



**Universitat**  
de les Illes Balears

DOCTORAL THESIS

2018

VARIETIES OF EMPATHY IN BOTTLENOSE  
DOLPHINS

*(Tursiops truncatus)*

Ana Pérez Manrique





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Doctoral Programme of Cognition and Human Evolution

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Thesis Supervisor: Antoni Gomila

Thesis tutor: Antoni Gomila

Doctor by the Universitat de les Illes Balears



*A mi familia, Sonia,  
y delfines*



## Acknowledgments

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## Scientific papers related to the contents of this dissertation

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Results obtained in the present thesis have resulted in the following papers:

1. **Pérez-Manrique, A. & Gomila, A.** (2016). Comments on the article: “Oxytocin-dependent consolation behavior in rodents”. *Science (E-Letter)*, 8 March 2016.  
<http://science.sciencemag.org/content/351/6271/375/tab-e-letters>
2. **Pérez-Manrique, A. & Gomila, A.** (2018). The Comparative Study of Empathy: Sympathetic Concern and Empathic Perspective-taking in Non-Human Animals. *Biological Reviews*. **93**, 248–269.
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## Conference presentations related to the contents of this thesis

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1. **Pérez-Manrique, A. & Gomila, A.** “False belief attribution in bottlenose dolphins (*Tursiops truncatus*) using a novel paradigm”. **Oral presentation**. Behaviour 2015. 9–14 August 2015. Cairns, Australia.
2. **Pérez-Manrique, A. & Gomila, A.** “Object permanence in bottlenose dolphins (*Tursiops truncatus*)”. **Poster**. 8th European Conference on Behavioural Biology ECBB. 12–15 July 2016. Vienna, Austria.
3. **Pérez-Manrique, A. & Gomila, A.** “The comparative study of empathy: sympathetic concern and targeted helping in non-human animals”. **Oral presentation**. 24th annual meeting of the European Society of Philosophy and Psychology ESPP. 10–13 August 2016. St. Andrews, Scotland.
4. **Pérez-Manrique, A. & Gomila, A.** “Bottlenose dolphins do not behave prosocially in an instrumental helping task”. **Oral presentation**. Behaviour 2017. 30 July – 4 August 2017. Estoril, Portugal.





**Universitat de les  
Illes Balears**

Dr. Antoni Gomila Benejam de la Universitat de les Illes Balears

DECLARO:

Que la tesis doctoral que lleva por título “Varieties of empathy in bottlenose dolphins (*Tursiops truncatus*)”, presentada por Ana Pérez Manrique para la obtención del título de doctor, ha sido dirigida bajo mi supervisión y que cumple con los requisitos necesarios para optar al título de Doctor Internacional.

Y para que quede constancia de ello firmo este documento.

Firma

Dr. Antoni Gomila Benejam

Palma de Mallorca, 27 de octubre de 2017



## RESUMEN

---

Los cetáceos, junto con los primates, son considerados como uno de los grupos animales que poseen las capacidades cognitivas más complejas de todo el reino animal. Además, existen desde la antigüedad infinidad de relatos que describen casos donde delfines y ballenas ayudan o salvan a compañeros o incluso a humanos en apuros. Esta visión positiva de los cetáceos perdura hoy en día, y presenta a los cetáceos como animales capaces de comportamientos empáticos complejos. Sin embargo, no se ha investigado en profundidad si estos animales en verdad muestran formas básicas o complejas de empatía. Una de las principales razones de esta falta de estudios sobre empatía en cetáceos o en otras especies animales es que la investigación en este campo se ha desarrollado sin seguir un programa sistemático y usando múltiples paradigmas y diferentes conceptos de los fenómenos implicados. A esto hay que añadirle que evaluar las respuestas de ciertas especies como los cetáceos ante emociones negativas es una tarea complicada debido a problemas éticos y metodológicos. Por ello, el objetivo principal de esta tesis es ahondar en el estudio de las capacidades empáticas de los cetáceos buscando la manera de evitar estos problemas y dificultades. Con este punto de partida, esta disertación integra una propuesta teórica con un enfoque empírico para investigar diferentes procesos empáticos en la especie de cetáceo más estudiada, el delfín mular (*Tursiops truncatus*).

En particular, la primera sección de la tesis se centra en el estudio comparativo de formas básicas y complejas de empatía animal, resaltando que estos comportamientos podrían ser importantes adaptaciones evolutivas en especies sociales. En concreto, el Capítulo 2 se centra en las formas básicas de empatía como el contagio emocional, mímica, y la sincronía social y el Capítulo 3 en las formas complejas como la preocupación y la toma de perspectiva empática. Esta sección trata primero de clarificar la terminología y la taxonomía de estas formas de empatía proponiendo criterios operativos aplicables tanto a humanos como a otras especies animales. También aporta una revisión exhaustiva de la literatura sobre formas básicas y complejas de empatía en animales y discute el estado de la cuestión. Además, durante la primera parte de esta disertación, se presta especial atención a la interacción entre la vida social y la evolución de ciertos procesos cognitivos y emocionales relacionados con la empatía. Finalmente, esta sección también trata de construir un marco teórico robusto que sirva como guía para realizar futuros estudios sobre empatía animal, evitando algunos de los principales problemas asociados a la investigación empírica de los procesos empáticos en animales. En general, esta sección aporta una visión integradora de este campo resaltando la importancia del estudio comparativo de estos procesos a la hora de tratar de dilucidar la historia evolutiva y las funciones adaptativas de la empatía en el reino animal.

El marco teórico desarrollado en la primera sección de esta tesis se aplicó al estudio en cetáceos de diferentes procesos cognitivos y emocionales relacionados con la empatía. En concreto, la segunda sección presenta cinco estudios empíricos y observacionales llevados a cabo en un grupo de delfines mulares en cautividad. Los resultados de estos estudios mostraron que los delfines parecen verse afectados por el estado emocional o de excitación de sus congéneres, especialmente por el de aquellos con los que están estrechamente afiliados. Además, en determinados contextos, la percepción de estrés en un congénere parece propiciar que los delfines que fueron testigo de dicha situación se comporten “empáticamente”. Estas respuestas afiliativas podrían haber mejorado la situación del delfín estresado, resultado que respaldaría la hipótesis de que estos comportamientos son empáticos. Los resultados de esta tesis, por tanto, consolidan a los delfines mulares como un modelo animal ideal para el estudio de los fenómenos empáticos y destacan la necesidad de realizar más investigaciones sistemáticas en este campo.

## RESUM

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Els cetacis, juntament amb els primats, són els grups d'animals que es considera que estan dotats amb capacitats cognitives més complexes. A més, des de temps antics es contenen històries sobre balenes i dofins que ajuden o salven altres congèneres i fins i tot humans en perill. Aquesta visió positiva dels cetacis persisteix avui en dia i els presenta com animals capaços de les més complexes conductes empàtiques. Ara bé, no comptem a penes amb estudis científics sobre si aquesta visió és correcta. Una de les raons principals d'aquesta situació és la diversitat de paradigmes utilitzats, la diversitat de concepcions dels fenòmens utilitzats, i la absència d'un programa sistemàtic de recerca. A més, mesurar emocions negatives en algunes espècies, com els cetacis, s'enfronta a problemes ètics i metodològics. Per tant, el principal objectiu de la tesi és aprofundir en l'estudi de les capacitats empàtiques dels cetacis, trobant la manera d'evitar aquests problemes i dificultats. Amb aquest punt de partida, aquesta tesi integra una proposta teòrica amb un enfoc empíric per investigar l'empatia en el cetaci més estudiat, el dofí (*Tursiops truncatus*).

Així, la primera secció de la tesi revisa l'estudi comparatiu de les formes elementals i complexes d'empatia, emfasitzant que aquestes conductes podrien ser adaptacions evolutives importants de les espècies socials. Més precisament, el capítol 2 es centra en formes bàsiques d'empatia com el contagi emocional, la imitació motora i la sincronia, i el capítol 3 considera les formes complexes d'aquesta capacitat com la preocupació simpatètica i la presa de perspectiva empàtica. Ambdós pretenen clarificar primer la terminologia i la taxonomia d'aquestes formes d'empatia, proposant criteris operacionals que permetent aplicar-los tant a humans com a no humans; a continuació, es fa una revisió comprensiva de la literatura respectiva, i es discuteix l'estat de la qüestió. Finalment, s'elabora un robust marc teòric que pretén servir de guia per orientar els futurs estudis d'empatia animal, oferint una manera d'evitar els problemes detectats al principi. Globalment, els capítols de la primera secció proporcionen una visió integral d'aquest camp d'estudi, destacant la importància de l'estudi comparat d'aquests processos per poder elucidar la història evolutiva i la funció adaptativa de l'empatia en les diferents espècies que la inclouen en el seu repertori conductual.

El marc teòric desenvolupat en la primera part de la tesi serveix per fonamentar els estudis empírics sobre els diferents processos cognitius i emocionals involucrats en l'empatia en cetacis que constitueixen la segona part. Així, la secció segona de la tesi presenta cinc estudis empírics duit a terme en un grup de dofins captius. Els resultats d'aquests estudis mostren que els dofins es veuen afectats per l'estat emocional i d'activació dels seus companys de grup, especialment pels d'aquells amb qui es té una afiliació estreta. A més, en certs contextos, la percepció d'un company de grup alterat elicitava una resposta empàtica en els dofins que ho veuen. Aquestes respostes afiliatives semblen fins i tot conduir a que el dofí alterat es senti millor, cosa que avala la hipòtesis que aquestes conductes són empàtiques. En conjunt, els resultats dels estudis consoliden l'interès dels dofins com models animals ideals per l'estudi de l'empatia i mostren el camí per un estudi més sistemàtic de la qüestió.

## ABSTRACT

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Cetaceans, together with primates, are considered to be one of the animal groups endowed with the most complex cognitive capacities across the animal kingdom. Furthermore, since ancient times nautical lore is full of stories about whales and dolphins helping or saving companions or even drowning humans. This positive vision of cetaceans still persists today and depicts cetaceans as animals able to carry out complex empathic behaviours. However, the extent to which these marine mammals display basic or complex forms of empathy has not been extensively assessed. One of the main reasons for the lack of studies on the empathic capacities of cetaceans and other animal species is that research on animal empathy has developed using different paradigms, different concepts of the phenomena involved, and the absence of a systematic program. Moreover, assessing responses towards negative emotions in some species like cetaceans is a thorny issue due to ethical and methodological problems. Therefore, the main objective of the present thesis is to deepen in the study of empathic capacities of cetaceans trying to avoid some of the main issues related to research on empathy in non-human species. With this premise in mind, this dissertation combines a theoretical and an empirical approach to investigate empathic processes in the most studied cetacean, the bottlenose dolphin (*Tursiops truncatus*).

In particular, the first Section of the present thesis centres on the comparative study of basic and complex forms of animal empathy, highlighting that these behaviours could be important evolutionary adaptations for social species. More precisely, Chapter 2 focuses on basic forms of empathy such as emotional contagion, mimicry and social synchrony and Chapter 3 on complex forms of this capacity like sympathetic concern and empathic perspective-taking. This section first tries to clarify the terminology and taxonomy of these forms of empathy, providing operative criteria for these phenomena that are applicable to both human and non-human animals. It also provides a comprehensive review of the literature on basic and complex forms of empathy in non-human animals and discusses whether these studies really offer examples of empathic behaviours. Furthermore, throughout the first part of this dissertation, special attention is given to the interplay of social life and the evolution of certain cognitive and emotional processes related to empathic behaviours. Finally, it also aimed to build a robust theoretical framework that serves as a guideline to carry out future studies on animal empathy, avoiding some of the main problems associated with the empirical research on empathic processes in non-human species. Overall, this section provides an integrative view of the field highlighting the importance of the comparative study of these processes for elucidating the evolutionary history and adaptive functions of empathy across the animal kingdom.

The theoretical framework developed in the first Section of this dissertation was applied to the study of different cognitive and emotional processes related to empathy in cetaceans. In particular, the Second section of this thesis presents five empirical and observational studies in a group of captive bottlenose dolphins. The results of these studies shown that dolphins seem to be affected by the emotional or arousal state of conspecifics, especially from that of close affiliated partners. Furthermore, in certain contexts, the perception of distress in a conspecific appeared to elicit empathy-like behaviours in witness dolphins. These affiliative responses could have led to the improvement of the situation of the distressed dolphin, supporting the hypothesis that these behaviours are empathy based. The outcomes of this thesis thus consolidate bottlenose dolphins as ideal animal models for the study of empathic phenomena and posit the necessity of more systematic research on the field.



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## SECTION I: ANIMAL EMPATHY

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*“There is no fundamental difference between man and animals in their ability to feel pleasure and pain, happiness, and misery.”*

— Charles Darwin





## CHAPTER 1

# GENERAL INTRODUCTION

### 1. Empathy models and views

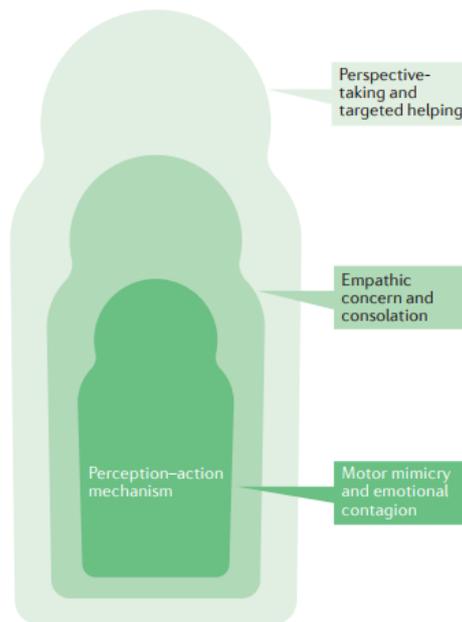
In 1873, Robert Vischer coined the German term “*Einfühlung*” meaning “feeling oneself into” (Vischer, 1873). The term was later translated into English as “empathy”, and popularized by Theodor Lipps and Vernon Lee (Hammond & Kim, 2014). While the term began in the field of aesthetics –basically in an effort to account for expressive perception, such as when we perceive a melody as sad– currently, empathy is broadly defined as the ability to understand and share the feelings of another (Oxford dictionary). In spite of the late date at which this term was coined, empathy is a capacity that has been studied for decades under a different rubric. Before the twentieth century, the term “sympathy” was used extensively to refer to the process by which we can put ourselves in the place of the other and somehow experience what the other feels (Hammond & Kim, 2014). As early as 1759, authors like Adam Smith and later Charles Darwin began to wonder about the “universal human capacity” for sympathy, its relation with the moral sense, and its continuity among species (van der Weele, 2011). In recent years, research on empathic processes in non-human animals has received much attention, becoming one of the hottest topics in comparative cognitive studies. There is still, however, a lack of consensus within the scientific community on empathy’s nature and definition. In addition, research on empathic processes in non-human animals has developed using different procedures, different conceptions of the phenomena involved and a lack of a systematic program.

Evolutionary biologists are currently returning for inspiration to Charles Darwin’s ideas set out in his work “The Descent of Man, and Selection in Relation to Sex” (Darwin, 1871). In this book, Darwin defends that many social animals sympathize with each other’s distress, danger, pain, fear or pleasure. For Darwin, as for Adam Smith (Smith, 1759), the meaning of the word sympathy is more closely defined by the German word *Einfühlung*, “feeling oneself into”, than by the current definition, feelings of pity and sorrow for someone else’s misfortune (Johnson, 2013). In fact, Darwin stated that “Almost every one would experience the same feeling in the highest degree in witnessing a man being tortured or going to be tortured. In these cases there is no danger to ourselves; but from the power of the imagination and of sympathy we put ourselves in the position of the sufferer, and feel something akin to fear” (Darwin, 1897, p. 304). This statement describes thus the process by which an individual takes another’s perspective or “feels into” the emotional state of another, which actually is the original meaning of *Einfühlung* (Johnson, 2013). According to Darwin, this capacity is innate in both humans and other animals and there is a phylogenetic continuity between them in this regard. Some of Darwin’s ideas on sympathy are very similar to those currently defended by influential theorists of empathy, such as Frans de Waal. Like de Waal, Darwin divided sympathy into several levels of complexity. The first level comprises the social instincts that lead an animal to feel sympathy for others and perform various services for them, such as helping conspecifics in several ways. Darwin

highlighted that these feelings and services would be only provided to the members of the same association and not extended to all the individuals of the same species. The second level involves highly developed mental faculties that allow the individual to recall past actions and motives that, in turn, might influence his or her experience. Finally, the third level arises with the development of language, that could guide the individuals' actions. However, social instincts still prevail in this level and "give the impulse to act for the good of the community" (Darwin, 1871, p.41 ). The habit also plays an important role in guiding the behaviour of individuals, strengthening social instincts and sympathy. Thus, for Darwin sympathy is an adaptive process involving innate social instincts that prompts feelings of sympathy towards familiar individuals and lead the animal to perform some services for them. What could be more surprising is that Darwin already suggested that sympathy is a capacity that involves several processes of varying complexity, both affective and cognitive that are interrelated. In Darwin words: "the social animals which stand at the bottom of the scale are guided almost exclusively, and those which stand higher in the scale are largely guided, by special instincts in the aid which they give to the members of the same community; but they are likewise in part impelled by mutual love and sympathy, assisted apparently by some amount of reason"(Darwin, 1871), p. 49). That is, as modern accounts of empathy, the Darwinian model implies an incremental view of sympathy, stating that simple forms of sympathy are only based on automatic impulses (social instincts) and are displayed by some social animals. In turn, complex forms of sympathy, besides instincts, also require mental capacities and are displayed by social species with well-developed mental abilities. Thus, Darwin's approach also implies a phylogenetic continuity of this phenomenon, with the most basic forms of sympathy being shared with many social animal species, and the most complex ones only present in some "higher social animals" and humans. Interestingly, Darwin emphasized the important influence of familiarity and past experience on sympathy. These two factors are currently considered to enhance empathic responses in human and other animals (Preston & de Waal, 2002). Furthermore, Darwin highlighted the importance of sociability for displaying sympathy for others and the utility of the comparative approach to better understand this human faculty. Although Darwin recognized the difficulties of measuring or judging whether animals have any feeling for suffering others, he provided many anecdotal reports of animals advertising danger to others or performing rescue or helping behaviours. Some of these behaviours are currently considered to be examples of empathic processes. Finally, he also speculated on the evolutionary function of sympathy in social species. Darwin believed that sympathy was of high importance for aiding and defending each other, and thus the groups composed of the most sympathetic individuals would thrive best and rear the greatest number of offspring. Therefore, in species that could benefit from living in society, sympathy might have been increased by natural selection.

One of the strongest advocates of Darwin's evolutionary view of empathy is Frans de Waal. He defines empathy as "the capacity to be affected by and share the emotional state of another, assesses the reasons for the other's state, and identify with the other adopting his or her perspective" (de Waal, (2008, p. 281). de Waal contends that even if a behaviour only satisfies the first element of this definition, it can still be considered empathic. In line with Darwin's ideas, he has developed a model that distinguishes degrees of complexity in forms of empathy and assumes the evolutionary continuity of this capacity between species. This model is called "The Russian doll model of empathy" and states that instead of evolution having replaced simpler forms of empathy with advanced ones the latter are products of the former and are still dependent on them (de Waal, 2007). Thereby, several forms of empathy are structured as a Russian-doll made up of three layers: 1) emotional contagion, where the emotional state of an individual induces a similar state in another; 2) sympathetic concern, that arises when emotional contagion is combined with the ability to evaluate the other's situation and with attempts to understand the cause of others' emotions; and 3) empathic perspective-taking, where an individual is able to adopt another's point of view (de Waal, 2007) (**Figure 1**). According to Preston and de Waal (2002), the core feature of empathy is the ability to share emotional experiences, that is based on an ancient perception-action coupling mechanism (PAM) located at the core of the doll. This mechanism is supposed to couple perception and action processes. Applied to the case of

empathy, this mechanism would be activated by the perception of other's emotional state, and would automatically activate in the subject the neural representations of that state, giving rise in this way to a shared emotional experience (Preston, 2007). This statement is reminiscent of those of Adam Smith, Alexander Bain or Theodor Lipps proposing that we retain former states of pain or pleasure and those states are later reactivated when we see pain or pleasure in others (Smith, 1759; Bain, 1868; Lipps, 1903). Currently, this multi-layered vision of empathy is widely accepted.

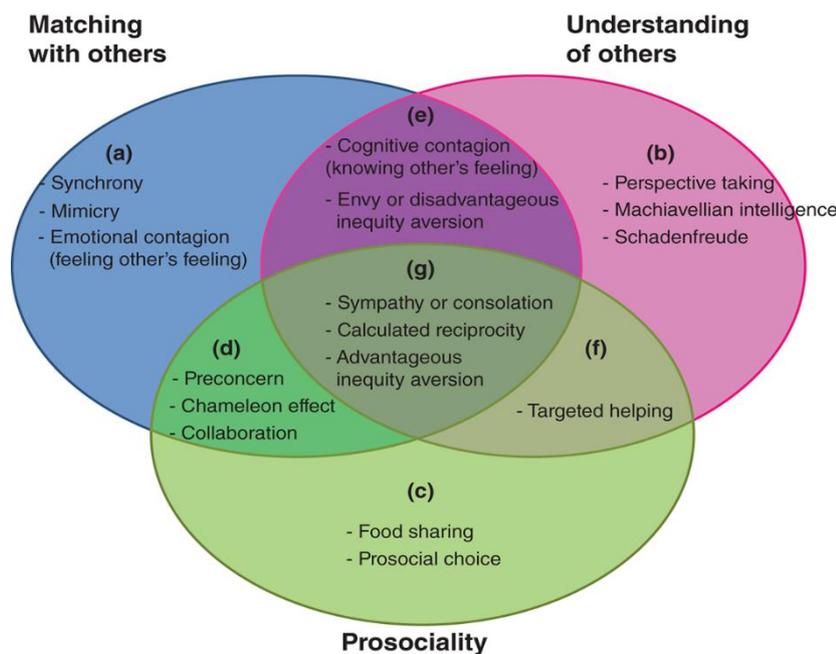


**Figure 1.** The Russian-doll model of the evolution of empathy (taken from de Waal & Preston, 2017).

essential information for higher brain processes included in the third level (Panksepp & Panksepp, 2013). Furthermore, tertiary processes could modulate the functioning of the lower levels. According to these authors thus empathy is constituted by psychological processes of varying complexity across brain levels, that range from emotional contagion and affect sharing to the highest levels of psychological processing.

Recently, Shinya Yamamoto (2017) has proposed another way of reorganizing the empathy-related phenomena. Instead of a linear development model such as de Waal's Russian Doll model, Yamamoto proposes a combination model in which independent factors are laid out horizontally and in parallel. In this manner, the different levels of complexity in empathy could be the outcome of different combinations of those factors. As de Waal, Yamamoto also uses empathy as an umbrella term that covers a wide range of phenomena. However, Yamamoto's model assumes that the different factors involved in empathy might have evolved independently of each other, and without a phylogenetic continuity. This combination model is composed by three organizing factors: (1) matching with others: intentionally or unintentionally matching one's mental, behavioural and/or environmental state with another's; (2) understanding of others: appreciation of another's states based on the capacity of self-other distinction; and (3) prosociality: a basic tendency to benefit others (Figure 2). Yamamoto tries to categorize most of the empathy-related processes using these three factors and their combinations and map them to appropriate contexts. These factors can be conceptually separated but overlap in practice and their combinations give rise to other empathy-related phenomena. For example, the combination of the first and the second factor drives animals to engage in social comparison with others. This combination gives rise to cognitive contagion (knowing other's feeling) and envy or disadvantageous inequity aversion (negative responses to an inequitable situation in which an individual has concern about having less of a commodity than other

(Yamamoto, 2017)). These processes require self-other distinction both in the emotional and cognitive domains. Preconcern arises from the combination of matching with others and prosociality and leads animals to automatically approach individuals in pain or distress instead of escaping from them. Preconcern is thus an automatic response that does not require a cognitive understanding of another's needs and situations, and that drives animals to approach others in distress in order to extinguish their own negative arousal that matches that of the distressed party. The chameleon effect (automatic and unconscious motor mimicry) and collaborative behaviour are also related to this combination of factors. Animals endowed with the ability to understand others and prosocial tendencies could be able to provide targeted helping, that is, helping directed at an individual with a specific need (Yamamoto, 2017). Finally, the union of the three factors gives rise to sympathetic concern or consolation, calculated reciprocity and advantageous inequity aversion (aversive response to a situation in which the responder inequitably has something better than another, which leads to proactive prosociality (Yamamoto, 2017)). The latter two processes are closely related to cooperation, and allow an individual to behave prosocially to diminish the detected differences between oneself and other individuals. According to Yamamoto (2017), support for this model consists of evidence that some animal species display one of the proposed factors but not another and other species show the opposite pattern.



**Figure 2.** Three major factors and their combinations for empathy-related phenomena (taken from Yamamoto, 2017).

Despite their differences regarding the neural mechanisms that mediate these behaviours and its phylogenetic continuity, these three main theories of empathy share the idea that empathy covers three sorts of processes of different cognitive complexity: emotional contagion, sympathetic concern and empathic targeted helping. Accordingly, in the following chapters, we have structured our revision of empathy in non-human animals along these three main of processes.

## 2. The study of animal empathy

Rats preferring to free trapped companions than to eat chocolate chips, voles “consoling” distressed partners, dolphins helping injured companions to breathe... reports like these have

fascinated us since ancient times. Already in his *Historia Animalium* (Aristotle, 1897), the Greek philosopher Aristotle considered the temper of animals, highlighting the gentleness of the lion, the sensitivity of the elephant or the kindness of the dolphin in saving companions from fishermen or compassionately supporting dead calves to prevent them from being devoured. However, fear of anthropomorphism restricted research on non-human animal empathy for decades (Panksepp, 1998; de Waal, 1999). But recently, the field has overcome this concern, stimulating public interest and promoting observational and empirical studies.

One of the reasons of the recent progress in the study of animal empathy is that, although there is still a lack of consensus on the precise nature and definition of empathy, broad views of this term are increasingly being accepted and used. These views divide empathy into several cognitive and emotional interrelated components that can change depending on context, species and during ontogeny (Preston & de Waal, 2002; Panksepp & Lahvis, 2011). According to this approach, the simplest forms of empathy, such as emotional contagion, should be found in a wide variety of species, while the most complex empathic behaviours, i.e. those involving not only emotional processes but also higher cognitive abilities, are not expected to be widespread across the animal kingdom. Dividing empathy into several processes of varying complexity is a very useful strategy for the study of animal empathy (Panksepp & Lahvis, 2011). It allows researchers to apply biological approaches to elucidate the existence of homologous behaviours in different species. In this manner, some authors prefer to focus on the emotional aspects of empathy (emotional empathy), assessing how animals perceive and react to the emotional expressions of others, while others study the cognitive components of this capacity (cognitive empathy). This approach ultimately serves to assess a possible phylogenetic continuity of this ability, as Darwin suggested (Preston & de Waal, 2002).

However, research on empathic processes in animals has developed using multiple paradigms and concepts of the phenomena involved, and the lack of a systematic program. For instance, only a few studies include well-controlled experiments; and it is still extremely difficult to set up a general paradigm that serves to test different species in the same way with a minimum of reliability so that results can be properly compared. Due to the lack of verbal capacities of non-human animals most of the paradigms used in the study of human empathy are not useful for animal studies, and sometimes the non-verbal ones still seem too cognitively demanding for most animal species.

The study of empathy in non-human species is inevitably linked to research on emotional processes in animals. The scientific study of emotions in animals has also been ignored for decades and still faces many impediments. These impediments range from a lack of consensus on a definition of emotion, lack of interest in the mental lives of animals during years or methodological problems (Kuczaj *et al.*, 2013). However, since Darwin's pioneering work "The Expression of the Emotions in Man and Animals" (Darwin, 1897) to date much progress has been made in this field. Researchers have used a wide variety of methods to measure and assess emotional responses in non-human animals. These methods can be divided into two categories: physiological and behavioural measures (Dawkins, 2006). It is possible to assess animal emotional responses to potentially emotion-inducing situations using physiological measures such as hormone levels, heart rate or brain activity (Kuczaj *et al.*, 2013). Another way of assessing animal emotional reactions is examining behavioural changes during arousing situations. Behavioural measures could be facial expressions, vocalizations, postures or changes in the pattern of spontaneous behaviours usually displayed by the species or changes in learned behaviours (Dawkins, 2006). Using both types of measurements, physiological and behavioural, could be the most accurate procedure for studying emotional processes in animals (Kuczaj *et al.*, 2013). Some researchers have also proposed that the new field of animal personality could provide a new insight into the study of animal emotions (Kuczaj *et al.*, 2013).

Despite the recent advances in the study of emotional processes in animals, there are only a reduced number of works assessing the emotional responses of certain species towards distressed

conspecifics or examining positive emotions in non-human animals. On the one hand, negative emotions like anxiety or fear are more easily observed and measured (Kuczaj *et al.*, 2013) than positive emotions that could be too subtle to detect. On the other hand, assessing negative emotions in some species is also a thorny issue due to ethical and methodological problems. It is unethical to create situations in which animals, like great apes or cetaceans, experience intense emotions such as distress, fear or pain to test their conspecific's responses. Thus, to assess these types of interactions we have to rely mostly on behavioural observations and anecdotal reports. But this sort of evidence is not fully satisfactory: besides the fact that chances to observe these incidents are rare, this type of reports has also been called into question. For example, it has been argued that there can be inconsistencies in the attention or interpretation of the observer; most of these data are based on a single record that is not always representative of the normal behaviour of the species; usually there are not enough cases recorded under similar circumstances to allow statistical analysis; and there are many difficulties for replication of this data (Bates & Byrne, 2007).

There are also some limitations regarding the use of physiological measures to study animal emotional processes (Paul, Harding, & Mendl, 2005a). The procedure used to collect physiological samples may, in turn, evoke an emotional reaction in the subjects and thus, the collected samples could not be reliable (Paul *et al.*, 2005a). Moreover, different emotional states could result in the same physiological response. For instance, both rewarding and punishing stimuli may trigger the same physiological response, a higher heart rate (Kuczaj *et al.*, 2013).

On the other hand, this field of research also is conditioned by the fact that an overwhelming number of terms are used to refer to empathic-related behaviours, many of which lack common currency or understanding. For example, "sympathy", "concern", or "sympathetic concern" are sometimes used interchangeably, assuming that they refer to a single process, while at other times the same terms are used to differentiate between processes. Certain terms appear only in the human empathy literature while others are used to study similar behaviours in non-human animals. This lack of consensus complicates the comparative study of empathic behaviours.

Finally, there also is an unsolved problem with assessing the motivations underlying complex empathic behaviours. While it is not easy to distinguish between the motivations and consequences of a behaviour in humans, this task may be even harder in other animals. In Chapter 3 we will deal explicitly with this difficulty and propose a way to address it operationally, so that progress can be made.

Despite these difficulties, a wealth of data has accumulated, so it's time to try to take it together and try to make sense of the larger picture.

### **3. Bottlenose dolphin, animal model for the study of empathy**

Aristotle in his *Historia Animalium* (1897) describes dolphins as sweet and familiar marine animals which display expressions of love and passion for their offspring. This positive vision of cetaceans, especially of dolphins, still persists today. This vision is reinforced by the numerous reports of possible cases of rescue or helping behaviours in dolphins. These anecdotal reports include situations in which dolphins saved companions releasing them from nets, biting through harpoon lines, or protected wounded conspecifics by staying with them and pushing away the ships instead of fleeing from the threat (de Waal, 2008). Dolphins have also been observed carrying or supporting injured and sick calves at the surface in order to aid them in breathing (Siebenaler & Caldwell, 1956; Connor & Norris, 1982; Cockcroft & Sauer, 1990; Lodi, 1992; Warren-Smith & Dunn, 2006; de Moura, Rodrigues, & Siciliano, 2009). Furthermore, the number of observational cases describing situations in which dolphins seem to come to the aid of a different species like whales in distress or drowning humans is increasing.

Although little is known about emotional processes in dolphins, some evidence suggests that emotions play an important role in their social interactions (Kuczaj *et al.*, 2013). Dolphins, especially bottlenose dolphins (*Tursiops truncatus*), are ideal candidates for the study of emotions since they are a highly social species that live in complex societies that rely on individual recognition, a long period of development, coalition formation and cooperative behaviours (Pack & Herman, 2006). In captivity, they also engage in several cooperative activities (Marino *et al.*, 2007; Kuczaj *et al.*, 2015a). It has been suggested that some dolphins' vocalizations, postures and tactile interactions are indicative of their emotional state or serve to communicate emotional information (Kuczaj *et al.*, 2013). Furthermore, many anecdotal reports suggest that these animals could be affected by the emotional state of other individuals (Lilly, 1963; Caldwell & Caldwell, 1966; Kuczaj *et al.*, 2015a). Therefore, the extent to which dolphins emotionally respond to others' emotional states and behaviour warrants further exploration.

In terms of cognition, bottlenose dolphins are similar to primates (Marino, 2002) and are endowed with very sophisticated and complex cognitive abilities. Dolphins have robust joint attention skills possessing the ability to understand the focus of another's gaze and they might be able of producing indicative pointing and referential gestures (Xitco *et al.*, 2001; Xitco, Gory, & Kuczaj, 2004; Pack & Herman, 2006). Bottlenose dolphins can learn actions through imitation (Herman, 2002), recognize themselves in mirrors (Reiss & Marino, 2001) and have a conscious awareness of its own recent behaviour (Herman, 2010). These are abilities required for an understanding of the self/other distinction and a precursor to understanding others as mental agents. Dolphins can also generalize learned rules to novel behaviours and novel experimental contexts, have been taught to report on actions performed by other dolphins and to report on the presence or absence of objects (Mercado III & DeLong, 2010). They are able of concept learning and understanding as well (Herman, 2010). This pattern of findings suggests the remarkable capacity and flexibility of dolphin cognition and points out that dolphins are endowed with cognitive capacities that are required for display complex forms of empathy. Therefore, due to both their emotional and cognitive capacities bottlenose dolphins are candidates of choice for the study of animal empathy.

#### 4. Research objectives

The current thesis seeks to contribute to the study of empathy in bottlenose dolphins. With this general aim in mind, the following objectives have been pursued:

- ❖ Clarify the terminology and taxonomy of different forms of empathy, providing operative criteria for these phenomena that are applicable to both human and non-human animals.
- ❖ Carry out a comprehensive review of the literature on basic and complex forms of empathy in non-human animals to integrate current findings and clarify the challenges and conditions yet to satisfy.
- ❖ Provide an integrative view of the field highlighting the importance of the comparative study of these processes for elucidating the evolutionary history and adaptive functions of empathy across the animal kingdom, and build a robust theoretical framework that serves as a guideline to carry out future studies on animal empathy.
- ❖ Apply this theoretical framework to the study of different forms of empathy in bottlenose dolphins.
- ❖ Carry out a series of studies on basic and complex forms of empathy in bottlenose dolphins to expand our knowledge on the emotional lives and empathic capacities of these marine mammals.

- ❖ Consolidate bottlenose dolphins as ideal animal models for examining empathic phenomena in the wild and in captivity, highlighting the necessity of more systematic research on the field in order to broaden our knowledge on this subject.



## CHAPTER 2

# BASIC FORMS OF EMPATHY

### 1. Introduction

Charles Darwin was a pioneer in the study of animal's emotions (Bekoff, 2000; Kuczaj *et al.*, 2013). Contrary to the common opinion of his time, Darwin (1872) argued that animals experience the same emotions as humans and that many social animals are able to sympathize with each other's distress, danger, pain, fear or pleasure as well (Darwin, 1896). According to his view, the most basic forms of sympathy are shared with many social species, and the most complex ones are only present in some "higher social animals" and humans (Darwin, 1872). Thus, he defended the existence of an evolutionary continuity of emotional expressions and sympathy between humans and other animals (Darwin, 1872,1896). After Darwin, the study of animal emotions became marginalized. Fear of anthropomorphism and the impossibility of measuring subjective experiences in animals, among other impediments, stopped research on this topic for many years (Bekoff, 2000; Kalueff *et al.*, 2012; Panksepp, 1998). From the end of the last century to the present, the study of animal emotions has overcome these concerns. Observational and experimental studies have been carried out and the topic has regained interest. At least in part, this move is due to the replacement of the subjective aspects used to measure emotions by more objective criteria (behavioural and physiological indicators) (Kalueff *et al.*, 2012) which has led to rapid progress in this field of study. In fact, a currently accepted view within the study of animals' emotions is to consider emotional processes as multifaceted, comprising physiological, behavioural and subjective components (Paul, Harding, & Mendl, 2005b). While these different elements form a whole, they are also potentially dissociable, allowing researchers to independently study different aspects of an emotional event (Paul *et al.*, 2005b).

Similarly, that animals emotionally respond to perceived emotional displays of conspecifics is currently a well-established fact (Darwin, 1872; de Waal, 2008; Preston & de Waal, 2002). Those emotional responses may vary in complexity but in many cases, are considered as examples of empathic behaviour (Preston & de Waal, 2002). Although there is still a lack of consensus among the scientific community on the precise nature and definition of empathy, this concept traditionally refers to an emotional reaction in response to another's emotional state that is more congruent with the other's situation than to one's own (Eisenberg & Strayer, 1987; Hoffman, 1987). Depending upon whether this shift involves the adoption of another's point of view, cognitive or projective empathy is distinguished from emotional empathy. Only cognitive empathy is thought to require such perspective-taking, or similarly mediating cognitive activity, while for emotional empathy, the emotional response is automatically elicited by the perception of the other's emotional expression. In fact, it has been proposed that two systems, an emotional and a cognitive system, mediate empathy (Shamay-Tsoory, 2011). Although these two systems may work together, they could also be

behaviorally, developmentally, neurochemically, and neuroanatomically dissociable (Shamay-Tsoory, 2011).

In this chapter we will focus on emotional empathy, understood as the capacity to be affected by and share the emotional experiences of others without cognitive mediation (de Waal, 2008; Shamay-Tsoory, 2011). Emotional contagion, broadly defined as the emotional state-matching of a subject with another, is thought to be the main illustration of this phenomenon (de Waal, 2008; Shamay-Tsoory, 2011). Attention will also be paid to social synchrony, the capacity to become entrained with one another (Phillips-Silver, Aktipis, & Bryant, 2010) and to motor mimicry, a motor reaction in which an individual unconsciously imitates the expressions or behaviours of another individual (Hess & Fischer, 2013). Mimicry and synchrony have been considered as primitive forms of emotional contagion since they are also thought to lead to an emotional convergence between individuals (Hatfield, Cacioppo, & Rapson, 1994).

Incremental views of empathy divide this capacity into several interrelated processes of varying complexity, both cognitive and affective. These views usually consider emotional contagion, motor mimicry and related processes as the foundational levels of empathy. For example, Panksepp and Panksepp (2013) conceive empathy as a complex capacity that relies on different but interrelated circuits of the mammalian brain. According to their view, emotional contagion constitutes the first level of empathy and is based on deeply subcortical emotional-affective brain functions. The “Russian doll” model of empathy proposed by de Waal (2007), conceives empathy as a multi-layered capacity. This model states that the most basic forms of this capacity, emotional contagion and motor mimicry would be grounded in an automatic neural mechanism that couples perception and action (PAM) (Preston & de Waal, 2002). Thus, the core feature of empathy would be the ability to share emotional experiences. In fact, de Waal defines empathy as “the capacity to be affected by and share the emotional state of another, assess the reasons for the other’s state, and identify with the other adopting his or her perspective” (de Waal, p.281). He admits that even if a behaviour only satisfies the first criterion of the former definition, it can still be considered an empathic one. On the other hand, models that assume independent emergences of empathic components, such as the one of Yamamoto (2017), also consider emotional contagion and motor mimicry as two of the main factors involved in empathy. This combination model is composed of independent factors or categories that in turn include a broad spectrum of phenomena related to empathy. One of these organizing categories is “matching with others”, a process which implies intentionally or unintentionally matching one’s mental, behavioural and/or environmental state with another’s. This category thus includes the most fundamental phenomena of emotional empathy such as synchrony, mimicry, emotional contagion or social facilitation (Yamamoto, 2017).

Overall, most of the current models of empathy assume that the core feature of emotional empathy is to share, match or be affected by the emotional experiences of another individual. Therefore, emotional contagion, motor mimicry and related processes are thought to be the main processes involved, either as the basic mechanisms above which more complex forms of empathy develop, or as separate but related processes that could or not contribute to more complex empathic behaviours. Given that these phenomena seem to be automatic processes that do not involve complex cognitive processing, they might allow the sharing of some emotional cues in a simple and unconscious fashion in animals. Therefore, in some social species, they could function as a primitive form of empathy prompting affiliation and leading to prosocial or cooperative behaviours. However, although emotional contagion, mimicry and synchrony are usually considered to be the most basic elements of human emotional empathy, in other species little is known about the link between these processes and empathic behaviours or whether they function as basic forms of empathy. Therefore, a review of the literature on emotional contagion, mimicry and related processes in non-human animals is timely to integrate current findings and to assess a possible link between these phenomena and empathy in non-human animals. Therefore, the first aim of this chapter is to clarify and describe these processes,

focusing on why they have been proposed to function as primitive forms of empathy and why they have been linked to more complex empathic behaviours. Secondly, we carry out a comprehensive review of the available evidence on emotional contagion, mimicry and social synchrony in non-human animals and discuss whether these studies really offer examples of basic forms of empathy comparable to those found in humans.

## 2. Mimicry

Mimicry consists in unwittingly adopting the movements, expressions or behaviour of another individual. Thus, it is considered to be the minimal criterion of exhibiting a motor match to the movements of another individual (Fuhrmann *et al.*, 2014). Unlike true imitation, it does not require that the mimicker share a similar goal with the mimicked individual (Whiten *et al.*, 2004). Adam Smith, the celebrated moral philosopher, was the first to pay attention to this phenomenon, which he thought as the most primitive form of sympathy (Smith, 1759). For Smith, it was a kind of reflex (Bavelas *et al.*, 1987). In the eighteenth century, the word sympathy was used instead of the term empathy, which derived from the German word “Einfühlung” meaning “feeling oneself into”. This term developed as a form of implicit understanding of another's emotional expression and involved motor mimicry of those expressive movements (Lipps, 1903; Bavelas *et al.*, 1987). Nowadays some authors like Hatfield, Cacioppo, and Rapson (1994) also link both capacities and define “primitive emotional contagion” as “the tendency to automatically synchronize and mimic expressions, vocalizations, postures and movements with those of another person and, consequently, to converge emotionally” (p.5). That is, when an observer matches another's emotional expression, its own emotional state could be modulated as well, giving rise to emotional contagion (McIntosh, 2006). It has been empirically confirmed that during social interactions humans tend to unconsciously mimic the behaviours of others (Chartrand & Bargh, 1999; Lakin *et al.*, 2003; Bourgeois & Hess, 2008). This phenomenon is also known as “chameleon effect” (Chartrand & Bargh, 1999). However, there is no scientific consensus on the role of mimicry in emotional contagion and more precisely on whether mimicry leads to emotional contagion. In fact, in humans the available evidence is contradictory. While some studies have found no relationship between mimicry and emotional contagion (Hess & Blairy, 2001; McIntosh, 2006), others have provided positive evidence of this link (Laird *et al.*, 1994; Sato *et al.*, 2013; De Coster *et al.*, 2013). Furthermore, motor mimicry is evoked by a broad class of phenomena ranging from emotional expressions to synchronized movements and body postures (Bavelas *et al.*, 1987). Thus, motor mimicry seems to be a very ubiquitous phenomenon, raising the question of whether there is more than one process involved in it (Bourgeois & Hess, 2008).

Following Smith and Lipps' view of motor mimicry, this phenomenon has also been causally linked to empathy. For instance, motor mimicry and emotional contagion entail the inner core of de Waal's “Russian-doll” model of the evolution of empathy (de Waal, 2007; de Waal & Preston, 2017). This model suggests that both processes represent the simplest manifestations of empathy (de Waal & Preston, 2017; Preston & de Waal, 2002). In support of this view, several studies have provided evidence that relates motor mimicry to the empathic capacities of individuals. For example, people who scored high in empathic capacities exhibit motor mimicry to a greater extent than others do (Chartrand & Bargh, 1999; Dimberg, Andréasson, & Thunberg, 2011; Sun *et al.*, 2015; Rymarczyk *et al.*, 2016) and some studies have shown that humans with empathy deficit disorders may also present an impairment of automatic mimicry (McIntosh *et al.*, 2006; Rozga *et al.*, 2013). Furthermore, some studies have suggested that motor mimicry may decrease racial bias (Inzlicht, Gutsell, & Legault, 2012), reduce victim blaming (Stel, van den Bos, & Bal, 2012) and increase affective responses to seeing another individual in pain (De Coster *et al.*, 2013).

In humans, it has been proposed that motor mimicry could have evolved from a communicative tool to serve a social function, increasing affiliation and thus facilitating group living (Lakin *et al.*, 2003). That is, mimicry may function as “social glue” increasing affiliation, liking and rapport between individuals (Lakin *et al.*, 2003). For example, it has been shown that, after a social interaction in which an individual mimicked the actions of another, both individuals became more affectively attuned and reported more feelings of having bonded with each other than after a control interaction (Stel & Vonk, 2010). This relationship could be bi-directional that is, mimicry might promote affiliation and affiliation could be displayed through mimicry (Lakin *et al.*, 2003).

Motor mimicry has also be linked to prosocial behaviour (Duffy & Chartrand, 2015). It has been shown that, in humans, mimicry led to increased helping and cooperative behaviour, not only towards the mimicker but also toward uninvolved individuals (Carpenter, Uebel, & Tomasello, 2013; Fischer-Lokou, Martin, & Guéguen, 2011; Guéguen, Martin, & Meineri, 2011; Kirschner & Tomasello, 2010a; Müller, Maaskant, van Baaren, & Dijksterhuis, 2012; van Baaren, Holland, Kawakami, & Knippenberg, 2004; van Baaren, Holland, Steenaert, & van Knippenberg, 2003). According to the previous assumptions about the functionality of mimicry, it has been suggested that mimicry would be displayed preferentially to familiar or in-group individuals, with whom the individual interacts and cooperates more (Bourgeois & Hess, 2008). Moreover, considering the broad range of phenomena that elicit motor mimicry, it is expected that several other factors like context or the type of stimuli displayed influence mimicry levels as well. In fact, in humans, emotional facial mimicry is affected by familiarity with the other person, and by the type of emotional expression displayed (Bourgeois & Hess, 2008). More precisely, negative emotion expressions were mimicked only when displayed by a familiar individual, while positive emotions were always mimicked, suggesting that mimicry is not always purely reflex-like (Bourgeois & Hess, 2008).

Although the precise nature and mechanisms involved in mimicry, and its connection with emotional contagion are still not well known, there seems to be a consensus on its role in social interactions, that justifies reviewing whether it is present in non-human animals. As mentioned above, mimicry is a very ubiquitous phenomenon ranging from mimicry of purely motor movements to mimicry of emotional expressions. Therefore, herein we will focus on evidence of mimicry that has been related to some extent with empathic processes. In the following sections, thus we first provide a description of some processes related to mimicry and then we review the main evidence available on mimicry in non-human animals.

## 2.1. Contagious yawning and rapid facial mimicry

Two interesting phenomena related to involuntary motor mimicry are contagious yawning (CY) and rapid facial mimicry (RFM). The former consists in yawning after hearing or seeing another individual doing this action (Campbell & de Waal, 2011). Its mechanism and function remain up to date mostly unknown but it seems clear that it has a social component, given that it occurs principally in social contexts (Guggisberg *et al.*, 2010). CY has been observed in several mammal species and in only one species of birds (reviewed in Massen & Gallup, (2017).

In humans, this phenomenon has been associated with empathy (Helt, Eigsti, Snyder, & Fein, 2010; Norscia & Palagi, 2011; Platek, Critton, Myers, & Gallup, 2003). This claim has empirical support: As empathic behaviours, CY is elicited more strongly by familiar individuals than by strangers, and the emotional bond between individuals affects the frequency, occurrence and latency of CY (Norscia & Palagi, 2011). Susceptibility to yawn contagion presents a developmental increase (Anderson & Meno, 2003; Helt *et al.*, 2010), just as empathic capacity, displaying a great increase at the age of four; age in which several cognitive abilities related to empathy begin to manifest (Widen & Russell, 2003). Humans who performed better at Theory of mind and self-recognition, abilities

supposedly required for complex empathy, displayed more CY (Platek *et al.*, 2003). Moreover, neurobiological studies have shown that, in humans, CY is associated with activity in the neural networks linked to empathy and social skills (Nahab, Hattori, Saad, & Hallett, 2009; Platek, Mohamed, & Gallup, 2005). Finally, yawn contagion seems to be impaired in individuals with empathy disorders such as schizotypy and autism (Platek *et al.*, 2003; Senju & Maeda, 2007).

RFM is an involuntary, fast, and automatic response, in which an individual mimics another's facial expressions (Mancini, Ferrari, & Palagi, 2013a). Its main feature is the rapidity of the response that distinguishes it from other forms of mimicry (Dimberg, Thunberg, & Grunedal, 2002). In humans, this facial mimicry has been proposed as the sensorimotor loop that induces in the observer the corresponding positive emotional state associated to that facial expression, giving rise to emotional contagion (Decety & Meyer, 2008). RFM could be grounded in the automatic perception-action coupling mechanism that takes place in the motor brain regions (Ferrari, Bonini, & Fogassi, 2009). There is evidence from functional brain imaging studies in humans showing that, during the observation of emotional facial expressions, shared motor representations are activated, not only in premotor and parietal areas, but also in cingulate and insular cortices which are involved in processing emotions and visceromotor sensations (Mancini, Ferrari, & Palagi, 2013b). RFM in humans could serve to avoid misunderstandings, promote social affiliation, increase the level of cooperation and seems to reflect the empathic capacity of individuals (Mancini *et al.*, 2013b). This hypothesis is partially supported by behavioural experiments showing that the frequency of RFM is higher among familiar than among unfamiliar individuals (McIntosh, 2006; Feldman, 2007).

## 2.2. Studies on mimicry in non-human animals

### 2.2.1. Motor mimicry

Two studies have assessed the link between mimicry and affiliation in two species of non-human primates: tufted capuchin monkeys (*Sapajus apella*) and rhesus macaques (*Macaca mulatta*), finding an affiliative effect of being mimicked in both species. Paukner *et al.* (2009) carried out a set of experiments in which one human actor mimicked the actions of the monkey while it was manipulating a ball and another actor did contingent actions with the ball but did not mimic the monkey. Then, they tested whether mimicry had influenced the preferences of the capuchins for one of the actors. Results showed that capuchins looked significantly longer at the imitator while they were being mimicked, they spent significantly more time in front of the imitator after the test (proximity to others is a reliable indicator of affiliative relationships in these primates (Fragaszy, Visalberghi, & Fedigan, 2004)), and they preferred to exchange tokens for food significantly more with the mimicker. Remarkably, in the first token exchange, without having experienced a mimicry phase, they did not show a preference for either actor. The second study (Sclafani *et al.*, 2015) tested the hypothesis that, in infancy, being mimicked can impact social interactions promoting new-born visual engagement and affiliation. The findings concurred with the hypothesis: being mimicked significantly affected the motor and affiliative behaviour of infant macaques. They displayed more affiliative gestures and looked longer at an experimenter during and after being mimicked than in the control condition.

In summary, these studies show that some monkey species realize when they are being mimicked, and that being mimicked prompts affiliation towards the mimickers even when they belong to another species.

### 2.2.2. Contagious yawning and rapid facial mimicry

#### a. Non-human primates

Campbell and de Waal (2011) examined whether CY in chimpanzees (*Pan troglodytes*) is elicited more strongly by familiar than by unfamiliar individuals, as it is in humans (Norscia & Palagi, 2011). Their findings supported the previous premise: chimpanzees yawned more after watching videos of familiar individuals. In a second experiment, chimpanzees watched videos of familiar and unfamiliar humans and gelada baboons (*Theropithecus gelada*) (Campbell & de Waal, 2014), and they yawned contagiously in response to both human groups but not after seeing baboon yawns. Madsen *et al.* (2013) also demonstrated the existence of this cross-species yawn contagion observing that juvenile, but not infant chimpanzees yawned contagiously after seeing familiar and unfamiliar humans yawning. The previous results suggested that chimpanzees could be subject to a developmental increase in susceptibility to CY. When the stimuli involved human yawns, there was no familiarity bias as the one observed in conspecific interactions, maybe because chimpanzees treat all humans as if they were in-group members (Campbell & de Waal, 2011). A bias toward familiar individuals was also observed in another ape species, the bonobo (*Pan paniscus*). Bonobos responded contagiously to conspecifics' yawns, yawning more frequently in relaxing than stressful periods. This effect increased with the closeness of the relation between individuals and if the stimulus subject was a female, as expected for a female bonded society (Demuru & Palagi, 2012). Palagi *et al.* (2009) obtained in a group of gelada baboons similar results to those reported for humans and apes. They provided evidence of CY in the presence of both visual and acoustic yawn signals from conspecifics. The level of CY correlated with the level of grooming contact between individuals. Thus, yawn contagion in baboons was more common among individuals with greater levels of affiliation. Moreover, female baboons were more likely to yawn than males. This result is consistent with the social structure of baboon groups, and with the fact that, in humans, it has been suggested that females have higher empathic reactions than males (Eisenberg, 2000). CY was only registered in adult baboons, an outcome that concurs with the previous data on apes and with studies in human infants showing that children younger than 5 years old do not show yawn contagion (Anderson & Meno, 2003). Interestingly, empathy also presents a series of developmental changes during ontogeny (Decety & Michalska, 2010; Lennon & Eisenberg, 1987).

On the other hand, few studies have provided data on RFM in non-human animals and its specific function is poorly understood. During play, non-human primates display a characteristic play-face homologous to the human facial expression associated with laughter (Mancini *et al.*, 2013a). The play-face, through RFM, also seems to activate in the perceiver the same motor programs and the same positive emotional state that the one of the individual in interaction (Mancini *et al.*, 2013b). This sharing could be adaptive since it allows individuals to fine-tune their own motor programs which, in turn, increases cooperation and avoids misunderstandings during play (Mancini *et al.*, 2013a). The first evidence of RFM in non-human animals was provided by a study with orangutans (*Pongo pygmaeus*) (Davila-Ross, Menzler, & Zimmermann, 2008). The authors assessed the occurrence of RFM studying the orangutan open-mouth face display (OMF) during dyadic play. Results indicated that orangutans mimicked OMFs of their partners rapidly. Two later studies with gelada baboons reported that RFM was also present during play in this species. Mother-infant play sessions presented the highest levels of RFM and the fastest responses (Mancini *et al.*, 2013b), and play interactions containing RFM lasted longer than those with DFM (delayed facial mimicry) (Mancini *et al.*, 2013a). Due to the scarce number of studies on RFM, more research is needed to assess its function in primates and its link with empathic processes. Even so, during social encounters, some non-human

primate species appear to rapidly mimic another's facial expressions suggesting that, in these species, RFM could play a similar role to that of emotional facial mimicry in humans.

### b. Canids

The study of Joly-Mascheroni *et al.* (2008) was the first to report evidence of CY in dogs (*Canis lupus familiaris*) in response to human yawns. However, two later studies failed to replicate these results (Harr, Gilbert, & Phillips, 2009; O'Hara & Reeve, 2011). Later, an experiment showed that dogs yawned contagiously in response to familiar and unfamiliar human yawns (Madsen & Persson, 2013). A developmental effect was also observed: only dogs above 7 months presented the contagious effect. Finally, two studies (Silva, Bessa, & de Sousa, 2012; Romero, Konno, & Hasegawa, 2013) found some evidence supporting the empathy-based explanation of CY: dogs yawned contagiously in response to the sound or the sight of a human yawning, and this effect was enhanced when the model was a familiar individual (e.g. their owner). Romero *et al.* (2014) demonstrated the presence of CY in wolves (*Canis lupus*). Wolves sharing a strong social bond displayed a higher frequency of CY, and females responded to yawns faster than males. Data on wolves suggest that, as empathy, CY correlates with the level of emotional proximity between individuals and that females could be more responsive to this kind of social stimulus.

### c. Parrots

It has been observed that budgerigars (*Melopsittacus undulatus*) tend to automatically mimic the actions of another bird (Mui *et al.*, 2008). Furthermore, Miller *et al.* (2012) observed that, under semi-natural flock-living conditions, budgerigars' yawns were temporally clumped. That is, budgerigars were more likely to yawn within few seconds of another bird's yawn, suggesting that yawns were socially influenced and that yawning in these birds might be contagious. Recently, the experimental evidence of CY in these parrots was finally provided by Gallup *et al.* (2015). This study assessed the presence of CY using as stimuli an individual yawning and video clips of conspecific's yawns. The results demonstrated that yawning was contagious, but there was no evidence of a familiarity bias. Budgerigars could be less sensitive to familiarity since they live in large and changing groups of unrelated individuals (Gallup *et al.*, 2015). This result could also be due to the fact that the experimental subjects were housed in the same room and, therefore, they could have established some degree of social closeness through vocal communication (Gallup *et al.*, 2015).

### d. Rodents

Moyaho *et al.* (2015) demonstrated the occurrence of CY in rats (*Rattus norvegicus*). CY was stimulated by olfactory cues but inhibited by visual ones. This result could be partially explained by the impaired vision of albino rats. Moreover, they observed a totally unexpected behaviour: pairs of cage-mate rats failed to show yawn contagion but pairs of stranger rats displayed auditory CY and higher rates of smell-facilitated auditory CY. That is, instead of finding a familiarity bias in the contagion they observed the opposite pattern. Taking into account the great importance of olfaction in mammals' social interactions, it should not be surprising to find a stimulatory role of olfaction on auditory CY in rats (Moyaho *et al.*, 2015). The fact that stranger rats but not cage-mates showed CY suggests that, in rodents, this phenomenon could rely on a mechanism not related to empathy. For example, yawning might have a communicative function, advertising greater physiological capacity during male-male conflicts (Moyaho *et al.*, 2015).

### 3. Social synchrony

Synchrony is broadly defined as the matching of rhythmic behaviour (e.g. movements or vocalizations) in time (Reddish, Bulbulia, & Fischer, 2014). Social synchrony or entrainment is a special case of spatiotemporal coordination where the rhythmic signals originates from another individual (Phillips-Silver *et al.*, 2010). In the case of spontaneous synchronization, it occurs unconsciously and neither requires higher cognitive processes nor particular goals (Nagasaka *et al.*, 2013).

Studies exploring synchrony in humans are numerous. During social interactions humans tend to spontaneously synchronize their movements, and this effect has been proposed to increase cohesion and affiliation facilitating communication and reciprocal responses (Richardson, Marsh, & Schmidt, 2005; Richardson *et al.*, 2007; Oullier *et al.*, 2008; Miles *et al.*, 2011; Nagasaka *et al.*, 2013). A broad class of synchronized movements (walking, dancing, finger tapping) seem to increase prosociality, cooperative behaviours and likeability among the individuals involved (Hove & Risen, 2009; Wiltermuth & Heath, 2009; Kirschner & Tomasello, 2010; Cirelli, Einarson, & Trainor, 2014; Rabinowitch & Meltzoff, 2017). Furthermore, synchronous interaction in groups may elicit cues of group membership promoting cooperative behaviours among group members (Reddish *et al.*, 2014). On the other hand, synchrony might also evoke generalized prosociality even towards individuals outside the synchronous group (Wiltermuth & Heath, 2009; Reddish *et al.*, 2014). The results of a recent meta-analysis (Rennung & Göritz, 2016) have confirmed a medium effect of synchrony on prosocial attitudes and behaviours in humans. However, this study has also highlighted that experimenter effects (influence of unblinded experimenter's expectations on subjects' responses) and intentionality (synchrony occurs as a consequence of a common goal) can moderate these effects. Thus, raising the question of whether in some experiments the effects of synchrony on prosociality may in part be caused by a methodological artefact (Rennung & Göritz, 2016).

Several hypotheses have been proposed to explain the effect of synchrony on prosocial behaviours and cooperation. Valdesolo and DeSteno (2011) hypothesized that synchrony marks others as similar to self, enhancing altruistic behaviours toward synchronous individuals. That is, synchrony might elicit low-level appraisals of similarity leading individuals to perceive themselves as united, an effect that would in turn increase affiliation, emotional responding and helping behaviours toward synchronous partners. It has been also proposed that synchrony may facilitate emotional contagion and attentiveness towards synchronous individuals (Hatfield *et al.*, 1994; Reddish *et al.*, 2014). Therefore, individuals could be more inclined to communicate and/or to empathize with their synchronous partners, an effect that would lead to an increase in cooperative and helping behaviours among synchronized individuals. At the brain level, it has been suggested that the link between synchrony and prosocial behaviour could be based on the activation of the reward system during synchronized activities (Kokal *et al.*, 2011). Performing synchronized movements could be socially rewarding and facilitate prosocial behaviour between the synchronized individuals (Kokal *et al.*, 2011). The caudate nucleus (part of the reward system) could relate synchronized activity to basic reward processing, influencing future decision to help the synchronous partner (Kokal *et al.*, 2011). Endorphin release (endogenous opioid neuropeptides) has also been proposed as a factor linking synchrony to prosocial behaviours and social bonding. Several studies have provided evidence supporting this hypothesis by showing that, after performing synchronized movements, individuals displayed higher pain tolerance than individuals performing the same activity alone (Cohen *et al.*, 2010; Dunbar *et al.*, 2012a, 2012b; Sullivan & Rickers, 2013; Tarr *et al.*, 2015). This higher pain tolerance has been inferred as an indicator of endorphin activity (Sullivan & Rickers, 2013).

Therefore, activation of the endogenous opioid system through synchronized behaviour might increase positivity towards others, promoting social bonding and subsequent prosocial behaviours (Sullivan & Rickers, 2013).

There is a growing body of evidence pointing that several species of parrots and mammals are able to synchronize their motor activity with an auditory rhythm (Patel *et al.*, 2009; Schachner *et al.*, 2009; Hasegawa *et al.*, 2011; Cook *et al.*, 2013; Hattori, Tomonaga, & Matsuzawa, 2013; Stoeger & Manger, 2014). These studies suggest that several species could also spontaneously synchronize their movements or vocalizations with those of other individuals during social interactions. Furthermore, there are dozens of examples of collective synchronized behaviours in the animal kingdom as schooling in fish (Pitcher & Parris, 1993), flocking in birds (Emlen, 1952) or flashing in fireflies (Moiseff & Copeland, 2010). These synchronized behaviours could play several distinct evolutionary functions. Synchronous movements could provide protection to the group by allowing collective responses to danger, by increasing vigilance or by decreasing the risk of predation through confusion and dilution effects (Fellner, Bauer, & Harley, 2006). Moving in synchrony may also provide aero- or hydrodynamic advantages favouring energy conservation (Fellner *et al.*, 2006; Daghooghi & Borazjani, 2015). For species that produce synchronous calls or flashing signals to attract females, synchrony could minimize predation risks by confusing predator's auditory localization abilities, maximize peak signal amplitude or serve for the identification of conspecifics (Greenfield, 1994; Merker, 2000; Moiseff & Copeland, 2010; Ravnani, Bowling, & Fitch, 2014). Furthermore, in species in which females prefer males which perform the leading call in a closely synchronized sequence, synchrony could also be an epiphenomenon created by competitive interactions between males (Greenfield & Roizen, 1993; Greenfield, 1994). On the other hand, it has been proposed that, as in the human case, synchrony may also play a role in pair bonding, affiliation and cooperation in non-human animals (Sullivan & Rickers, 2013; Tarr *et al.*, 2015).

### 3.1. Studies on social synchrony in non-human animals

#### a. Non-human primates

Under controlled laboratory conditions, Nagasaka *et al.* (2013) provided positive evidence of the occurrence of spontaneous social synchrony in a non-human primate. In this experiment, Japanese macaques (*Macaca fuscata*) were first trained in a button-pressing task. After training, two macaques facing each other were tested simultaneously in this task. Researchers quantified synchronization by rhythm changes in button-pressing behaviour. Results demonstrated that monkeys were synchronized and that this behaviour was dependent on the partner. It was also found that visual information from the partner induced a higher degree of synchronization than auditory information. Another study reported that a 3 years-old chimpanzee spontaneously mimicked and synchronized its movements with those of a model (another chimpanzee or a human experimenter) while the model was cracking nuts (Fuhrmann *et al.*, 2014).

Some cohesive pair-living primate species like gibbons (Hylobatidae) were reported to engage in duetting behaviour. Duetting is defined as an interactively organized pair display in which one partner coordinates its vocalizations in time with those of the other partner (Wickler, 1980; Méndez-Cárdenas & Zimmermann, 2009). Several functions have been proposed to explain duetting in primates such as territorial advertisement, strengthening of pair or family bonds or both (Farabaugh, 1983; Geissmann, 2000; Malacarne, Cucco, & Camanni, 1991; Ravnani *et al.*, 2014; Wachtmeister, 2001). Mated pairs of siamangs (*Hylobates syndactylus*) for example, produce well-patterned duets by combining their partially sex-specific repertoire in relatively rigid, precisely timed and complex vocal interactions (Geissmann, 2000). Mated siamangs synchronise the beginning and end of their song

sequences, and during some phases of the duet, they also synchronise their vocalisations (Geissmann, 2000). Other members of the family group could also join in the songs and these songs seem to elicit song bouts of neighbouring groups (Geissmann, 2000). A study has provided positive evidence of the relation between duetting and pair bonding in this primate species showing that duetting was positively correlated with accepted indicators of pair bond strength in primates (Geissmann & Orgeldinger, 2000). Data on duetting behaviour in a group of polygynous black-crested gibbons (*Nomascus concolor jingdongensis*) also supported the pair bonding hypothesis as well as the mate defence and group cohesion hypotheses (Fan *et al.*, 2009). These results suggest that, in fact, duetting behaviour in gibbons may serve multiple functions and these functions may vary depending on the context and the behavioural ecology of each species (Geissmann, 2000). Duetting behaviour has also been described in dispersed pair-living primates such as the Milne Edwards' sportive lemur (*Lepilemur edwardsi*) (Méndez-Cárdenas & Zimmermann, 2009). It has been shown that, in these lemurs, duetting behaviour increased during the offspring care period and that pair partners synchronized their behavioural activities after duetting. Therefore, in this species, duetting may serve to coordinate activities between mated pairs dispersed in space, but also to strengthen pair bonds and maybe to limit infanticide (Méndez-Cárdenas & Zimmermann, 2009).

Overall, there is a lack of studies on spontaneous social synchronization in non-human primates. Nevertheless, some evidence suggests that, as humans, other primate species may tend to spontaneously synchronize their movements with those of another individual during social interactions. However, more studies are needed to confirm the occurrence of social synchronization during social contexts in ape and monkey species and its link with prosocial and cooperative behaviours, as suggested by human data. On the other hand, data on duetting behaviour on gibbons suggests that calling in synchrony may enhance pair or group bonding and thus, serve as a basic mechanism of empathy promoting affiliation between individuals in an automatic and simple way.

## **b. Birds**

Many monogamous birds engage in pair displays after mate choice. These displays often involve synchronic movements and are performed in different contexts (Wachtmeister, 2001). For example, many aquatic birds like grebes, mergansers or loons, display complex courtships in which both sexes perform synchronized movements such as preening the same feathers, swimming or diving in unison. Given that these behaviours are also observable after the mating season, it has been proposed that they may serve to synchronize hormonal changes of the male and the female or for strengthening the pair bond (Mc Allister, 1958; Wickler, 1980; Greenquist, 1982; Wachtmeister, 2001; Kear, 2005; Evers *et al.*, 2010). Flamingos (Phoenicopteridae) execute highly synchronous mixed-sex group displays throughout the year, but the rate of these displays increase during the pre-breeding period (Wickler & Seibt, 1980; Stevens, 1991; Perrot *et al.*, 2016). It has been suggested that these displays stimulate synchronous nesting and facilitate pair formation. Furthermore, there is evidence pointing to a relationship between these synchronous displays and breeding success (Stevens, 1991). Greeting and triumph ceremonies are also examples of displays in monogamous birds that include synchronous movements and are not only associated with pair formation (Malacarne *et al.*, 1991; Wachtmeister, 2001). Many of these synchronized visual displays are coupled with duetting, that is temporally and thematically coordinated in a sequential manner (Wickler, 1980; Wachtmeister, 2001). Greeting ceremonies are common, for example, in several species of herons and are performed by both partners when they rejoin after a period of separation (Mock, 1976; Rodgers, 1977; Wachtmeister, 2001). Interestingly, these ceremonies are often characterized by the male bringing nest twigs and passing them to the female. This behaviour persists even when the nest is in good condition and does not require additional twigs for repair (Rodgers, 1977). The function

of this ceremonies is not yet clear (Wachtmeister, 2001) and again, one of the hypotheses is that they serve to reinforce the pair bond after a period of separation (Rodgers, 1977). Several species of penguins (Spheniscidae) also perform mutual displays calling or trumpeting together in synchrony. These displays are usually observed at the beginning of the breeding season but they also may serve to strengthen the affiliative bond when a member of the couple returns to the nest after an absence period (Favaro, Ozella, & Pessani, 2014). Triumph ceremonies are common among geese and swans (Anatidae) and consist of coordinated displays of the pair after having evicted and intruder (Lorenz, 1966; Wachtmeister, 2001). Triumph displays include vocal and motor sequential patterns of behaviour, some of these patterns are often performed by the pair in a synchronized manner (Kear, 2005). These ceremonies were first described in territorial contexts but seem to occur at any stage of a pair bond and not exclusively after aggressive encounters (Radesäter, 1975; Wachtmeister, 2001). For example, it has been reported that geese and swans also perform these ceremonies at times of distress and when partners or family members rejoin after a period of separation (Lorenz, 1966; Radesäter, 1975; Wachtmeister, 2001). Some synchronous displays in birds may also serve to restore relationships after aggressive events. For example, after an aggressive encounter, rooks (*Corvus frugilegus*) tend to engage in a synchronized display which includes bowing and tail-fanning accompanied by vocalizations (Seed, Clayton, & Emery, 2007). This behaviour seems to buffer the tension during the post-conflict period and has been suggested to advertise affiliation and alliances to other group members (Seed *et al.*, 2007).

Many bird species, especially those living in tropical areas, perform duets characterized by coordinated vocal displays of alternating or simultaneous song (Wachtmeister, 2001). Duetting seems to occur after pair formation and throughout the duration of the pair bond (Wachtmeister, 2001). Many hypotheses have been proposed for the function of duetting behaviour in birds such as cooperative territory defence, enhance or advertise the pair-bond, keep contact with each other, mate guarding or synchronize reproductive physiology of the mates (Wickler, 1980; Farabaugh, 1982; Malacarne *et al.*, 1991; Wachtmeister, 2001; Logue, 2005; Mennill & Vehrencamp, 2008; Templeton *et al.*, 2011). Some bird species also engage in synchronous chorusing, a complex and coordinated behaviour that occurs when more than two individuals combine their vocalisations into an acoustic display (Bradley & Mennill, 2009). Given that several birds are involved, choruses could serve as a cooperative group signal for enhancing within-group cohesion, maintaining social bonds and playing a role in joint resource defence (Bradley & Mennill, 2009).

The fact that synchronous displays in birds often occur in many different contexts suggests that they could be multi-purpose signals that serve independent functions in different situations. The pair-bonding hypothesis has received considerable interest since it seems to be the only existing explanation consistent with much of the empirical evidence with respect to temporal pattern and form of these behaviours (Wachtmeister, 2001). It has been also proposed that synchronous displays may have become necessary for maintaining reproductive cooperation and for keeping the relationship between pair partners (“theory of manipulation”) (Wachtmeister, 2001). That is, these displays could function as a manipulating behavioural mechanism necessary to elicit partner assistance and maintain the pair bond (Wachtmeister, 2001). In fact, many synchronized displays in bird species seem to be related to or promote subsequent cooperative activities such as joint territory or resource defence, cooperative breeding of the offspring or nest building. Performing coordinated displays might synchronize the physiology of the pair partners or the group members, a process that in turn could promote affiliation between synchronous partners or strengthen social bonds and group cohesion. Ultimately, this process could lead to an increase in the probability of cooperation and prosociality between synchronous individuals. Therefore, many synchronic behaviours in birds may

function as basic forms of empathy. Overall, bird synchronous displays offer an interesting study model for testing the effect of synchronous movements or vocalizations in subsequent cooperative, prosocial and affiliative behaviours. More research is needed to assess the mechanisms, factors and functions underlying the different synchronized motor or vocal behaviours observed in several bird species.

#### 4. Emotional contagion

Contagious crying among babies and the spread of fear in a group of animals are two of the most common examples given to illustrate emotional contagion. As its name implies, emotional contagion is traditionally seen as the automatic spreading of emotions. But, in the scientific literature, there are two distinct ways of characterizing and defining this process. On the one hand, emotional contagion is seen as a behavioural change, not as an affective experience (Lahvis, 2017). Thus, emotional contagion is defined as the tendency to automatically mimic and synchronize expressions, vocalizations, postures or movements with those of another individual (Hatfield *et al.*, 1994) or as a reflexive behavioural change in which an individual spontaneously displays a behaviour that resembles the behaviour showed by another individual (Lahvis, 2017). Although sometimes the behavioural change can be accompanied by a change in the emotional state of the subject or lead to the emotional convergence between individuals (Hatfield *et al.*, 1994), this is not a necessary condition to talk about emotional contagion. According to this view, emotional contagion and mimicry are two equivalent and indistinguishable processes. On the other hand, emotional contagion is seen as an emotion sharing process. It is defined as the emotional state-matching between individuals (de Waal, 2008) or as an automatic response resulting in a similar emotion being triggered in the observer as a direct result of perceiving the displayed emotion in another individual (Li *et al.*, 2014). Therefore, emotional contagion involves the adoption, in whole or in part, of another's emotional state (de Waal, 2008; Hatfield *et al.*, 1994). Sometimes, this emotional state-matching might be also accompanied by a behavioural state-matching but, in this case, emotional contagion and motor mimicry are considered to be related but different processes.

Even though emotional contagion may encompass several psychological and physiological components that are interrelated, as neurophysiological activity, facial and postural expressions and behavioural responses (Hatfield *et al.*, 1994), the mechanisms involved in this process do not appear to be very complex. In fact, a crucial feature of emotional contagion is that it does not require a discrimination between one's own and another's emotions (Hatfield *et al.*, 1994). According to Preston and de Waal (2002), the main mechanism underlying emotional contagion is the PAM. Therefore, emotional contagion requires direct sensory engagement that triggers automatic and involuntary motor and emotional processes (Coplan, 2006). Seeing the emotional displays of another individual may reactivate neural representations of past experiences in the bystander which, in turn, generates a bodily state that matches that of the observed individual (de Waal, 2008). According to this approach, emotional contagion implies that individuals contemporaneously share the same emotional state (Panksepp & Lahvis, 2011). In fact, there is empirical evidence showing that there is a neural similarity between self-generated and vicarious emotions (Carr *et al.*, 2003; Decety & Chaminade, 2003; Decety & Jackson, 2006; Singer *et al.*, 2004; Wicker, Keysers, Plailly, & Royet, 2003). Furthermore, several studies have supported the claim that, in humans, emotions are contagious (e.g. Hatfield *et al.*, 1994; Hess & Blairy, 2001; Wild, Erb, & Bartels, 2001; Barsade, 2002; de Gelder *et al.*, 2004; Dezechache *et al.*, 2013; Martin *et al.*, 2015). However, due to the difficulties associated with the process of measuring online emotions, it is not yet clear whether emotional contagion produces the relevant emotional experience in the receiver or simply primes core affect mechanisms (Decety & Svetlova, 2012). That is, it is not well established whether the

emotional response triggered by the perception of another's emotional state is isomorphic or not to the perceived affective state (de Vignemont & Singer, 2006). Some authors propose that to qualify as empathic, the elicited state must be isomorphic to that of the other person (de Vignemont & Singer, 2006; Panksepp & Lahvis, 2011). Given that emotional contagion has been proposed as the main process underlying emotional empathy, this empathic category is also often characterized by a "state-matching" between individuals (Panksepp & Lahvis, 2011). This vision of empathy, focused on the individual's affective experience, is close to the seminal approach of Lipps (1903), in which the term empathy (*Einfühlung*) also implied that the perception of an emotional display in another individual automatically activate the same emotion in the perceiver, without any intervening labeling, associative or cognitive perspective-taking processes. Most of the current models of empathy have adopted to some extent this approach assuming that the emotional aspects of empathy are based on an emotional state-matching between individuals (de Vignemont & Singer, 2006; de Waal, 2008).

Incremental views of empathy often consider emotional contagion as the lowest common denominator of all empathic processes (de Waal, 2008). On the other hand, other views of empathy acknowledge that emotional contagion may be an important component of some empathic behaviours but also admit that other complex forms of empathy might not be underlain by it (de Vignemont & Singer, 2006; Yamamoto, 2017). If emotional contagion underlies some complex forms of empathy, it is possible that this process leads to prosocial behaviours such as helping. In fact, the emotional engagement induced by state-matching processes may be necessary to motivate subsequent prosocial or cooperative behaviours (de Waal, 2008). Experiencing emotional reactions consistent with the state of another may elicit other-oriented concern and thus provide motivation for alleviating the other's need or distress (Eisenberg *et al.*, 1989) or helping others (Barsade, 2002; de Vignemont & Singer, 2006). In the human literature, there is some empirical support for this claim (Barsade, 2002; Decety & Svetlova, 2012; Eisenberg *et al.*, 1989; Eisenberg & Miller, 1987). Furthermore, given that an important feature of the empathic response is that it is amplified by greater similarity, familiarity or social closeness with the other individual (de Waal, 2008; Preston & de Waal, 2002), emotional contagion processes are expected to be elicited more strongly by familiar individuals. Some accounts of empathy state that the initial emotional response triggered by the perception of another's emotional or behavioural displays must be subjected to some degree of emotional regulation, contextual appraisals and/or cognitive processing in order to talk about empathy (de Vignemont & Singer, 2006). In general, it is assumed that the primary emotional response towards another's emotional display is downregulated and modulated by several factors to give rise to most complex forms of empathy (de Vignemont & Singer, 2006; Decety & Svetlova, 2012; Eisenberg *et al.*, 1989). At this point, the literature usually distinguishes between two different resulting emotional responses: sympathy or sympathetic concern, an other-oriented emotional reaction to another's emotional state or condition (Eisenberg *et al.*, 1989) and personal distress, a self-focused, aversive emotional response triggered by the perception of another's distress (Batson, 1991). Personal distress is associated with the desire to alleviate one's own aversive arousal not with the goal of mitigating the other's suffering, and therefore it is not usually considered as a form of empathy (Batson, Fultz, & Schoenrade, 1987). It also involves an emotional reaction to another's emotional state, but it is characterized by feelings of personal distress that do not necessarily match the ones of the other individual, neither trigger subsequent empathic behaviours or lead to the understanding of the other's emotional state.

In brief, emotional contagion may function as a basic form of empathy allowing the sharing of emotional responses in an automatic and simple way. Furthermore, emotional contagion processes may underlie more complex empathic behaviours and motivate to some extent prosocial behaviours. Sharing a similar emotional state with another individual may be an important motivator to, for

example, engage in costly helping responses. Moreover, these emotional contagion processes do not seem to be cognitively demanding and thus might be found in a wide number of animal species.

In the following section, we review the most relevant studies on emotional contagion in non-human animals. We focus on whether emotional contagion processes, similar to those described in humans, are present in other species and whether they lead to an emotional state-matching between individuals. Furthermore, we also pay special attention to the available evidence linking emotional contagion with affiliative and prosocial behaviours.

#### 4.1. Studies on emotional contagion in non-human animals

##### a. Non-human primates

There are several anecdotal reports describing possible cases of emotional contagion in non-human primates, especially in chimpanzees. Mothers briefly whimpering when they hear their offspring whimper (de Waal, 2008); chimpanzees becoming excited when seeing another individual becoming aroused just before the presentation of food (O'Connell, 1995); or the scaling up of group arousal through the emission of pant-hoot vocalizations (calls emitted during social excitement) (Fritz & Koelsch, 2013). The pioneer empirical studies on emotional contagion in non-human primates *per se* were the infamous experiments with rhesus macaques conducted during the 60's. Those studies assessed the ability to communicate emotional information between individuals measuring monkeys' behavioural responses towards distressed conspecifics. Masserman, Wechkin and Terris (1964) first trained macaques to press a lever that delivered food. Then, if the macaque pressed that lever a conspecific received an electric shock. They observed that macaques stopped pressing the lever. In a subsequent experiment (Masserman *et al.*, 1964), one lever delivered a huge amount of food and a shock to another macaque, and a second chain delivered a smaller quantity of food but no shock to the other monkey. After witnessing the other monkey receiving the shock, two monkeys stopped pulling either chain, one for 5 days and other for 12 days. The inhibition response was greater if a familiar macaque received the shock or if the observer had previously experienced it. Visual cues were more likely to trigger this response. The authors concluded that the sight of a distressed monkey affected the behaviour of the observer up to the point that most of the monkeys would suffer hunger rather than secure food at the expense of shocking a partner. Miller *et al.* carried out a set of experiments in which two monkeys engaged in a cooperative-conditioning paradigm. The experiments showed that: 1) monkeys do react to the emotional expressions of other individuals (Mirsky, Miller, & Murphy, 1958; Miller, Banks, & Ogawa, 1963); 2) monkeys that were conditioned to react to conspecific's distress signals did not respond when a monkey puppet or an albino rat received the shock (Miller, Murphy, & Mirsky, 1959); and 3) macaques exhibited the same heart rate (HR) response when experiencing distress and when perceiving expressions of distress in others (Miller, 1967; Miller, Banks, & Kuwahara, 1966). Although these data suggest the existence of an emotional state-matching between monkeys, we must be cautious when interpreting these results since several authors noticed some objections in the procedure of these experiments. In many cases, the details of the monkeys' facial expression are lacking so we cannot be sure if the responder monkey guided its behaviour using emotional expressions or other motor actions (Hauser, 2000).

Three studies empirically assessed the behavioural and physiological responses of chimpanzees to the sight and sound of emotional expressions of conspecifics. Berntson *et al.* (1989) exposed infant chimpanzees to conspecifics' emotional vocalizations and recorded changes in HR and behaviour. Conspecific laughter had an acceleratory influence in HR and evoked vocalizations from the infants similar to adult threat-barks. Further analysis revealed that the acceleratory response resulted from sympathetic activation and was reminiscent of a defensive reaction. Thus, laughter vocalizations

elicited in infants defensive-like reactions rather than affiliative responses. Conversely, screams evoked decelerating responses likely arisen from an increase in parasympathetic activity and no vocalizations were registered during this condition. This result is consistent with previous data in chimpanzees (Berntson & Boysen, 1989) and humans (Bryan & Newman, 1989). These findings indicate that cardiac responses of infant chimps differentiate between scream and laughter stimuli and that these differential responses to conspecific vocalizations arise very early in development. However, these HR measures did not provide reliable indicators of the precise nature of the underlying behavioural or emotional reactions (Berntson & Boysen, 1989). In another study (Parr & Hopkins, 2000), chimpanzees' tympanic membrane temperature (Tty) was measured while they watched three types of emotional videos: positive, neutral or negative. Tty is an index of sympathetically mediated changes in brain temperature that, in turn, indicates changes in the physiological arousal of chimpanzees (Hopkins & Fowler, 1998). Right Tty increased significantly in response to the negative emotional videos and left Tty increased in response to the positive emotional videos, but not significantly. This suggests a lateralization of emotional processing in chimpanzees. Moreover, during the negative videos chimpanzees responded with strong visual orientation, piloerection, pant-hooting and bluff-displays, indicators of a high arousal state. On the other hand, chimpanzees displayed a strong visual orientation, play invitations, play faces and solicitations to the video monitor in response to the positive emotional videos. During the neutral videos, no clear behavioural responses were registered. In a similar experiment (Parr, 2001), chimpanzees watched three categories of negative emotional videos. A decrease in peripheral skin temperature (an indicator of negative arousal) was recorded when chimpanzees viewed videos of individuals injected with needles or videos showing needles but not when watching videos of a conspecific chasing the veterinarian. There were no significant differences in the responses to the sight of conspecific injected and the sight of needles themselves. Thus, it was not clear that the physiological changes were triggered by the perception of another's distress rather than by the sight of an aversive stimulus like needles. Nevertheless, these chimpanzees correctly matched the video with a picture of a conspecific's emotional expression which had the same valence.

In general, both experimental and observational reports show that non-human primates are affected by the emotional displays of conspecifics. Some of the previous data are suggestive of emotional contagion as the evidence provided by Parr and Hopkins' study in which chimpanzees showed negative behavioural indicators in response to negative emotional videos and displayed affiliative behaviours in response to positive emotional displays. That is, the emotional state of observers appeared to match that of the chimpanzees who appeared in the videos. However, more controlled studies are needed to clarify the mechanisms involved in these responses as well as the factors that influence these reactions (familiarity, gender, previous experience...).

## **b. Canids**

Dogs are a very interesting animal model to study inter-species emotional contagion since during a long period of time they have shared a close bond with humans. In fact, it has been reported that during positive interactions there is a physiological and hormonal synchronization between dogs and their owners (Odendaal & Meintjes, 2003; Nagasawa *et al.*, 2015). Moreover, dogs seem to be able to discriminate human emotions (Deputte & Doll, 2011) and emotional expressions of human faces (Müller *et al.*, 2015). An experimental paradigm used with human infants (Zahn-Waxler, Hollenbeck, & Radke-Yarrow, 1984) was adapted to investigate the responses of dogs to human emotional behaviours (Custance & Mayer, 2012). Dogs were exposed to 4 conditions: two in which their owner or a stranger pretended to cry and two in which they hummed a song. Dogs oriented significantly more often toward their owner or the stranger during the crying condition. Furthermore, during the

crying condition most of the dogs approached the person in a submissive way. When the stranger was pretending to cry, dogs sniffed, nuzzled and licked him instead of seeking out their owner for comfort. Intriguingly, during the crying condition two dogs produced mild distress vocalizations. The authors suggested that dogs' reactions were driven by emotional contagion. Sümeği, Oláh, and Topál (2014) assessed whether the owner's stress-related emotional changes could be contagious to the dog. As several studies have shown, a significant effect of perceived stress on subjects' cognitive performance in memory tasks (McEwen & Sapolsky, 1995), researchers measured changes in dogs' cognitive performance in a spatial memory task as an indicator of contagion-induced changes in their stress level. Dogs were subjected to a stressful period in which they were separated from their owners. This procedure improved dogs' performance in a spatial working memory task. More remarkably, task completion was also affected by dog owners' anxiety state: dogs performed better when the self-reported anxiety of their owner was higher suggesting that dogs were influenced by the owners' emotional state. Yong and Ruffman (2014) provided further evidence for the existence of emotional contagion in dogs. In this work, the authors assessed whether dogs showed signs of emotional contagion responses to three auditory stimuli: a human infant crying, a human infant babbling and "white noise". They found that in both, humans and dogs, cortisol levels increased significantly from the baseline but only after the crying condition. Moreover, dogs displayed a specific behaviour in response to crying, they behave in a submissive and alert manner. A recent study tested whether dogs experience emotional contagion and direct empathy-like behaviours towards familiar partners (dogs that lived together) after hearing conspecifics' distress whines (Quervel-Chaumette *et al.*, 2016). To assess the occurrence of emotional contagion, dogs' physiological (cortisol levels) and behavioural responses (alertness and stress-related behaviours) were recorded and analysed. The experiment consisted in two phases: 1) the playback phase in which the subject was exposed to the experimental sounds; and 2) the reunion phase in which the subject was reunited with its familiar partner. While dogs displayed higher behavioural alertness and more stress-related behaviours in the whine compared with the control condition, none of the observed behavioural responses was influenced by familiarity. Although familiar whines tended to maintain dog's cortisol concentration at a higher level than stranger whines, in contrast to a previous study (Yong & Ruffman, 2014) no increase in salivary cortisol levels was found. During the reunion phase, subjects spent more time near their partner and engaged in more affiliative behaviours in the whine than in the control condition. In addition, in the first session of the experiment, subjects that were exposed to familiar whines spent more time directing affiliative behaviours towards their familiar partners than subjects exposed to stranger whines. Finally, Huber *et al.* (2017) exposed dogs to positive and negative sounds of humans or conspecifics and measured their behavioural responses. Dogs' responses toward human and conspecific emotional sounds were similar but differed from their responses to control sounds. Independently of the valence of the stimuli, dogs froze more in response to conspecific than to human emotional sounds. Given that freezing behaviour is usually found in social conflicting situations, these results could be indicative that, in dogs, hearing unfamiliar conspecifics might elicit higher tension than hearing unfamiliar human sounds (Huber *et al.*, 2017). Dogs displayed more behavioural indicators of negative emotional states in response to human or conspecific negative stimuli than to control or positive sounds. However, researchers did not measure behavioural indicators of positive emotional states to assess the occurrence of positive emotional contagion in dogs. The authors concluded that dogs' behavioural responses were triggered by emotional contagion since they behaved differently depending on whether the sound had an emotional component or not, or whether its valence was positive or negative.

Overall, these findings suggest that dogs can be attuned and affected by the emotional states of others. Some of the previous evidence point to a possible emotional-state matching between dogs and humans or conspecifics: similar physiological changes were registered in both human and dog

participants in interaction, dogs seemed to acquire their owners' anxiety state and displayed stress-related behaviours in response to distress or negative sounds of conspecifics or humans. Furthermore, some of these emotional reactions in response to another's distress lead to affiliative contacts toward the distressed party suggesting a possible link between emotional contagion and prosocial responses in dogs. However, we also face some contradictory and non-conclusive results that do not allow us to distinguish whether dogs adopted the same emotional state as demonstrators or they merely displayed stress reactions towards what they perceived as aversive stimuli (e.g. human crying). Either way, these studies on dogs' emotional responses to the emotional state of humans and conspecifics open a very interesting area of research that deserves more attention.

### c. Elephants

Elephants have a complex social behaviour and share close bonds with family members, features which make them a very interesting study species for empathy research (Plotnik & de Waal, 2014). However, there are not many empirical studies with well-defined controls assessing these emotional behaviours, and most of the available data comes from anecdotal reports. Although anecdotal reports have been called into question for several reasons (see Bates and Byrne, 2007), Douglas-Hamilton *et al.* (2006) carried out a more rigorous observational report using long-term associations records, GPS tracking data and direct observations of a group of African elephants (*Loxodonta africana*). This paper reports the behavioural responses of different elephants and their families towards a dying and deceased matriarch. In particular, an unrelated matriarch displayed an intriguing behaviour likely related to emotional contagion. When the distressed matriarch fell down, the unrelated female rapidly approached her displaying clear signs of excitement, as tail raised, emission of vocalizations and temporal gland secretion (related to stress, excitement or fear in elephants (Gorman, 1986)). Then, the unrelated matriarch tried to lift her up. This report shows a behavioural change in the presence of a suffering conspecific and what is more, gland secretion suggests that the behavioural changes were accompanied by autonomic modifications driven by the perception of suffering in another individual. Moreover, the distressed matriarch also displayed temporal gland secretion suggesting a possible state-matching between both individuals. Sikes, in 1971 (Schulte, 2000) described a similar case in which an elephant was mortally wounded and could not rise. The other members of the group tried to lift it up but they failed in their attempt so they start circling the injured individual, as has been seen in dolphins during stressing situations (Caldwell & Caldwell, 1964). In regard to experimental evidence of emotional contagion in elephants, we can only mention the study of Plotnik and de Waal (2014). They investigated affiliative tendencies between Asian elephants (*Elephas maximus*) after distressing events. They reported that the behavioural and emotional state of an observer elephant matched those of an individual that has undergone a distressful event. More specifically, bystanders adopted the agitated behaviour of the distressed individual (e.g. ears presented forward, erected tail, vocalizations, urination and defecation). Furthermore, bystanders engaged in significantly more reassuring responses towards other individuals following a distress event than during control periods. That is, elephants provided more affiliative responses to distressed individuals. These findings suggest the existence of emotional contagion between both individuals and link this emotional response to subsequent prosocial behaviours. However, this study lacked well-defined controls to distinguish between the observer's behaviours triggered by the perception of distress in others from the behaviours elicited by the distressing event itself.

Jointly, these studies indicate that elephants are affected by the sight of a suffering individual. During those situations, they displayed both behavioural and physiological signals of distress that, in occasions, appeared to match those of the distressed individual suggesting the occurrence of an

emotional state-matching. Furthermore, the observed subsequent prosocial behaviours relate this possible emotional contagion process to more complex empathic behaviours such as sympathetic concern or targeted helping. However, we must be cautious at the time of interpreting previous data due to the lack of rigorous controls in the experimental procedure of Plotnik and de Waal (2014) and the nature of the other observational records. More research is needed thus to assess the occurrence of an emotional state-matching between elephants in other relevant emotional situations.

#### d. Rodents

The studies on rodent empathy have become consolidated as an ideal model for assessing empathic processes in animals and the neural substrates involved. In recent years, a large body of data on emotional contagion of pain and fear in rodents has been accumulated. These studies have emphasized the extent to which rodents can be attuned to the affective state of others suggesting the presence of emotional contagion (reviewed by Panksepp & Lahvis, (2011); Mogil, (2012); Keum & Shin, (2016); Meyza *et al.*, (2016)).

Most of the studies on emotional contagion of fear in rodents can be divided into three categories, depending on the type of stimulus to which the observer animal is exposed (Meyza *et al.*, 2016). The first category includes experiments in which rodents observe a conspecific (demonstrator) experiencing aversive stimulation (e.g. foot-shocks), in occasions paired with a conditioned stimulus (e.g. tone). This paradigm serves to assess the observer's responses to demonstrators' fear and pain reactions. As rodents usually express fear by freezing (defensive immobility) (Sivaselvachandran *et al.*, 2016), this is the most used behavioural parameter in experiments assessing emotional contagion of fear. In two seminal studies (Church, 1959; Rice, 1964), a rat had to press a lever to obtain food while observed another rat receiving electrical shocks. Both studies showed that the exposure to a conspecific's distress decreased the observers' rate of lever pressing, behaviour that was interpreted as a signal of fear (Estes & Skinner, 1941). However, in the experiment of Rice (1964), it was not clear whether this effect and the observers' fear-related responses were due to the features of the apparatus or triggered by the sight of the distressed conspecific. Interestingly, rats that received a synchronous shock with a partner expressed a strong drop in lever pressing compared to the other groups, even when rats were deprived of food (Church, 1959). This result suggests that a shared experience with another rat may enhance emotional contagion in these rodents. Some recent studies showed that neither the visual (Sanders *et al.*, 2013) nor auditory (Chen, Panksepp, & Lahvis, 2009; Atsak *et al.*, 2011) exposure to a familiar or unrelated conspecific receiving foot-shocks elicited freezing responses in observer rodents. Thus, these results do not support the existence of emotional contagion. However, another series of studies provided positive evidence of this phenomenon. HR changes were registered in witness mice (*Mus musculus*) while unrelated demonstrators experienced the shocks. Only mice from a gregarious genetic strain (B6) and not mice from a less social genetic strain (BALB) displayed an HR deceleration with repeated exposures to conspecific distress vocalizations (Chen *et al.*, 2009). These findings are consistent with human data showing a link between HR deceleration and empathic concern for others (Panksepp & Lahvis, 2011) and suggest that genetic background may influence the magnitude of some emotional responses in rodents. In fact, Keum *et al.*, (2016) found that different inbred mouse strains differed in the level of freezing behaviour displayed while they observed a demonstrator receiving shocks. If observer mice and rats previously had a similar shock experience, they displayed freezing behaviour in response to the sight of a familiar or unrelated demonstrator receiving foot-shocks (Atsak *et al.*, 2011; Sanders *et al.*, 2013; Carrillo *et al.*, 2015). That is, previous experience with the aversive event might influence the occurrence of emotional contagion in rodents, as seen in humans (Preston & de Waal, 2002). In addition, demonstrator's behaviour was modulated by the behaviour of the observer rats: they froze

more if witnesses froze more (Atsak *et al.*, 2011). Sanders *et al.* (2013) did not find any familiarity bias in the freezing levels of observer mice. On the other hand, several studies have shown that non-experienced mice (Jeon *et al.*, 2010; Jeon & Shin, 2011; Gonzalez-Liencrez *et al.*, 2014; Keum *et al.*, 2016) and rats (Yusufishaq & Rosenkranz, 2013) also display freezing behaviour while observing demonstrators receiving foot-shocks. Interestingly, when visual inputs were blocked, observers' fear responses substantially decreased, suggesting an important role of visual cues in this process (Jeon & Shin, 2011). These studies also reported a familiarity bias in mice fear responses (Jeon *et al.*, 2010; Jeon & Shin, 2011; Gonzalez-Liencrez *et al.*, 2014). Observers showed more freezing behaviour when they were socially related to demonstrators (siblings, mating partners or cagemates) than when they were unrelated. These fear responses were compatible with emotional contagion since freezing of both mice occurred at the same time, pointing to a social transfer of fear between them (Jeon *et al.*, 2010; Keum & Shin, 2016). Thus, consistent with the human empathy literature (Preston & de Waal, 2002), familiarity between observer and demonstrator seemed to enhance emotional contagion in mice (Jeon *et al.*, 2010; Jeon & Shin, 2011; Gonzalez-Liencrez *et al.*, 2014). In rats, the magnitude of the observers' freezing responses was modulated by the rearing conditions (Yusufishaq & Rosenkranz, 2013). Isolation-reared rats showed significantly less freezing behaviour observing a demonstrator during a fear conditioning procedure compared to pair-housed rats. Finally, repeated exposure to familiar rats receiving foot-shocks resulted in a gradual reduction of observers' freezing responses (Carrillo *et al.*, 2015). Although this result could suggest a disappearance of the emotional response to the distressed demonstrator, it was observed a continuous increase in the frequency of observers' yawning suggesting that this mechanism could be an alternative stress coping strategy (Carrillo *et al.*, 2015). Previous studies assessed rodents' responses to conspecifics' distress or fear using physical stressors (e.g. shocks). However, in these paradigms, rodents' behavioural and physiological responses may differ from those obtained using social stressors. Two studies used social defeat as a social stressor to assess the effects on the physiological, cognitive and behavioural responses of observer male mice (Warren *et al.*, 2013) and rats (Patki, Solanki, & Salim, 2014). After several days of testing, observers showed increased anxiety and depression-like behaviours strikingly similar to that of defeated conspecifics. Both witnesses and demonstrators also displayed increased levels of serum corticosterone (as part of the stress response). This result suggests that observing a conspecific being attacked induces a negative emotional state in witnesses similar to that displayed by the defeated individual (Warren *et al.*, 2013). In addition, being exposed and experiencing social defeat had long-lasting behavioural and neuroendocrine effects affecting learning and memory function as well.

In the second group of studies on emotional contagion of fear, demonstrators are first fear-conditioned and then subjected to a fear-memory retrieval task in which only the conditioned stimulus is presented (e.g. a tone). During the fear-memory retrieval, the observers' reactions to a frightened demonstrator are registered. In these studies, the display of freezing behaviour by the observer is also interpreted as an evidence of social transfer of fear between rodents. Overall, it has been shown that rats with previous experience with the aversive event but not naïve rats display significant freezing in response to the reactions of the frightened individual (Kim *et al.*, 2010; Pereira *et al.*, 2012; Jones *et al.*, 2014). Other rodent species, the prairie vole (*Microtus ochrogaster*), showed an increase in freezing responses when observing a fear-conditioned conspecific freezing during the presentation of the conditioned stimulus (Burkett *et al.*, 2016). This freezing response occurred concurrently with that of the demonstrator. A more controversial issue is which demonstrator's responses trigger the freezing behaviour of observers. It has been proposed that the fear-induced 22-kHz ultrasonic distress calls (USVs) may play an important role in fear transmission in rats (Kim *et al.*, 2010). This hypothesis is supported by the fact that observers' freezing responses were blocked by lesions and reversible inactivation of the medial geniculate nucleus (MGN) of the thalamus, which

prevented auditory information flow to the forebrain (Kim *et al.*, 2010). Conversely, some studies (Pereira *et al.*, 2012; Jones & Monfils, 2016) showed that most of the rats did not emit distress calls at all during the fear-memory retrieval task, casting doubt on the role of USVs in the social transmission of fear. An alternative explanation is that other auditory cues, apart from USVs, could be involved in this process. In fact, Pereira *et al.* (2012) reported that freezing of the demonstrator could be detected through the lack of movement-evoked sound. They performed the test in the dark and found that both, observers and demonstrators, showed freezing upon the presentation of the tone, suggesting that visual cues are not necessary to respond to a frightened conspecific. What was even more interesting is that playback of the sound of a rat moving abolished freezing in observers, although the demonstrator displayed freezing at that time. Moreover, freezing by observers in response to the immobile state of demonstrators resumed when playback stopped. Finally, in an experimental condition in which observer rats were tested alone while a movement-evoked sound was played continuously, experienced but not naïve rats froze during the periods of silence and when the silence gaps were filled with an arbitrary sound (Pereira *et al.*, 2012). Thus, the absence of auditory motion cues was necessary and sufficient to induce fear in observers, suggesting that the sudden cessation of the sound of a moving conspecific might be perceived as threatening (Pereira *et al.*, 2012).

Finally, in the third group of experiments, observer rodents were exposed to a distressed conspecific which have undergone an aversive event (e.g. fear conditioning episode). In this case, the demonstrator was still stressed due to the previous aversive and/or painful event. Thus, this protocol serves to evaluate the observer's responses to demonstrator's distress cues. For example, in rats, observers' exploratory behaviour increased (Knapska, Mikosz, Werka, & Maren, 2010; Knapska *et al.*, 2006) and the startle response (fast motor response to unexpected stimuli intensified by fearful stimuli which serves as a measure of emotional states) was enhanced after the exposure to a distressed conspecific (Knapska *et al.*, 2006). These behavioural outcomes have been interpreted as an increased arousal/vigilance state that could have been transferred by the stressed demonstrator (Knapska *et al.*, 2010; Knapska *et al.*, 2006). However, another study found that observers displayed similar social exploratory behaviours during the interaction with distressed and control rats, suggesting that the emotional state of the demonstrator did not influence the observers' behaviour (Mikosz *et al.*, 2015). It has also been reported that, after being exposed to a distressed cagemate, male but not female rats displayed an amygdalar activation similar to that of demonstrators, being the amygdala a part of the limbic system involved in fear processing and emotional reactions (Knapska *et al.*, 2006; Mikosz *et al.*, 2015). As regards to mice, a study (Meyza *et al.*, 2015) assessed the different behavioural and neurobiological reactions of two different strains of mice in response to a stressed demonstrator: the BTBR characterized by an asocial profile and the normo-social B6 mice. Researchers found differences in the responses of both strains. B6 but not BTBR presented an increase in the number and duration of social and digging behaviour in presence of a stressed conspecific. B6 and BTBR also showed a distinct pattern of neuronal response: only B6 observer mice and B6 stressed demonstrator itself displayed an increased activation in the prefrontal cortex and the amygdala. However, this pattern differed from the one previously observed in rats, suggesting the existence of different species-specific strategies of fear transmission in rodents (Knapska *et al.*, 2006; Meyza *et al.*, 2015). These results point again to a genetic influence on the magnitude of emotional responses in mice. Burkett *et al.* (2016) reported positive evidence of emotional contagion in prairie voles. Observers that interacted with a stressed familiar conspecific mimicked its anxiety and fear like behaviours: they matched the increase in self-grooming and freezing displayed by the demonstrator. When observers were separated from distressed demonstrators across a clear, perforated barrier presented a significantly elevated plasma corticosterone which correlated with that of the stressed conspecific.

These results suggest a behavioural and physiological state-matching between prairie voles, that is consistent with emotional contagion processes (Burkett *et al.*, 2016).

Social interaction with a frightened, distressed or emotionally aroused conspecific could result in long-lasting changes of behaviour modulating learning and memory (Meyza *et al.*, 2016). Vicarious fear learning and social acquisition of defensive, avoidance or conditioned fear responses have been interpreted as a proof of emotional contagion. This social transfer and the subsequent learning of emotional responses have been observed in rats and mice (Bredy & Barad, 2009; Bruchey, Jones, & Monfils, 2010; Chen *et al.*, 2009; Ito, Erisir, & Morozov, 2015; Jeon *et al.*, 2010; Jones & Monfils, 2016; Jones *et al.*, 2014; Kavaliers, Colwell, & Choleris, 2003; Kavaliers, Colwell, & Choleris, 2005; Knapska *et al.*, 2010; Nowak, Werka, & Knapska, 2013; Panksepp & Lahvis, 2016; Yusufshaq & Rosenkranz, 2013). However, more studies are needed in order to clarify the elements through which social interaction with emotionally aroused individuals improves or impairs learning (Meyza *et al.*, 2016).

Emotional contagion of pain in rodents has been studied by assessing changes in pain sensitivity or pain thresholds in individuals that have been exposed to a conspecific in pain. Two studies assessed social modulation of pain in mice administering an identical noxious stimulus to two animals and then testing them in dyads or in isolation (Langford *et al.*, 2006; Martin *et al.*, 2015). Modulation of pain sensitivity (hyperalgesia) was observed solely in familiar dyads (cagemates) but not in stranger dyads or in mice tested in isolation (Langford *et al.*, 2006; Martin *et al.*, 2015). Furthermore, pain behaviours (writhing) co-occurred significantly in time, were influenced by those of the cagemate and dependent on visual information (Langford *et al.*, 2006). Intriguingly, observation of a cagemate in pain also altered pain sensitivity in a different modality (Langford *et al.*, 2006). It has been proposed that elevated stress levels in stranger dyads could be responsible for the absence of emotional contagion of pain (Martin *et al.*, 2015). In fact, blockade of glucocorticoid synthesis or receptors for adrenal stress hormones elicited the same pain behaviours among stranger and familiar pairs of mice and humans. Moreover, the induction of stress impaired the previously observed behavioural responses in familiar pairs (Martin *et al.*, 2015). Several factors influenced this social modulation of pain in mice: severity of the social threat (Langford *et al.*, 2011), stress levels (Martin *et al.*, 2015), familiarity (Langford *et al.*, 2006; Martin *et al.*, 2015), gender (Langford *et al.*, 2011) and dominance relationship (Watanabe, 2014). In turn, observer rats were exposed to a social interaction with an individual (cagemate or stranger) that had received a subcutaneous injection of bee venom (Li *et al.*, 2014). After this interaction, observers were isolated and treated with the same venom. Only observers exposed to cagemates showed a change in pain-related behaviours. They displayed enhanced supra-spinally and spinally mediated pain-related behaviours; increased mechanical but not thermal pain sensitivity, and enhanced spinal dorsal horn nociceptive neuronal activity. This enhancement of spinal nociception was likely mediated by the medial prefrontal cortex and not by the amygdala and the entorhinal cortex. Given that both, cagemate and non-cagemate observers, displayed similar stress-related responses and anxiety-like behaviours the reported changes in pain sensitivity did not appear to be influenced by stress or anxiety. Therefore, Li *et al.* proposed that the modulation of pain thresholds in naïve witness after the exposure to a conspecific in pain was not likely a process of emotional contagion but rather mediated by an integrated emotional process involving also cognitive and memory functions. The fact that the induced pain behaviours of observers were recorded in a new emotional cue-absent testing box, not during the interaction with demonstrators and that observers' response was dependent on familiarity, so memory retrieval (recognition) could be required in the subsequent session of testing supported their statement. This hypothesis is also supported by the involvement of the medial prefrontal cortex, which plays an important role not only in emotion

but also in cognitive and memory functions, but not of the amygdala or entorhinal cortex (Li *et al.*, 2014).

Unlike the above-reviewed studies, Saito *et al.* (2016) tested whether rats display positive or negative emotional contagion after hearing conspecific USVs (50 kHz USVs emitted in positive contexts and 22 kHz USVs emitted in negative contexts) via a cognitive bias task. This task serves to measure affective states via operant conditioning. Rats were conditioned to respond differently to two sounds, each of which signalling either a positive or a negative outcome. It is expected that rats in positive emotional states would perceive an ambiguous cue (frequency falling between the two conditioned stimuli) as being positive (optimistic bias), and rats in negative states would perceive it as being negative (pessimistic bias). The results showed that indeed after being exposed to positive vocalizations rats responded to ambiguous cues as positive, and negative after being exposed to negative vocalizations. Thus, this outcome suggests that conspecific's USVs may evoke positive and negative emotional contagion, changing the affective states in receiver rats.

Finally, several studies have provided evidence pointing to a possible link between emotional contagion and subsequent prosocial responses in rats. In experiments in which observer rats showed emotional contagion-like responses to another's pain or distress, some of them also displayed behaviours such as nursing, allogrooming, or physical proximity which are likely to relieve or buffer the other's pain or distress (Atsak *et al.*, 2011; Burkett *et al.*, 2016; Knapska *et al.*, 2010). Furthermore, the study of Ben-Ami Bartal *et al.* (2016) suggested that rats may need to experience an emotional response triggered by the emotional reactions of a cagemate trapped in a restrainer to learn how to open it and free their partner.

Overall, these findings suggest that the emotional state of an individual affects the behaviour and physiology of another rodent. However, there are also many contradictory and not conclusive results. These contradictory data may be due to the use of different methods and paradigms. For example, using a different intensity of the aversive stimuli (e.g. shocks) may, in turn, imply a change in the salience of the behavioural response of the demonstrator and thus has a different effect in the observer's response (Panksepp & Lahvis, 2011). Sometimes it is also difficult to properly compare the data since the reviewed studies measured different parameters, used different devices and housing conditions or were trying to answer different research questions. Another problem with interpreting the available data is that, in many occasions, evidence for emotional contagion is reported through indirect measures instead of simultaneously measuring behavioural and physiological responses in both individuals to assess an emotional state-matching between them. However, there is some evidence pointing in that direction: observer and demonstrator prairie voles displayed a behavioural and physiological state-matching after a distressing procedure; freezing behaviour in observer and demonstrator mice co-occurred in time; witness mice and rats displayed behavioural and physiological indicators of a negative emotional state similar to those showed by social-defeated individuals; and mice observing a cagemate experiencing pain displayed changes in pain sensitivity and showed pain behaviours that co-occurred in time with those of the demonstrator. On the other hand, demonstrator's pain displays sometimes triggered fear not pain responses in the observers, so alternative hypothesis based on other processes cannot be ruled out for the moment. Several factors such as previous experience, familiarity, genetic background, sensory modality or rearing conditions seemed to modulate the emotional responses of rodents towards distressed conspecifics. However, the influence of such factors on rodents' responses varied greatly depending on the experiment. In some studies, emotional responses were enhanced, or simply present, if the observer was exposed to a familiar individual but, in other experiments, such familiarity bias was absent. Similarly, in several experiments, some rodents needed previous experience with the distressing procedure to respond to the demonstrator's distress, while in others naïve rodents displayed emotional responses toward the

distressed individual. In several studies, some of these factors were necessary for the observer to emotionally react to the distressed individual. Therefore, future studies should try to determine the nature, factors and mechanisms involved in rodents' responses to perceived distress in others. Finally, some of the reviewed evidence suggests a possible link between emotional contagion and prosocial behaviours. However, due to the scarce number of articles assessing the influence of emotional contagion processes on prosociality in rodents, more research is needed to confirm this relationship.

#### e. Swine and bovid

In the field of animal welfare, some interesting research has been done on the reactions of farm animals to distressed conspecifics. Anil *et al.* (1997;1996), for example, investigated the stress responses of pigs (*Sus scrofa domestica*) and sheep (*Ovis aries*) witnessing the slaughter of conspecifics. They did not find any stress-related changes in pigs or sheep, although the levels of stress-related hormones and HR tended to be high during the process. Both studies lacked rigorous controls so they were not able to distinguish between effects due to the own experience of the observer and those triggered by the witness of the slaughter. Therefore, if it is not possible to establish the sources of the observed physiological outcomes, we cannot distinguish whether these effects represent an example of emotional contagion.

On the other hand, Reimert *et al.* (2013) found some evidence showing that pigs could be sensitive to emotional contagion. This study assessed the responses of naïve pigs to the anticipation and experience of rewarding and aversive events by a trained pen mate. One pig had experience with the auditory and visual cues that anticipated both events, and the naïve pig observed the reactions of its experienced partner during the anticipation and experience of the events. This paradigm served to assess the extent to which pigs were affected not only by negative emotions but also by conspecifics' positive emotions. During the anticipation and experience of events, the behaviour of both pigs matched. During the anticipation of rewarding events, both pigs displayed behaviours indicative of positive emotions (e.g. play). Conversely, during the anticipation or experience of the aversive event, both pigs displayed indicators of negative emotions such as tail low, ears back, increased level of defecation, and urination, and more low-pitched vocalizations emission. Salivary cortisol measurements supported these behavioural observations, indicating that both pigs were aroused by the events. The authors ruled out the possibility that naïve pigs were just copying the behaviours from the experienced pigs since, during the events, observer pigs could not see the demonstrator pigs only hear them. In a follow-up study, Reimert *et al.* (2015) used a similar paradigm but, in this case, naïve pigs were given intranasal doses of oxytocin (neurohormone that has been related to empathic processes). Oxytocin doses did not significantly affect pigs' behaviour, except by increasing the number of low-pitched vocalizations. Surprisingly, it affected the behaviour of the trained pigs which had not received oxytocin. Thus, the authors concluded that oxytocin may play a role in pig auditory or olfactory communication. These oxytocin's inter-individual effects on behaviour and physiology have been also observed in rats (Ägren & Lundeberg, 2002) and humans (Weisman, Zagoory-Sharon, & Feldman, 2012; Schneiderman *et al.*, 2014). In a subsequent study, Reimert *et al.* (2017) examined whether the emotional state of a pig subjected to either a positive or negative treatment affected the emotional state of their naïve pen mate in the period after the treatment. During this period, the treatment-subjected pig and its pen mate seemed to be emotionally affected. That is, naïve pigs seemed to be both negatively and positively affected by the treated pigs. These results support the occurrence of emotional contagion for negative and positive emotions between pigs. However, the positive emotional state elicited in the naïve pigs could also be due to the exposure to traces of peat and chocolate raisins present on the treated pig body after the treatment rather than triggered by emotional contagion.

In summary, some of the previous results point to the occurrence of a behavioural and physiological state-matching between observer and demonstrator pigs, suggesting the presence of positive and negative emotional contagion processes in these animals. Moreover, it is possible that the observed effects of negative and positive events may extend beyond the end of the event in both the exposed animal and its group members.

## f. Birds

Using a similar paradigm to that of Church (1959) with rats, Watanabe & Ono (1986) tested pigeons (*Columba livia*) obtaining equivalent results. First, pigeons were trained to peck a lever that supplied food. Then, these pigeons were repeatedly exposed to another individual being shocked during their daily training sessions. Pigeons showed a suppression of the response, not pecking the lever after witnessing the demonstrator's distress responses. However, this suppression decreased with repeated exposure. During the second phase of the experiment, the same pigeons were divided into three groups and subjected to different treatments. Results showed that if pigeons are first exposed to a conspecific receiving shocks, and then receive experience with the same aversive stimulus, they show again a suppression of response when witnessing another's pain reactions. That is, when observer pigeons have experience with the distressing procedure, conspecifics' distress becomes an aversive stimulus to them.

Wascher (2008) assessed the responses of semi-tame free-roaming greylag geese (*Anser anser*) while they observed social and non-social events. HR responses were significantly greater in social contexts. Significantly higher maximum HR and a greater HR increase were recorded in response to agonistic interactions in which the pair partner or a family member was involved, as compared with unfamiliar individuals interacting. HR was also significantly higher when the bystander observed unrelated higher-ranking individuals interacting. The authors remained cautious of interpreting the HR results as an indication of emotional involvement, but they highlighted that the specificity of the arousal caused by witnessing social interactions points in that direction.

Perez *et al.* (2015) assessed the responses of female zebra finches (*Taeniopygia guttata*) to males' stress-induced calls. Calls of males treated with corticosterone, a glucocorticoid involved in stress responses, elicited an increase of corticosterone levels and behavioural changes in females compared to control calls. Females showed this effect only when the calls were emitted by their mate, not by an unfamiliar male. Females' responses matched those of stressed males suggesting the occurrence of emotional contagion between the pair.

Edgar *et al.* carried out a set of studies assessing emotional responses of hens (*Gallus gallus domesticus*) after the perception of distress in their chicks or familiar individuals. First, they evaluated whether hens responded to an aversive stimulus (air puff) directed at their chicks (Edgar *et al.*, 2011). Hens displayed increased alertness, decreased preening behaviour and a reduction in eye temperature only during the conditions in which they were either exposed to the air puff or to the sight of their chicks receiving the air puff. Exclusively during this last condition, hens showed increased HR and emitted more vocalizations, although chicks produced few distress vocalizations. Despite the fact that the valence of hen's responses is not clear, some of the observed physiological and behavioural changes have previously been used as signs of emotional responses in animals (Edgar *et al.*, 2011). What is more, adult hens avoid environments associated with that behavioural changes (Nicol *et al.*, 2009). A subsequent study (Edgar, Paul, & Nicol, 2013) investigated whether hens' behavioural and physiological responses to chick distress were mediated by their knowledge about the chicks' situation and by chicks' distress cues. Results showed that hen's vocalizations and walking behaviour increased, and preening behaviour decreased when they perceived their chicks to be threatened,

regardless of their chicks' responses to the situation. Reduced levels of preening may be indicative of a negative state in hens (Nicol *et al.*, 2009; Edgar *et al.*, 2011). Hens' increased calling and walking rate may serve to stimulate chicks to move away from the perceived danger and to enhance chicks' learning of the potentially threatening situation (Edgar *et al.*, 2013). Hens displayed stress-induced hyperthermia only when their perception of threat matched that of their chicks, suggesting that hens' responses were influenced and enhanced by chicks' distress cues. Furthermore, chicks' behaviour was also influenced by their mother's expectations. Chicks spent more time emitting distress vocalizations and less time preening when they were placed in the environment that their mother associated with threat. Conversely, chick preening was significantly increased by the hens' perception of safety even though the chicks' own expectation was that they were threatened. Therefore, when hen and chicks' expectations did not match, hens' responses could influence chicks' arousal state either inducing or buffering chicks' distress. In brief, these outcomes suggest that hens' behavioural and physiological responses were not solely driven by chicks' distress signals but by an integration of these cues with the hens own learned associations of the situation (Edgar *et al.*, 2013). The authors suggested that hens produced a potentially adaptive, flexible and context-dependent response instead of a simple and automatic response driven by distress cues. Although no significant correlations between hen and chicks' behaviour were found, some of the previous results could be indicative of an emotional state-matching between them. On the other hand, hens did not display behavioural or physiological reactions in response to the mild distress of an unrelated but familiar conspecific (Edgar *et al.*, 2012). Conversely, hens displayed more sitting posture indicating that they were in a more relaxed state than during the other experimental conditions. Moreover, hens did not respond even though distressed conspecifics emitted more alarm and warning calls than the chicks in the previous experiment. Thus, emotional reactions in hens were not facilitated by alarm calls. These findings suggest that outside the mother-offspring bond and in this specific context, chickens do not show emotional contagion responses towards adult familiar conspecifics subjected to mildly aversive stimulus.

Two experiments examined positive emotional contagion within the context of play behaviour in two social species of birds: kea parrots (*Nestor notabilis*) and ravens (*Corvus corax*). Schwing *et al.* (2017) assessed whether play vocalizations of keas may elicit emotional contagion. Acoustic playback of play calls increased significantly the amount of play among both juveniles and adult wild keas compared with the control sound stimuli, suggesting a positive emotional contagion. After hearing the play call, many keas started playing with other birds, objects or perform aerial acrobatics instead of joining in play that was already underway. Therefore, these vocalizations seemed to induce playfulness rather than "invite" to play, supporting the authors' hypothesis that play calls may act as a contagion process of positive emotional states. Osvath and Sima (2014) investigated whether the spread of play might be a case of positive emotional contagion in ravens. In the experimental condition, an item known to elicit object play in the individual holding it was introduced in the aviary. They hypothesized that if a category of play in one individual induces a different category of play in another, this indicates the spread of a playful mood rather than a species-specific motor response. The outcomes fitted the authors' hypothesis showing that ravens engaged in all categories of play during the experimental condition but not during the control conditions. Thus, this result points to play mood contagion rather than a spread of specific motor patterns and suggests the occurrence of positive emotional contagion in ravens.

In summary, experiments on emotional contagion in birds suggest that they could also be affected by the emotional or arousal state of conspecifics. The responses of female zebra finches towards distressed familiar males, the spread of positive playful states in keas and ravens or the reciprocal influence of hens and chicks' responses towards threatening situations point to a possible emotional state-matching between individuals. On the other hand, results such as that hens did not display any

emotional or behavioural reaction to familiar conspecifics in distress do not support the occurrence of emotional contagion. Furthermore, in the studies of Watanabe and Ono (1986) and Wascher (2008), it was not clear whether birds were reacting to the conspecific distress responses or to some aversive cues of the observed situation. Therefore, more research is needed to assess emotional contagion processes in birds and its associated features.

## 5. Discussion

Our objectives in this chapter were to 1) clarify and describe basic motor and emotional processes usually related to empathy, specifically emotional contagion, mimicry and social synchrony; 2) highlight the criteria by which these processes could be considered as primitive forms of empathy or be linked to more complex empathic behaviours; 3) review relevant studies on emotional contagion, mimicry and related processes in non-human animals; and 4) discuss whether the available evidence really offers examples of basic forms of empathy comparable to those found in humans.

Emotional contagion and mimicry have been generally considered as the lowest common denominators of all empathic behaviours (de Waal, 2008). Therefore, the comparative study of these processes has been proposed as a useful tool for elucidating the evolutionary history of empathy across the animal kingdom. Emotional contagion, mimicry and synchrony are thought to be automatic processes that do not require complex cognitive processing and thus allow the sharing of emotional responses in a rapid and simple way. Furthermore, these phenomena may elicit an emotional engagement between individuals that could be necessary to motivate some subsequent prosocial or cooperative behaviours. The ability to share emotional states during social interactions and to “feel into” another’s affective state is considered by many authors as the main feature of empathy. Therefore, these simple emotional and motor processes could function as basic forms of empathy if they lead to the sharing of emotional states between individuals.

In general, many of the studies reviewed herein support this claim. These studies show that some animals seem to be affected by the emotional displays of others, suggesting that the sharing of emotions could be widespread among social species. Furthermore, data on CY, RFM, motor mimicry and synchrony point out that, in social contexts or while interacting with others, certain social animals are likely to spontaneously synchronize or mimic another’s expressions or movements. These mimicry-related processes may increase affiliation and rapport between individuals, strengthening, in turn, social bonds and group cohesion and restoring relationships and buffering tension after aggressive encounters. Importantly, there is evidence suggesting that mimicry and emotional sharing processes could also lead to an increase in the probability of cooperation and prosociality between individuals, as seen in the human literature. On the other hand, we face a lack of studies assessing spontaneous mimicry and synchrony during social interactions or examining the influence of these processes and emotional contagion on prosocial and cooperative behaviours in non-human species. Therefore, the link between these behaviours and empathy in non-human animals remains greatly unexplored. One important limitation is that most of the data on spontaneous mimicry and synchrony came from studies on CY or synchronized pair or group displays. And, in fact, the link between CY and empathy has been recently called into question by pointing out inconsistencies in its conceptual basis and revealing a pattern of inconclusive evidence regarding this connection (discussed in Massen & Gallup, 2017). Furthermore, synchronized displays have been traditionally considered as fixed behavioural repertoires related to courtship and pair formation and thus the link between these behaviours and cooperative or prosocial behaviours has not been extensively assessed. Therefore, the lack of evidence on this issue makes difficult to establish solid conclusions regarding the occurrence, nature and function of spontaneous mimicry and synchrony in non-human animals.

Even so, most of the evidence we have reviewed herein point out that human mimicry and synchrony share many similarities with related behaviours observed in other animals. Different studies have highlighted that, in non-human species, mimicry and synchrony may also function as “social glue” increasing affiliation, liking and rapport between individuals. For example, rhesus macaques and capuchin monkeys have been reported to display more affiliative behaviours towards persons that mimicked them. Furthermore, studies on synchrony have shown that, in many animals, behaviours including synchronous displays such as greeting or triumph ceremonies, courtship displays, synchronized swimming and duetting or chorusing, may serve to strengthen or restore pair, family or group bonds and to buffer tension after aggressive encounters. The fact that most of these synchronized behaviours are displayed in arousing or affiliative contexts (e.g. reunions, post-conflict or distress periods, during the formation and throughout the pair-bond), supports this claim. In this way, synchrony may serve to strengthen and reinforce social bonds, enhancing social tolerance and group cohesion in a simple and automatic way. In turn, it has been suggested that, in humans, affiliation could be displayed through mimicry and synchronized behaviours. Interestingly, some data indicate that in non-human species this bidirectional relationship could be present as well. In fact, some synchronized behaviours observed in birds or primates are likely to signal alliance or group membership. Therefore, synchronized displays may serve as an intra-group signal for enhancing within-group cohesion and/or as an out-group signal for advertising social relationships to other individuals. Data on CY and RFM in non-human species indicates that these processes may be influenced by the same factors that modulate empathic capacities such as familiarity, age and gender. Moreover, synchronized behaviours also seem to be preferentially displayed by closely bonded individuals (e.g. pair mates or in-group and family members). Finally, in humans it has been shown that mimicry and interpersonal synchrony may lead to increased helping and cooperative behaviour, suggesting a possible link between these motor processes and prosocial behaviour. Based on the reviewed evidence, it seems that synchrony might also lead to cooperative and prosocial behaviours in certain non-human species. For instance, synchronous displays might be related and precede the performance of subsequent cooperative behaviours such as joint territory or resource defence and nest building in some birds. However, evidence on this link is scarce and thus more studies are needed to reach robust conclusions on this issue.

Mimicry has been considered by some authors as a primitive form of emotional contagion. According to this view, the automatic synchronization and mimicry of some expressions, vocalizations, postures and movements with those of another individual could lead to an emotional convergence (Hatfield, Cacioppo, & Rapson, 1993). However, there is virtually no data assessing a causal relationship between mimicry or synchrony and emotional contagion processes in non-human species. Mimicking or performing synchronized displays during social interactions may promote a physiological synchronization between interaction partners inducing thus the same affective emotional state in both individuals. This emotional state-matching could increase affiliation between partners, and thus they could be more likely to engage in prosocial behaviour. In humans, this physiological synchronization could involve the activation of the reward and the endogenous opioid system (Kokal *et al.*, 2011; Sullivan & Rickers, 2013). Therefore, it has been suggested that the link between synchrony and prosocial behaviour in the brain could be based on the activation of these systems (Kokal *et al.*, 2011; Sullivan & Rickers, 2013). In certain non-human species, it is possible that performing synchronized activities also activates one or both systems. In this way, synchronized behaviours might be perceived as socially rewarding, increasing positivity toward others and promoting bonding and subsequent prosocial behaviours in animals. A study has provided evidence suggesting a link between oxytocin and automatic motor mimicry in humans (De Coster *et al.*, 2014). Thus, oxytocin may also be involved in mimicry and synchrony processes in humans and other species. However, little is known about the neural and physiological mechanisms underlying mimicry

and synchrony in non-human species, and thus this issue deserves more attention. Another possible effect through which mimicry and synchrony may promote affiliation and prosociality is by increasing perceptions of similarity, joint identity or group membership that, in turn, leads individuals to perceive themselves as united (Valdesolo & DeSteno, 2011). Synchronous movement may bind individuals together and thus could serve as a dynamic marker of affiliation increasing emotional responding and prosocial behaviours toward synchronous others (Valdesolo & DeSteno, 2011). Therefore, synchronous movements could serve as a cooperation-enhancing mechanism and favour other-oriented emotional reactions providing a motivation to engage in subsequent prosocial behaviours. Synchronous movements could also function as social cues that signal joint purpose and elicit coordinated and goal-directed actions (Valdesolo & DeSteno, 2011) without involving emotional processes. Therefore, more research is needed to assess the existence of a causal link between mimicry or synchrony and emotional contagion or emotional responding in non-human species, as well as the directionality of this relationship.

The diversity of mimicry and synchronous processes and the fact that they have been observed in many different contexts suggest that these behaviours could be multi-purpose serving independent functions in different situations and vary depending on the behavioural ecology of each species. For example, synchronous displays of monogamous birds or primates might not only serve to synchronize pair partners' hormonal changes before mating but also to keep their relationship during the breeding season. Performing synchronized displays could elicit positive emotional states and reduce stress levels and aggressive tendencies in both individuals. Therefore, these individuals could be more prone to engage in affiliative interactions and costly cooperative or prosocial behaviours. Furthermore, being in the same affective state that another individual might facilitate effective communication avoiding misunderstandings during social interactions and thus decreasing the risk of serious aggression. Therefore, these behaviours may elicit partner assistance and limit conflicts or infanticide, functions that are crucial for breeding success. Thus, for animals living in groups, mimicry and synchrony could be an important adaptation for maintaining social relationships, fostering social tolerance, decreasing aggression, avoiding misunderstandings, and increasing cooperation and assistance between group members.

In general, most of the evidence reviewed herein suggest that many non-human animals are affected by the emotional displays of other individuals. However, while several empathy models take for granted that emotional contagion leads to an emotional state-matching between individuals, experiments testing the occurrence of such process by simultaneously recording the emotional responses of both individuals are scarce. The lack of assessment of this emotional state-matching between individuals in most studies is thus remarkable and should be addressed in future work. Nevertheless, some of the reviewed studies reported possible cases of emotional state-matching in chimpanzees, elephants, birds, rodents or pigs. However, there are also many uncontrolled, contradictory or non-conclusive results on this issue. Hence, more controlled studies are needed to explicitly test the occurrence of emotional state-matching in non-human animals during both positive and aversive situations. We also noted that the procedures used to assess emotional contagion varied greatly between studies. While some paradigms directly registered physiological or behavioural changes in one or both individuals, others used indirect measures to examine the influence of another's emotional displays in the observer's responses. The lack of a systematic paradigm makes thus difficult to properly compare the available data. In fact, many of the contradictory and not conclusive results on emotional contagion studies may be due, among other reasons, to this unstandardized use of different methods and protocols. On the other hand, it is possible that two individuals present a physiological state-matching but do not display the same behavioural responses. For instance, an individual that has acquired another's fear state could flee from the situation instead of adopting the

other's immobile state. It could also be possible that different negative emotions trigger the same behavioural or stress responses in the observers. Therefore, assessing the occurrence of a negative emotional state-matching between individuals using only behavioural parameters is a difficult and controversial task. A possible way to overcome to some extent this ambiguity could be to examine individuals' reactions to positive emotions. Moreover, simultaneously measuring both physiological and behavioural responses to positive and negative emotions in observers and demonstrators could be a crucial tool to reliably establish the occurrence of an emotional state-matching between individuals.

Emotional contagion is often considered as an important component of empathic responses. It has been a common practice to link emotional contagion to empathy if they were modulated by the same factors. Familiarity, previous experience, context, ontogeny or gender are the main factors that have been proposed to influence empathic responses in humans and non-human species (Preston & de Waal, 2002). Many of the studies reviewed herein suggest that some of these factors, especially familiarity, could modulate emotional contagion processes as well. The fact that emotional contagion processes are displayed preferentially to familiar or in-group individuals is expected since these individuals are the ones with whom the individual interacts and cooperates more (Bourgeois & Hess, 2008). Data on rodents have suggested that the stress associated to a social interaction with a stranger individual inhibits emotional contagion responses and that blocking that stress response could elicit emotional contagion (Martin *et al.*, 2015). Given that oxytocin has anxiolytic effects in the brain (Neumann & Landgraf, 2012) and is involved in the development of social recognition and long-term social memory in rats (Gur, Tandler, & Wagner, 2014), this neurohormone may have a role in the reduction of stress levels between familiar pairs facilitating emotional contagion. In humans, for example, it was reported that oxytocin increased trust, cooperation and empathy towards in-group but not towards out-group members (De Dreu *et al.*, 2010). Oxytocin can also induce antisocial effects and promote defensive forms of aggression toward out-group members (De Dreu *et al.*, 2010), thus its effects might vary depending on the relationship between individuals (Shamay-Tsoory & Abu-Akel, 2016), which is consistent with the familiarity bias observed in several studies reviewed herein. In support of this view, "the social salience hypothesis of oxytocin" have highlighted the role of oxytocin in emotional contagion, pointing out the influence of context, relationship and identity of the observed individual on oxytocin's effects on behaviour. And, as these factors also affect emotional contagion and motor mimicry, oxytocin may have a key role in these phenomena too. Furthermore, this theory proposes that oxytocin mediates social interaction by providing an assessment of the value of that interaction and orienting the organism accordingly (Shamay-Tsoory & Abu-Akel, 2016). For instance, during positive supportive situations, oxytocin might increase the salience of safety signals attenuating stress. On the other hand, during threatening contexts this peptide may increase anxiety, eliciting orienting responses to threat (Shamay-Tsoory & Abu-Akel, 2016). A recent study in rats (Rickenbacher *et al.*, 2017) points in that direction showing that oxytocin has an effect on action selection in defence of offspring. More specifically, in threatening situations, mother rats switched from self-defence (freezing) to offspring protection when their pups were present. Blocking oxytocin signalling in the centro-lateral amygdala prevented the suppression of the self-defence response in the rats. Previous experience with the situation or the aversive procedure seems to also be an important factor modulating empathic capacities (Preston & de Waal, 2002). Data from some studies, mainly in rodents, have suggested that previous experience with the situation or the experimental procedure might influence the occurrence of emotional contagion as well. However, we noted a great variability in the effects of previous experience on the behaviour of rodents. For example, in several studies, some individuals needed previous experience with the distressing procedure to emotionally respond to the demonstrator's distress while in others, naïve individuals displayed emotional responses toward the distressed conspecific. This fact, added

to the involvement of the prefrontal cortex (Li *et al.*, 2014; Meyza *et al.*, 2015), and the finding that only the absence of auditory motion cues was sufficient to induce fear in experienced observer mice (Pereira *et al.*, 2012), cast doubt on the automaticity of this emotional transfer. Thus, some authors have suggested that the observers' emotional responses toward distressed individuals could be grounded in an integrated emotional process involving cognitive and memory functions as well (Li *et al.*, 2014). What is more, we can be facing different processes that lead to the same behavioural and physiological effects. For example, the animal's own experience with an aversive event might promote learning of specific cues signalling danger that are later recognized in another frightened individual. That is, a rat subjected to electrical shocks may display defensive immobility in response to the shocks and could learn to associate these aversive painful stimuli with the sudden cessation of its own motion sounds. Thus, when this rat again detects a sudden cessation of auditory motion cues, it might display the same behaviour: freezing. Therefore, a behavioural and emotional state-matching could occur through the perception of a learned threat signal and without involving emotional sharing between individuals. On the other hand, a rat could be affected by certain emotional cues signalling distress in others and react to those stimuli displaying similar emotional responses. In this case, the rat is expected to react whenever these emotional signals are present and irrespective of the situation. Thus, as in the human case, previous experience with the situation could enhance those emotional responses but it should not be a prerequisite to display emotional reactions towards a distressed individual if this individual displays signs of distress or discomfort.

In fact, many of the studies reviewed herein point to a social communication role of emotional contagion either in the form of advertising potential threats through pain or fear contagion or allowing individuals to stay attuned to the emotional state of others. Learning from events that elicit fear or pain responses have an important survival and adaptive value. For example, the social transfer of fear or pain is a very useful strategy that allows individuals to acquire valuable information about environmental threats without directly experiencing them. Therefore, those processes that allow the sharing of emotional information during such encounters would be crucial for the survival of the individual. The rapid sharing of emotions could facilitate the diffusion of vital information related to both positive and negative emotional situations since emotional events are usually remembered with higher accuracy and vividness than another type of situations (Buchanan, 2007). The fact that some neuroendocrine systems and limbic areas related to emotional contagion are also involved in memory encoding and consolidation during emotional events (Buchanan, 2007) reinforces this hypothesis. Thus, emotional contagion may function as a social learning mechanism for fear or pain transmission, avoiding trial and error strategies which could be fatal to the individual. In support of this view, a mathematical model has shown that in some cases, emotional contagion, understood as the process by which an individual adopts another's emotional state and takes a behaviour driven by that emotion, is the most adaptive and flexible strategy when dealing with an uncertain environment (Nakahashi & Ohtsuki, 2015). The advantage of adopting emotional contagion over other strategies, such as copying the behaviour of others, increased when individuals shared the same environment and when the observation of the other's behaviour was difficult or cognitively demanding. Thus, group-living could be one of the ecological features that favoured the evolution of emotional contagion, even in species with limited cognitive abilities (Nakahashi & Ohtsuki, 2015). Emotional contagion could also facilitate effective communication between individuals avoiding misunderstandings and favouring social coordination, and bonding. For example, evoking the corresponding emotional state during play may allow individuals to foresee playmates' intentions, fine-tune their own motor responses accordingly and avoid aggressive conflicts (Mancini *et al.*, 2013a). Thus, emotional contagion could function as a basic form of empathy, allowing individuals to stay attuned to the affective state of others in a simple manner. This emotional state-matching between individuals favours emotional resonance with others and allows the individuals to

“feel into” another’s affective state, as proposed by the seminal definition of empathy (Lipps, 1903). For social species, being in the same emotional state as their group could have an important adaptive value. For example, the rapid spread of fear among individuals could allow that all or most individuals in a group escape from a potential danger. Likewise, the spread of positive emotional states among group members could diminish stress and strengthen affiliative bonds between in-group individuals. Therefore, emotional contagion could be considered as an adaptive process that serves to socially adjust the physiological, and behavioural parameters of the individuals increasing their capacity to respond adaptively to different contexts and situations. This emotional transfer thus could be related to the behavioural ecology of the species and finely tuned to its precise ecological circumstances. Therefore, the type of emotions transferred between individuals might differ across species (Yamamoto, 2017), fact that might explain some of the variability observed in animals’ emotional contagion processes. For instance, due to its survival advantages, contagion of negative emotions such as fear could be widespread among animals and be displayed in several contexts; while the contagion of positive emotions could be restricted to a reduced number of social species.

Although there are not many studies explicitly assessing the link between emotional contagion and prosociality, some evidence points in that direction. For example, data on dogs, elephants and rodents indicated that experiencing emotional reactions consistent with the emotional state of another may lead to affiliative contacts towards the distressed individual (Custance & Mayer, 2012; Plotnik & de Waal, 2014; Burkett *et al.*, 2016; Quervel-Chaumette *et al.*, 2016). Furthermore, this emotional engagement could also be related to subsequent helping responses in rodents and elephants (Douglas-Hamilton *et al.*, 2006; Ben-Ami Bartal *et al.*, 2016). Therefore, the emotional engagement induced by emotional contagion could motivate subsequent prosocial or cooperative behaviours towards others (de Waal, 2008).

It is possible that emotional contagion triggers prosocial responses in an automatic way. For example, in certain species the emotional reaction evoked by the perception of another’s emotional state could automatically elicit approach and affiliative responses, providing thus social relief of stress and anxiety to distressed individuals (Kikusui, Winslow, & Mori, 2006). The observer could be impelled to provide these prosocial behaviours either since it is distressed by the perception of another’s negative emotional state and the easiest way to alleviate its own aversive arousal is by engaging in affiliative responses with the distressed individual, or just because the perception of certain cues automatically triggers those behaviours in the observer. These emotional responses could again be related to the behavioural ecology of the species and precisely tuned to its specific ecological circumstances. Therefore, depending on the species, emotional contagion processes could be displayed only under precise circumstances, and when interacting with certain individuals. This effect of the species’ socio-behavioural traits on emotional and affective responding is illustrated by the different responses of two vole species towards distressed individuals (Burkett *et al.*, 2016). In this case, males belonging to a monogamous species of voles (prairie voles) displayed affiliative responses towards distressed individuals but only if they were familiar female mates. Furthermore, these responses had a social buffering effect in both individuals suggesting that they are specifically targeted to their pair mate and serve to diminish stress in both partners. Conversely, solitary and promiscuous male meadow voles (*Microtus pennsylvanicus*) tested under long photoperiods that is, when they show lower levels of social tolerance, did not show differences in the duration of allogrooming based on the state of their partner. Given that this type of emotional contagion processes and their associated prosocial responses do not seem to be cognitively demanding, they might be found in a wide number of animal species. In this way, for some pair or group living species not endowed with complex cognitive abilities, automatic emotional contagion could serve to ensure assistance and social buffering in certain circumstances, without requiring a cognitive evaluation of the situation.

Furthermore, these responses can be maintained over time since they may have a rewarding effect for both individuals. In several animal species, including humans, there is evidence supporting this claim. In fact, it has been shown that social contact and interaction may activate the reward mechanisms in the brain stimulating the release of opioids and thus eliciting a strong rewarding effect on interacting individuals (Carden & Hofer, 1990; Nelson & Panksepp, 1998; Kikusui *et al.*, 2006). Moreover, it has been shown that stressed individuals are more highly attracted to other individuals than non-stressed animals, suggesting that stressed animals seek for social contact, likely to ameliorate their negative emotional state or to obtain positive neurochemical rewards (Davitz & Mason, 1955; Morris *et al.*, 1976; Kikusui *et al.*, 2006). Therefore, in social species, negative emotional contagion could function as a mechanism to automatically elicit prosocial responses in observers that lead to the stress alleviation of distressed group members or pair mates. That is, the perception of distress in another individual could evoke a negative emotional state in the observer who thus seek for social contact approaching the distressed individual. Physical proximity could lead to the decrease of both individuals' stress levels (social buffering) and also increase affiliation between them. Therefore, emotional contagion could represent an important adaptive trait that favours pair and group living by socially regulating stress levels and strengthening bonds between partners.

On the other hand, species endowed with well-developed cognitive abilities could display a greater variety of emotional and prosocial responses. In these species, the primary emotional reaction to another's emotional displays could trigger automatic behaviours and/or be subjected to further emotional and cognitive processing, eliciting a more effective other-oriented response adapted to the needs of the distressed party (Pérez-Manrique & Gomila, 2017). So, emotional contagion and related prosocial behaviours might not always be a purely reflex-like process and might vary depending on the specific context and circumstances. Therefore, in these species, emotional contagion may underlie more complex empathic behaviours such as consolation or targeted helping (de Waal, 2008; de Waal, 2007; de Waal & Preston, 2017). However, we found only a few studies on emotional contagion in species traditionally considered to be among the most "empathic" ones. Great apes and elephants may engage in complex empathic behaviours like sympathetic concern or targeted helping and therefore the study of emotional contagion and mimicry in these species could be helpful for assessing the possible link between these phenomena and complex forms of empathy. This lack of empirical data could be explained in part by the fact that protocols involving suffering or distressing situations cannot be applied to these animals for ethical reasons. Thus, to assess their reactions to the sight of a conspecific experiencing intense emotions such as distress, fear or pain we must rely mostly on behavioural observations and anecdotal reports. Nevertheless, these impediments could be partially overcome by testing, for instance, the reactions of these animals to conspecifics' positive emotions.

Overall, it seems that the communicative and affiliative functions of emotional contagion are not mutually exclusive. That is, in social species emotional contagion responses might serve to communicate crucial information such as the presence of potential threats to others, and at the same time, function as a way to elicit and promote effective assistance or affiliation between pair mates or group members. For example, Plotnik & de Waal, (2014) reported that the negative emotional cues emitted by a distressed elephant not only promoted that bystanders approached and directed affiliative responses to the distressed individual but also triggered "bunching" behaviour, a defensive display that consists in forming a close circle around both juveniles and other adults (McComb *et al.*, 2001; Plotnik & de Waal, 2014). Thus, in this case, the cues emitted by the distressed elephant seemed to serve for both to alert potential bystanders and to elicit reassuring responses. It seems, then, that emotional contagion comprises a broad range of processes that could vary depending on the ecological circumstances and socio-behavioural traits of the species, be based on different mechanisms of varying complexity, and be subjected or not to further emotional and cognitive

processing. Furthermore, depending on the species and the situation, these processes could lead to fixed or more flexible prosocial responses that could promote social buffering and have a rewarding effect in both individuals, facilitating thus group or pair living.

In summary, emotional contagion, mimicry and social synchrony could function as basic forms of empathy in many social animals, allowing individuals to “feel into” another’s affective state in a simple and automatic way. These simple emotional and motor processes could serve to ease affiliative behaviours, enhance social acceptance, maintain social relationships, facilitate effective communication or elicit conspecifics’ assistance. Moreover, in certain species, these phenomena might also underlie more complex empathic behaviours such as consolation or targeted helping. Thus, they could be important evolutionary adaptations for group or pair-living species. Emotional contagion, mimicry and social synchrony seem to be adapted to the behavioural ecology of the species and thus present a great variability across the animal kingdom. Therefore, depending on the species, these processes could be triggered by a great variety of stimuli, modulated by different factors or be based on distinct mechanisms.

Overall, more research is needed to expand our understanding of the mechanisms and functions of emotional contagion, mimicry and social synchrony and the extent to which these processes are present in a wide variety of animal species. But it is clear enough that the comparative study of basic forms of empathy contributes to the understanding of our social nature.



## CHAPTER 3

# COMPLEX FORMS OF EMPATHY

### 1. Introduction

Sympathetic concern and empathic perspective-taking are usually considered to be the most complex forms of empathy (de Waal, 2008), comprising behaviours such as consolation or empathic targeted helping, which are traditionally treated as uniquely human. These higher forms of empathy require both, emotional and complex cognitive processes (de Waal, 2008), therefore, they are not expected to be widespread across the animal kingdom. Recent results suggesting the occurrence of these high-level behaviours in species such as rodents call for a deeper review of the nature and mechanisms of these behaviours.

In this chapter, we do not propose new definitions of the terms ‘sympathetic concern’, ‘empathic perspective-taking’ and associated processes. Instead, we provide operative criteria that represent the best available approach for reviewing the existing evidence. By using these criteria, we can separate empathic behaviours from similar behaviours that are not empathy-based. As most studies on empathy in non-human animals do not provide data on the motivations underlying the observed or measured responses, in this chapter, we focus herein on the available data (reactions, responses and outcomes/effects). Thus, we leave aside the underlying behavioural motives in defining operative criteria to distinguish empathic from non-empathic behaviours in non-human animals. So first, we clarify the terminology used in this field and provide operative criteria of application. We then carry out a comprehensive review of the literature on complex forms of empathy in non-human animals: sympathetic concern and empathic perspective-taking. In particular, we focus on consolation and empathic targeted helping, as examples of these two major categories. Finally, we discuss whether these studies really offer examples of complex empathic behaviours comparable to those found in humans. With this chapter, we hope to provide an integrative view of the field and discuss the challenges and conditions to be addressed. We also hope to highlight the importance of the study of these processes for elucidating the evolutionary history of these capacities across the animal kingdom.

### 2. Sympathetic concern and personal distress

Sympathetic concern has been defined in opposition to personal distress. Definitions by Batson, Fultz, & Schoenrade (1987), de Waal (2008) or Eisenberg *et al.* (1989) underline that sympathetic concern is an emotional reaction elicited in response to the negative state of another, that motivates to improve its situation (a prosocial response), while personal distress involves a motivation to overcome such an emotional reaction. Sympathetic concern is seen as an other-oriented emotional reaction, which – in contrast to emotional contagion – does not necessarily mimic that of the

distressed partner, and leads to a prosocial response to alleviate the other's negative state. Personal distress is a self-focused reaction, which mimics the aversive state of the distressed partner. This emotionally aversive over-arousal focusses the observer on its own negative state, generally triggering a non-prosocial response which aims to alleviate its own distress.

Apparently, then, these processes respond to opposite motivations. While sympathetic concern is viewed as an other-oriented emotion fostering altruistic behaviour, personal distress is thought to be an ego-oriented reaction that motivates care for oneself, aiming to alleviate one's own distress, while disregarding the other's (Eisenberg, 2010). However, this distinction may be over simplistic. Even if sympathetic concern involves an other orientation, it may also produce self-benefits, such as punishment avoidance, aversive-arousal reduction or social reward seeking (Batson, 2010). Therefore, some authors claim that sympathetic concern is also self-interested. Conversely, personal distress behaviours, even if self-oriented, may benefit others as well. Herein, we do not consider underlying motives of behaviour in characterizing these phenomena. Instead, we attempt to operationalize sympathetic concern and personal distress in terms of the type of reaction and response triggered by the perception of others' distress and its main effects (**Table 1**). In this way, sympathetic concern and personal distress can be more easily distinguished: we can view sympathetic concern as a moderate emotional reaction elicited by the perception of another individual in distress, which gives rise to an other-oriented response; and personal distress as an over-arousal and intense negative emotional reaction that mimics that of the distressed party, and gives rise to a self-focused response. It is useful to make this distinction because the emotional reactions and behavioural dispositions involved in each case are different: an other-oriented response that alleviates the other's distress and perhaps the mild distress vicariously felt by the observer (sympathetic concern), or a self-focused reaction that generally elicits escape responses to move away from the source of distress (personal distress). Motivations play no role in drawing this distinction. Of course, there will always be the possibility of ambiguous cases. In some situations (for example, when the observer cannot escape from the distressed partner), personal distress can lead to prosocial effects if this is the easiest way to reduce the observer's negative emotional state (Eisenberg & Eggum, 2009). In such cases, it will be more difficult to differentiate personal distress from sympathetic concern; doing so would require experimental manipulation to change the context and to determine whether the reaction and response change accordingly.

It has also been claimed that an important element that differentiates sympathetic concern from personal distress is the respective level of effective emotional regulation. Some authors point out that one of the fundamental characteristics of sympathetic concern is the ability to distinguish, to some extent, between internally and externally generated emotions, that is, between personal and vicarious emotions (de Waal, 2008). This does not mean that an individual must perceive another's internal state (Batson, 2010), but be able to tell whether its affective state was triggered by its own, or somebody else's, situation. This ability allows individuals to respond differently depending on the source of the emotion and explains why only observers perform an other-oriented response, not the ones being observed. Development, extended life history and prefrontal functions, such as working memory, increase the flexibility and control of the emotional response, thus facilitating the emergence of sympathetic concern (de Waal, 2008). In general, the human data point to a positive relationship between sympathetic concern and regulatory capacities and an inverse relationship between personal distress and emotional regulation (Eisenberg, 2002). Higher forms of inhibitory control are thought to depend upon the frontal lobe of the cortex. As prefrontal size correlates with emotional regulation skills in development and phylogeny, sympathetic concern processes are expected to be displayed only in species with a well-developed prefrontal cortex (Preston & de Waal, 2002). However, it remains to be shown that the basic form of emotional regulation presupposed for sympathetic concern can only

be achieved by means of advanced prefrontal abilities. It is in principle possible that the distinction between vicariously generated and personal emotions could be done in a more automatic way. Indeed, there is evidence that different neuronal populations are activated in the human anterior cingulate cortex (ACC) when experiencing or when observing pain (Morrison & Downing, 2007). This allows the possibility that different neuronal populations could trigger different automatic responses depending on the source of the emotion (vicarious or personal). If so, then sympathetic concern could be found in a wider range of animal species than possible if prefrontal control structures are necessary. Whether sympathetic concern can be mediated by different neural circuits should be subject to further investigation.

**Table 1.** Definition and main components of consolation (sympathetic concern), personal distress and empathic targeted helping (empathic perspective-taking).

	Components		
	1. Reaction	2. Response	3. Outcome
<b>Consolation</b>	<ul style="list-style-type: none"> <li>- <b>Other-oriented reaction in response to other's distress/situation/needs:</b> moderate level of arousal; non-emotional match</li> <li>- Some level of emotional control regulation needed</li> </ul>	<ul style="list-style-type: none"> <li>- <b>Other-oriented response:</b> attempts to ameliorate the other's state (approach responses)</li> </ul>	<ul style="list-style-type: none"> <li>- Alleviation of the distressed party</li> </ul>
<b>Personal distress</b>	<ul style="list-style-type: none"> <li>- <b>Self-focused reaction in response to other's distress/situation/needs:</b> over-arousal; emotional state-matching</li> <li>- Emotional control regulation not needed</li> </ul>	<ul style="list-style-type: none"> <li>- <b>Self-focused response:</b> attempts to ameliorate one's own distress (escape responses)</li> </ul>	<ul style="list-style-type: none"> <li>- Alleviation of the individual's own distress</li> </ul>
<b>Empathic targeted helping</b>	<ul style="list-style-type: none"> <li>- <b>Other-oriented reaction in response to other's distress and after a cognitive appreciation of the situation:</b> moderate level of arousal</li> <li>- Emotional control regulation needed</li> </ul>	<ul style="list-style-type: none"> <li>- <b>Flexible other-oriented response:</b> fine-tuned help or care appropriate to the situation of the distressed party</li> </ul>	<ul style="list-style-type: none"> <li>- Improvement of the situation of the distressed party</li> </ul>

### 2.1. Consolation

Consolation or comfort behaviour (consolation-like behaviour outside the post-conflict context) is considered to be a major example of sympathetic concern. de Waal & van Roosmalen (1979) first applied this term to non-human primates, defining it as contact of the aggressed party with a third animal. They distinguished consolation from reconciliation, which is contact between former

opponents, although both interactions seemed to have a calming effect. Their definition excluded affiliative contacts between winners and a third party and did not consider which individual (aggressor or third party) initiated the affiliative contacts.

However, three types of post-conflict bystander affiliation can be distinguished: (1) appeasement – post-conflict contact offered by bystanders to aggressors (Romero, Castellanos, & de Waal, 2011); (2) solicited bystander/third-party affiliation – solicited affiliation by the distressed party to a bystander (Fraser & Bugnyar, 2010); and (3) unsolicited bystander/third-party affiliation – post-conflict affiliative contact spontaneously directed to victims by bystanders (Palagi & Cordoni, 2009). Each of these post-conflict contacts might have different functions: (a) although appeasement could also alleviate the aggressors' post-conflict stress, it is not usually considered as an example of consolation since it may function to reduce aggressive tendencies in the aggressor. (b) This behaviour would provide direct benefits to bystanders by preventing them from becoming the target of redirected aggression. If so, appeasement could be qualitatively different from affiliation between bystanders and victims (Romero *et al.*, 2011). (c) To alleviate post-conflict distress: victims of aggression are expected to experience higher levels of anxiety and more distress after the conflict than aggressors, and hence, they are likely to have a greater need for consolation (Romero *et al.*, 2011). Solicited bystander contacts may be functionally similar to unsolicited ones in that they could also reduce post-conflict distress (Palagi & Cordoni, 2009). But the underlying mechanism is likely to differ from consolation in that it may not require empathy since the initiative is not taken by the bystander but by the distressed party (Fraser & Bugnyar, 2010). Solicited affiliative contacts could range from the mere approach of the victim to the bystander to the emission of specific signals by the distressed party (Cordoni, Palagi, & Tarli, 2006). These solicitation signals carry a specific meaning: approach the sender. Therefore, solicited third-party affiliation simply requires that the bystander tolerates the approach of the other individual or recognizes the specific approach signal emitted by the other animal, irrespective of whether it is distressed or not. On the other hand, to be considered true consolation, the uninvolved party must spontaneously realize that the other needs reassurance and provide it. That is, the prosocial response should be driven by the perception of the other's distress and not by an explicit request from the distressed party for attention and support from a bystander.

Unsolicited bystander affiliation is expected to be performed by individuals who share a close relationship with the distressed party, as they are more likely to be responsive to the other's distress (Fraser & Bugnyar, 2010). Much attention has been paid to the role of familiarity in consolatory responses because sympathetic concern is related to empathy and, according to the literature, familiarity has robust effects in processes facilitating empathy in several contexts (Preston & de Waal, 2002).

In the field of animal empathy research, the term consolation thus has come to define a specific type of unsolicited third-party affiliation characterized by the alleviation of the victim's distress and the directionality of the bystanders' affiliations, directed mostly towards familiar individuals (kin or friends) (Palagi *et al.*, 2014). Furthermore, this view assumes that consolation is based on empathy. Therefore, some authors still prefer the ethology descriptive tradition of using the more neutral concept 'unsolicited third-party affiliation' (Palagi *et al.*, 2014). The above definition of consolation excludes reconciliation, appeasement and solicited affiliation, considering only the contacts of bystanders towards victims of aggression.

## 2.2. Sympathetic concern and consolation studies in non-human animals

We will consider a behaviour to be an example of sympathetic concern if it involves the following three components: (1) a moderate other-oriented emotional reaction in response to another's distress, situation or needs that does not mimic that of the distressed party; (2) a prosocial response including attempts to ameliorate the other's state (approach responses); (3) alleviation of the distressed party (Table 1). We focus first on features of the emotional reaction triggered by the perception of another's distress. Both behavioural and neurophysiological data give us information about the type of response. For example, in sympathetic concern, the behavioural displays of the bystander are expected to be less overt than those of the distressed party (moderate other-oriented emotional reaction). The bystander's anxiety indicators (e.g. level of stress hormones) also should be lower than those of the stressed individual. Secondly, we can assess the responses of the observers: sympathetic concern responses must be directed towards the distressed party. And third, we consider whether this response alleviates the other's distress. We can test for stress alleviation by observing the termination of agonistic or stress behaviours in the distressed party after the occurrence of a prosocial response or/and by physiological measures that test for decreases in physiological indicators of anxiety.

From Zahn-Waxler's seminal studies on the development of concern in children (Zahn-Waxler, Radke-Yarrow, & King, 1979; Zahn-Waxler, Hollenbeck, & Radke-Yarrow, 1984; Zahn-Waxler *et al.*, 1992; Zahn-Waxler & Radke-Yarrow, 1990), the study of sympathetic concern processes in humans and non-human animals, has been almost exclusively focused on consolation behaviour, as it is the main example of this category (de Waal, 2008). Therefore, here we review only consolation studies. Apart from the involvement of a third party, the crucial feature of consolation or comfort behaviour is its distress-alleviation effect. When this effect cannot be established, then we resort to the common practice of referring to unsolicited third-party affiliation (within the post-conflict context). As the study of consolation in non-human animals is mostly focused on unsolicited bystander affiliative contacts towards victims of aggression, there are few data available on consolatory behaviours outside the post-conflict context.

### a. Non-human primates

Consolation has been studied in detail in chimpanzees, starting from de Waal and van Roosmalen (1979). They analysed hundreds of post-conflict contacts in a semi-free-ranging colony of chimpanzees and pointed out that, after agonistic interactions, chimpanzees usually engaged in non-violent body contacts. de Waal & van Roosmalen (1979) distinguished between reconciliation among former opponents, and consolation, which consisted of contacts of an uninvolved individual towards the aggressed party. They stated that such interactions seemed to serve an important distress alleviation function in the short term, and a longer-term social homeostasis function. Because of the short duration of the post-conflict observation period and the lack of control data, de Waal & Aureli (1996) replicated this study. They proposed that, if post-conflict affiliative contact with bystanders alleviate the distressed party, three predictions follow: (1) more affiliative contacts are expected within a few minutes of the conflict than after longer time periods or during control periods; (2) more contacts are expected following intense aggressive encounters (given that the distress of the victim is likely to be proportional to conflict intensity); and (3) more contacts are expected between bystanders and victims of aggression than between bystanders and aggressors. Their data on chimpanzees supported the results of de Waal & van Roosmalen (1979) and met their three predictions. Furthermore, they observed that bystanders often did not show overt signs of distress before approaching the victim, suggesting that the main role of this behaviour is not the bystander's comfort but the alleviation of the distressed party. These results led the authors to conclude that chimpanzees console victims of aggression. Recent work has provided further evidence for the existence of this type of behaviour in

chimpanzees showing that, in captivity, third-party affiliation occurred more often between individuals that were socially close (kin and affiliation partners) (Fraser, Stahl, & Aureli, 2008; Romero & de Waal, 2010; Romero, Castellanos, & de Waal, 2010), was more typical of females (Romero *et al.*, 2010) and reduced behavioural measures of stress in recipients of aggression (Fraser *et al.*, 2008). However, studies with wild chimpanzees do not provide corroborative evidence: in one wild group third-party affiliation was found to be very rare (Arnold & Whiten, 2001), and in another, third-party affiliation was observed but was delayed compared to captivity data (Kutsukake & Castles, 2004).

Several studies have described the occurrence of unsolicited third-party affiliations after conflicts in other ape species: bonobos (Palagi, Paoli, & Tarli, 2004; Clay & de Waal, 2013; Palagi & Norscia, 2013) and gorillas (*Gorilla gorilla* and *Gorilla beringei*) (Watts, 1995a,5b; Cordoni *et al.*, 2006; Mallavarapu *et al.*, 2006). In bonobos, close relationships positively affected only unsolicited affiliation rates along an empathic gradient, being mostly offered to kin, then friends and, finally to acquaintances (Palagi *et al.*, 2004; Clay & de Waal, 2013; Palagi & Norscia, 2013). Unsolicited bystander affiliation effectively reduced the distressed party's anxiety in bonobos (measured through self-scratching behaviour, an indicator of anxiety) (Palagi & Norscia, 2013). Data on unsolicited bystander affiliation in gorillas are not conclusive due to the fewer studies and inconsistent results between wild mountain gorillas (Watts, 1995a,5b) and captive groups of western gorillas (Cordoni *et al.*, 2006; Mallavarapu *et al.*, 2006). Overall, unsolicited third-party affiliation has been reported for both wild and captive gorillas but the extent to which this behaviour leads to stress alleviation in the distressed party is not yet clear.

de Waal & Aureli (1996) compared their chimpanzees' results with data on post-conflict behaviour of several species of macaques in the wild and in captivity and found important differences in unsolicited bystander affiliation. Unlike chimpanzees, affiliative contacts between macaque bystanders and victims of aggression did not occur more often following a conflict than during control periods. Instead, macaques avoided the scene of a conflict in which they were not involved. Other studies have also failed to find positive evidence of unsolicited third-party affiliation as a post-conflict consolatory mechanism (reviewed by Watts, Colmenares, & Arnold, 2000). These negative results led to the conclusion that consolation behaviour is virtually absent in monkeys. Recent studies have challenged this, reporting the existence of unsolicited bystander affiliation in stump-tailed macaques (*Macaca arctoides*) (Call, Aureli, & de Waal, 2002), mandrills (*Papio anubis*) (Schino & Marini, 2012) and Barbary macaques (*M. sylvanus*) (McFarland & Majolo, 2012). In the latter study, bystanders initiated post-conflict affiliations more frequently with victims with whom they shared high-quality relationships than with other individuals, just as in great apes and humans. None of these three studies found evidence of stress-alleviation effects of bystander affiliation. Palagi *et al.* (2014) reported such an effect in Tonkean macaques (*M. tonkeana*), one of the most tolerant macaque species, but not in the despotic Japanese macaque. In Tonkean macaques, unsolicited third-party affiliation reduced indicators of anxiety (scratching) in the conflict victims and was mainly directed towards friends (measured by the amount of grooming exchanged between individuals), especially towards females who experienced higher levels of anxiety compared to males. These results support the 'Social Constraints Hypothesis' (de Waal & Aureli, 1996), which proposes that unsolicited bystander affiliation depends on the social structure of the species, being more likely to be found in tolerant than in despotic species since the risks of further aggression for potential bystanders are lower (Fraser *et al.*, 2009).

Thus, unsolicited third-party affiliation in chimpanzees (Fraser *et al.*, 2008), bonobos (Clay & de Waal, 2013; Palagi & Norscia, 2013) and Tonkean macaques (Palagi *et al.*, 2014) reduced behavioural

indicators of stress in the victims, satisfying a crucial feature of consolation: distress alleviation. It also met the familiarity bias criterion, being offered mostly to familiar conspecifics. However, in the case of bonobos and Tonkean macaques, no data were collected assessing features of the observers' reaction towards the distressed victim. As noted above, this is crucial to distinguishing personal distress from sympathetic concern. For chimpanzees, however, observers' reactions are available. de Waal & Aureli (1996) reported that bystanders often did not show overt signs of distress before approaching the distressed individual and waited until the most intense displays of distress stopped. While de Waal & Aureli (1996) did not detail subtle indicators of emotion (behavioural or physiological) in the bystander, their observations of its reaction towards the distressed party suggest that chimpanzees have some inhibitory control over their emotional reactions, so that their approaching responses were not due to personal distress, but to sympathetic concern. Thus, to date, chimpanzees are the only species that show consoling behaviour according to the three proposed criteria. There are only two studies (Koski & Sterck, 2007; Fraser *et al.*, 2008) that assess stress-alleviation effects of third-party affiliation in chimpanzees. These studies used behavioural indicators of stress, not psychophysiological ones. Furthermore, Fraser *et al.* (2008) found positive evidence for a stress-alleviating effect of third-party affiliation, whereas Koski & Sterck (2007) did not. Therefore, it would be of great interest to measure not only behavioural but also physiological parameters to characterize the emotional reaction of the bystander better and the effectivity of the observer's responses in alleviating the victim's distress. Such research, especially in wild animals, could clarify the occurrence and effects of this type of behaviour in chimpanzees and other primate species and outside post-conflict contexts.

## b. Canids

Wolves and dogs engage in post-conflict third-party affiliation and the dynamics of this behaviour show a strong similarity with that observed in great apes (Palagi & Cordoni, 2009). Wolves show solicited and unsolicited bystander affiliation (Palagi & Cordoni, 2009; Baan *et al.*, 2014). Unsolicited third-party contacts occurred between friends (measured by body contact rates) (Palagi & Cordoni, 2009). In addition, third-party affiliation provided immediate benefits to the victims reducing the probability of renewed aggression and restoring social cohesiveness, suggesting that unsolicited affiliation with a third party buffers social tension in the group. In dogs, third-party affiliations were more often directed towards the victim of a conflict than towards the aggressor (Cools, Van Hout, & Nelissen, 2008) but the influence of familiarity in these post-conflict contacts could not be assessed. A recent paper has shown that wolves and dogs perform differently in a cooperative string-pulling task, being wolves the ones that better cooperate with their conspecifics (Marshall-Pescini *et al.*, 2017). This result may be related to the different socioecology of the two species and thus, it would be of great interest to assess in the future possible differences in consolation behaviour between these two species.

Outside the post-conflict context, Custance & Mayer (2012) evaluated the reactions of dogs towards apparently distressed humans. Dogs were exposed to four conditions: two in which their owner or a stranger pretended to cry, and two in which their owner or a stranger hummed a song. All conditions were preceded by a two-minute period during which the owner and stranger chatted. Dogs oriented significantly more often towards the person (looking at, approaching and touching them) during the crying condition than during the humming or talking periods regardless of the person's identity. Dogs approached the crying person in a submissive way, producing in some cases mild distress vocalizations. When the stranger was pretending to cry, dogs sniffed, nuzzled and licked them (instead of seeking out their owner for comfort), even if the stranger ignored them. This evidence is inconclusive since, as suggested by Custance & Mayer (2012), the dogs may have

previously been positively reinforced for approaching crying individuals and thus, their response could be the result of previous learning rather than spontaneous comfort behaviour.

Quervel-Chaumette *et al.* (2016) assessed whether dogs displayed comfort behaviours towards familiar conspecifics (dogs that lived together) after being exposed to conspecifics' distress vocalizations or control sounds. The distress vocalizations consisted of whines produced by their familiar partners or by "stranger" dogs. Dogs presented higher behavioural alertness, more stress-related behaviours, and an increase in comfort behaviours towards the familiar dog (longer time spent in proximity and expressing affiliative behaviour) after being exposed to conspecifics' whines than when exposed to control sounds. Dogs displayed more comfort behaviours towards their partner after hearing familiar whines compared to stranger whines. Furthermore, familiar whines tended to maintain a dog's cortisol (a stress-related hormone) concentration at a higher level than stranger's whines.

Overall, none of the above studies provided clear positive evidence of a distress-alleviation effect of third-party affiliation in dogs or wolves. Thus, for the moment, we cannot talk of consolation in these species. However, canids seem to be affected by and respond to other's distressing situations, providing unsolicited third-party contacts to conspecifics or even to members of other species like humans, instead of trying to alleviate their own stress. Furthermore, the results of Quervel-Chaumette *et al.* (2016) suggest that dogs' comfort behaviours were not just an automatic response driven by emotional contagion. After being exposed to whines, dogs opted to comfort their familiar partner without any solicitation or distress signal emitted by the other dog, instead of going to their owner for comfort. Future studies should examine the effect of unsolicited affiliation in canids and features such as the existence of a familiarity bias in those contacts.

### c. Elephants

Despite anecdotal reports describing possible empathic behaviours in elephants, empirical studies assessing the occurrence of emotional behaviours such as consolation are scarce. Bates *et al.* (2008) used observational reports collected over a 35-year period in Kenya with African elephants. These reports suggest that adult females tend to comfort immature individuals, more precisely calves under two years old. Comfort behaviour was preceded, in most cases, by the calf giving a distress vocalization or displaying alarm postures. In some situations, calves received comfort without displaying any obvious distress cues. In all but one case, the calf and the adult shared a valuable relationship. Plotnik & de Waal (2014), studied affiliative tendencies in Asian elephants after a distressing event. They assessed the occurrence of other-regarding responses to an individual's distress irrespective of its cause. Results showed that elephants affiliated significantly more with a conspecific through directed physical contact and vocal communication following a distress event than in control periods. But, in many cases, the authors could not identify a clear stimulus for a distressing event. Therefore, it was difficult to distinguish whether the individuals were reacting directly to the stimulus or to the conspecific's distress. However, the researchers contend that the directionality of the contacts and their nature strongly suggest attention towards the emotional states of other elephants and that this behaviour could be akin to consolation responses observed in apes.

Research on sympathetic concern behaviour in elephants is still in its infancy. For the moment, the few existing studies suggest that elephants react to perceived distress cues in their conspecifics providing in some cases comfort-like behaviours. It remains to be further clarified whether this response is empathically mediated and has the effect of reducing the stress of the receptor.

#### d. Rodents

In rodents, behaviours likely to relieve pain in conspecifics such as nursing, grooming, licking or physical proximity, have been observed in studies assessing the emotional responses of individuals to another's distress (Walker *et al.*, 2003; Knapska *et al.*, 2010; Atsak *et al.*, 2011). For example, Knapska *et al.* (2010) observed that rats spent significantly more time directing allogrooming (social behaviour considered to have an investigative and affiliative role; towards partners that had undergone an electric shock than towards non-shocked individuals. Atsak *et al.* (2011) noticed that rat witnesses that had previous experience with foot-shocks spent significantly more time in the area close to a distressed rat than any other witness groups (non-shock groups or non-experienced groups) during and after the shock period. In a first attempt to test consolation-like behaviours empirically in rodents Burkett *et al.* (2016) compared the spontaneous responses of two species of voles, the social and monogamous prairie vole and the solitary and promiscuous meadow vole towards stressed conspecifics (which received foot-shocks). Prairie voles spent significantly more time directing allogrooming towards distressed familiar partners (mates or siblings) than to control individuals (non-shocked), but not toward stressed strangers. This affiliative pattern was also observed in a previous study on social buffering of the stress response in prairie voles (Smith, Lieberwirth, & Wang, 2013). Conversely, meadow voles did not show differences in the duration of allogrooming based on the state of their partner. Anxiety behaviour was normalized in distressed prairie voles that interacted with observers, pointing to an alleviation effect of the observers' affiliative behaviours. According to Burkett *et al.* (2016), the combination of an increase in prairie voles' directed affiliation with a social-buffering effect supports the designation of this behaviour as a consolation behaviour.

However, this study has important limitations (Pérez-Manrique & Gomila, 2016): only the responses of male meadow voles were tested despite potential gender differences in the allogrooming response. In fact, female and male meadow voles' responses towards familiar individuals differed in a previous study (Ferkin, 1988). Ultrasonic vocalizations (USVs) were not controlled so that it cannot be excluded that the affiliation was solicited. In addition, the affiliative responses of observer voles might be a by-product of the observer's mechanism of coping with its own distress. As discussed in Section 2.1, in situations in which the observer cannot escape from the distressed party, like the voles in these two experiments (tested in small cages), personal distress could lead to apparently prosocial behaviours, if this is the easiest way to reduce one's own stress. In fact, in the study of Burkett *et al.* (2016), bystanders separated from the stressed party by a clear barrier had significantly higher levels of plasma corticosterone which correlated strongly with that of the distressed vole. This is indicative of physiological state-matching. This stress reaction was absent in observers in full contact with distressed voles, suggesting that the contact with the distressed party served to alleviate the observer's own stress. Finally, meadow voles undergo seasonal changes in their social structure: in winter (short photoperiods) they become socially tolerant, often participating in communal nursing and rearing of pups (especially females) (Anacker & Beery, 2013). These seasonal behavioural changes are associated with changes in oxytocin receptor levels and influenced by oxytocin administration (Parker *et al.*, 2001; Beery & Zucker, 2010; Anacker & Beery, 2013). However, Burkett *et al.* (2016) only tested male meadow voles under long photoperiods, i.e. when they are expected to show lower levels of social tolerance. Therefore, the possibility that meadow voles display affiliative responses towards distressed individuals cannot yet be ruled out. Assessing the existence of these responses in meadow voles (males and females) under short photoperiods would help to clarify the nature of voles' affiliative responses towards distressed individuals. It would also be of great interest for investigating the function of consolation-like responses as an adaptive mechanism facilitating group living.

In summary, evidence of sympathetic concern in rodents is still highly limited but research on emotional processes in these animals emerges as a promising field of study allowing the use of several experimental paradigms and controls that cannot be applied to other species.

#### e. Corvids

Two studies have found strong evidence for unsolicited third-party affiliation in social species of birds: rooks (*Corvus frugilegus*) (Seed, Clayton, & Emery, 2007) and ravens (Fraser & Bugnyar, 2010). During the post-conflict period, rooks engaged in third-party affiliation employing a specific behaviour named “bill twining”, in which two birds interlock their beaks. Both former opponents and uninvolved bystanders initiated the affiliative contacts. These behaviours appeared significantly more during the post-conflict period, suggesting that the use of this behaviour could serve to advertise third-party affiliation to other members of the group. In ravens, Fraser & Bugnyar (2010) found that post-conflict affiliation offered to the victim was more likely to occur if the bystander shared a valuable relationship with the victim and after intense conflict. Subsequent studies (Logan, Emery, & Clayton, 2013a; Logan, Ostojić, & Clayton, 2013b) using a slightly different methodology, showed that jackdaws (*Corvus monedula*) and Eurasian jays (*Garrulus glandarius*) engage in third-party affiliation initiated by both combatants and bystanders. Colonial jackdaws showed third-party affiliation with mates; despotic and territorial jays with any individual, not just mates. This result partially fitted the authors’ hypothesis that jackdaws will show third-party affiliation but not jays since these birds lack high-quality relationships outside of the breeding season when they were tested. Young jays were involved in most of the conflicts suggesting that aggression and post-conflict affiliation resulted from the formation of pairs and the establishment of a dominance hierarchy so that once it has been established, conflicts and post-conflict affiliation disappear.

However, the observed pattern of third-party affiliation in these birds is very similar to that of primate species, suggesting that they could be sensitive to the emotions of others. At present, we have no evidence for a consolatory effect of this post-conflict behaviour in corvids. Furthermore, other main features defining consolation behaviour are missing, such as specific data on the directionality of third-party affiliation in jackdaws and jays or the nature of the reaction of the bystander in these affiliative interactions.

#### f. Parrots

Budgerigars, a social species of Australian parrot, also show post-conflict third-party affiliation initiated by both bystanders and combatants (Ikkatai, Watanabe, & Izawa, 2016). The occurrence patterns of initiated bystander affiliation were specific to the post-conflict context. Third-party affiliations were initiated significantly more often by males towards loser partner females but less towards winner females than would be expected outside the post-conflict context. Conversely, observer females did not behave in this manner, initiating affiliations more often with winner partner males. Moreover, combatants tended to initiate affiliations with partners but loser males suppressed this behaviour. According to the authors, these gender differences in post-conflict behaviour could be rooted in sex differences regarding socio-behavioural features, like female dominance over males. Therefore, third-party affiliation in budgerigars seems to be a more fixed behaviour dependent on specific signals and gender than true consolation behaviour.

### 3. Empathic perspective-taking

Empathic perspective-taking is a term traditionally used to refer to an ensemble of complex cognitive and emotional abilities including perspective-taking, self-awareness, mental-state

attribution, emotional-responding and well-developed emotional control regulation. For example, de Waal (1996) defined it as the capacity to take another's perspective (understanding another's specific situation and needs as different from one's own) combined with vicarious emotional arousal. It has also been said that a heightened self-awareness allows individuals to relate to the other's emotional state without losing sight of the actual source of this state (de Waal, 2008). Animals capable of self-recognition could have an introspective awareness of their own mental states and be able to adopt other's perspective (Decety & Moriguchi, 2007). So, in theory, animals endowed with these capacities possess the requirements to not only respond emotionally towards an individual in distress but also to carry out a cognitive appreciation of the situation and the specific needs of the distressed individual, acting accordingly within the relevant context.

### 3.1. Empathic targeted helping: rescue and epimeletic behaviour

Empathic targeted helping is considered to be the primary example of empathic perspective-taking (de Waal, 2008). It has been defined as "help and care based on a cognitive appreciation of the other's specific need or situation" (de Waal, 2008, p. 285). By definition, targeted helping requires the animal to understand, to some extent, the others' needs or goals given the situation, in order to help effectively (Yamamoto, Humle, & Tanaka, 2012). The thorny issue is how to distinguish real empathic targeted helping from simpler forms of empathy. A way to address this issue is to focus on the flexibility of the prosocial response: to qualify as targeted helping, a behaviour must be fine-tuned to the situation of the distressed individual, and change as the situation changes. We can assume then, that empathic targeted helping involves the combination of sympathetic concern with a cognitive appreciation of the specific situation (de Waal, 2008).

Empathic targeted helping can appear in two forms: rescue behaviour and epimeletic behaviour. The former is defined as "the rescue of one animal by another" (Nowbahari *et al.*, 2009, p.1 ) and it involves four components: (1) the victim is in distress (is in a situation that implies immediate physical risk to itself); (2) the rescuer's behaviour is suited to the circumstances of the victim's distress; (3) the rescuer places itself at risk by engaging in this behaviour; and (4) the rescue is not inherently rewarding to the helper [see Nowbahari & Hollis (2010) for a deeper look at rescue behaviour]. Epimeletic behaviour is also known as care behaviour and is characterized as "intra-, interspecific, or intergeneric behaviour that involves attention or assistance" (Lodi, 1992, p. 284) or "helping and caregiving directed to distressed individuals" (de Waal & Aureli, 1996, p.81 ). It has been called 'nurturant' if attention or care is directed towards young individuals and 'succorant' if directed towards adult individuals in distress (Caldwell & Caldwell, 1966). Examples of epimeletic behaviour are assisting mobility, caregiving or assisting ill, disabled or stunned individuals, and pre-emptive protection. This last behaviour is defined as protection provided by an individual before any harm has come to a conspecific (Bates *et al.*, 2008). In these cases, the protector may be empathic in the sense of predicting the distress that the other will suffer if the situation is not stopped (Bates *et al.*, 2008). It might be argued that, in some cases, consolation could be considered as an example of epimeletic behaviour as well (de Waal & Aureli, 1996). Such is the case if reassurance contacts are the most adequate response that an observer could provide to a distressed party in a specific situation.

The study of well-developed cognitive capacities in non-human animals is fraught with difficulties and controversies. Therefore, we will assume as a working hypothesis that perspective-taking can take place in different ways so that a wider set of social species can be considered.

### 3.2. Empathic targeted helping studies in non-human animals

According to **Table 1**, a behaviour should meet the following three requirements to be considered an example of empathic targeted helping: (1) a moderate emotional reaction towards another in

distress; (2) a fine-tuned help response appropriate to the situation of the distressed animal, which should lead to (3) the improvement of the situation of the distressed animal.

#### a. Non-human primates

There are many anecdotal reports describing situations where non-human primates, particularly chimpanzees, seemed to help others (de Waal, 1996). However, due to ethical and methodological issues, most of the available experimental studies on helping behaviour in primates are focused on instrumental helping and other-regarding preferences. Instrumental helping, a behaviour performed by an individual that enables another to reach a goal that cannot be achieved otherwise (Greenberg *et al.*, 2010), differs from empathic targeted helping in that the latter always requires some emotional involvement of the observer, which reacts towards the perceived distress of the other individual. Both instrumental helping and empathic targeted helping require a cognitive evaluation of the other's situation and may require other-regarding preferences. Concern for the welfare of others (other-regarding preferences), refers to whether an individual is sensitive to another's payoffs (Yamamoto & Tanaka, 2010). Helping others at a very low or no cost to oneself is an example of this capacity. Experimental studies on other-regarding preferences in non-human primates have provided mixed results depending on the context and paradigm used. In chimpanzees, studies testing other-regarding preferences in a food context have produced mostly negative evidence (Silk *et al.*, 2005; Jensen *et al.*, 2006; Vonk *et al.*, 2008; Amici, Visalberghi, & Call, 2014). However, other studies have shown that chimpanzees do seem to help others even in contexts where there is food involved (Warneken & Tomasello, 2006; de Waal, Leimgruber, & Greenberg, 2008; Yamamoto, Humle, & Tanaka, 2009; Yamamoto *et al.*, 2012; Greenberg *et al.*, 2010; Horner *et al.*, 2011; Melis *et al.*, 2011; Claidière *et al.*, 2015). In some studies, orangutans (*Pongo abelii*, *P. pygmaeus*) (Amici *et al.*, 2014; Kim *et al.*, 2015), bonobos, western gorillas, spider monkeys (*Ateles geoffroyi*) (Amici *et al.*, 2014), cotton-top tamarins (*Saguinus oedipus*) (Cronin *et al.*, 2009; Stevens, 2010), Japanese macaques (Burkart & van Schaik, 2013), and capuchin monkeys (Burkart & van Schaik, 2013; Drayton & Santos, 2014) did not show other-regarding preferences. However, marmosets (*Callithrix jacchus*) (Burkart *et al.*, 2007; Burkart & van Schaik, 2013), capuchin monkeys (de Waal *et al.*, 2008; Lakshminarayanan & Santos, 2008; Takimoto, Kuroshima, & Fujita, 2010; Brosnan *et al.*, 2010; Suchak & de Waal, 2012; Claidière *et al.*, 2015) and bonobos (Tan & Hare, 2013) were found to show other-regarding preferences under different experimental conditions. In the context of instrumental helping, chimpanzees spontaneously helped an unrelated conspecific, or a human, irrespective of being rewarded or whether helping was costly (Warneken & Tomasello, 2006; Warneken *et al.*, 2007). These apes also showed flexible helping depending on conspecifics' needs and this helping behaviour varied depending on the situation (Yamamoto *et al.*, 2009, 2012; Melis *et al.*, 2011). Some studies emphasize the importance of request behaviour for promoting this type of behaviour (Yamamoto *et al.*, 2009, 2012) and others showed that chimpanzees seldom help others without a direct request (Greenberg *et al.*, 2010). A study with capuchin monkeys (Barnes *et al.*, 2008) demonstrated that they are able to instrumentally help human experimenters in the absence of a reward but failed to take into account the perspective of others when they expect to get food for themselves. Furthermore, they prioritized the potential cost to themselves over the benefit to the conspecific that needs help. Capuchin monkeys also failed to help a conspecific in a minimal-cost instrumental helping task, not sharing tokens that allow the other monkey to obtain food from an apparatus (Skerry, Sheskin, & Santos, 2011).

Apart from the above data on instrumental helping and other-regarding preferences, there is a lack of systematic studies on empathic targeted helping *per se* in non-human primates. Pruetz (2011) provides an anecdotal report which could be one of the few detailed cases of empathic targeted

helping in chimpanzees in the wild. Over two days, an adolescent male was seen helping an injured mother carry her infant. The mother was unable to keep up with the rest of the group and stopped frequently, leaving her infant on the ground each time. The young male picked up the infant and carried her for approximately one-third of the distance the group moved. He was not observed to carry the baby again during a subsequent 8-week period. Furthermore, this adolescent had never been observed to carry this or any other baby before this incident. In this community of chimpanzees, other males had been observed to carry infants but never for the duration shown by this young male. The male was not matrilineally related to the mother but the cohesion of this community is three times greater than that reported for chimpanzees at other study sites. Pruetz (2011) highlights that the issue of concern here is the recognition of the mother's state and her needs by the male. Neither the mother nor the infant emitted emotional signals to indicate distress, so the young male apparently perceived the difficulty of the mother and anticipated her goal. Vogel & Fuentes-Jiménez (2006) described a case of rescue behaviour in white-faced capuchin monkeys (*Cebus capucinus*). A mother and her baby were rescued by the beta male of their social group after being isolated by male attackers of another group that were attempting to grab the infant. The beta male appeared soon after the female emitted alarm calls, and the attackers left the female and infant to chase him. Marzec *et al.* (2016) reported a striking case of possible rescue behaviour in wild orangutans (*Pongo pygmaeus wurmbii*). An old female with her infant received protection from an unrelated male while she was being attacked by a young female which, in turn, received active support from another male. The defender male could have been attracted by the screams of the victim. The intervention of this male reduced the physical aggression directed at the old female and he remained and protected the distressed orangutan and her infant during a three-day period.

Other reports provide possible instances of 'pre-emptive' protection during mother-infant interactions. Hirata (2009) describes cases where mothers pull the infants away from potentially dangerous plants and a situation in which a mother witnessed her infant playing with a chain and removed it from the infant. The infant was still clumsy in her motor actions so her hand or fingers could possibly have been damaged. It is usual that chimpanzee, orangutan and spider monkey mothers help young individuals to move from one tree to another (Carpenter, 1935; Bard, 1995; de Waal, 2008). Although in many cases the infant or the juvenile vocalizes, soliciting help, the mother seems to observe and analyse the situation, anticipating possible danger, the reason for the infant or juvenile's distress and intervenes appropriately to address it. Other examples of possible nurturant or succorant behaviour are provided by caring for sick, injured or disabled individuals. In the Tai forest chimpanzees have been seen licking, cleaning and preventing flies from accessing the wounds of other individuals, sometimes for extended periods (Boesch, 1992). These chimpanzees seem to adapt their behaviour to the specific needs of the injured individual: dominant males prevent other group members from disturbing the wounded individual, and the whole group wait for the injured individual to begin to walk again (Boesch, 1992). There are also reports in which chimpanzees and Japanese macaques care for disabled infants (Turner, Gould, & Duffus, 2005; Matsumoto *et al.*, 2016). In such cases, mothers seemed to respond to the abnormal behaviours, limited physical abilities, and particular needs of the infant.

The lack of empirical and systematic observational data on empathic targeted helping in non-human primates prevents us from reaching robust conclusions. The available information suggests that at least some of the components listed in Table 1 for empathic targeted helping are present in apes' helping behaviour. Experiments on instrumental helping in chimpanzees and anecdotal descriptions suggest that these apes are able to make a cognitive evaluation of the situation and needs of other individuals, adapting their helping behaviour to the specific context. Helping behaviour in monkeys does not seem to be as flexible as that of chimpanzees. The observations of Pruetz (2011),

Boesch (1992) and Marzec *et al.* (2016) also imply that great apes, at least chimpanzees and orangutans, understand the situation of others in distress, providing help in a flexible way. In these reports, the helping behaviour provided by chimpanzees improved the wounded individual's situation, allowing it to keep up with the group and reach the feeding site, and in the orangutan's case, the intervention of the male stopped the physical attacks towards the old female. These reports do not provide information about the helping individuals' emotional reaction towards the distressed animal. In particular, the young chimpanzee seemed to recognize the needs of the injured female without any emitted distress signal and the male orangutan may have been attracted by the screams of the old orangutan. It is thus difficult to establish the nature of these males' reactions towards the distressed females.

### **b. Elephants**

Elephants live in very closely bonded societies and their interest in ailing companions or in the carcasses and bones of dead conspecifics is well known (Bates *et al.*, 2008). There is a remarkable number of anecdotal reports describing elephants assisting suffering conspecifics (Douglas-Hamilton *et al.*, 2006). Elephants possess complex cognitive capacities (Plotnik, de Waal, & Reiss, 2006), and it has been demonstrated that they are able to solve tasks acting cooperatively (Plotnik *et al.*, 2011). Thus, it seems reasonable to hypothesize that their behaviour towards distressed conspecifics could be an example of empathic targeted helping. Observational reports of wild elephants include instances in which familiar or unrelated elephants assisted or tried to lift suffering companions (Schulte, 2000). For example, Douglas-Hamilton *et al.* (2006) reported the behavioural responses of different elephants and their families towards a dying matriarch. After the distressed animal collapsed, an unrelated matriarch rapidly approached her in some degree of excitement [tail raised, vocalizing and showing temporal gland secretion (related to stress, excitement or fear in elephants; (Gorman, 1986)]. She tried to lift the matriarch and stayed with her even though her family was gone. These behaviours have also been observed in captivity, even between an Asian and an African elephant (Schulte, 2000), so this helping behaviour can occur irrespective of genetic similarity (Douglas-Hamilton *et al.*, 2006). Mothers or other adult elephants have also been reported to help to lift calves when they could not stand by themselves, had fallen into ditches or could not climb in or out of rivers or swamps (Bates *et al.*, 2008). In most cases, the elephants' behaviour seemed to adapt specifically to the problem faced by the calves (Bates *et al.*, 2008). Elephants protect young or injured individuals in potentially dangerous situations when the victims are unable to defend themselves effectively (Bates *et al.*, 2008). Most reports involve mothers protecting their calves or retrieving them, but there are also instances in which darted adults were guarded and helped by familiar or unrelated individuals (Douglas-Hamilton *et al.*, 2006; Bates *et al.*, 2008). There are also reports of 'pre-emptive' protection in which the individuals acted before any harm had come to the conspecific, such as stopping play fights between calves, pushing individuals or predators away from new-borns, keeping offspring away from young individuals and preventing calves from moving into dangerous areas (Bates *et al.*, 2008). The protector could be using its past experience in order to act effectively in each situation, rather than simply be responding to the direct perception of distress signals emitted by the calf because in most of these instances distress signals were absent. Another behaviour that could be an example of empathic targeted helping is the removal of foreign objects from the body of other elephants. Bates *et al.* (2008) described three examples of this behaviour including the removal of a dart, a spear and a plastic bag. The authors claim that it could be possible that in situations where there is a visible wound or damage, or the object presents a potential danger, elephants are compelled to touch the object. They may be able to detect dangerous foreign objects using emotional and behavioural signals from the injured animal and this recognition triggers the

action to remove them. However, interaction with foreign objects could be dangerous to the individual that removes or touches the object (Bates *et al.*, 2008).

Some of the anecdotal data described above could be considered as positive evidence for the three components listed in **Table 1** for targeted helping. In some situations, elephants react emotionally towards distressed conspecifics, as in the case of the dying matriarch described by Douglas-Hamilton *et al.* (2006). The helping animal displayed moderate signs of stress and temporal gland secretion, suggesting that the behavioural changes were accompanied by autonomic modifications driven by the perception of distress in the other individual and thus, fitting the first requirement. Regarding the second component, these reports show that elephants responded appropriately in many situations, adjusting their behaviour to the specific case and, more surprisingly, seeming to anticipate the future consequences of potentially dangerous situations (Bates *et al.*, 2008). Elephants not only helped familiar individuals but also unrelated conspecifics as humans do, suggesting a generalized response to distress (Douglas-Hamilton *et al.*, 2006). Finally, some of the helping behaviours described above could have improved the distressed animal's situation, meeting the requirements of the third component. However, almost all the examples discussed above are from only two studies. It is clearly desirable to carry out systematic studies focusing on the emotional and cognitive components of these helping responses in elephants to provide convincing evidence and expand our knowledge of empathic targeted helping in these social animals.

### c. Rodents

Targeted helping requires sophisticated cognitive capacities that are not thought to be present in rodents. However, their behavioural ecology and new empirical evidence suggest that some rodents, particularly rats, could be interesting subjects to investigate the roots of helping behaviour (Panksepp & Lahvis, 2011; Panksepp & Panksepp, 2013; Kirk, McMillan, & Roberts, 2014; Hernandez-Lallement *et al.*, 2015; Márquez *et al.*, 2015; Sivasevachandran *et al.*, 2016).

Rice & Gainer (1962) assessed the ability of rats to act effectively in reducing the suffering of a conspecific. In this pioneering work, a rat was suspended in the air (stressful situation) and another individual could help by pressing a lever that lowered the distressed rat. The helper rat lowered the distressed rat more often than a plastic block (control stimulus) and the helper stayed close to and oriented towards the suffering conspecific. Rats that had previous experience with a conspecific's distress were 10 times more likely to lower the distressed partner compared to controls. Lavery & Foley (1963) suggested that such helping responses were due to auditory stimulation in the experimental condition (distress calls of the suspended rat), as opposed to the control situation (silent object). More recently, Schneeberger, Dietz & Taborsky (2012) tested rats using an iterated Prisoner's Dilemma. In the first experiment, actor rats were paired with cooperative or defective partners. The actor rat could help its partner by pulling a tray with food towards the cage, the cost of which was manipulated by varying the resistance of pulling. In the second experiment, the researchers manipulated the levels of food deprivation of partners and assessed the potential effects of conspecifics' condition (body mass) in the actor's willingness to help. Rats provided more help to cooperative than to defective conspecifics, and the amount of help decreased with increasing costs when the partner was a defector. The need (hunger) and body condition of the partner influenced the amount of help provided by the actor rat: hungry rats received more help if they were underweight, whereas if the receiver was satiated, actor rats provided more help for heavy partners. The authors hypothesized that, as body mass correlates with dominance in rats, helping a dominant partner could reduce the probability of punishment for defection or might improve the social reputation of the helper. A study on the factors that drive prosociality in rats has pointed to the role of social cues (e.g. behavioural displays of intention) as modulators of prosocial behaviour (Márquez

*et al.*, 2015). In this study, rats tested in a prosocial choice task displayed a high proportion of prosocial choices but the display of recipients' food-seeking behaviour was necessary to drive those prosocial responses.

In order to test for targeted helping behaviour in rodents, Ben-Ami Bartal, Decety & Mason (2011) placed a free rat in a chamber with a distressed cagemate trapped in a restrainer. The free rat learned, after several sessions, to open the restrainer and free the cagemate. Rats opened the restrainers containing cagemates even when social contact was prevented, but, in general, did not open empty or object-containing restrainers. When free rats were presented with two containers, one containing chocolate and the other containing their cagemate, they opened both and typically shared the chocolate. Consistent with the hypothesis that females are more responsive to emotional stimuli than males (Eisenberg, 2000), the proportion of females that opened the restrainers was significantly higher. Observer rats apparently acted in a more agitated way when their cagemates were restrained, which could be considered evidence for emotional contagion. Further work complemented and supported these results (Ben-Ami Bartal *et al.*, 2014) showing that rats also helped trapped strangers, but did not help strangers of a different strain. Nevertheless, after being housed with rats of a different strain, these rodents helped strangers of that strain, demonstrating that rats can expand helping behaviour from one familiar individual to phenotypically similar others. Genetic relatedness alone was not required for helping, proving, according to the authors, that strain familiarity is a requisite for the expression of pro-social behaviour in rats.

The study of Ben-Ami Bartal *et al.* (2011) has been criticized. Silberberg *et al.* (2014) in a follow-up study concluded that their results and those of Ben-Ami Bartal *et al.* (2011) could be better explained in terms of neophobia and the pursuit of social contact, instead of in terms of empathic helping. Silberberg *et al.* (2014) showed that: (1) free rats did not learn to release the trapped rat when social contact was prevented during the learning phase; (2) trapped rats often returned to the restraint tube following release, suggesting that the tube was not aversive later in the experiment; and (3) observer rats continued to make the freeing response even when this action was no longer effective. These findings do not support a conclusion of empathy. It should be noted, however, that in the experiment of Silberberg *et al.* (2014), the door could be opened by contacting a metal strip attached to the door, so it is possible that some of the responses were accidental.

If rats' helping behaviour is mainly driven by social contact as proposed by Silberberg *et al.* (2014), rats should open restrainers similarly for distressed and non-distressed cagemates (Sivaselvachandran *et al.*, 2016). Sato *et al.* (2015) tested this prediction. In a first experiment, the cagemate was soaked in a pool of water (distressing condition) and the observer could open a door to allow their cagemate into a safe area. Rats opened the door significantly faster in the soaking condition than in control conditions (no cagemate in the pool area, neither cagemate nor water in the pool area, stuffed toy rat in the empty pool area). The experiment also showed that the rats disliked being soaked and that those with previous experience of soaking learned how to open the door faster. In a second experiment, the cagemate was just placed in an adjacent cage. Only one out of eight observer rats showed door-opening behaviour suggesting that rats did not learn door-opening behaviour when the cagemate was not in distress. In a third experiment, a group of rats were conditioned to open the door for a soaked cagemate and another group was conditioned to open the door for a food reward. Both groups were then tested in an arrangement in which they had to choose between opening a door that freed the cagemate from the pool or a door that gave them access to a food reward. Only the first group showed a significantly higher proportion of door opening to the cagemate, suggesting that the learning phase influences later behaviour. Sato *et al.* (2015) concluded that their findings support the view that rats show empathic helping. Recently, Schwartz *et al.* (2016) replicated the study of Sato *et al.* (2015) and disputed their conclusions. They highlighted that the use of a different

apparatus in the second experiment of Sato *et al.* (2015) may have influenced the results obtained. Using an E maze, Schwartz *et al.* (2016) also showed that rats preferred to release another rat standing in a pool of water than a rat standing on dry ground but this preference was maintained by two separate outcomes: the social contact offered by the freed rat and the reinforcing value of a pool of water. Although in Sato *et al.*'s first experiment observer rats sometimes opened the pool chamber even when there was no distressed cagemate present, they did not observe a preference for the pool area, rather noting that the rats showed a tendency to avoid water.

In sum, the results from these rat studies remain controversial and inconclusive. The fact that rats only help distressed individuals (Sato *et al.*, 2015) or provide help even when social contact was prevented (Ben-Ami Bartal *et al.*, 2011) is compatible with an empathy hypothesis. By contrast, the possibility that the outcome experienced during the learning process may influence future helping responses, as illustrated by the rats that failed to learn how to help distressed partners when the outcome was not social contact (Silberberg *et al.*, 2014), supports the social-contact hypothesis. Another limitation of some of these studies is that the same rats were tested repeatedly across sessions using the same restraining tube (Ben-Ami Bartal *et al.*, 2011, 2014; Silberberg *et al.*, 2014). The trapped rats showed habituation, even returning to the tube when the helper rat had opened the door. This casts doubt on whether the observer rat was really helping the trapped rat in response to its distress if the latter was not in an aversive situation.

The presence of distress calls during the learning process may have influenced these results. Lavery and Foley (1963) showed that rats spontaneously learned to press a bar to stop the auditory playback of distress squeals, suggesting that squeals are aversive to some extent and rats will act to stop them. These calls can evoke emotional contagion processes, inducing negative emotional states in the receivers (Kim *et al.*, 2010; Atsak *et al.*, 2011; Saito *et al.*, 2016). Therefore, it is possible that, after hearing the calls of their cagemates, observer rats experienced personal distress during the early learning phase and acted to stop emission of the squeals. If their actions during this phase not only stop the disturbing calls but also allow them to interact with their cagemate, rats might perceive these helping responses as a highly rewarding experience (Vasconcelos *et al.*, 2012). Physical contact and social interaction are known to have a calming effect in these rodents (Hofer & Shair, 1980; Carden & Hofer, 1992; Beery & Kaufer, 2015). Thus, in situations in which they experience personal distress, rats could act not only to stop the distressing stimuli but also to look for social interaction with their partners to reduce their own negative arousal. Therefore, knowing the behavioural and physiological features of the emotional reaction of the observer rat towards a distressed partner is necessary to distinguish between personal distress and a moderate emotional reaction associated with empathetic targeted helping.

Rats respond differently depending on the needs of their partner (Schneeberger *et al.*, 2012) and their previous experience with the distressing procedure (Rice & Gainer, 1962; Sato *et al.*, 2015) suggesting some degree of flexibility in their response and some cognitive evaluation of the situation. Sato *et al.* (2015) found that rats that had previously been soaked were quicker to learn how to open the door for a soaked cagemate than were naïve rats. However, this paradigm consisted of role-reversal sessions, and soaked rats could have learned about door opening through observation of their own helper rat, thus learning more quickly than naïve rats (Sato *et al.*, 2015). When rats' responses lead to the termination of a distressing situation such as being soaked or suspended, there is obviously an improvement of the distressed party's state, fulfilling the third requirement of empathic targeted helping (**Table 1**). However, this outcome could be a by-product of attempts by the rat to reduce its own stress and thus is not yet a true example of empathic targeted helping.

In summary, rodents represent promising models to study the roots of empathic target helping, allowing researchers to measure behavioural and physiological data, use different controls and test the role of distress calls in prompting helping responses in social animals. Auditory recordings and physiological measurements are crucial for assessing the nature of the reaction and responses of these animals towards distressed others to allow us to determine whether empathic targeted helping occurs in rodents.

#### 4. Discussion

Our objectives in this chapter were to (1) clarify the terminology used in this field by providing operative criteria of application; (2) review relevant studies on sympathetic concern and empathic perspective-taking in non-human animals using these criteria, and (3) discuss whether the available evidence offers examples of complex empathic behaviours.

We reviewed relevant studies in light of whether they meet the three requirements established in **Table 1** to qualify as examples of consolation and empathic targeted helping. A summary of our main findings is provided in **Table 2**. Note that in most of the reviewed studies, the first requirement is lacking: most studies assessing consolation or empathic targeted helping in non-human animals did not record the existence of an emotional reaction of the observer towards the distressed party. We are not suggesting that there is a lack of studies assessing emotional reactions in non-human animals *per se*, nor that animals do not display emotional reactions to a distressed individual. Instead, we note that studies assessing consolation and empathic targeted helping usually overlook the emotional component of the behaviour by not reporting data on the emotional response of the involved individuals, undermining our ability to reach firm conclusions. Furthermore, among studies that did report the observers' emotional reactions, only a minority included physiological data, making it difficult to establish solid conclusions regarding the nature of those reactions. As discussed in Section 2., the distinction between a moderate emotional reaction and an intense negative emotional reaction that mimics that of the distressed party could help us to distinguish between empathic behaviours and personal distress processes. The lack of assessment of this emotional component in most studies thus is remarkable and should be addressed in future work, especially considering that, for humans, there is a broad agreement on the presence of an emotional response to another person as a crucial component of empathy (Lamm, Batson, & Decety, 2007).

It is important to establish the compliance of all three criteria in order to interpret a certain behaviour as empathic. We use as an example the helping behaviour of some sand-dwelling ants (*Cataglyphis cursor*, *Cataglyphis floricola*, *Tetramorium* sp. E, *Lasius grandis*, *Formica cinerea*). Experimental studies conducted in the laboratory (Nowbahari *et al.*, 2009; Nowbahari, Hollis, & Durand, 2012; Miler, 2016) and in the field (Hollis & Nowbahari, 2013; Taylor *et al.*, 2013) have shown that several species of ants engage in a type of helping behaviour, termed by the authors "precision rescue", to free entrapped nestmates. Ants directed rescue behaviours such as sand-digging and limb-pulling towards individuals restrained by a nylon snare in a sand field. Interestingly, when these behaviours are ineffective, rescuer ants begin to bite precisely at the nylon snare. Furthermore, rescuers discriminate between victims based on their state and identity, providing help only to distressed nestmates and not to motionless nestmates, members of different colonies, common prey items, ants from a different species or the empty apparatus (Nowbahari *et al.*, 2009). Thus, ants displayed what seems to be sophisticated helping responses towards familiar distressed individuals. This rescue behaviour is fine-tuned to the specific situation of the victim and, if the biting attempts directed toward the snare are ultimately successful, the rescue is likely to alleviate the victim's distress. Therefore, it appears that the second requirement (fine-tuned help appropriate to the situation of the distressed party) and the third requirement (improvement of the distressed party's situation)

established in the definition of targeted helping (Table 1) are met. These responses are very similar to those displayed by rats in the studies of Ben-Ami Bartal *et al.* (2011, 2014) and Sato *et al.* (2015). However, as Vasconcelos *et al.*, (2012) pointed out, these two sets of results led to quite different interpretations. Whereas Ben-Ami Bartal *et al.* (2011, 2014) discuss their findings in terms of empathically motivated helping, Nowbahari *et al.* (2009) refrained from hypothesizing about the motivation underlying the ants' behaviour and focused on the functional aspects of the rescue behaviour.

**Table 2.** Studies on consolation and empathic targeted helping reviewed in this chapter. See Chapter 4 for a description of the cetaceans' studies. ✖ : Negative evidence; ✓ : Positive evidence; ?: No evidence available.

Species	1. Reaction	2. Response	3. Outcome
<b>Consolation</b>			
Chimpanzee ( <i>Pan Troglodytes</i> )	✓ de Waal & Aureli (1996)	✓ de Waal & van Roosmalen (1979), de Waal & Aureli (1996), Kutsukake & Castles (2004), Fraser <i>et al.</i> (2008), Romero & de Waal (2010), Romero <i>et al.</i> (2010)	✓ Fraser <i>et al.</i> (2008) ✖ Koski & Sterck (2007)
Bonobo ( <i>P. paniscus</i> )	?	✓ Clay & de Waal (2013), Palagi <i>et al.</i> (2004), Palagi & Norscia (2013)	✓ Clay & de Waal (2013), Palagi & Norscia (2013)
Mountain Gorilla ( <i>Gorilla gorilla beringei</i> )	?	✓ Watts (1995b)	?
Western Gorilla ( <i>G. gorilla gorilla</i> )	?	✓ Cordoni <i>et al.</i> (2006), Mallavarapu <i>et al.</i> (2006)	?
Stump-tailed macaque ( <i>M. arctoides</i> )	?	✓ Call <i>et al.</i> (2002)	?

Mandrill ( <i>Papio Anubis</i> )	?	✓ Schino & Marini (2012)	✗ Schino & Marini (2012)
Barbary macaque ( <i>M. sylvanus</i> )	?	✓ McFarland & Majolo (2012)	✗ McFarland & Majolo (2012)
Tonkean macaque ( <i>M. tonkeana</i> )	?	✓ Palagi <i>et al.</i> (2014)	✓ Palagi <i>et al.</i> (2014)
Japanese macaque ( <i>M. fuscata</i> )	?	✗ Palagi <i>et al.</i> (2014)	✗ Palagi <i>et al.</i> (2014)
Wolf ( <i>Canis lupus</i> )	?	✓ Palagi & Cordoni (2009)	?
Dog ( <i>C. familiaris</i> )	✓ Custance & Mayer (2012), Quervel-Chaumette <i>et al.</i> (2016)	✓ Cools <i>et al.</i> (2008), Custance & Mayer (2012), Quervel-Chaumette <i>et al.</i> (2016)	?
African elephant ( <i>Loxodonta africana</i> )	?	✓ Bates <i>et al.</i> (2008)	?
Asian elephant ( <i>Elephas maximus</i> )	?	✓ Plotnik & de Waal (2014)	?
Bottlenose dolphin ( <i>Tursiops truncatus</i> )	?	✓ Tamaki <i>et al.</i> (2006), Yamamoto <i>et al.</i> (2015)	?
Sperm whale ( <i>Physeter macrocephalus</i> )	?	✓ Pace <i>et al.</i> (2005)	?

Rat ( <i>Rattus norvegicus</i> )	?	✓ Knapska <i>et al.</i> (2010), Laviola <i>et al.</i> (2004), Atsak <i>et al.</i> (2011), Walker <i>et al.</i> (2003)	?
Prairie vole ( <i>Microtus ochrogaster</i> )	✗ Burkett <i>et al.</i> (2016)	✓ Smith <i>et al.</i> (2013), Burkett <i>et al.</i> (2016)	✓ Smith <i>et al.</i> (2013), Burkett <i>et al.</i> (2016)
Meadow vole ( <i>M. pennsylvanicus</i> )	✗ Burkett <i>et al.</i> (2016)	✗ Burkett <i>et al.</i> (2016)	✗ Burkett <i>et al.</i> (2016)
Rook ( <i>Corvus frugilegus</i> )	?	✓ Seed <i>et al.</i> (2007)	?
Raven ( <i>C. corax</i> )	?	✓ Fraser & Bugnyar (2010)	?
Budgerigar ( <i>Melopsittacus undulatus</i> )	?	✗ Ikkatai <i>et al.</i> (2016)	?

Targeted helping

Chimpanzee ( <i>P. Troglodytes</i> )	?	✓ Warneken & Tomasello (2006), Yamamoto, <i>et al.</i> (2009,2012), Melis <i>et al.</i> (2011), Greenberg <i>et al.</i> (2010), Pruettz (2011), Hirata 2009; de Waal (2008), Boesch (1992)	✓ Warneken & Tomasello (2006); Yamamoto, <i>et al.</i> (2009, 2012), Melis <i>et al.</i> (2011), Greenberg <i>et al.</i> (2010), Pruettz (2011), Hirata (2009), de Waal (2008), Boesch (1992)
Capuchin monkey ( <i>Cebus capucinus, C. apella</i> )	?	✗ Barnes <i>et al.</i> (2008), Skerry <i>et al.</i> (2011)	✓ Vogel & Fuentes-Jiménez (2006)

Orangutan ( <i>Pongo pygmaeus wurmbii</i> )	?	?	✓ Marzec <i>et al.</i> (2016)
African elephant ( <i>L. africana</i> )	✓ Douglas-Hamilton <i>et al.</i> (2006)	✓ Schulte (2000), Bates <i>et al.</i> (2008), Douglas-Hamilton <i>et al.</i> (2006)	✓ Douglas-Hamilton 2006, Bates <i>et al.</i> (2008)
Asian elephant ( <i>E. maximus</i> )	?	✓ Schulte (2000)	
Bottlenose dolphin ( <i>T. truncatus</i> )	✓ Kuczaj <i>et al.</i> (2015a), Hooper (2011)	✓ Caldwell & Caldwell (1966), Connor & Norris (1982), Siebenaler & Caldwell (1956), Warren-Smith & Dunn (2006), Kuczaj <i>et al.</i> (2015a), Lilly (1963), Hooper (2011)  ✗ Connor & Norris (1982)	✓ Kuczaj <i>et al.</i> (2015a), Caldwell & Caldwell (1966), Siebenaler & Caldwell (1956), Lilly (1963)
Pacific white-sided dolphin ( <i>Lagenorhynchus obliquidens</i> )	?	✓ Baird (1998)	?
Indo-Pacific humpback dolphin ( <i>Sousa chinensis</i> )	?	✓ Wang <i>et al.</i> (2013)	?
Long-beaked common dolphin ( <i>Delphinus capensis</i> )	?	✓ Park <i>et al.</i> (2012)	?

Humpback whale ( <i>Megaptera novaeangliae</i> )	?	✓ Pitman <i>et al.</i> (2016)	✓ Pitman <i>et al.</i> (2016)
Rough-toothed dolphin ( <i>Steno bredanensis</i> )	?	✓ Connor & Norris (1982)	?
Rat ( <i>R. norvegicus</i> )	?	✓ Rice & Gainer (1962), Schneeberger <i>et al.</i> (2012), Sato <i>et al.</i> (2015), Ben-Ami Bartal <i>et al.</i> (2011, 2014) ✗ Schwartz <i>et al.</i> (2016), Silberberg <i>et al.</i> (2014)	✓ Rice & Gainer (1962), Schneeberger <i>et al.</i> (2012), Sato <i>et al.</i> (2015) ? Ben-Ami Bartal <i>et al.</i> (2011, 2014) (2014), Silberberg <i>et al.</i> (2014)

It is true that ants' responses seemed to be other-directed and fine-tuned to the specific needs of the victim, but we should also consider the flexibility of those responses. These help responses do not appear to change radically depending on the context. Subsequent studies revealed that this rescue behaviour is elicited only under specific circumstances related to the ant species' behavioural ecology: loose sandy-soil habitats and close proximity to pit-digging antlions, a common predator of many ant species, are critical factors in whether an ant species displays rescue behaviour (Hollis & Nowbahari, 2013). Thus, rescue behaviour has evolved in those ant species that face high risks of possible entrapment by sand collapse and as an antipredator strategy (Taylor *et al.*, 2013). Furthermore, rescue behaviour is constrained by division of labour: help was received and dispensed only by certain colony members (Nowbahari *et al.*, 2012). Ants belonging to a different colony were vigorously attacked and, individuals belonging to the youngest inactive caste were ignored. The mechanism underlying this rescue behaviour remains unknown but it has been hypothesized that it is mediated by the release of facilitating pheromones by the entrapped ant (Miler, 2016). When they are in distress, ants secrete alarm pheromones through the Dufour and poison glands and these two glands seem to be involved in the observed rescue behaviour (Nowbahari *et al.*, 2012). The alarm signals are colony-specific and their secretion increases with worker age (Nowbahari *et al.*, 2012; Miler, 2016). In addition, the fact that anesthetized ants elicited no help supports the hypothesis that active pheromone release by the victim triggers the rescue behaviour (Miler, 2016). Therefore, ants' helping responses are likely elicited by the detection of alarm pheromones and not by a moderate emotional reaction in response to other's distress or requiring the well-developed cognitive abilities expected for empathic targeted helping. Thus, ants' rescue behaviour does not meet the first requirement. Ants do display a sophisticated form of rescue but it is not based on complex empathic processes, their responses lack the emotional component. The ants' helping behaviour is an adaptive specialization finely tuned to

their precise ecological circumstances: the caste member's probability of becoming or finding, a nestmate in need of help (Nowbahari *et al.*, 2012). Overall, this example shows us that some behaviours that appear cognitively complex can be explained by much simpler mechanisms (Vasconcelos *et al.*, 2012). Simple mechanisms can lead to responses and outcomes very similar to those expected for empathic behaviours but this does not mean that they are the same. Thus, we should be careful when comparing similar behaviours displayed by different species since, although the observable features may be identical, their nature may differ and be derived from very different mechanisms. In attributing empathic motivations to a specific behaviour, we tend to be more permissive for mammals than for other classes such as insects. But, we must attempt to avoid such species biases and consistently apply the same criteria. The use of different criteria, definitions and paradigms in the field of animal empathy may mean that behaviours that rely on different mechanisms but that have similar features are considered to be identical. Returning to the example of ants, it should not be surprising that many social animals display seemingly complex helping behaviours that are not empathy-based. For example, in social species, distress calls could play the same role as alarm pheromones in ants and automatically elicit sophisticated approaching or helping responses in the receivers. These responses will be related to the behavioural ecology of the species and fine-tuned to its specific socio-behavioural traits. For example, the affiliative behaviours observed in voles, budgerigars and Eurasian jays towards distressed group members are consistent with the socio-behavioural features and group structure of these species. Chimpanzees' caring behaviour for wounded individuals also differs depending on the ecological features of their habitat. While Tai chimpanzees care for wounded group members independent of kin relationship, a non-kin member with a wound elicits a reaction of fear or disgust in Gombe chimpanzees. This differential pattern of behaviour may be explained by the high predation pressure that Tai, but not Gombe, chimpanzees experience from leopards (Boesch, 1992). Animals could obtain survival and reproductive benefits by caring or helping group members with whom they are likely to be genetically related (Vasconcelos *et al.*, 2012). Thus, for group-living species, the adaptive value of this affiliative or helping behaviour is evident. If certain selective pressures are present, it is likely that social animals may develop strategies that favour survival not only for the individual but also for the rest of the group. These behaviours could range from simple, automatic and fixed responses not based on empathy, such as perception-action mechanisms involving alarm signals that trigger approach and rescue responses, to flexible behaviours requiring more complex emotional and cognitive processes. With increased emotional and cognitive abilities and a greater level of effective emotional regulation, animals can respond flexibly to distressed individuals in different contexts, even if alarm signals are identical or absent.

It seems, then, that the ability to attend and respond to the emotional state of others was a major evolutionary step for group-living animals. This capacity is an important adaptive strategy in the maintenance of complex social systems allowing animals to predict others' future behaviour (Waller, Whitehouse, & Micheletta, 2016) and to attend to others' needs in changing circumstances. The affective experiences may help to build, strengthen or repair social bonds, also providing a variety of reproductive benefits (Lahvis, 2016). The combination of a capacity to respond to others' emotional states with the ability to carry out a cognitive evaluation of the situation will lead to a more robust and flexible behavioural response to an urgent situation (Lahvis, 2016).





## SECTION II: EMPATHY IN BOTTLENOSE DOLPHINS (*Tursiops truncatus*)

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“Among the sea-fishes many stories are told about the dolphin, indicative of his gentle and kindly nature, and of manifestations of passionate attachment to boys, in and about Tarentum, Caria, and other places”.

— Aristotle





## CHAPTER 4

# EMPATHIC CAPACITIES OF CETACEANS

### 1. Introduction

The divergence between cetaceans and primates occurred about 65 million years ago. Even so, the parallels between these two groups of mammals are striking, suggesting a great degree of convergence in their cognitive and social capacities (Marino, 2002). Primates and cetaceans share complex social organizational patterns, engaging in several forms of social interaction such as cooperative hunting, alliance formation or alloparental care (Siebenaler & Caldwell, 1956; Riedman, 1982; Boesch, 1994, 2002; Marino, 2002; Gazda *et al.*, 2005; Sargeant *et al.*, 2005; van Schaik & Kappeler, 2006; Fernandez-Duque, Vallengia, & Mendoza, 2009; Jaeggi, Burkart, & Van Schaik, 2010; Pitman & Durban, 2012; Connor & Krützen, 2015). They also exhibit an extended period of postnatal development and a long lifespan. This life history pattern entails a strong reliance on learning about the physical and social environment (Marino, 2011). Furthermore, their extended period of postnatal development involves a long period of parental care that might promote affiliative and cooperative behaviours toward juvenile or adult group members (Charvet & Finlay, 2012). Both primates and cetaceans also possess several behavioural traditions, some of which are considered to be acquired and passed through a process of culture transmission (Whiten, 2000; Rendell & Whitehead, 2001; Marino, 2002). In terms of cognition, they are endowed with very sophisticated communicative and learning abilities, exhibiting outstanding cognitive capacities both in the wild and in experimental situations (Marino, 2011). Primates and cetaceans are two of the few orders of animals capable of passing the mirror test (Inoue-Nakamura, 1997; Reiss & Marino, 2001). Passing this test has been generally considered as an indicator of self-recognition, a basic form of self-awareness (Gallup, 1970).

Given these parallels in the social and cognitive domain, cetaceans and primates may be expected to also share complex empathic capacities. In fact, there are many anecdotal reports on possible cases of rescue or helping behaviour in cetaceans (Caldwell & Caldwell, 1966). But, on the other hand, there are only a few empirical studies assessing empathic processes in this suborder of mammals. It has been proposed that social complexity could underlie the evolution of rudimentary forms of morality and altruism and that these phenomena are, in turn, based on empathy (Marino, 2002; Hunter, 2010). Therefore, the study of empathic capacities in species of primates and cetaceans could serve to better understand the evolution of empathy and morality. The study of the similarities between these distant groups of animals could also shed light on the alternative evolutionary pathways to complex social, cognitive and moral capacities. However, most of the studies and reviews on empathy have only focused on primates and rodents. Therefore, a review of the possible cases of empathic behaviour in cetaceans is thus timely to complement primate and rodent models of empathy, to clarify theoretical models, and to integrate current findings.

The aim of this chapter is, therefore, to review the available evidence on empathic capacities in cetaceans and discuss whether the available evidence qualifies such behaviour as empathic. As we did

in previous chapters, first, we carry out an exhaustive review of the literature on basic forms of empathy in cetaceans: emotional contagion and spontaneous synchronization. Second, we also review the available evidence on complex forms of empathy: sympathetic concern and empathic perspective-taking. In particular, we focus on consolation and empathic targeted helping, as the best examples of each category. With this review, we aim to provide an integrative view of the research on empathic capacities of cetaceans, serving as a theoretical framework for future studies on empathy in these animals. In so doing, we pave the way to motivate the empirical studies we have carried out on empathic capacities of bottlenose dolphins, which will be presented in the next chapter.

## 2. Basic forms of empathy in cetaceans

### 2.1. Spontaneous synchronization in cetaceans

Synchronized movement like swimming or breathing, has been described in several species of cetaceans in a great variety of contexts (reviewed in Fellner, Bauer, & Harley, 2006). Synchronous behaviours in cetaceans may play different roles depending on the context. It has been proposed that moving in synchrony might provide a hydrodynamic advantage to synchronized groups over those moving in loose aggregations (Fellner *et al.*, 2006). Synchronized movements could also enable rapid coordinated responses, and offer protection from predators (Fellner *et al.*, 2006; Senigaglia *et al.*, 2012). Synchrony may also be important in social contexts as an indicator of male alliances or coalitions and could have implications within hierarchical relationships (Connor, Smolker, & Bejder, 2006; Fellner *et al.*, 2006). In several species of dolphins, the synchronous surfacing and elaborate synchronous displays performed by male alliances are more common during social behaviour, and likely directed towards females (Connor *et al.*, 2006).

Synchronized behaviours in cetaceans could also have an important role in easing affiliative behaviours and strengthening and advertising social bonds (Connor *et al.*, 2006). In fact, synchronous swimming has been used as a measure of affiliative behaviour and social bonding in dolphins (Holobinko & Waring, 2010). For example, in captivity, affiliative relationships between dolphins have been characterized through synchronized swimming and breathing, physical contact and the frequency and duration of swimming together (Pryor & Shallenberger, 1991). Bottlenose dolphins use to move synchronously while rubbing or caressing each other and during play episodes (Fellner *et al.*, 2013). Finless porpoises (*Neophocaena phocaenoides*) dive synchronously when particular members are reunited, despite that in this species the social structure appears to be undeveloped, being mother-calf pairs the only stable social unit (Sakai *et al.*, 2011). In addition, it has been observed that, during reconciliation episodes following an aggressive conflict, synchronous swimming was one of the most frequently performed behaviour by pairs of bottlenose dolphins (Holobinko & Waring, 2010). These findings suggest that synchronous swimming may also serve to restore relationships between former opponents, constituting a usual post-conflict affiliative behaviour. Furthermore, synchronized swimming has been recently proposed as a reliable indicator of affective states in dolphins (Clegg, Rödel, & Delfour, 2017). Using a cognitive bias test (a measure of the effects of emotional experiences on cognitive functioning), Clegg *et al.* (2017) observed that higher frequencies of synchronous swimming in dolphins were associated with more optimistic-like judgements towards ambiguous cues in a spatial location judgement bias test. These outcomes suggest that synchronous swimming could result in higher social bonding and affiliation that in turn lead to a positive internal affective state and thus to more optimistic judgements (Clegg *et al.*, 2017). Nevertheless, it was not clear whether synchronous swimming induced affective states and/or was induced by them. Finally, a study on the development of synchrony in bottlenose dolphin calves (Fellner *et al.*, 2013) showed that synchronous swimming is an important component of early mother-

calf interactions. Synchronous swimming placed the calf in a good position for physical contact with its mother, facilitating affiliative contacts between the pair. Thus, these early experiences of synchronous swimming could prepare calves to establish social relationships, strengthen bonds and mediating social interactions in adulthood (Fellner *et al.*, 2013). Fellner *et al.* also hypothesized that synchronous swimming could allow calves to perceive what the mother perceives from the same perspective, linking perception to motor action and resulting in a unique shared experience. Then, it is possible that in dolphins, as in humans, synchronous movement represents an important element for shared attention facilitating learning of adaptive behaviours (Fellner *et al.*, 2013).

Overall, synchronous movements may allow cetaceans to be attuned to the affective state of their partners thus pointing toward a functional convergence of synchrony in cetaceans and primates. Synchrony seems to play an important role promoting affiliation and cooperation, signalling alliance membership and social relationships, strengthening bonds between individuals and restoring relationships after agonistic interactions. Therefore, it is tempting to postulate that synchrony could be an adaptive trait that facilitates group living and constitutes a basic form of empathy in social species like cetaceans. More research is needed to assess the relationship between synchronous swimming and affective states. That is, whether swimming in synchrony induces positive emotional states or is induced by them, or whether it is a by-product of moving in an aquatic environment.

## 2.2. Emotional contagion in cetaceans

There is virtually no data regarding emotional contagion in cetaceans. This might be due to methodological problems at the time of interpreting emotional expressions in these animals. The anatomical differences between cetaceans and primates are patent, cetaceans cannot gesture easily and their facial musculature prohibits facial expression altogether (Simmonds, 2006). Changes in body posture and vocalizations are better indicators of emotional state in these mammals but to date, little is known about the features and reliability of these parameters (Kuczaj, 2013). Therefore, it is really difficult for humans to detect emotional states within the members of this mammal order (Simmonds, 2006). Besides, as in the case of primates, protocols involving suffering or distressing situations cannot be applied for ethical reasons. Thus, researchers must rely on behavioural observations and not invasive paradigms. However, many anecdotal reports suggest that cetaceans could be affected by the state of other individuals. For example, it has been observed that in response to dead or sick individuals, dolphins often display circling behaviour (swimming in circles) or swim frantically (Caldwell & Caldwell, 1964; Kuczaj *et al.*, 2015a). These behaviours have been interpreted as signs of distress or excitement in these animals (Caldwell & Caldwell, 1964; Lodi, 1992), suggesting that, indeed, the emotional state of one individual has an effect on the arousal state of another.

Currently, evidence of emotional contagion in cetaceans is practically non-existent. Therefore, this issue deserves further investigation. A way to overcome the main concerns associated to the study of cetaceans' emotional responses towards distressed conspecifics could be to record the reactions of observer individuals while one of the members of the group is being subjected to a scientific or medical procedure. Some of these procedures, such as brief capture-release events of wild dolphins for health assessment or management procedures in marine parks such as blood sampling or transferring animals to other facilities, may represent a source of short-term distress for these animals.

### 3. Complex forms of empathy in cetaceans

#### 3.1. Sympathetic concern in cetaceans

Consolation in cetaceans has not been empirically demonstrated, but third-party affiliation with victims of conflicts has been reported in bottlenose dolphins (Tamaki, Morisaka, & Taki, 2006; Yamamoto *et al.*, 2015). However, its function and main features, as the direction of affiliative contacts, require further research. Outside post-conflict contexts, there are anecdotal instances of cetaceans appearing to comfort distressed individuals. Pace, Miragliuolo & Mussi (2005) provided a systematic report on this type of interaction. They observed a group of five sperm whales (*Physeter macrocephalus*), entrapped in a drift net during a two-day period. All the animals showed clear signs of stress and had numerous lesions on their body, in particular on their tails. Divers managed to free two individuals on the first day. These individuals remained near the trapped whales watching the divers' work, touching the entangled tails and rubbing their sides with the melon. The function of tactile contacts in cetacean species has not been studied in detail but it may have an affiliative role analogous to that of allogrooming in primates (Dudzinski *et al.*, 2009). For example, Herzing (1996) reported that a spotted dolphin calf (*Stenella frontalis*) repeatedly emitted distress calls until another animal calmed him by pectoral rubbing. During post-conflict periods, flipper-rubbing among bottlenose dolphins seemed to ease tension and restore friendly relationships between former opponents (Tamaki *et al.*, 2006). Thus, the rubbing behaviour provided by the free individuals towards the distressed ones may have a comforting effect and be displayed by cetaceans towards distressed individuals. It would be of great interest if more systematic studies assessed comfort behaviour and the possible consolatory effect of rubbing in cetaceans.

#### 3.2. Empathic perspective-taking in cetaceans

Cetaceans are candidates for exhibiting empathic targeted helping not only because they are endowed with complex cognitive abilities (Delfour & Marten, 2001; Xitco, Gory, & Kuczaj, 2001; Reiss & Marino, 2001; Herman, 2002; Pack & Herman, 2006; Marino *et al.*, 2007) but also because they engage in several cooperative activities (Marino *et al.*, 2007; Kuczaj, Winship, & Eskelinen, 2015b). Indeed, descriptions of helping behaviour in cetaceans are common (Siebenaler & Caldwell, 1956; Caldwell & Caldwell, 1966; Connor & Norris, 1982; Kuczaj *et al.*, 2001). Chances to observe these incidents are rare, but fortunately, many researchers systematically report this type of event in relation to rescue and epimeletic behaviour in cetaceans.

Nurturant behaviour has been observed toward both live and dead calves (see Reggente *et al.*, (2016) for a review). The most commonly observed nurturant behaviours in cetaceans are the mother's habit of holding her calf at the surface supposedly to aid it in breathing (Siebenaler & Caldwell, 1956), and lifting a new-born to the surface immediately after birth (Deakos *et al.*, 2010). But cases in which individuals supported sick or injured calves at the surface have also been reported. For instance, a female bottlenose dolphin (presumed mother) assisted an injured juvenile, while three other dolphins placed themselves between the couple and a research vessel in a protective manner. When the juvenile was euthanized the group appeared agitated, showing short dives of irregular direction (Warren-Smith & Dunn, 2006). Joan Gonzalvo and his team observed that dolphins displayed different responses in two situations in which a calf died but the cause of the death was different (Hooper, 2011). In the first case, the calf presented wounds suggesting that it died suddenly and violently. Its mother interacted with the corpse for two days. In the second instance, the calf died after an illness period, some adults supported it till it died but after its death, the corpse sank and neither the mother nor the rest of the group tried to recover it and left the area. These observations

suggest that dolphins' responses towards distressed calves could be context dependent. Interspecific cases of nurturant behaviour have also been observed: two Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) took turns to support a neonatal harbour porpoise (*Phocoena phocoena*) at the surface (Baird, 1998) and a group of Indo-Pacific humpback dolphins (*Sousa chinensis*) were reported to assist a finless porpoise (*Neophocaena phocaenoides sunameri*) calf for more than 3 hours (Wang *et al.*, 2013). The group seemed to adjust to the calf's situation by swimming slowly and showing no signs of aggressive behaviour.

There are many anecdotal reports of succorant and rescue behaviour in cetaceans, in particular of bottlenose dolphins (Siebenaler & Caldwell, 1956; Caldwell & Caldwell, 1966). Even Aristotle provided one of such reports (Aristotle, 1897). He described how a pod of dolphins came into the harbour of Caria after a member of the group had been captured and wounded. The pod remained in the harbour till the fishermen freed the wounded individual and then all escaped together. Reports like the one described by Aristotle are very common in dolphins. For example, one group stayed with an individual injured in an explosion buoying it to the surface to breathe, instead of leaving the area as they did on another occasion in which dynamite exploded but none of them was injured. When the animal was recovered they rapidly left the area. A school of dolphins charged and milled around a vessel where fishermen were trying to release an individual hooked on a fisherman's line until the dolphin was freed. A sick captive dolphin ceased to echolocate and consistently rammed the side of the tank, sometimes causing bleeding. During these occasions, another dolphin put itself between the sick dolphin and the tank wall. It circled the tank with the sick animal until it started swimming normally. When the dolphin's health worsened and it started sinking and listing, the other dolphin intermittently buoyed up it until it died. Two recent and more systematic studies of succorant behaviour in dolphins are the ones by Park *et al.* (2012) and Kuczaj *et al.* (2015a). Park and his team filmed for the first time a group of long-beaked common dolphins (*Delphinus capensis*) apparently trying to help a paralyzed female. The group of dolphins supported it forming a sort of raft, swimming while carrying it on their backs. Kuczaj *et al.* (2015a) described a similar incident in bottlenose dolphins where helping behaviours towards a distressed female included raft formation, lifts, and stimulating pushes. These behaviours seemed to be directed towards bringing the dolphin to the surface to breathe and appeared to stimulate it to move. Sometimes, four or five individuals pushed the distressed dolphin towards the surface together, suggesting possible cooperative behaviour among the helpers. While some of the dolphins supported the distressed individual others stayed nearby swimming slowly or, on several occasions, circling or milling, behaviours that have been interpreted as signals of distress or excitement in cetaceans (Siebenaler & Caldwell, 1956; Cockcroft & Sauer, 1990; Fertl & Schiro, 1994; de Moura, da Silva Rodrigues, & Siciliano, 2009). The distressed dolphin frequently produced what were almost certainly distress calls. The frequency of the whistle production was positively correlated with the frequency of the supporting behaviours of the helper dolphins, suggesting an important role for these calls in eliciting helping behaviours. Lilly (1963) recorded dolphin distress calls containing two whistles repeated until a distressed animal received sufficient aid. He reported that the helper usually assisted the distressed dolphin in an appropriate way and adapted to its specific needs. In general, the first response of an animal after hearing a distress call was to stop vocalizing and searching for the dolphin emitting the call. Then, it pushed the head of the distressed dolphin to the surface and an exchange of whistles between both individuals took place. According to Lilly, after this exchange, the helper usually assisted the distressed dolphin in a more appropriate way and according to its specific needs. For example, a dolphin held a distressed one on the proper side to allow it breathing, and two dolphins took turns to hold a distressed female against a wall or supported her between them to prevent her blowhole from being submerged. Lilly pointed out that the three times that a sick animal was isolated, it was found dead the next morning. Nonetheless, in all but two cases that a healthy dolphin could interact with the sick one, the later

survived highlighting the effectivity of the help provided. By contrast, reports also exist in which individuals did not help a distressed animal, such as a male bottlenose dolphin that, instead of assisting a female emitting distress signals, abandoned her (Connor & Norris, 1982).

Finally, there are also instances of some dolphin species apparently helping others to give birth or removing foreign objects from the body of others as in the case of a captive rough-toothed dolphin (*Steno bredanensis*) that pulled a hypodermic syringe from a pen-mate during medical treatment and then behaved aggressively towards the veterinarian (Connor & Norris, 1982).

In regard to baleen whales, Fertl and Fulling, (2007) reported a curious case of interspecific succorant behaviour by a humpback whale (*Megaptera novaeangliae*) directed towards a sea turtle (unidentified species). The whale used its fore flippers to try to turn over the turtle that appeared to have buoyancy problems and finally managed to flip it. It has been reported that humpback whales may also engage in a type of interspecific rescue behaviour (Pitman *et al.*, 2016). These whales have been observed to harass attacking killer whales even if their prey was from another species (other whales, pinnipeds or teleost fish). Their mobbing response sometimes differed depending on the prey species. If the prey was a humpback whale, the approaching humpbacks always acted aggressively towards the killer whales, driving them off on some occasions. But if the prey was not a humpback, the whales showed a range of responses: moving away, staying nearby, or aggressively confronting the orcas. Pitman *et al.* (2016) suggested that humpbacks may respond to acoustic cues of attacking mammal-eating orcas. Sometimes, the prey could escape thanks to this harassing response. However, there was no apparent benefit for the humpbacks, rather the contrary: they were often attacked by orcas during these interactions, sometimes they travelled long distances to interfere with the attack and, on some occasions, they spent a huge amount of time harassing the orcas. There is also a report of a humpback whale harassing short-finned pilot whales (*Globicephala macrorhynchus*), when a pod were attacking a pair of grey whales (*Eschrichtius robustus*) (Pitman *et al.*, 2016), suggesting that such harassing is not only restricted to killer whales.

All three requirements defined for targeted helping in **Table 1** thus seem to be present in some of the reports described above. Regarding the first component, it is important to note that there are virtually no data on emotional responses or emotional contagion in cetaceans. However, some surfacing behaviours, and bubble and swimming patterns like circling or milling seem to signal stress or excitement in these animals and these behaviours were observed in some of the reports cited above. Kuczaj *et al.* (2015a), for example, reported that several dolphins stayed near a distressed female, taking turns to assist it, swimming slowly and, on several occasions, circling or milling. These responses suggest that, while the observers did not seem to be over-aroused due to emotional contagion, they did show some signs of stress pointing to an emotional reaction in response to the distressed party. Nonetheless, solid evidence is needed to conclude that such behaviours are an indication of a moderate emotional reaction rather than signs of personal distress.

Several hypotheses have been proposed to explain the cetacean behaviour of pushing or holding dead or alive conspecifics: displaced nurturant behaviour (Deakos *et al.*, 2010), curiosity towards novel objects (Siebenaler & Caldwell, 1956), surrogate behaviour in response to perinatal mortality (Smith & Sleno, 1986). All of these hypotheses assume that this behaviour is an automatic response triggered by a specific stimulus such as a calf's death or the perception of an immobile or floating object. However, an automatic response is not always elicited by the presence of a corpse or an object (Caldwell & Caldwell, 1964). A more complex interpretation of this pushing behaviour is that it depends on an appreciation or understanding of the circumstances of the distressed individual, differing depending on context. This is the second requirement for a behaviour to be considered as true targeted helping. In most reports of potential cases of rescue and epimeletic behaviour, animals

seem to behave flexibly and according to the specific situation (lifting an injured companion in the correct manner to allow it to breath, preventing a sick individual from injury from ramming against the side of the tank, interposing themselves between an individual and a threat, acting together to form a raft to carry a paralyzed individual, etc.). Moreover, such supporting behaviour was directed towards individuals requiring different types of assistance or even towards distressed individuals from other species. Sometimes the helper took risks in doing so and in several cases the entire group became involved, apparently adjusting their behaviour to the circumstances of the distressed individual. These features could indicate that cetaceans are aware of the needs of the distressed individual, and act to alleviate its suffering if they can (Ritter, 2007). The assisting behaviour usually ceased when the individual recovered or died, indicating that the response was restricted to the circumstances in which the individual needed help, meeting the third criterion for targeted helping. Recent studies have highlighted the potential of signature whistle rate and loop number as indicators of stress in bottlenose dolphins (Esch *et al.*, 2009) and, as suggested by Lilly (1963) and Kuczaj *et al.* (2015a), such calls may give rise to helping behaviour. Although distress calls are likely to play an important role in rescue and epimeletic behaviour in cetaceans, they do not alone explain the observed behavioural flexibility of the responses and why these behaviours are sometimes directed towards other species or towards corpses that do not emit distress calls. In fact, it has been reported that captive dolphins are more likely to respond to the distress calls of some conspecifics than others (Sayigh *et al.*, 1999; Kuczaj *et al.*, 2001; Janik & Sayigh, 2013). For example, a group of captive dolphins that in previous occasions provided assistance to other animals, ignored the distress calls of a sick dolphin that finally died (Kuczaj *et al.*, 2001). Further studies should include auditory recordings to clarify the role and spectrum of distress calls in cetacean species. Finally, some of these reports detail cases in which individuals appeared to risk their lives to help another animal. Apparently, these behaviours did not provide immediate benefits to the rescuers, on the contrary, the helping responses implied high costs to the helpers. The problem here is to determine whether these rescue responses were triggered by the perception of distress in others, in turn eliciting a moderate emotional response in the bystanders that elicited their helping. In the case of rescuer humpback whales, for instance, we do not have data on any emotional nature of their reaction and thus, we cannot yet define these as empathic targeted-helping.



## CHAPTER 5

### EMPIRICAL STUDIES ON BOTTLENOSE DOLPHINS

In the next sections, we report a series of experimental studies assessing different varieties of empathy and related cognitive capacities in a group of captive bottlenose dolphins. Following the theoretical framework developed in the preceding chapters, we carried out five studies on basic and complex forms of empathy in bottlenose dolphins:

- ❖ The first study examines the emotional responses of bottlenose dolphins towards a conspecific in distress. This study is a preliminary attempt to establish a paradigm that overcomes some of the main problems associated with the assessment of emotional responses in cetaceans. With this aim in mind, we took advantage of the transfer of one dolphin in the marine zoo “Marineland” to record the behaviours of observer dolphins during the period in which their partner was isolated and confined in a small tank before the transfer. This observational study thus serves to assess the compliance of two of the three requirements defined in Chapter 3 for a behaviour to be considered as an example of sympathetic concern or empathic targeted helping. That is, the display of (1) a moderate emotional reaction in response to another’s distress, and (2) other-oriented responses including attempts to ameliorate the other’s state. The assessment of the third requirement, alleviation and improvement of the situation of the distressed party, is beyond the reach of this approach.
- ❖ The second study focuses on consolation behaviour, considered to be the main example of sympathetic concern. Most evidence on consolation in primates and birds come from studies of unsolicited post-conflict affiliative interactions between bystanders and victims of aggression. Thus, we conducted an observational study of the post-conflict affiliative patterns of a group of captive bottlenose dolphins. Since current evidence of unsolicited bystander affiliation in bottlenose dolphins is scarce and inconclusive, this study aimed to confirm the occurrence of such behaviour in dolphins and to examine its function and main features. With this paradigm, we can assess the compliance of the second and the third criteria of sympathetic concern as defined in Chapter 3. That is the presence of (2) other-oriented responses such as approach responses and attempts to comfort the distressed party, and (3) the alleviation of the distressed individual. The assessment of the first requirement, a moderate emotional reaction in response to another’s distress, is beyond the reach of this observational paradigm.
- ❖ In the third and fourth studies, we investigated whether bottlenose dolphins are able to pass tasks requiring well-developed cognitive capacities such as Theory of mind (ToM) and secondary representation. These capacities are usually viewed as pre-conditions for higher forms of empathy such as empathic perspective-taking. Given that the attribution of false beliefs to another individual is considered to be one of the main indicators of ToM, we tested dolphins in a false belief task. The fourth was a follow-up study to further investigate the reasons for their failure to pass this task. In particular, given that the classical false belief task involves the displacement of an object, we tested the ability of dolphins to track invisible displacements.
- ❖ The fifth study further explored empathic perspective taking in dolphins from another standpoint. It examined whether bottlenose dolphins behave prosocially in a minimal-cost

instrumental helping task. Instrumental helping is a behaviour performed by an individual that enables another to reach a goal that cannot be achieved otherwise and, as empathic targeted helping, it requires a cognitive evaluation of another's situation and the elicitation of other-regarding preferences (prosocial motivation). Therefore, instrumental helping paradigms are a good option to examine some of the factors and situations that favour empathic targeted helping responses in dolphins without eliciting distress in the experimental subjects, and requiring more elemental forms of perspective taking.

## 1. Study 1: Dolphins' emotional and "other-oriented" responses towards a distressed conspecific.

### 1.1. Introduction

It is a well-known fact that animals emotionally respond to the perceived distress of conspecifics (Darwin, 1897; Preston & de Waal, 2002; de Waal, 2008). One of the most common affective reactions towards others in distress is emotional contagion, which takes place when one individual is affected by another's emotional or arousal state (de Waal, 2008). This phenomenon involves several interrelated components as neurophysiological activity, facial and postural expressions and behavioural responses (Hatfield *et al.*, 1994). Interestingly, these emotional responses are considered to be basic forms of empathic behaviours (Preston & de Waal, 2002). From this point of view, the primary emotional response towards another's distress, may be down-regulated and modulated by several factors to give rise to more complex forms of empathy. In this manner, when emotional contagion is subjected to some degree of emotional regulation and combined with a simple cognitive appraisal of the other's situation we talk about sympathetic concern (de Waal, 2008). Sympathetic concern is thus defined as a moderated emotional reaction elicited by the perception of another's distress, which gives rise to a prosocial response that usually alleviates the other's distress and maybe the mild distress vicariously felt by the observer (Pérez-Manrique & Gomila, 2017) (see **Table 1**). It is expected that individuals who share a close relationship (kin or friends) with the distressed party experience a stronger emotional reaction since they are more likely to be responsive to the other's needs (Preston & de Waal, 2002; Fraser & Bugnyar, 2010). Therefore, familiarity with the distressed party is expected to be a strong modulator of observers' emotional responses (Preston & de Waal, 2002).

Despite recent advances in the study of emotional processes in animals, there are only a reduced number of works assessing the emotional responses of certain species towards distressed conspecifics. Among other reasons, the scarcity of studies may be due to ethical and methodological problems. It is unethical to create situations in which animals such as cetaceans experience intense emotions (e.g. distress, fear or pain) to test their conspecific's responses. Thus, in order to assess these types of interactions, we must rely mostly on behavioural observations and anecdotal reports. However, chances to observe these incidents are rare, and evidence coming from this type of reports has been called into question for several reasons (see **Chapter 1**).

If the study of animal emotion is fraught with difficulties, research on the emotional processes in cetaceans is an even thornier issue. There are several methodological problems when interpreting emotional expressions in cetaceans. First, the anatomical differences between cetaceans and primates are obvious. As previously pointed out, their facial musculature does not allow them to display overt facial expressions so that it is difficult for humans to detect emotional reactions on the basis on these expressions (Simmonds, 2006). For this reason, it has been proposed that changes in body posture, surfacing or aerial behaviours, bubble and swimming patterns and vocalizations could be better emotional markers in these mammals (Kuczaj *et al.*, 2012; Frohoff, 2004; Waples and Gales, 2002). But there are few studies assessing the specific context in which dolphins perform these non-vocal behaviours (Lusseau, 2006). Swimming patterns like circling, milling or swimming frantically have been interpreted by some researchers as signals of distress or excitement (Cockcroft and Sauer, 1990; de Moura *et al.*, 2009; Dezecache *et al.*, 2013; Fertl and Schiro, 1994; Siebenaler and Caldwell, 1956, Kuczaj *et al.*, 2015a; Lodi, 1992). For example, these behaviours have been observed in bottlenose dolphins in response to dead or sick individuals (Caldwell & Caldwell, 1964; Kuczaj *et al.*, 2015a). When surprised, curious or excited, dolphins also emit bubble bursts (McCowan *et al.*, 2000).

Captive and wild spotted dolphins (*Stenella spp*), under known circumstances of stress, have been observed to display behaviours like headslaps, tailslaps, breaching, rapid swimming, porpoising, chuffing and bunching (**Table 3**). Furthermore, spotted dolphins positioned themselves as far from the distressing stimulus as was possible. These behaviours were interpreted as signs of agitation, stress, fear or frustration (Pryor & Shallenberger, 1991; Curry, 1999; Oliveros & Maldonado, 2002). In Hector's dolphins (*Cephalorhynchus hectori*), aerial behaviours (e.g. leaps), tailslaps and bubble blowing were associated with a high level of motivation and displayed in different contexts like aggression, sexual behaviour or excitement (Slooten, 1994). Percussive behaviours, surface behaviours that produce sound by slapping a body part on the water surface, might be also a form of non-vocal communication among dolphins advertising a motivational and/or an intentional state when, for example, vision is useless (Norris & Dohl, 1980; Herzing, 2000; Lusseau, 2006).

**Table 3.** Descriptions of stress-related behaviours in dolphins.

Behaviour	Description
<b>Headslaps</b>	The animal emerges in the normal position at about 30°- 45° angle to the water surface, and then flexes its head sharply downward, slapping its chin and lower beak against the water. After Norris & Dohl, (1980).
<b>Tailslap</b>	Tail arched at the surface bringing the flukes above the surface. The flukes are brought down smartly against the water producing a clearly audible sound. After Norris & Dohl, (1980).
<b>Leap</b>	Jump entirely out of the water. After Samuels & Spradlin, (1995).
<b>Bubble burst</b>	Dolphin produces a cloud of bubbles through blowhole similar to the release of air from scuba equipment. After Kuczaj <i>et al.</i> , (2015a).
<b>Bunching</b>	Animals travelling rapidly grouped tightly together and breathing in sharp puffs. After Pryor & Shallenberger, (1991).
<b>Porpoising</b>	Rolling or leaping across the surface. After Pryor & Shallenberger, (1991).
<b>Chuffing</b>	Loud exhalation. After Pryor & Shallenberger, (1991).
<b>Breaching</b>	Jump, the dolphin usually comes out of water obliquely and returns back to water on its side. Very often, only half or two-thirds of the body length is out of the water. After Pryor & Shallenberger, (1991).
<b>Milling</b>	Diving up and down in a concentric area. After Santurtún & Galindo, (2002).
<b>Circling</b>	Swimming in circles. After Caldwell & Caldwell, (1964).

Some of the previous behaviours are displayed in different situations, are ambiguous or could be part of a multimodal sequence of behaviour, thus caution should be used when interpreting these behaviours as expressive of emotional states (Lusseau, 2006; Kuczaj, 2013). Therefore, it is of great importance to identify non-vocal behaviours that are consistently displayed in different contexts but with the same affective valence (Paul *et al.*, 2005a; Kuczaj, 2013). It is also crucial to reliably know

the stimuli or situations which trigger the behaviours to better understand the link between the observed behaviours and the emotion they may express.

Even though there is little data on emotional responses towards others' distress or emotional contagion processes in cetaceans, many anecdotal reports suggest that these animals could be affected by the emotional state of others (see **Chapter 4, section 2**). For instance, Kuczaj *et al.* (2015a) described the reactions of a group of dolphins towards a distressed conspecific. While some of the individuals were supporting the distressed dolphin, others stayed nearby circling or milling. These behaviours could be interpreted as cases of epimeletic behaviour and emotional contagion respectively. Similar anecdotal reports of helping and epimeletic behaviours in dolphins are common. Many reports have described situations in which dolphins and whales helped or protected companions or members of another species, instead of fleeing from the threat, or supported injured or sick calves at the surface to aid them in breathing (see **Chapter 4, section 3**). Bottlenose dolphins have been reported to emit distress calls in stressful situations (Lilly, 1963; Kuczaj *et al.*, 2015a). These calls seem to elicit helping behaviours in other individuals and, in fact, distressed dolphins usually repeat the distress calls until they receive sufficient aid (Lilly, 1963). Signature whistles, individually distinct stereotyped whistles (Caldwell & Caldwell, 1970), might function as both contact calls to maintain group cohesion (Janik & Slater, 1998), and distress calls to elicit a helping response and more urgent approach by others (Kuczaj *et al.*, 2015a). Thus, the rate and loop number of signature whistles could be a potential indicator of stress in bottlenose dolphins (Esch *et al.*, 2009; Janik, 2009; Kuczaj *et al.*, 2015a).

Spending time in close proximity to a distressed individual is considered to be an affiliative response that could have a distress-alleviating function (Kikusui *et al.*, 2006; Simpson *et al.*, 2014). This phenomenon is known as “social buffering” and has been found in several species of mammals and birds (Kikusui *et al.*, 2006). For many social species, the presence of a valuable social partner can mitigate the behavioural and physiological responses to distressful stimuli (Rukstalis & French, 2005), and helps animals to recover from stressful experiences (Kikusui *et al.*, 2006). Cues from different sensory modalities promote social buffering, and these cues vary among animal species (Kikusui *et al.*, 2006). In species such as dolphins for which vocal communication is essential to transmit social information, vocal cues could lead to social buffering. This phenomenon, termed as “vocal buffering”, has been observed in pairs of familiar Wied's black-tufted-ear marmosets (*Callithrix kuhlii*) (Rukstalis & French, 2005). In isolated marmosets, the exposition to their pair mate's signature vocalization but not to that of an unfamiliar individual decreased the magnitude of the physiological stress response (Rukstalis & French, 2005). As marmosets, bottlenose dolphins also have signature vocalizations for individual identification (signature whistles), and they have been reported to respond preferentially to these whistles when emitted by certain individuals (Sayigh *et al.*, 1999). Thus, in cetaceans, close proximity and the emission of these vocalizations could have a social buffering effect in stressed conspecifics.

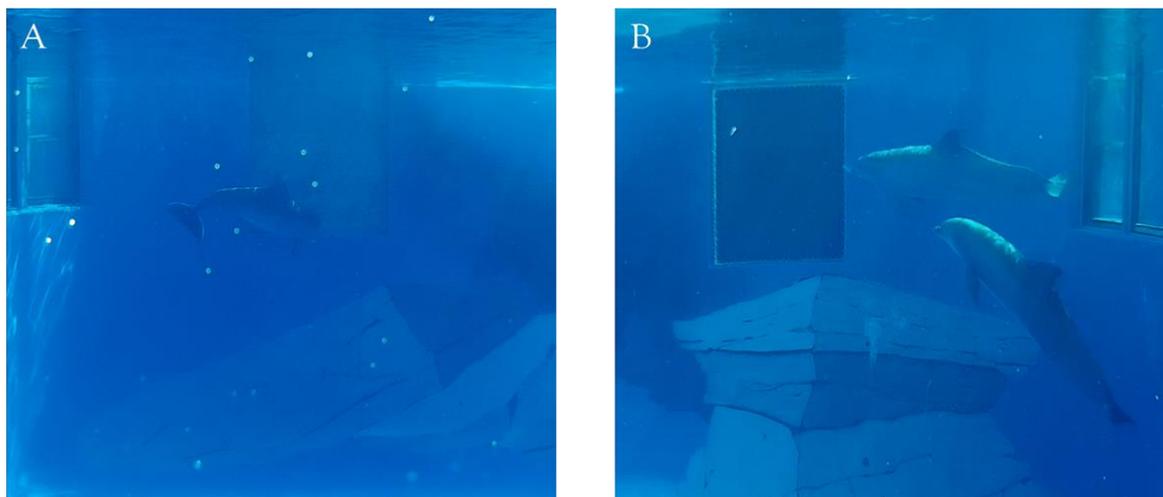
Due to the lack of data on emotional responding in cetaceans, it would be of great interest to carry out more empirical studies to expand our knowledge on this subject. A way to overcome these difficulties and assess emotional responses in captive cetaceans could be to take advantage of certain management procedures in zoos such as the transfer of animals between pools. Capturing, restraining, and removing dolphins from water are actions that may take place occasionally in marine zoos, and they are a potential source of short-term stress for these animals (Thomson & Geraci, 1986; Ortiz & Worthy, 2000; Waples & Gales, 2002; Esch *et al.*, 2009). Therefore, reporting the behavioural reactions of observer animals during these episodes offers the chance to identify useful emotional indicators (e.g. aerial or percussive behaviours, bubble patterns) and empathic-like

behaviours in cetaceans. Therefore, in this study, we observed the behavioural responses of three captive bottlenose dolphins during the confinement and transfer of two of their partners. In particular, we focussed on two dependent variables: bystanders' behaviours that may express distress, and bystanders' behaviours that may indicate help or comfort attempts, including the time spent near the distressed individual. The main objectives of the study were: (1) to carry out an initial attempt to assess emotional responses in dolphins avoiding the main problems related to the study of emotions in this species; (2) to elaborate an ethogram of the most common behaviours displayed by observers while their partner experienced a stressful event; (3) to consider whether dolphin's emotional reactions to other group members in distress are modulated by the degree of affiliation between the individuals involved; (4) to examine whether these responses were dependent on the presence of a distressed conspecific and the level of partner's distress rather than a general stress response to non-social aspects of the procedure; and (5) to assess the influence of the quality of the relationship with the distressed individual on observers' help and comfort attempts.

## 1.2. Method

### *Subjects and facility*

We observed three captive Atlantic bottlenose dolphins, two adult males (*Mateo* and *Blue*), and one adult female (*Estel*), at Marineland Mallorca. The dolphins were captive born and were kept in a display pool constituted by three outdoor interconnecting tanks: a main display tank (1.6 million litres of water, 324.43 m<sup>2</sup> surface area, 5 m deep), a medical tank (37.8 thousand litres of water, 18.91 m<sup>2</sup> surface area, 2 m deep) and a small tank (636.8 thousand litres of water, 127.37 m<sup>2</sup> surface area, 5 m deep). These interconnected pools could be divided by canvas or wooden sliding gates (see **Figure 3**). Canvas gates are often used in the park during daily training routines or during the show to separate the dolphins in different groups. For this reason, this group of dolphins are familiar with them. On the other hand, the wooden gates are only used during procedures that require the emptying of the medical tank, such as medical procedures or transfers. Thus, this type of gate is associated with the occurrence of stressful events.



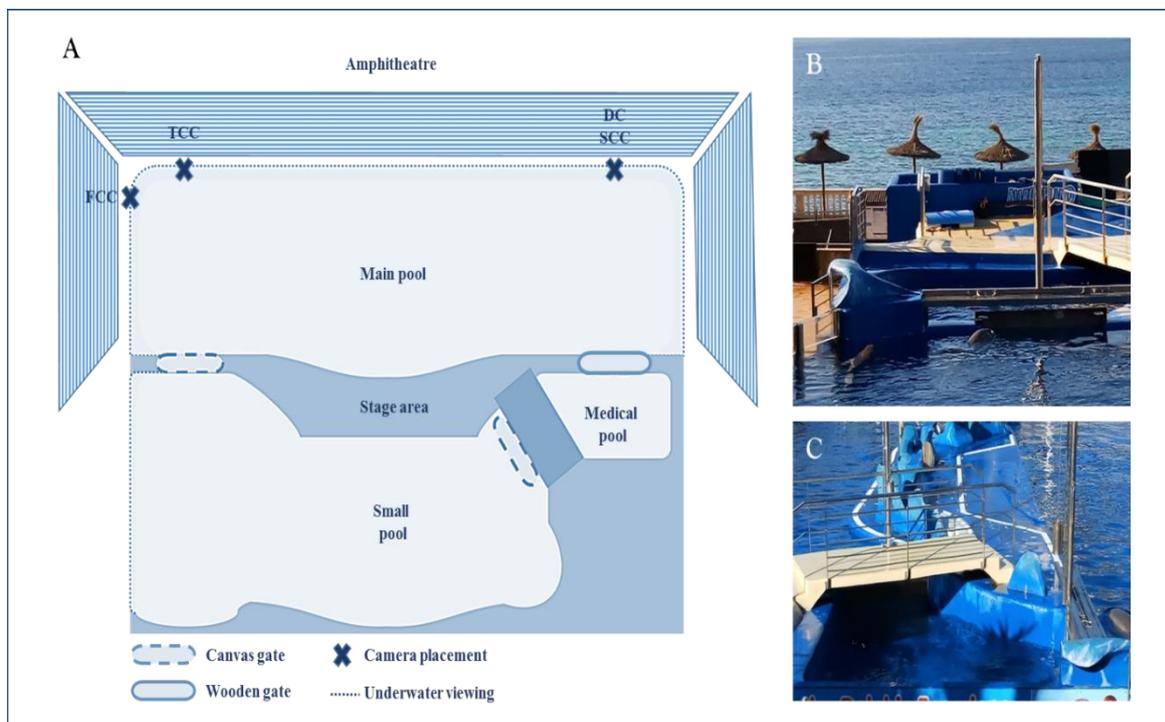
**Figure 3.** Underwater view of the wooden (A) and the canvas gate (B).

During the transfer procedure, a pregnant female (*Sacha*) was confined in the medical tank while the other three dolphins remained in the main tank. This female was later moved to a second facility (1.85 million litres of water) also located in the park. In addition, an adult female (*Blava*) was

transferred from this facility to the small tank. This dolphin had been housed in this pool before and moved to the other facility in mid-2014 (see **Table 4** for subjects age, sex and location during the transfer period). Underwater viewing at the main and the small pool was possible through the transparent walls around the rim of the pools (see **Figure 4** for the facility).

**Table 4.** Age, sex and location of the subjects during the transfer procedure. **M:** male; **F:** female.

Subject	Sex	Age (years)	Pool
Blue	M	24	Main pool
Mateo	M	12	Main pool
Estel	F	12	Main pool
Sacha	F	11	Medical pool
Blava	F	12	Small pool



**Figure 4. A:** The display pool and disposition of the gates and cameras during the observation periods; **B:** front view of the wooden gate separating the medical tank from the display pool; **C:** the medical tank. (DC: distress condition; FCC: first control condition; SCC: second control condition; and TCC: third control condition).

*Transfer procedure*

On April 27, 2016, the pregnant female *Sacha* was moved to an outdoor pool closed to the public. It was expected that, in this facility, the pregnant female would be less exposed to potential stressors. In addition, the adult female *Blava* housed in this facility was transferred back to the display pool. The display pool was divided into three areas as follows: the main pool was separated from the medical tank by a wooden gate and from the small tank by a canvas gate. In turn, the medical tank was separated from the small one by a wooden gate (see **Figure 4**). Until the transfer took place, both

dolphins were separated from the rest of the group and confined to the medical tanks. During this period, one of the trainers remained with the isolated dolphins to provide for their well-being. Then, approximately half an hour before the transfer, the emptying of the medical tank began. After the total emptying of the tank, dolphins were lifted out of the tank with a crane, placed on a stretcher and moved to the other facility. *Blava* was transferred first and released in the small tank of the display pool. Then, *Sacha* was lifted and moved to the other facility (see **Table 5** for the timeline of events). Handling was carried out in a careful way by the dolphin trainers avoiding unnecessary discomfort and stress and was supervised by the Technical Director of the Marineland marine mammals' unit.

**Table 5.** Timeline of events during the transfer procedure on April 27, 2016.

Time	Events
17:15	Emptying of the medical tank begins
17:19	Recording of the “distress condition” starts
17:28	End of the “distress condition”
17:30	A trainer arrives at the medical tank
17:46	Trainers arrive carrying <i>Blava</i> on a stretcher
17:48	<i>Blava</i> is released in the small pool
18:01	<i>Sacha</i> is lifted out of the water by a crane
18:04	<i>Sacha</i> is moved to the other pool on a stretcher
18:11	Recording of the “first control condition” begins
18:20	End of the “first control condition”

### *Behavioural study*

This study tries to shed light on dolphins' responses towards a distressed conspecific. With this aim, we registered the behavioural reactions of three captive dolphins kept in the main pool after their partner was isolated and confined in an adjacent medical tank before being moved to another facility (“distress condition”). In particular, we were interested in behaviour that may be expressive of stress and an effort to help. We also measured the amount of time dolphins spent near the gate behind which the distressed partner was held, since it could be an indicator of affiliative or comfort responses towards the partner in distress. In order to distinguish between the responses triggered by the perception of another's distress from the stress responses elicited by other features of the procedure, we also registered dolphins' behavioural responses and the time spent near the gates in

three control conditions. Therefore, we registered observers' behavioural responses in four different conditions as follows:

- 1) In the distress condition (DC), we recorded the dolphins' responses to one isolated female (*Sacha*) during the last period of the emptying of the medical tank in which she was confined. During this period, *Sacha* was held in the small tank with shallow water. Given that procedures such as isolating, restraining, and removing dolphins from water has been shown to be sources of short-term stress for these animals (Thomson & Geraci, 1986; Ortiz & Worthy, 2000; Waples & Gales, 2002; Esch *et al.*, 2009), it is likely that this female experienced distress during this period. Given that *Sacha* was separated from the rest of the group by a wooden gate that limited visual and physical contact but allowed to some extent acoustical contact between individuals, the other three dolphins could perceive the possible distress vocalizations and percussive behaviours produced by her.
- 2) In the first control condition (FCC) we registered the reactions of the same three dolphins towards a mildly distressed female (*Blava*). This adult female was moved from another facility to the small tank of the display pool. Although *Blava* had also been subjected to a stressful period of confinement and transport, the recordings in this condition started sometime after *Blava*'s release (see **Table 5**), to make sure that her stress levels would have decreased by the time the record was made. Furthermore, the fact that she was placed in a relatively large pool in which her movements were not restricted and she was familiar with the enclosure and the social group, also contributed to assuring that her stress levels were lower than those of *Sacha*. The small tank was separated from the main tank by a canvas gate that also limited visual and physical contact but allowed acoustical communication between dolphins located on opposite sides of the gate, as in the previous condition. This control condition thus serves to assess whether the bystanders' responses are contingent on the level of stress of the enclosed individual, or are rather a generic response to the presence of another individual behind the gates.
- 3) In the second and third control conditions (SCC and TCC), the three dolphins that were bystanders in the two previous conditions were kept in the main tank together with *Blava*. This tank was separated from the other two by the same gates used in the previous conditions (a wooden and a canvas gate), but this time there was no dolphin at the other side of the gates. In the SCC, we recorded dolphins' behaviours and the amount of time spent in the vicinity of the wooden gate, and in the TCC we measured the same parameters for the canvas gate. These control conditions serve to distinguish between dolphins' responses triggered by the perception of a partner in distress from responses elicited by non-social features of the procedure such as restricted access to the other pools, or the presence of an aversive stimulus like the wooden gate. *Blava*'s behaviour was not included in the statistical analysis.

We made the following predictions:

- 1) If dolphins are affected by the perception of a conspecific in distress, bystanders are likely to display stress-related behaviours in the DC. The stress level of the distressed party could influence bystanders' responses (emotional contagion) and thus they are expected to respond more strongly in situations in which their partner displays an elevated level of distress. In the DC and in the FCC a considerable amount of time elapsed since the closing of the gates until the start of the video-recordings. Therefore, one of the main differences between these two conditions that could have affected bystanders' arousal state, was the different stress level of the confined dolphins. Thus, in the DC bystanders are likely to display more stress-related responses than in the FCC, that is when the other dolphin is expected to be more distressed. On the other

hand, in the SCC and TCC, the video-recordings started soon after the closing of the gates and there were no dolphins behind the gates. Since the wooden gates are only used in the park in stressful situations like transfers or medical procedures that require the emptying of the medical tank, it is reasonable that the sight of these gates triggers stress and fear reactions in this group of dolphins. Therefore, if the wooden gate is indeed perceived as aversive by the dolphins, it is expected that, in these two control conditions, dolphins display a great number of stress or fear responses. Furthermore, given that in the SCC we recorded the dolphins' responses that occurred near the wooden gate, we expect to observe more stress-related behaviours in the SCC than in the TCC.

- 2) If dolphins' reactions towards the emotional displays of another individual also involve an other-oriented response (empathic-like response), bystanders are expected to remain near the distressed party, and perhaps engage in attempts to help or comfort her (see **Chapter 3**). Therefore, bystanders are likely to spend more time near the gate and perform more "other-oriented" responses in the DC than in the rest of conditions. Familiarity, affiliation or social closeness with the other individual seems to amplify emotional and empathic responses. Thus, bystanders sharing a valuable relationship with the distressed dolphin are expected to show more prosocial responses (e.g. more time in the vicinity of the distressed individual or help and comfort attempts) than non-valuable partners, since these individuals are more likely to be responsive to each other's distress.
- 3) If dolphins' behavioural responses are triggered by other social factors such as the simple presence of another individual behind a gate, bystanders are likely to display similar behavioural responses in both the DC and the FCC, irrespective of the stress level of the partner. On the other hand, if dolphins' behavioural responses are elicited by non-social factors such as restricted access to other sides of the pool, bystanders' behavioural responses should not differ between the four conditions. Finally, if dolphins' other-oriented responses are rather behavioural reactions specifically directed towards a specific type of gate, dolphins' reactions directed at the wooden gates should differ from those directed at the canvas gates, regardless of the presence of a distressed conspecific.

#### *Data collection and behavioural observations*

On April 27, 2016, during the transfer procedure, two underwater videos of the main pool were recorded between 17:19 pm and 18:46 pm. Approximately at the same time on May 25, 2016, another two underwater videos were recorded during a training session in which dolphins were subjected to circumstances similar to those of the transfer procedure, but in this case, no transfer took place. During this session, the main pool was also separated from the other tanks by a wooden and a canvas gate, just as during the transfer procedure, but all dolphins remained in the main pool. This training session aimed to familiarize the dolphins with the presence of the wooden gate and thus diminish their stress responses in future transfers or similar procedures involving this gate.

All behavioural observations were recorded by the same person (APM) from underwater viewing windows of the main pool using waterproof cameras SJCAM SJ4000. During the transfer procedure on April 27, only one camera was available. This camera was placed in front of the wooden gate in the DC, and focusing the canvas gate in the FCC. During the training session on May 25, two cameras were available, and each camera was placed in front of one of the two gates (see **Figure 4**). Video recordings only covered the vicinity of one of the gates, that is approximately one-third of the entire area of the enclosure. Additional data on the transfer procedure and the training session was registered in situ by APM.

Overall, a total of four videos were recorded: one video of the events occurring near the wooden gate during the emptying of the medical tank where *Sacha* was isolated (DC); one video of the events taking place in the vicinity of the canvas gate after *Sacha* was transferred to the other pool and while *Blava* was in the small tank (FCC); and two videos of the events occurring near the wooden or the canvas gate during the training session (SCC and TCC respectively). It was intended that the videos of the four conditions had the same length, were recorded under similar circumstances, and avoiding potential distractors such as the presence of trainers or other workers in the vicinity of the pools. Therefore, of the total video length recorded prior to *Sacha*'s transfer, only 9 minutes 42 seconds were used for the DC. During this specific period, *Sacha* remained alone in the medical tank, there were no trainers nearby and *Blava* had not yet been released in the small pool. Video-recording of the FCC started 23 minutes after *Blava*'s release in the small pool, 10 minutes after *Sacha* was lifted out of the water and 6 minutes after people left the area (see **Table 5** for a timeline of events). During the recording of the SCC and TCC, no trainers were present and the video-recordings started 1 minute after the closing of the two gates to avoid registering confounding behaviours triggered by the presence of the trainers or elicited by the sound of the closing gates.

Video data were coded for all dolphins' behaviours directed at the gates using an all occurrence sampling method (Altmann, 1974). We registered the identity of the dolphin and the type of behaviour performed. We tried to identify possible cases of "other-oriented" behaviours. "Other-oriented" behaviours were defined by the occurrence of investigative behaviours or attempts to help or comfort the distressed party: spending time in the area in which the distressed dolphin was confined (e.g. near the gate), attempting to open the gate (e.g. ramming or pushing the gate) or to make visual contact with the distressed individual. To calculate the total amount of time that each individual spent in the vicinity of a gate, all videos were analysed using "Kinovea" free software (<http://www.kinovea.org>). This program allowed us to draw a grid on the gates and delimit the study area. In this manner, we ensured that the study area was the same in all conditions. We only included in the analysis those periods of time in which a dolphin remained facing the gate for more than five seconds. Each period started when the dolphin's snout entered the grid and ended when it came out. To register the occurrence of stress-related behaviours, we also ensured that the study area was the same in all conditions.

*Index of affiliation relationships:* To examine the effect of valuable relationships on dolphins' responses toward a distressed individual confined on the other side of the gate, we calculated the index of affiliation relationships between the four dolphins (three bystanders and *Sacha*) following the procedure described in Yamamoto *et al.* (2016). Synchronous swimming is considered to be a reliable indicator for higher affiliation and social bonding in dolphins groups (Connor, Smolker, & Bejder, 2006; Holobinko & Waring, 2010; Sakai *et al.*, 2010; Clegg, Rödel, & Delfour, 2017). Thus, relative frequencies of synchronous swimming were recorded for calculating the index of affiliation relationships in this group of dolphins. Data of synchronous swimming between dolphins were recorded using group 0-1 sampling (Altmann, 1974) at 3-minute intervals. Data were collected months before the transfer procedure. Observations were conducted by the same person (APM) and occurred for approximately 70 min between 8:00 and 11:00 from March 2015 to June 2015. For calculating the index of affiliation relationships for each pair, the number of 1-0 sampling periods in which synchronous swimming between individuals A and B occurred ( $X_{AB}$ ) was divided by the number of 1-0 sampling periods in which the individuals A and B were observed ( $Y_{AB}$ ) (Whitehead & James, 2015; Yamamoto *et al.*, 2016). To categorize the affiliative level for each dyad, we calculated the quartile points of the affiliation indexes. Dyads whose affiliation index was higher than the second quartile score were considered "high affiliated", and those whose affiliation score was less than the

second quartile as “low affiliated” (Kutsukake & Castles, 2004). Synchronous swimming data was collected using both direct observation and video-recordings.

### *Data analysis*

Statistical analysis of behavioural data was limited by the small sample size. Furthermore, given that video-recordings only covered one-third of the entire area of the enclosure, we were unable to record all occurrences of stress-related behaviours. Nevertheless, for each condition, records of the main behavioural events (stress-related behaviours and “other-oriented” behaviours) were obtained from the video-recordings. This data was used descriptively to express the total number and the percentage of times where the behaviour was seen performed by one or more dolphins in each condition.

We tested our predictions on the amount of time dolphins spent near the gates in each condition using a series of Linear mixed models (LMMs). When data were not normally distributed, transformations were performed to approximate them to a normal distribution. The transformation applied prior to analysis was square root transformation for the variable “amount of time spent facing the gate”. Appropriateness of this transformation was then confirmed by graphical assessment and Shapiro-Wilk’s test for normality.

We assessed whether the presence of a partner in distress and its stress level had an effect on the amount of time bystanders spent facing the gate behind which their partner was confined. With this aim, we run an LMM to compare the amount of time each dolphin spent in front of the gate between the four different conditions (dependent variable). The fixed effect was the experimental condition (DC, FCC, SCC or TCC) and we included the identities of the bystanders as random effects.

We run a second LMM to assess the effects of social and non-social factors (fixed effects) on the time spent in the vicinity of the gates (dependent variables) per condition. Thus, for each condition, we included as a social factor a binomial variable indicating the presence or absence of an individual behind the gate (yes/no). The non-social factor was the type of gate at which the dolphins directed the behaviours (wooden or canvas gate). We included the identity of the bystander as random effects. The best model (most parsimonious) was selected using Akaike’s information criteria (AIC) values. The AIC allowed us to identify the most parsimonious model that best explains the variance of the dependent variable while penalizing for the number of variables in the model (Clay & de Waal, 2013).

For all LMMs, we run likelihood ratio tests comparing the full model (random and fixed effects) with the null model (only random effects) to test for overall significance of the model’s fixed effects (Clay & de Waal, 2013). LMMs analyses were run using R 3.4.1. statistical software (R Core Team, 2017) using the “lmerTest” package (Kuznetsova, Brockhoff, & Bojesen, 2016).

### **1.3. Results**

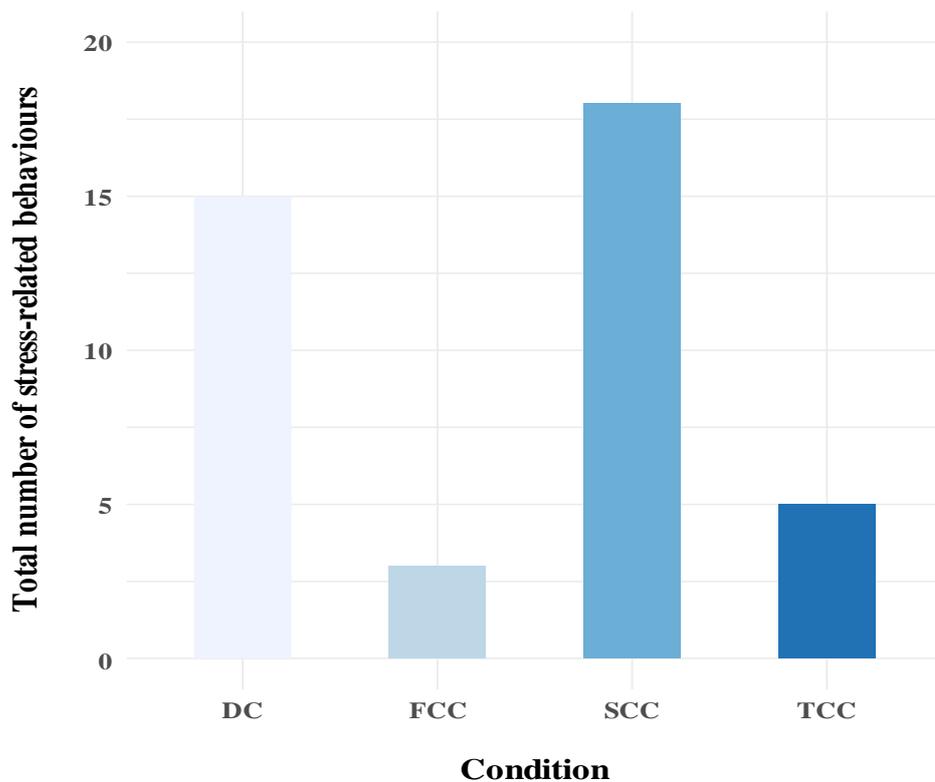
During the emptying of the medical tank, *Sacha* emitted multiple audible vocalizations and continuously slapped the water surface with its tail. On the other hand, *Blava* swam at high speed immediately after being released in the small tank, but during the following period, she continued to swim at a moderate speed without performing tailslaps or any other percussive behaviour. Therefore, the behaviour of both dolphins differed, suggesting that in fact, they were experiencing different levels of stress.

**Table 6** shows the index of affiliative relationships for the four dolphins. *Estel* and *Blue* were highly affiliated with *Sacha* while the affiliative index between *Sacha* and *Mateo* was lower.

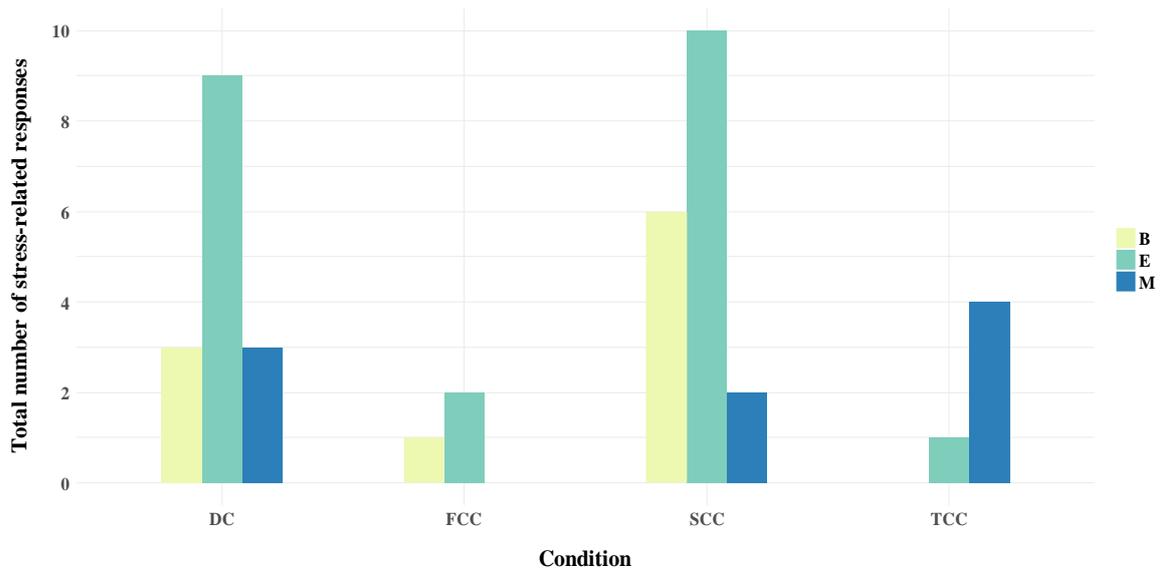
**Table 6.** Index of affiliative relationships (IA).

Dyad	IA	Affiliation
Blue - Mateo	0.476	High
Estel - Sacha	0.382	High
Blue - Sacha	0.131	High
Estel - Mateo	0.067	Low
Mateo - Sacha	0.066	Low
Blue - Estel	0.03	Low

In **Table 3** are listed some the possible stress-related behaviours observed in this study. Leaps, headslaps and bubble bursts were the main behaviours identified in the video-recordings. Of the 41 observed stress-related behaviours, 43.9 % were performed in the SCC, 39.02% in the DC, 12.2% in the TCC, and 4.87% in the FCC. Leaps were only observed in DC and SCC conditions. **Figure 5** shows the total number of stress-related behaviours registered in each condition while **Figure 6** shows the total number of stress behaviours displayed by each individual per condition. Of the 15 observed stress-related behaviours in the DC, 60% was performed by *Estel*, the dolphin that shared the strongest affiliative relationship with *Sacha*.



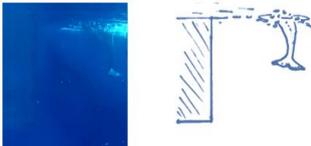
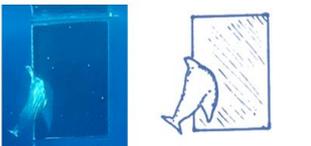
**Figure 5.** Total number of stress-related responses per condition



**Figure 6.** Total number of stress-related responses per individual per condition (E = Estel, M = Mateo, B = Blue).

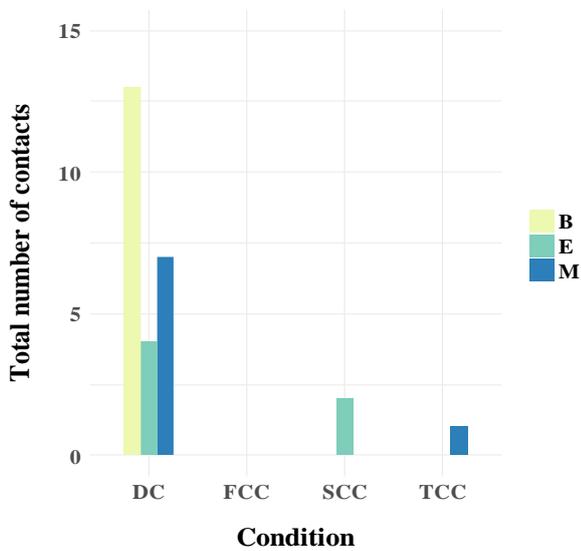
We identified two types of behaviours that could be related to the presence of a distressed dolphin on the other side of the gate: (1) attempts to make visual contact with the distressed dolphin such as spyhopping above the wooden gate and beaching near the medical tank; and (2) behaviours directed at the gate: strongly ramming the gate or gently contacting the gate with head and body (see **Table 7** for descriptions of behaviour).

**Table 7.** Description of the “other-oriented” behaviours recorded in this study.

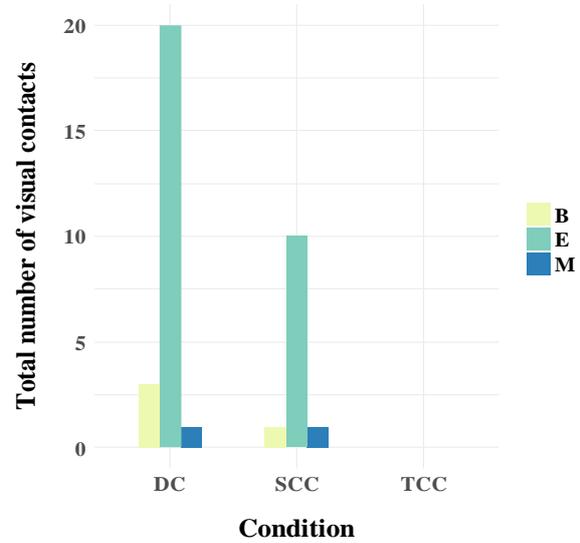
Other-oriented behaviours		
Behavior	Description	Image
<b>Spyhopping</b>	Investigation behaviour where a dolphin is vertical in the water with its head above the water surface. After Jensen et al., (2013)	
<b>Beaching</b>	Partial or nearly complete intentional stranding. After Paulos et al., (2010).	
<b>Ram</b>	Abrupt and forceful contact with the gate using rostrum or head. After Samuels & Spradlin, 1995	
<b>Contact</b>	Gentle contact with the gate using head or body**	

\*\* denotes a behaviour that was specifically coded for this study

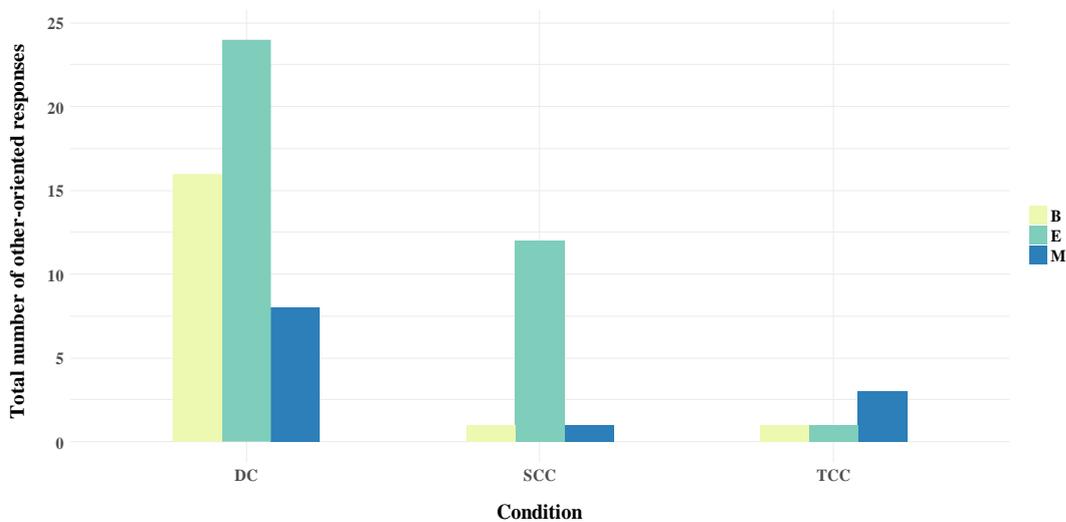
Of the 36 observed attempts to make visual contact with the other side of the gates, 66.67 % were performed in the DC and 36.36 % in the SCC; no attempts were observed in the TCC. Although we neither observed beaching behaviour nor spyhopping attempts in front of the gate in the FCC, since the camera accidentally moved, there was a blind spot in the area to the right of this gate, and thus, in this area, we could not record possible spyhopping attempts as we did in the rest of conditions. Beaching behaviour was only performed by Estel in the DC. Of the 29 observed contacts directed at the gate, 82.76 % were performed in the DC, 10.34 % in the TCC and 6.9 % in the SCC. No contacts directed at the gate were observed in the FCC. Figures 7 and 8 show the total number of attempts to make visual contact with the other side of the gates (excluding the FCC) and the total number of contacts directed at the gate performed by each individual per condition. Overall, we observed 48 “other-oriented” behaviours in the DC of which 50% were performed by Estel, 33.33% by Blue and 16.67% by Mateo. Figure 9 shows the total number of “other-oriented” behaviours performed by each individual per condition.



**Figure 7.** Total number of contacts directed at the gates per individual per condition (E = Estel, M = Mateo, B = Blue).

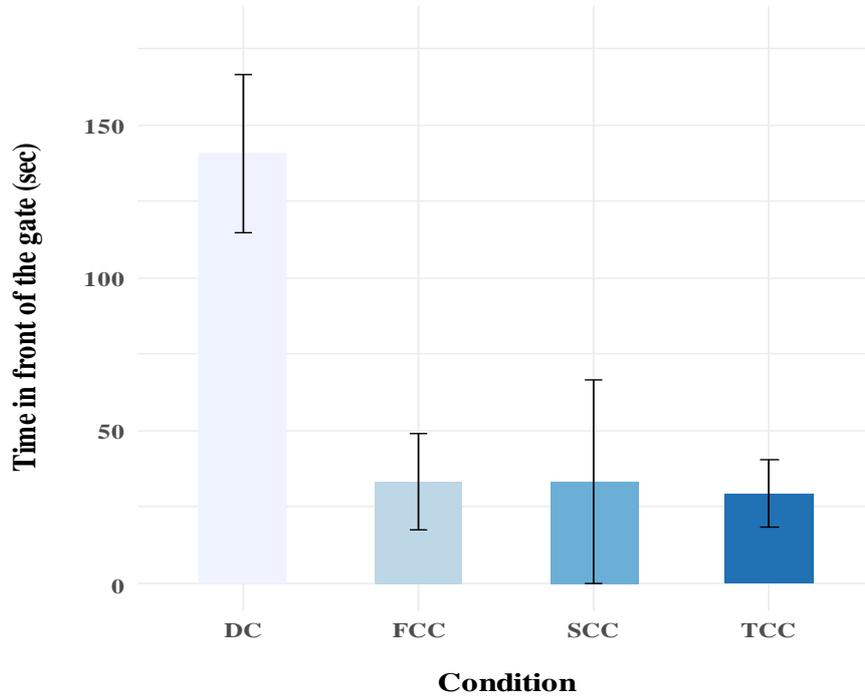


**Figure 8.** Total number of attempts to make visual contact with the other side of the gates per individual per condition (excluding the FCC) (E = Estel, M = Mateo, B = Blue).

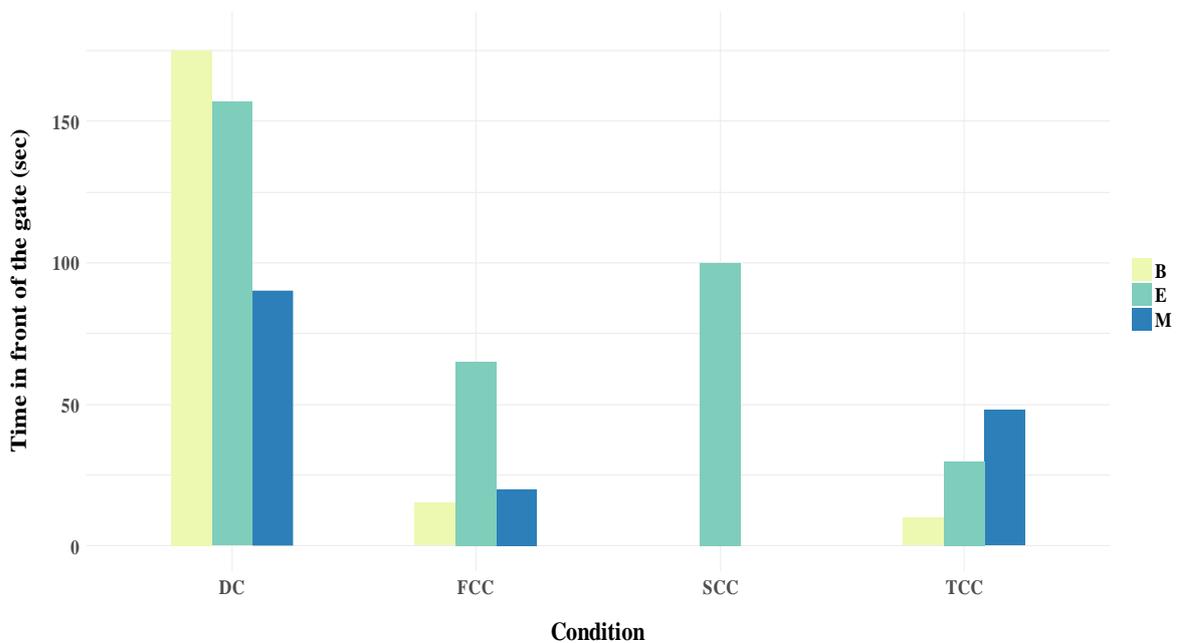


**Figure 9.** Total number of “other-oriented” behaviours per individual per condition (excluding FCC) (E = Estel, M = Mateo, B = Blue).

We measured the amount of time that dolphins spent facing the gates in each condition. Of the total length of the video-recordings, the mean percentages of time that dolphins spent facing the gate were 24.17% for the DC, 5.73% for both the FCC and SCC and 5.04 % for the TCC (**Figure 10**). **Figure 11** shows the total amount of time spent by each individual per condition.

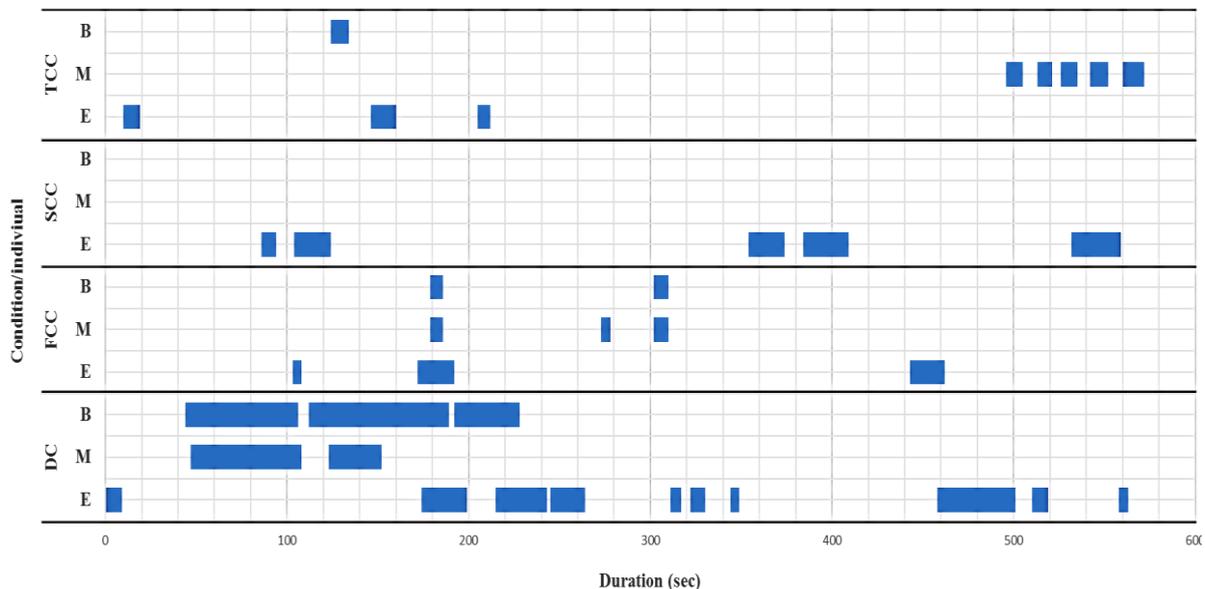


**Figure 10.** Mean time spent facing the gate per condition. Error bars represent standard errors (SE) of the mean.



**Figure 11.** Total amount of time in seconds spent facing the gate by each individual per condition (E = Estel, M = Mateo, B = Blue).

The individuals that shared a close affiliative relationship with Sacha spent more time near the gate (*Estel*: 26.98 % and *Blue*: 30.07 %) than the individual that was not closely affiliated with her (*Mateo*: 15.46%) (**Figure 11**). **Figure 12** shows the chronology of the time each dolphin spent facing the gate in each condition for the total length of the video-recordings.



**Figure 12.** Chronology of the time periods (seconds) in which each dolphin was in front of the gate per condition (E=*Estel*, M=*Mateo*, B=*Blue*).

We conducted an LMM to compare the total time bystanders spent facing the gates in the different conditions. The distress condition (DC) had an effect on the amount of time dolphins spent facing the gate. This model was significantly better at predicting the data when compared to the null model (AIC=69.617,  $\chi^2(3) = 10.959$ ,  $p = 0.01$ ). Bystanders were significantly more likely to remain in close proximity to the gate in the DC than in the FCC ( $\beta = 6.279$ , SE= 2.404,  $t = 2.612$ ,  $p = 0.04$ ), SCC ( $\beta = 8.415$ , SE= 2.404,  $t = 3.501$ ,  $p = 0.01$ ), and TCC ( $\beta = 6.559$ , SE= 2.404,  $t = 2.729$ ,  $p = 0.03$ ).

We run a second LMM to examine whether other social and non-social factors predicted the amount of time bystanders spent facing the gates in each condition. The presence of a partner behind the gates and the type of gate used in the experimental conditions did not have a significant effect on the total time spent near the gates by bystanders (presence:  $\beta = 4.348$ , SE= 2.200,  $t = 1.976$ ,  $p = 0.08$ ; type:  $\beta = 2.212$ , SE= 2.200,  $t = 1.005$ ,  $p = 0.35$ ). When all possible models were compared using the AIC, the most parsimonious model was the one including only the presence of another dolphin behind the gate. However, this model did not predict the data significantly better than the null model (AIC=72.862,  $\chi^2(1) = 3.714$ ,  $p = 0.05$ ).

#### 1.4. Discussion

Several studies have shown that procedures like confinement, separation from the group, and removing dolphins from water elicit stress responses in both captive and wild dolphins (Thomson & Geraci, 1986; Curry, 1999; Ortiz & Worthy, 2000; Oliveros & Maldonado, 2002; Waples & Gales, 2002; Esch *et al.*, 2009). What is not yet well established is whether the arousal state of a dolphin subjected to this type of stressful events can influence another's dolphin arousal state (emotional contagion), or whether this emotional reaction elicited by the perception of a conspecific in distress could give rise to other-oriented behaviours (sympathetic concern or empathic targeted

helping) (Pérez-Manrique & Gomila, 2017). The results of this study support most of our predictions suggesting that bottlenose dolphins are indeed affected by the emotional state of another dolphin, especially if they are closely affiliated with each other. Moreover, we also obtained evidence that, in these situations, dolphins may engage in empathic-like behaviours such as attempts to comfort or help the distressed party.

We predicted that if dolphins are affected by the perception of another's distress, bystanders are likely to display more stress-related behaviours in the DC than in the FCC since, in the former, the confined dolphin is expected to be more stressed. In general, our results fitted this prediction showing that bystanders displayed more stress-related responses in the presence of a more distressed partner than in the presence of a mildly stressed dolphin. However, we were unable to record all occurrences of stress-related behaviours per condition, so we lack quantitative behavioural data to confirm the observed frequency of stress responses. Therefore, we can only conjecture about the reasons why we registered more stress-related behaviours near the gates in certain conditions than in others.

In general, our results supported the hypothesis that certain factors related to the transfer, such as the presence of the wooden gate, elicit stress-related behaviours in this group of dolphins. In the video-recordings, we identified three types of behaviours previously proposed as indicators of stress in dolphins: leaps, headslaps, and bubble bursts (Pryor & Shallenberger, 1991; Curry, 1999; Oliveros & Maldonado, 2002). Bubble bursts were observed in all the conditions excepting the FCC. In most cases, dolphins produced the bubble bursts when they were close to the water surface and before emerging to breathe. Headslaps were not observed in the TCC and leaps were only observed in the DC and SCC. Tailslaps were observed only once in the FCC during an aggressive encounter between the males and the female kept in the main pool. Thus, it is likely that this behaviour was an aggressive display directed by one of the males to this female, rather than a stress-related behaviour. On the other hand, *Sacha* performed multiple tailslaps while confined in the medical tank. It has been hypothesized that percussive behaviours like tail slapping might have a communicative role and are performed to get the attention of the rest of the group (Herzing, 2000). If this is correct, *Sacha's* behaviours during the DC could be signs of frustration or stress that served to communicate her state to the other members of the group.

Since the wooden gates are only used in the park in stressful situations, it is expected that the mere sight of these gates triggers stress and fear reactions in this group of dolphins. Consistent with previous predictions, most of the stress-related behaviours were observed in the two conditions in which the wooden gate was present: the SCC (43.9%) and the DC (39.02%), while less than one-third of the registered behaviours were performed in the TCC (12.2%) and in the FCC (4.87%). Dolphins could have shown more stress-related behaviours in the SCC than in the DC since, in the former, only a minute elapsed between the closing of the gate and the onset of the recording while in the DC a considerable amount of time elapsed between the start of the recording and the closing of the gate. Given that we were unable to record all occurrences of stress-related behaviours, it is possible that we observed more behaviours in the SCC and in the DC simply because dolphins spent more time in the area recorded in these two conditions. However, when we controlled for the time each dolphin was videotaped in each condition, we obtained the same pattern of results. The SCC had the highest mean rate of stress responses per minute recorded (2.00) followed by the DC (1.52), the TCC (0.92), and finally the FCC (0.29). Furthermore, in the DC *Estel*, that was highly affiliated with *Sacha*, showed the highest rate of stress-related responses per minute recorded (1.78) followed by *Mateo* (1.26) and *Blue* (0.93). It is also possible that dolphins displayed more stress responses in the DC than in the FCC due only to the proximity of the wooden gate, the presence of water sounds in the medical enclosure, or due to the different start times of the video-recordings in both conditions and not because in the DC the confined dolphin showed a higher level of stress. We cannot entirely

rule out this possibility since, for ethical and methodological reasons, we could not record a control condition in which an undisturbed dolphin was behind the wooden gate during a considerable amount of time or register dolphins' responses near the wooden gate at the same time as we recorded the FCC. These control conditions, together with the FCC, would serve to assess the effect of the stress level of the confined partner in the arousal state of the bystanders, controlling for the influence of the presence of the wooden gate and the amount of time elapsed since the closing of the gates in the dolphins' stress responses. To control for the effect of water sounds in the medical enclosure, in future studies a possible control could be having a human in the tank. Nevertheless, our data suggest that these factors alone cannot explain the differences registered between stress-related behaviours in the DC and in the FCC. For example, the individual that shared the highest IA with *Sacha* was the one that in the DC showed the highest rate of stress-related behaviours per minute recorded. Emotional contagion processes are expected to be elicited more strongly by familiar individuals since these individuals are likely to be more sensitive to the other's state (see **Chapter 2**). Therefore, this result is consistent with the occurrence of emotional contagion between dolphins in the DC. Nevertheless, the methodological constraints previously mentioned make difficult to draw uncontroversial conclusions on this issue based solely on our data.

We predicted that if bystanders' reactions towards the distressed party involve an other-oriented response, bystanders are expected to remain near the conspecific in distress and perform attempts to help or comfort her. According to this prediction, dolphins should spend more time near the gate in the DC than in the rest of conditions. More precisely, the more the affiliation with *Sacha*, the more time bystanders are expected to remain near her. Our results also supported these predictions, showing that bystanders were significantly more likely to remain in close proximity to the gate in the DC than in the rest of conditions. In particular, dolphins spent more time near the confined dolphin in the DC than in the FCC, suggesting that the stress level of the isolated individual did influence dolphins' responses. Moreover, in the DC, the individuals who were more closely affiliated with *Sacha*, *Estel* and *Blue*, spent more time facing the gate behind which she was confined than *Mateo*, the individual barely affiliated with *Sacha*. In addition, our results also showed that neither the mere presence of another dolphin behind the gates nor the type of gate alone can explain the amount of time spent by bystanders in each condition. These results suggest that, indeed, the presence of a distressed individual behind the gate was the main factor influencing the amount of time dolphins spent in its vicinity.

Dolphins might have spent a great amount of time near the distressed dolphin in the DC since they were concerned about the situation of their partner. Physical proximity to a distressed individual and specific vocal cues could lead to social buffering (Kikusui *et al.*, 2006). In the present study, it is likely that bystanders closely bonded to the distressed dolphin, in addition to remaining as near as possible from her, also emitted vocalizations. These vocalizations could have had a social buffering effect on the stressed dolphin (vocal buffering). If this is the case, bystanders' responses could be considered as a sort of consolatory behaviour, since they would meet two of the main features of true consolation: a distress alleviation function and a clear directionality of the response, directed mostly towards a closely bonded individual (see **Chapter 3, section 2.1**). However, this is only a speculative hypothesis since we were unable to record neither the vocalizations emitted by bystanders in the different conditions nor possible changes in the stress response of the isolated dolphin.

Another aim of this study was to assess whether bystanders directed "other-oriented" behaviours towards the distressed partner, in addition to spending time in its proximity. These behaviours were defined by the presence of expressions of interest towards the situation of the distressed party or attempts to help the distressed dolphin. We identified four different behaviours that fitted in this category. As possible expressions of interest, we observed attempts to make visual contact with the

conspecific in distress such as spyhopping above the gate or beaching behaviour. Beaching consisted of intentionally stranding in the area near the medical tank where the distressed partner was confined, which allowed the individual to have visual access to the medical tank. This behaviour was only observed in the DC, that is when the distressed conspecific was kept in the medical tank. Beaching was only performed by *Estel*, the individual that shared the highest IA with *Sacha*. Furthermore, spyhopping behaviours were mainly recorded in the DC condition, were not observed in the TCC, and again, were mostly performed by *Estel*. We also observed that, on several occasions, dolphins forcefully rammed the gates with their heads. These responses could be considered as an example of helping behaviour if, when ramming the gate, what the dolphins were trying to do was to open it and free their partner. Dolphins rammed the gate mainly in the DC (75%), this behaviour was observed neither in the FCC nor in the SCC and only two times in the TCC. Forcefully ramming the wooden gate with the head could imply a physical risk to the dolphins. Interestingly, dolphins did not ram the wooden gate in the SCC and only rammed the canvas gate twice in the TCC, this gate is made of a more elastic material and thus the risk of suffering physical damage ramming this gate is lower. In the DC, the three bystanders rammed the gate the same number of times. Thus, no differences were observed depending on the quality of the affiliative relationship of each individual with *Sacha*. Bystanders also performed other types of contacts with the gates that consisted in gently pushing the gate with the head, leaning their head on the gate and spinning around, or contacting the gate with the side of their bodies. Again, dolphins performed these behaviours mainly during the DC (85.7%), they did not contact the gate in the FCC, and in the TCC they gently pushed the gate with the head only once and twice in the SCC. In the DC, *Blue* was the individual that directed more contacts at the gate, followed by *Mateo* and then *Estel*. However, when all these responses (visual and gate contacts) were pooled into a single behavioural category called “other-oriented behaviours”, *Estel* was the individual which performed more “other-oriented” behaviours in the DC followed by *Blue* and *Mateo*. Thus, the observed behavioural pattern followed an affiliative bias, being mostly performed by individuals sharing a closer relationship with *Sacha*. It is not clear why dolphins performed these behaviours, and with the available data, we can only speculate about their possible functions. The fact that these behaviours were mainly performed in the DC and by the individuals that were highly affiliated with *Sacha*, suggests that they are related to the presence of the distressed dolphin behind the gate. In this manner, bystanders’ behaviours directed at the gate could be attempts to push and open the gate, or frustration displays in response to the situation of the distressed party.

Overall, dolphins spent more time in the vicinity of a gate and performed more “other-oriented” behaviours when a distressed partner was confined behind that gate than in the rest of conditions. Furthermore, the two individuals that were highly affiliated with *Sacha* spent more time near her and displayed more “other-oriented” behaviours than the less affiliated individual. That is, the individuals that were more likely to be responsive to *Sacha*’s distress were the ones that remained with her a greater amount of time and displayed more “other-oriented” responses. Thus, as empathic responses, these behaviours seemed to be promoted by close social bonds (Preston & de Waal, 2002; Fraser & Bugnyar, 2010). The stress level of the confined dolphins seemed to influence bystanders’ responses since they spent more time near the gate and displayed more “other-oriented” behaviours in the DC than in the FCC. That is when the isolated dolphin was expected to be more stressed. Furthermore, it has been reported that in certain situations dolphins used to position themselves as far from a distressing stimulus as possible (Pryor & Shallenberger, 1991; Curry, 1999). Thus, if the wooden gate is perceived as aversive by the dolphins, as suggested by the stress-related behaviours recorded in the SCC, dolphins are expected to stay away from this gate. In fact, both males did not spend any time in close proximity to this gate in the SCC and *Estel* spent less time near this gate in the SCC than in the DC. The fact that bystanders spent a considerable amount of time near the wooden gate in the DC, even when this gate was aversive to them, also supports the hypothesis that the behavioural

responses registered in the DC are “other-oriented” behaviours elicited by the perception of another’s distress. All these outcomes are consistent with an empathic-like response towards a distressed conspecific, suggesting that bystanders’ behaviours could be empathy based.

Although our results are consistent with empathy-based explanations, the underlying mechanisms of the observed behaviours nevertheless remain hard to elucidate and alternative explanations should be considered as well. For example, distress calls could have played a significant role in eliciting the observed responses. These responses could be simple and automatic behaviours that do not require empathy. It is known that dolphins emit distress calls in aversive situations and these vocalizations may give rise to approach responses and helping behaviour of other conspecifics (Lilly, 1963; Kuczaj *et al.*, 2015a). More specifically, dolphins in distress emit their distinctive signature whistle encoding their level of distress in whistle rate and number of loops (Esch *et al.*, 2009; Janik, 2009). When isolated, dolphins also produce contact calls to maintain group cohesion. Therefore it has been proposed that signature whistles could function as both distress and contact calls (Janik & Slater, 1998; Esch *et al.*, 2009; Sayigh & Janik, 2009). In fact, it is likely that in the DC and in the FCC the confined dolphins emitted these vocalizations. If distress and contact calls automatically elicit approach responses in bystander dolphins, then all bystanders should approach the gate simultaneously in these two conditions. **Figure 12** shows that, indeed, only in the DC and FCC there were periods of time in which more than one dolphin was simultaneously facing the gate. Moreover, in the FCC there was a period in which all the bystanders were located in front of the gate. These results suggest that, in fact, the confined dolphins emitted vocalizations that triggered approach responses in bystander dolphins. Thus, it could be also argued that bystanders spent a greater amount of time near the distressed individual in the DC than in the FCC since, in this condition, the confined dolphin produced more distress vocalizations than in the FCC and the perception of those calls elicited automatic and urgent approaches in bystanders.

However, the fact that in the DC bystanders responded differently depending on the level of affiliation with the distressed dolphin rather suggests that the observed behaviours are not automatic responses. Similarly, the bystanders did not perform any “other-oriented” behaviour in the FCC and spent approximately the same amount of time near the gate in the FCC than in the other two control conditions. Further studies are needed to clarify the nature of dolphins’ responses to distress calls. These studies should serve to clarify whether dolphins respond to the perception of another’s distress is multimodal or privilege a sensory channel over others, as well as whether the different sensory channels involve different degrees of control, requiring in some cases a flexible cognitive evaluation of the situation of the distressed party to provide fine-tuned help. In this latter case, these behaviours could be considered as an example of empathic targeted helping (see **Chapter 3**).

Overall, studies empirically assessing the emotional responses and empathic-like behaviours of cetaceans towards conspecifics in distress are scarce. This study was conceived as an initial attempt to improve on this situation by developing a new paradigm. With this new paradigm, we aimed to overcome some of the main problems associated with the empirical study of emotional responses in cetaceans. This paradigm emerges thus as a useful tool for assessing dolphins’ responses towards a distressed individual.

Most of our results are consistent with an empathy-based explanation of dolphins’ responses towards a distressed partner. In the first place, it seems clear enough that bottlenose dolphins are affected by the emotional state of their conspecifics, suggesting thus the occurrence of emotional contagion. In the second place, dolphins seemed to perform “other-directed” behaviours towards the distressed party. Some of those “other-oriented” behaviours involved possible attempts to comfort the stressed dolphin and to open the gate which created the stressful situation for the partner,

suggesting that dolphins are aware of the needs of their distressed partner and may try to alleviate its suffering. The emotional reactions elicited by the perception of the partner's distress could have promoted those empathic-like responses. These emotional reactions did not match those displayed by the distressed dolphin, and therefore they could have been subjected to some degree of emotional regulation. If this is so, these "other-oriented" behaviours would also qualify as instances of sympathetic concern (consolation) (see **Table 1**). The fact that the dolphins more closely affiliated with the distressed conspecific were the ones performing more "other-oriented" behaviours, suggests that the affiliative relationship with the distressed individual was a strong modulator of dolphins' behavioural responses. This result supports the empathy-based explanation of these responses since familiarity with the distressed party also modulates empathic processes like consolation (Preston & de Waal, 2002). Furthermore, this result is also consistent with multiple anecdotal reports of epimeletic behaviour in cetaceans (see **Chapter 4, section 3**). Although suggestive, our data fail to provide clear evidence of whether dolphins' "other-oriented" responses were examples of flexible targeted helping. A different approach is required to study this question, which will be raised in posterior studies.

## 2. Study 2: Consolation and conflict-resolution in bottlenose dolphins

### 2.1. Introduction

Living in groups has been suggested to provide many survival benefits to social animals. Some of those benefits are protection, mate choice, aid in the rearing of young, reduction of the risk of predation, energetic benefits in locomotion or higher probabilities to find food (Rubenstein, 1978; Parrish & Edelman-Keshet, 1999). On the other hand, conflicts of interest over access to resources, mating partners or positions in the dominance hierarchy are also common in group-living species. Such conflicts may result in aggressive encounters within group members, which are costly in terms of energy expenditure, risk of injury and damage to social relationships between opponents (de Waal, 2000; Wittig & Boesch, 2003; Fraser *et al.*, 2008). In animals that rely on cooperation and mutual assistance for their survival, the occurrence of aggression might be constrained by the need to maintain these social relationships (de Waal, 2000; Weaver, 2003). The reproductive and survival success of both opponents thus may depend on how aggressive conflicts are stopped (Lorenz, 1963) and resolved (Huntingford & Turner, 1987). Social species are then expected to evolve ways to control or mitigate the damaging consequences of in-group aggression (de Waal, 2000; Weaver, 2003). Post-conflict management has been proposed to reduce the cost of conflicts and prevent further aggression by means of several affiliative interactions that take place after an aggressive encounter (Wittig & Boesch, 2003). After the end of the aggressive event thus former opponents may display a variety of post-conflict interactions such as reconciliation, third-party affiliation or redirected aggression, that may alleviate post-conflict distress, reduce aggressive tendencies in both parties, or restore relationships between former opponents (Wittig & Boesch, 2003). These interactions may also involve bystanders.

One of the main costs associated with aggression is post-conflict distress of former opponents. Distress alleviation of both parties is therefore expected to be one of the functions of post-conflict interactions exhibited by social species. Reconciliation and third-party affiliations may serve this purpose (de Waal & van Roosmalen, 1979). Reconciliation is defined as the exchange of affiliative contacts between former opponents shortly after the conflict (de Waal & van Roosmalen, 1979). It has been proposed that, in addition to reducing post-conflict stress levels, reconciliation may repair damage to relationships between former opponents (de Waal & van Roosmalen, 1979; Aureli, Cords, & van Schaik, 2002). Reconciliation is one of the most studied post-conflict management mechanisms in non-human species and has been reported in multiple species of primates (chimpanzees, (de Waal & van Roosmalen, 1979; Kutsukake & Castles, 2004); bonobos (Palagi *et al.*, 2004); mountain gorillas (Watts, 1995b); macaques, *Macaca nemestrina*, *M. mulatta*, *M. silenus*, *M. arctoides*, *M. fascicularis*, *M. fuscata*, *M. tonkeana* (de Waal & Yoshihara, 1983; de Waal & Ren, 1988; Judge, 1991; Cords, 1992; Aureli, 1992; Aureli *et al.*, 1993; Abegg, Thierry, & Kaumanns, 1996; Thierry & Demaria, 2001); redfronted lemurs, *Eulemur fulvus rufus* (Kappeler, 1993); baboons, *Papio anubis*, *P. hamadryas hamadryas*, *Theropithecus gelada* (Swedell, 1997; Castles & Whiten, 1998; Romero, Colmenares, & Aureli, 2009); patas monkeys, *Erythrocebus patas* (York & Rowell, 1988); vervet monkeys, *Cercopithecus aethiops* (Seyfarth & Cheney, 1989); golden monkeys, *Rhinopithecus roxellana* (Ren *et al.*, 1991); and capuchin monkeys, *Sapajus apella* (Verbeek & de Waal, 1997)). Subsequent studies have also reported reconciliation in other species of mammals such as spotted hyenas (*Crocuta crocuta*) (Wahaj, Guse, & Holekamp, 2001), domestic dogs (Cools *et al.*, 2008), wolves (Cordoni & Palagi, 2008), horses (*Equus caballus*) (Cozzi *et al.*, 2010), red-necked wallabies (*Macropus rufogriseus*) (Cordoni *et al.*, 2014), domestic goats (*Capra hircus*) (Schino, 1998), and birds (ravens (Fraser *et al.*, 2011); budgerigars (Ikkatai *et al.*, 2016).

Sometimes, bystanders are involved in the restorative behaviours. In fact, we can distinguish three main categories of post-conflict bystander affiliation: (1) appeasement: post-conflict contact offered by bystanders to aggressors (Romero, Castellanos, & de Waal, 2011); (2) solicited bystander affiliation: solicited affiliation by the distressed party to a bystander (Fraser & Bugnyar, 2010); and (3) unsolicited bystander affiliation: post-conflict affiliative contact spontaneously directed to victims by uninvolved bystanders (Palagi & Cordoni, 2009). When unsolicited bystander affiliation implies the alleviation of the victim's distress, this post-conflict interaction is also called consolation. Consolation is the most representative example of sympathetic concern (concern about another's state and attempts to ameliorate this state (de Waal, 2008)), a phenomenon that has been related to empathy (de Waal, 2008). Sympathetic concern involves a moderate emotional reaction elicited by the perception of another individual in distress that gives rise to an other-oriented response, which generally results in the alleviation of the other's distress (Pérez-Manrique & Gomila, 2017) (Table 1). Thus, the uninvolved party must spontaneously realize that the victim of the conflict needs reassurance and provide it (Fraser *et al.*, 2011). So, this process requires some degree of sensitivity to the emotional needs of other individuals, a capacity traditionally considered to be a uniquely human trait (Fraser & Bugnyar, 2010). Furthermore, this process seems to be cognitively demanding and may involve an effective level of emotional regulation, which allows individuals to distinguish, to some extent, between internally and externally generated emotions and respond differently depending on the source of the emotion (de Waal, 2008). Therefore, unlike other post-conflict interactions, consolation is not expected to be displayed by a great number of non-human species. Indeed, it has been only described in a few animal species (see **Chapter 3, section 2.1**). de Waal & van Roosmalen (1979) first applied the term consolation to non-human primates, defining it as contact of the aggressed party with a third animal. Their definition excluded affiliative contacts between winners and a third party and did not consider which individual (aggressed or third party) initiated the affiliative contacts. Currently, in the field of animal empathy research, the term consolation is used to define a specific type of unsolicited third-party affiliation initiated by the bystander and characterized by the alleviation of the victim's distress (Palagi *et al.*, 2014).

Although appeasement could also alleviate the aggressors' post-conflict stress, it is not usually considered as an example of consolation since it might rather reduce aggressive tendencies in the aggressor. Furthermore, this behaviour would provide direct benefits to bystanders by preventing them from becoming the target of redirected aggression. If so, appeasement could be qualitatively different from consolation (Romero *et al.*, 2011). Solicited bystander contacts may be functionally similar to unsolicited ones in that they could also reduce post-conflict distress (Palagi & Cordoni, 2009). However, given that the initiative is not taken by the bystander but by the distressed party, its underlying mechanism is likely to differ from consolation in that it may not require empathy (Fraser & Bugnyar, 2010). Solicited third-party affiliation may simply require that the bystander tolerates the approach of the other individual or recognizes the specific approach signal emitted by the other animal, irrespective of whether it is distressed or not. On the other hand, to be considered true consolation, the prosocial response should be driven by the perception of the other's distress and not by an explicit request from the distressed party for attention and support from a bystander (Pérez-Manrique & Gomila, 2017).

Although the term consolation implies a distress-alleviating function, affiliation from bystander to victim may not always have a consoling effect and could have alternative functions not requiring empathy (Fraser & Bugnyar, 2010). For example, unsolicited bystander affiliation could be a form of kin-mediated reconciliation, if a familiar individual (kin or unrelated valuable partners) of both the aggressor and the victim are more likely to affiliate with their relative's opponent (Fraser & Bugnyar, 2010). This type of interaction allows repairing former opponents' relationship avoiding

the risk of renewed aggression between them (Fraser & Bugnyar, 2010). Indeed, it was reported that in savannah baboons friendly grunts from the aggressor's kin to the victim restored tolerance between former opponents (Wittig *et al.*, 2007), and in chimpanzees, bystanders who shared a valuable relationship with the aggressor were the ones who initiated affiliation with the victims (Wittig, 2010).

As already mentioned, bystander affiliation might also function as a self-protection strategy for bystanders (Koski & Sterck, 2009). That is, bystanders might also provide affiliative contacts towards victims of conflict in order to avoid becoming a target of redirected aggressions (Call *et al.*, 2002; Koski & Sterck, 2009). In fact, in a group of chimpanzees, those individuals who had a higher overall risk of receiving aggression from opponents were the ones who provided bystander affiliation, and these affiliative contacts effectively decreased their chance of receiving aggression from those opponents (Koski & Sterck, 2009). However, bystander affiliation was also provided to victims by their own kin, and these affiliations did not appear to be self-protective. Thus, bystander affiliation could be a more heterogeneous behaviour than previously thought (Koski & Sterck, 2009).

According to the "Valuable Relationship Hypothesis", all post-conflict interactions should occur more often between individuals with more valuable relationships (Aureli *et al.*, 2002). In fact, several studies have reported that some primates and ravens directed more post-conflict contacts towards individuals with whom they exchange high rates of affiliative behaviour at baseline than with other conspecifics (de Waal & Yoshihara, 1983; de Waal & Ren, 1988; Arnold & Whiten, 2001; Aureli *et al.*, 2002; Fraser *et al.*, 2011). As reconciliation might serve to restore former opponents relationships, this type of interaction is expected to occur when the opponents are mutually valued social partners, since the loss of a more valuable relationship entails a larger loss of benefits for both individuals (Aureli *et al.*, 2002). In turn, unsolicited bystander affiliation is also expected to be performed by individuals who share a close relationship with the distressed party, as they are more likely to be responsive to the other's distress (Fraser & Bugnyar, 2010). Moreover, much attention has been paid to the role of familiarity in consolation because this behaviour is related to empathy and, familiarity has strong effects in processes favouring empathy (Preston & de Waal, 2002). Thus, in addition to its distress alleviation function, consolation is characterized by the directionality of the bystanders' affiliations, directed mostly towards familiar individuals (kin or friends).

Wild bottlenose dolphins live in fission-fusion groups characterized by frequent changes in group composition, flexible dominance relationships, and high levels of cooperation (Johnson & Norris, 1986; Holobinko & Waring, 2010). In dolphins' fission-fusion societies, individuals generally tend to associate in small groups whose composition changes dynamically (Lusseau *et al.*, 2003). Despite the nature of their fission-fusion society, dolphins are dependent on their social partners, and they establish complex and stable relationships with some group members (Norris & Dohl, 1980; Weaver, 2003). Conflicts are common among bottlenose dolphins (Samuels & Gifford, 1997) like other species sharing a similar social organization. Therefore, dolphins are expected to display post-conflict mechanisms that allow them to develop and maintain long-lasting complex social networks despite frequent conflict (Weaver, 2003; Holobinko & Waring, 2010). In general, the most stable associations are among same-sex members, and between mother and calf pairs (Smolker *et al.*, 1992). Female bottlenose dolphins display a large variability in their association patterns and establish less stable relationships than males (Smolker *et al.*, 1992; Lusseau *et al.*, 2003). Some females live in groups in which, although the school composition is fluid, they have long-term relationships with some specific individuals (Wells, 1991). Furthermore, certain groups of females tend to associate more with each other than with other female groups (Wells, 1991). At the other end, some females are solitary or have few or no valuable associates (Connor *et al.*, 2000; Lusseau *et al.*, 2003). Some males form strong and long-lasting bonds with other males, whereas others tend to

be solitary (Wells, 1991; Connor *et al.*, 2000). Males often form strong alliances with two or three individuals, and several of these alliances can cooperate forming multiple-level alliances to herd and control females and/or attack other alliances (Wells, 1991; Connor *et al.*, 1992, 2011; Lusseau *et al.*, 2003; Connor & Krützen, 2015). Associations between males and females are generally weak and related to the reproductive state of females (Smolker *et al.*, 1992; Connor *et al.*, 2000; Lusseau *et al.*, 2003). However, dolphins' social organization could vary depending on the ecological constraints and habitat features of each population (Weaver, 2003; Lusseau *et al.*, 2003). For example, bottlenose dolphins living in low-productivity systems in which survival may require a greater level of cooperation, have been reported to form larger and more stable mixed-sex groups in which all members are relatively closely associated (Lusseau *et al.*, 2003; Augusto, Rachinas-Lopes, & dos Santos, 2012; Louis *et al.*, 2017).

These cetaceans possess good memory skills and individual recognition (Sayigh *et al.*, 1999; Herman, 2010; Mercado III & DeLong, 2010), capacities that are considered to be the minimum requirements necessary to display post-conflict contacts (de Waal & Yoshihara, 1983; Weaver, 2003). Furthermore, although there are few data on emotional responses in bottlenose dolphins, many anecdotal reports suggest that they are affected by the emotional state of conspecifics, providing prosocial responses towards distressed individuals in several contexts (Lilly, 1963; Caldwell & Caldwell, 1966; Kuczaj *et al.*, 2015a). Therefore, bottlenose dolphins seem to be good candidates to show consolation responses towards victims of aggression, especially when the victim is a valuable partner.

Using current primate behaviour research methods (Samuels & Flaherty, 2000), recent studies have shown that captive bottlenose dolphins reconcile after aggression (Samuels & Flaherty, 2000; Weaver, 2003; Holobinko & Waring, 2010; Yamamoto *et al.*, 2015, 2016). Both aggressors and victims initiate reconciliation and these affiliative contacts decrease the probability of renewed aggression between former opponents, suggesting that this behaviour helps to reduce the aggressive tendencies of both winners and losers after a conflict (Yamamoto *et al.*, 2015). In addition, former opponents that share a more valuable relationship reconciled more frequently, supporting the valuable relationship hypothesis (Yamamoto *et al.*, 2016). Affiliative contacts between former opponents typically occurred soon after aggression (Samuels & Flaherty, 2000; Weaver, 2003; Yamamoto *et al.*, 2015) and consisted of affiliative behaviours such as flipper-rubbing, contact-swimming, approaches or synchronous breathing (Samuels & Flaherty, 2000; Weaver, 2003; Tamaki *et al.*, 2006; Holobinko & Waring, 2010).

So far, little evidence is available about other types of post-conflict contacts between bottlenose dolphins. Two studies (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015) reported the occurrence of third-party affiliation in captive bottlenose dolphins. Yamamoto *et al.* (2015) observed that victims, but not aggressors, tended to initiate affiliations toward bystanders during the post-conflict period (solicited bystander affiliation). These contacts reduced renewed aggressions by winners to losers, and thus seem to function as a protective strategy of the victim (Yamamoto *et al.*, 2015). An alternative hypothesis to explain why only the victims solicited affiliation from bystanders is that victims were more distressed after the conflict than aggressors and affiliating with a bystander served to reduce their own post-conflict distress. Bystanders tended to affiliate with both winners and losers after the aggressive encounters. These affiliative contacts reduced renewed aggressions by winners to losers and vice versa suggesting that, in bottlenose dolphins, unsolicited bystander affiliation may function as appeasement of former opponents (Yamamoto *et al.*, 2015). However, Yamamoto *et al.* (2015) did not examine the occurrence of redirected aggression and thus it was not possible to assess whether bystanders offered affiliation to former opponents as a self-protection strategy. Tamaki *et al.* (2016)

examined the function of a specific affiliative contact, flipper-rubbing, during the post-conflict period. Flipper-rubbing between former opponents or between one of the opponents and a third-party significantly increased the latency to further aggression, suggesting that these affiliative interactions may serve to ease tension in the group, reducing thus the probability of the recurrence of another conflict (Tamaki *et al.*, 2006).

In brief, it seems that dolphins tend to reconcile after an aggressive encounter and this post-conflict affiliation may ease tension and restore former opponents' relationships. On the other hand, evidence of unsolicited bystander affiliation in bottlenose dolphins is scarce and inconclusive. Although the previous studies (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015) observed that some captive bottlenose dolphins sometimes provided unsolicited bystander affiliation towards victims of aggression, Tamaki *et al.* (2006) did not conduct a quantitative analysis of this behaviour, they only reported its occasional occurrence. Therefore, only the study of Yamamoto *et al.* (2015) provided positive evidence of unsolicited bystander affiliation in bottlenose dolphins. In addition, another study (Holobinko & Waring, 2010) found no evidence of such contacts in another group of captive bottlenose dolphins. Furthermore, there are no studies assessing the two main features defining consolation: its distress alleviation function and the directionality of the post-conflict affiliative contacts, that is, whether they are mostly directed to valuable partners. Therefore, unsolicited bystander affiliation with victims of conflicts in dolphins requires further research to reliably establish its occurrence, function and main features.

Assessing the consolatory function of unsolicited bystander affiliation, though, may not be an easy task, especially in some species such as dolphins, which often show no clear behavioural signs of distress or these indicators are difficult to identify (Simmonds, 2006). For this reason, the theoretical framework for determining the function of bystander affiliation proposed by Fraser *et al.* (2009) seems to be an ideal tool for assessing consolatory responses in dolphins. This framework states that the quality of the relationships between the individuals involved in the post-conflict interaction and the patterns of behaviour displayed could determine its occurrence and function. Bystander affiliation with a victim of aggression can be associated with three different functions: (1) distress alleviation (consolation), (2) relationship repair and (3) self-protection, and this framework allows to tell which is the relevant one in a given occasion. When a bystander offers affiliation to a victim of aggression with whom it shares a valuable relationship, these affiliative contacts are suggested to have a distress alleviation function (consolation), since valuable partners are more likely to be responsive to each other's distress (Fraser *et al.*, 2009; Fraser & Bugnyar, 2010). On the other hand, when a bystander which shares a valuable relationship with the aggressor affiliates with the victim, it is likely that the function of this post-conflict interaction is to ease group tension and restore former opponents' relationships. Thus, in this case, bystanders may act as proxies for the aggressor in reconciling the opponents (Fraser & Bugnyar, 2010). Finally, if the function of unsolicited bystander affiliation is to avoid redirected attacks from the original conflict victim, it is expected that those bystanders that are more likely to become the next target of these attacks offer affiliation to the victim, although they do not share a close relationship with her (Fraser *et al.*, 2009; Fraser & Bugnyar, 2010).

Our main objective in this study is to assess the occurrence of unsolicited bystander affiliation in a group of captive bottlenose dolphins and its possible consolatory function, applying for the first time in a cetacean species this predictive framework. In this study, thus we first examined the occurrence of unsolicited bystander affiliation and other types of post-conflict interactions (reconciliation, appeasement and solicited bystander affiliation) to expand our knowledge on the post-conflict management mechanisms of captive bottlenose dolphins. We also determined the influence of certain factors related to the conflict (conflict intensity, the occurrence of another type of post-conflict affiliation) and social variables (relationship quality) on the occurrence of unsolicited

bystander affiliation. If unsolicited bystander contacts have a distress alleviation function, it is predicted that: (1) bystanders would offer more affiliative contacts after more intense conflicts since the victim is expected to experience more distress, and (2) bystander affiliation with the victim may be more likely to occur when the bystander shares a valuable relationship with her (Fraser & Bugnyar, 2010). If unsolicited bystander contacts with the victim serve for restoring former opponents' relationship, it is predicted that the bystander is likely to share a valuable relationship with the aggressor. Finally, if unsolicited bystander affiliation function as a self-protection strategy of the bystander, it is expected that bystanders who do not share a valuable relationship with the victim and are often the target of her attacks provide more affiliative contacts to the victim of the conflict. Furthermore, if solicited or unsolicited bystander affiliation with victims serves as a self-protection strategy for bystanders or victims from winners' further attacks, it is expected to find lower levels of renewed or redirected aggression by winners in affiliated than in unaffiliated post-conflict periods. Finally, we also tested the hypothesis that post-conflict affiliation with winners have a calming effect on the aggressor, reducing the probability that winners engage in renewed or redirected aggression

## 2.2. Method

### *Subjects and facility*

We observed a group of four Atlantic bottlenose dolphins (two adult males, and two adult females) housed at Marineland Mallorca (see **Table 8**, for subjects' sex and age).

**Table 8.** Age and sex of the experimental subjects. M: male; F: female.

Subject	Sex	Age (years)
Blue	M	25
Mateo	M	13
Blava	F	13
Estel	F	13

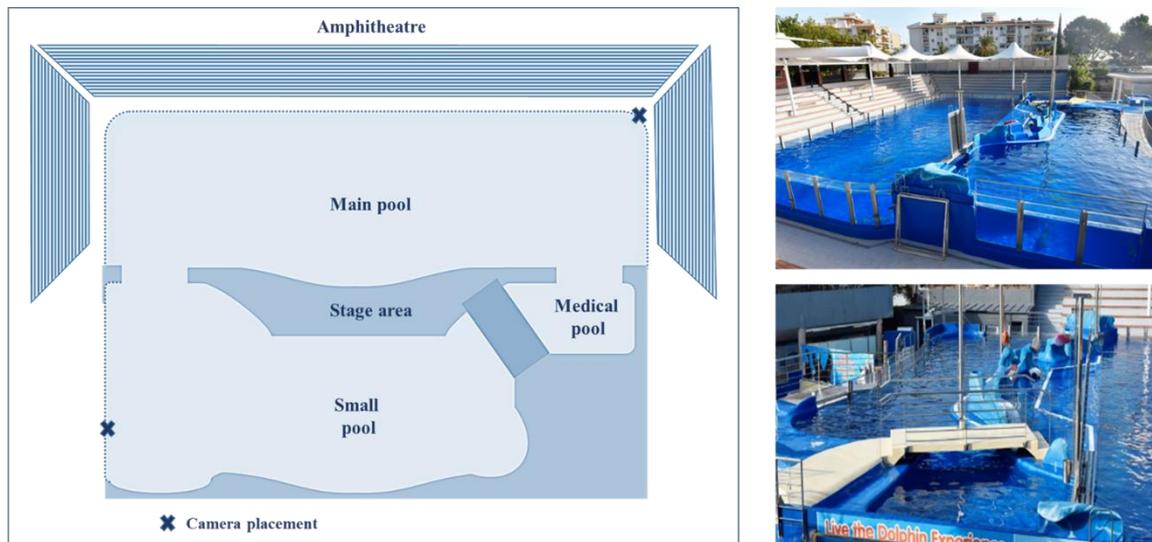
The dolphins were kept in three outdoor interconnecting pools: a main performance pool (1.6 million litres of water, 324.43 m<sup>2</sup> surface area, 5 m deep), a medical pool (37.8 thousand litres of water, 18.91 m<sup>2</sup> surface area, 2 m deep) and a small pool (636.8 thousand litres of water, 127.37 m<sup>2</sup> surface area, 5 m deep). During the observational periods, the dolphins had free access to the three pools. Underwater viewing at the main and the small pool was available through the transparent walls around the rim of the pools (see **Figure 13**).

### *Behavioural observations*

#### *Data collection*

Behavioural data were collected in situ by APM from May 2016 to November 2016. In addition, all observational periods were recorded using two waterproof cameras SJCAM SJ4000 through the acrylic walls of the pools and covered approximately the entire area of the dolphins' enclosure (see **Figure 13**). Observations were conducted at the main pool between 8:00 am and 11:00 am. Due to the schedules and dynamics of the park, we were unable to collect data outside this period. Dolphin

social behaviour was generally registered and videotaped daily for 30 min - 2 h each day. Only data from sessions that lasted at least 30 min were included in the analysis. Morning training and medical sessions did not have a rigid schedule and were variable in length. We did not collect any data during these procedures and resumed the observational session few minutes after the end of these events.



**Figure 13.** Facility and camera placement in this study.

We recorded all occurrences of aggressive conflict and the identities of the aggressor and the victim (initial recipient of aggression) (Fraser *et al.*, 2008). Aggressive interactions were defined by the occurrence of chasing, biting, and hitting, as established in previous studies (Samuels & Gifford, 1997; Tamaki *et al.*, 2006; Holobinko & Waring, 2010; Yamamoto *et al.*, 2015, 2016) (see **Table 9**). In order to not confuse playful or affiliative behaviours with aggressive interactions, we only classified a behaviour as “aggressive” when the recipient of the attack resisted or clearly avoided the aggressor (e.g. “flee” or “flinch” as defined in **Table 9**) (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015, 2016). In addition, chasing interactions were treated as aggression only if the interaction included threatening behaviour (e.g. jawclaps), and were excluded if dolphins alternated roles, behaviour that has been suggested to be an indicator of play behaviour (Tamaki *et al.*, 2006). In conflicts involving more than one aggressor-victim dyad, each dyad was considered separately (Veenema, Das, & Aureli, 1994). We also recorded the intensity of each conflict (low = threatening and chasing or only one aggressive contact, high = threatening, chasing, biting or/and hitting). We used the post-conflict-matched control method established by de Waal & Yoshihara (1983) to collect post-conflict and baseline data. Post-conflict observations (PC) were conducted after the last aggressive exchange between opponents and consisted of a 10-min period during which we recorded all affiliative and aggressive interactions between two individuals involving either one or both former opponents (Yamamoto *et al.*, 2015). Affiliative contacts were defined as contact swimming, synchronous breathing and swimming (at least 30” of continuous swimming) or flipper-rubbing, as established in previous studies (Tamaki *et al.*, 2006; Holobinko & Waring, 2010; Sakai *et al.*, 2010; Yamamoto *et al.*, 2015, 2016) (see **Table 9**). Renewed aggression was defined as the first aggression between former opponents during the PC period, and redirected aggression as the first aggression between a former opponent and a bystander. We also recorded the identity of the individual initiating the affiliative or aggressive contact (Yamamoto *et al.*, 2015, 2016). If the agonistic interaction was resumed within 2 minutes after the end of the last aggressive exchange, it was considered that the conflict was not ended, and the PC observation was cancelled (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015, 2016).

**Table 9.** Descriptions of aggressive, affiliative and submissive behaviour of bottlenose dolphins in this study.

Behaviour	Definition
<b>Aggression</b>	
<b>Threatening</b>	One dolphin abruptly opens its mouth at another dolphin ahead. This behaviour is often accompanied by shaking head movements and by jaw clapping (an abrupt closure of jaw with a loud sound). After Samuels & Gifford, (1997).
<b>Chasing</b>	One dolphin pursues another rapidly and persistently. This pursuit is usually accompanied by threats. After Samuels & Gifford, (1997).
<b>Hitting</b>	One dolphin abruptly makes contact with another with great force using tail, peduncle, or head. After Samuels & Gifford, (1997) and Yamamoto <i>et al.</i> (2015).
<b>Biting</b>	One dolphin abruptly makes contact with another with great force using teeth, sometimes resulting in rake marks. After Samuels & Gifford, (1997).
<b>Submission</b>	
<b>Flinch</b>	One dolphin immediate cringe, cower or recoil in response to the action of another dolphin. This behaviour usually adopts the form of an abrupt movement of one or more body parts (e.g. head) away from the other. After Samuels & Gifford, (1997).
<b>Flee</b>	Dolphin's abrupt, rapid, and immediate departure to > 1 m in response to the action of another dolphin. Includes: leap above water, breach out of the water, or flee to another pool. After Samuels & Gifford, (1997).
<b>Affiliation</b>	
<b>Contact swimming</b>	Two dolphins swim in synchrony less than 1/2 m apart, in a staggered position (one animal slightly forward of the other), and with intermittent physical contact. After Holobinko & Waring, (2010).
<b>Synchronous breathing and swimming</b>	Two dolphins swim in parallel at close proximity (< 0.6 m) and synchronizing their breath (< 2 s) and swimming speed. After Sakai, <i>et al.</i> (2010).
<b>Flipper-rubbing</b>	One dolphin brought its pectoral fin into contact with another dolphin and moved it along the surface of the other's body. After Tamaki, <i>et al.</i> (2006).

Each PC observation had its corresponding matched control (MC) observation that was carried out on the next possible observation day, starting at the same time ( $\pm 30$  min) as the corresponding PC (de Waal & Yoshihara, 1983). During MCs, we recorded all the affiliative and aggressive contacts involving the same individuals involved in aggressive or affiliative interactions in the PC for the same length of time (10 minutes) and registering the identity of the individual initiating the interaction (Yamamoto *et al.*, 2015, 2016). If an aggressive contact took place in the 10 min before a scheduled MC, the MC was postponed until at least 10 min after the aggression, for up to 40 min after the time the corresponding PC was taken, or until the following observation day (Yamamoto *et al.*, 2015). If the affiliative interactions that started after the end of an aggressive encounter continued during the scheduled MC, the MC observation was postponed until the end of the affiliative contacts (Yamamoto *et al.*, 2015). PC were discarded if no MC was recorded within 15 days of the initial conflict. There were some blind spots in the pools where we could not record dolphins' behaviour. Therefore, in the few cases in which we were unable to identify the individual initiating the aggressive or affiliative event we discarded the observation.

*Index of affiliation relationships:* To examine the effect of valuable relationships on dolphins' post-conflict affiliative contacts, we calculated the index of affiliation relationships (IA) between the four dolphins following the procedure described in Yamamoto *et al.* (2016). Relative frequencies of synchronous swimming were recorded for calculating the index of affiliation relationships in this group of captive bottlenose dolphins. Data of synchronous swimming between dolphins were recorded using group 0-1 sampling (Altmann, 1974) at 3-minute intervals excepting PC periods. Observations were conducted by the same person (APM) and occurred for approximately 70 min between 8:00 and 11:00 from May 2016 to November 2016. For calculating the index of affiliation relationships for each couple, the number of 1-0 sampling periods in which synchronous swimming between individuals A and B occurred ( $X_{AB}$ ) was divided by the number of 1-0 sampling periods in which the individuals A and B were observed ( $Y_{AB}$ ) (Whitehead & James, 2015; Yamamoto *et al.*, 2016).

### *Data analysis*

#### *Occurrence of post-conflict affiliation*

In order to examine the occurrence of reconciliation, we followed de Waal & Yoshihara (1983) and classified each PC-MC pair in three categories. If the first affiliative contact between former opponents occurred earlier in the PC than the MC, or only in the PC the pair was labelled as "attracted". If the first affiliative contact between former opponents occurred earlier in the MC than the PC, or only in the MC the pair was labelled as "dispersed". Finally, the pair was labelled as "neutral" if the affiliative contact took place at the same time in the PC and the MC, or occurred in neither observation (Fraser & Bugnyar, 2010). Each PC-MC pair was similarly categorized for unsolicited bystander affiliation, solicited bystander affiliation, appeasement, renewed aggression and redirected aggression.

To assess the occurrence of these post-conflict interactions, we examined whether the probability of affiliation increased after aggression (Yamamoto *et al.*, 2015). We run a generalized linear mixed model (GLMMs) with a Poisson error structure and log-link function for each type of post-conflict interaction. The dependent variable was the number of attracted and dispersed pairs for each former opponent pair (reconciliation), for winners (appeasement or solicited bystander affiliation by winners), or for losers (unsolicited and solicited bystander affiliation by victims). The predictor variable was whether the affiliation occurred after or without conflict, indicated by the type of PC-MC pair (after conflict = attracted; without = dispersed). We included each pair of former opponents

(reconciliation), the identity of the winner (appeasement or solicited bystander affiliation by winners), or the identity of the victim (unsolicited and solicited bystander affiliation by losers) as random effects.

For purposes of comparison with other groups, we assessed pair rates of conciliatory tendencies using the Corrected Conciliatory Tendency measure (CCT). We used the CCT to calculate a measure of the frequency of reconciliation between former opponents controlling for baseline levels of affiliation (Veenema *et al.*, 1994). Following Veenema *et al.*, 1994, we calculated the CCT as follows:  $100 \times (\text{number of attracted pairs} - \text{number of dispersed pairs}) / (\text{total number of PC-MC pairs})$ . We also calculated the triadic contact tendency (TCT) for each type of bystander affiliation (appeasement, unsolicited and solicited bystander affiliation) following formula:  $100 \times (\text{number of attracted pairs} - \text{number of dispersed pairs}) / (\text{total number of PC-MC pairs})$  (Call *et al.*, 2002).

### ***When does unsolicited-bystander affiliation occur?***

We examined the influence of several factors on the occurrence of unsolicited bystander affiliation using GLMMs. The factors entered in the model were related to the conflict (occurrence of other affiliation with the victim, occurrence of affiliative contacts with the aggressor and conflict intensity) and to the social features of the group (relationship quality of the bystander with the victim, identity of the victim, aggressor and bystander). We used GLMMs with binomial error structure and a logit link function. The dependent variable was the occurrence of unsolicited bystander affiliation (yes/no). To control for baseline levels of affiliation, we considered unsolicited bystander affiliation to have occurred when the PC-MC pair was labelled “attracted”. The identities of the aggressor, the victim and the bystander were entered as random factors to control for variation in individual contribution to the dataset. The best model (most parsimonious) was selected using Akaike’s Information Criteria (AIC) values. The AIC allowed us to identify the most parsimonious model that best explained the variance of the dependent variable with the least number of variables in the model (Clay & de Waal, 2013).

### ***The influence of relationship quality on unsolicited-bystander affiliation***

We also investigated whether the quality of the relationship between victim and bystanders influenced the degree of unsolicited bystander affiliation provided to victims. We used two measures of the level of unsolicited bystander affiliation between partners: The Consolation Index (CI) and the Triadic Contact Tendency (TCT). The CI is calculated for each dyad as the frequency with which each individual was the first to provide bystander affiliation to each partner (frequency of consolation), divided by the frequency with which the individual was a bystander in a conflict in which that partner was the victim (opportunity to console) (Fraser *et al.*, 2008; Fraser & Bugnyar, 2010). This index controls for the opportunity to provide affiliation and for the potential effect of consolation by multiple bystanders but does not control for baseline levels of affiliation between partners (Fraser & Bugnyar, 2010; Clay & de Waal, 2013).

To control for baseline affiliation levels, we calculated the TCT for each possible victim-bystander dyad as the  $(\text{number of attracted pairs} - \text{number of dispersed pairs}) / (\text{total number of PC-MC pairs})$  (Call *et al.*, 2002). The TCT only takes into account the first affiliative interaction between that victim and each bystander, irrespective of preceding affiliations that may have occurred with another bystander. Therefore, these two complementary measures of bystander affiliation are necessary to control for both the baseline levels of affiliation and the effect of multiple consolation interactions (Fraser & Bugnyar, 2010; Clay & de Waal, 2013). We used Linear mixed models (LMMs) to assess the effects of the victim-bystander relationship (IA) (fixed effect) on the CI and TCT values

(dependent variables) (Fraser & Bugnyar, 2010; Clay & de Waal, 2013). The identities of the victim and the bystander were included as random effects.

We also compared the qualities of the bystander-victim and bystander-aggressor relationships, as measured through the IA using LMMs to test the hypothesis that bystanders who affiliate with victims of aggression act as proxies for the aggressors (Wittig *et al.*, 2007; Fraser & Bugnyar, 2010). The dependent variable was the value of the bystander's relationship with each opponent (IA) for every conflict in which unsolicited bystander affiliation occurred. The predictor variable or fixed effect was the nature of the relationship (bystander-victim or bystander-winner). We included the identities of the bystander, victim and winner as random variables.

### *The influence of post-conflict affiliation on renewed and redirected aggression*

Using GLMMs with binomial error structure and a logit-link function, we assessed whether winners were more likely to engage in subsequent aggression (renewed and/or redirected aggression) in PC periods in which there was no post-conflict affiliation with the victim and/or the aggressor. The dependent variables were the occurrence of renewed, redirected aggression or at least one of these types of post-conflict aggression by winners (yes/no). To control for baseline levels of aggression, we considered renewed and redirected aggression to have occurred when the PC-MC pair was labelled "attracted". The predictor variables were the occurrence of post-conflict affiliative contacts with the victim (unsolicited or solicited bystander affiliation and reconciliation) and the occurrence of post-conflict affiliative interactions with the aggressor (appeasement, solicited bystander affiliation and reconciliation). We included the identity of the winner and loser as random effects.

For all GLMMs and LMMs, we run likelihood ratio tests comparing the full model (random and fixed effects) with the null model (only random effects) to test for overall significance of the best model's fixed effects (Clay & de Waal, 2013). All GLMM and LMM analyses were run using R 3.4.1. statistical software (R Core Team, 2017). GLMMs were run with the "lme4" package (Bates *et al.*, 2015) and LMMs with the "lmerTest" package (Kuznetsova *et al.*, 2016).

## 2.3. Results

A total of 57 conflicts were collected on 4 recipients of aggression (with 9 aggressor-victim dyads from the potential 12 ones), with a mean of 14.25 PC-MC pairs per individual (range= 3-31) and a standard deviation of 12.42. 77.19 % of the MC observations were conducted within 3 days after the PC observation. **Table 10** shows the IA for each pair of members of the group.

**Table 10.** Index of affiliative relationships.

Dyad	IA
Blue-Mateo	0.474
Estel-Blava	0.434
Estel- Mateo	0.116
Blue-Estel	0.079
Mateo-Blava	0.05
Blue- Blava	0.001

### *Occurrence of post-conflict affiliation*

#### **Reconciliation**

Using a GLMM we compared the proportion of attracted (mean  $\pm$  SD= 0.27  $\pm$  0.25) and dispersed (mean  $\pm$  SD= 0.24  $\pm$  0.30) PC-MC pairs for reconciliation. We found that affiliation between former opponents was not more likely to occur after aggression than during control periods, indicating that reconciliation was absent in this group of dolphins ( $\beta = -0.09$ , SE= 0.44,  $z = 0.22$ ,  $p = 0.83$ ). Mean CCT %  $\pm$  SD per pair of former opponents was 7.61  $\pm$  35.23.

#### **Solicited bystander affiliation by winners**

For solicited bystander affiliation by winners, the proportion of attracted pairs per winner was 0.13  $\pm$  0.19 (mean  $\pm$  SD) and the proportion of dispersed pairs, 0.08  $\pm$  0.16 (mean  $\pm$  SD). We found that, after a conflict, winners were not more likely to solicit affiliation than during control periods (GLMM:  $\beta = 0.62$ , SE= 0.47,  $z = 1.32$ ,  $p = 0.19$ ). In this group of captive dolphins, winners did not tend to initiate affiliative interactions with bystanders after a conflict. Mean individual TCT %  $\pm$  SD for solicited bystander affiliation by winners was 5.12  $\pm$  25.00.

#### **Appeasement**

The proportion of attracted pairs per winner was 0.29  $\pm$  0.26 (mean  $\pm$  SD) and the proportion of dispersed pairs, 0.17  $\pm$  0.14 (mean  $\pm$  SD). Using a GLMM we found that bystanders were not more likely to provide affiliation to winners after a conflict than during control periods ( $\beta = -0.76$ , SE= 0.45,  $z = 1.70$ ,  $p = 0.09$ ), indicating the absence of appeasement in this group of dolphins. Mean individual TCT %  $\pm$  SD for appeasement was 12.07  $\pm$  38.39.

#### **Solicited bystander affiliation by victims**

The proportion of attracted pairs per victim was 0.27  $\pm$  0.16 (mean  $\pm$  SD) and the proportion of dispersed pairs, 0.11  $\pm$  0.08 (mean  $\pm$  SD). Using a GLMM we found that victims were significantly more likely to solicit affiliation from a bystander after a conflict than during control periods, indicating the presence of solicited bystander affiliation by losers in this group of dolphins ( $\beta = 1.15$ , SE= 0.47,  $z = -2.46$ ,  $p = 0.01$ ). Mean individual TCT %  $\pm$  SD for solicited bystander affiliation by victims was 15.75  $\pm$  22.24.

#### **Unsolicited bystander affiliation**

The proportion of attracted pairs per loser was 0.25  $\pm$  0.18 (mean  $\pm$  SD) and the proportion of dispersed pairs, 0.06  $\pm$  0.07 (mean  $\pm$  SD). Using a GLMM we found that bystanders were significantly more likely to provide affiliation to victims after an aggressive event than during control periods ( $\beta = 0.98$ , SE= 0.48,  $z = -2.05$ ,  $p = 0.04$ ), indicating the presence of unsolicited bystander affiliation in this group of captive dolphins. Mean individual TCT %  $\pm$  SD for unsolicited bystander affiliation was 18.73  $\pm$  17.90.

#### ***When does unsolicited-bystander affiliation occur?***

We used GLMM to examine the factors predicting unsolicited bystander affiliation. When all possible models were compared using the AIC, the best fitting model was the one including the relationship between victims and bystanders and the intensity of the conflict as fixed effects (AIC= 81.73,  $\chi^2(1) = 15.86$ ,  $p < 0.001$ ) (Table 11). This model fitted significantly better to the data than the null model ( $p < 0.001$ ). The relationship between victims and bystanders strongly predicted the occurrence of unsolicited post-conflict affiliation ( $\beta = 1.62$ , SE = 0.49,  $z = 3.32$ ,  $p < 0.001$ ). Bystanders sharing a close relationship with the victim were significantly more likely to provide unsolicited

affiliation to victims than bystanders who did not have a close bond with the victim of aggression. Unsolicited post-conflict affiliation was more likely to occur after intense conflicts than after conflicts characterized by lower intensity of aggression, however, this effect was not significant ( $\beta = 1.21$ ,  $SE = 1.02$ ,  $z = -1.19$ ,  $p = 0.23$ ).

**Table 11.** The best fitting GLMM model for the occurrence of unsolicited bystander affiliation.

		AIC	$\chi^2$ (1)	p	
<b>Best fitting model</b>		81.73	15.86	< 0.001	
Dependent variable	Fixed effects	$\beta$	SE	Z	p
Unsolicited bystander affiliation	Bystander-victim IA	1.62	0.49	3.32	< 0.001
	Intensity	1.21	1.02	-1.19	> 0.05
Random effects		Variance	SD		
Victim identity		0.18	0.42		
Bystander identity		0.007	0.08		
Winner identity		0.00	0.00		

*The influence of relationship quality on unsolicited-bystander affiliation*

We used LMMs to examine the influence of the victim-bystander relationship on the level of unsolicited bystander affiliation. When we used the CI as a measure of unsolicited bystander affiliation, we found that the model including the value of the relationship between the victim and the bystander was significantly better at predicting CI's values when compared to the null model ( $AIC = -11.195$ ,  $\chi^2(1) = 13.992$ ,  $p < 0.001$ ). Thus, unsolicited bystander affiliation was more likely to occur between victims and bystanders who shared valuable relationships ( $\beta = 0.812$ ,  $SE = 0.160$ ,  $t = 5.064$ ,  $p = 0.002$ ). When the TCT was used to control for baseline levels of affiliation, the best model was also the one including the value of the relationship between the victim and the bystander. This model ( $AIC = -7.556$ ,  $\chi^2(1) = 7.567$ ,  $p = 0.006$ ) predicted TCT's values significantly better than the null model. So, the previous result was confirmed, showing that bystanders were more likely to provide unsolicited post-conflict affiliation to victims with whom they share a more valuable relationship ( $\beta = 0.591$ ,  $SE = 0.186$ ,  $t = 3.185$ ,  $p = 0.015$ ). In addition, we found that bystanders who initiated unsolicited affiliation with victims of a conflict shared a more valuable relationship ( $\beta = 0.321$ ,  $SE = 0.021$ ,  $t = 14.942$ ,  $p < 0.001$ ) with the victim of aggression than with the aggressor.

*The influence of post-conflict affiliation on renewed and redirected aggression*

We used GLMM to examine the factors predicting the probability that winners engage in post-conflict aggression (renewed aggression, redirect aggression towards bystanders or both). The most parsimonious model was the one including the occurrence of post-conflict affiliation directed to the winner of the conflict ( $AIC = 75.888$ ,  $\chi^2(1) = 5.198$ ,  $p = 0.023$ ). This model predicted significantly better the occurrence of post-conflict aggression than the null model ( $p = 0.023$ ). Post-conflict aggression was significantly more likely to occur after conflicts in which winners did not receive post-conflict affiliation ( $\beta = 1.641$ ,  $SE = 0.766$ ,  $z = -2.141$ ,  $p = 0.032$ ). Only in one out of 57 PC periods (1.75%) a bystander was subsequently attacked by the victim of the conflict. Thus, it seems that in

this group of dolphins, victims of aggression do not redirect their attacks towards bystanders during the post-conflict period.

## 2.4. Discussion

Given the predictions established in the theoretical framework for determining the function of bystander affiliation (Fraser *et al.*, 2009), our results suggest that unsolicited bystander affiliation has a distress alleviation function in bottlenose dolphins. Thus, these outcomes support the idea that consolation is a well-established behaviour among bottlenose dolphins and that this behaviour may be based on empathy.

In more detail, reconciliation was not found in this group of dolphins, concurrently with Holobinko & Waring's (2010), and in contrast to Weaver (2003) and Yamamoto *et al.*, (2015, 2016) who did find evidence of reconciliation between former opponents in other groups of captive bottlenose dolphins. Conciliatory tendencies (CCT) in our study group (8%) were lower than those previously reported in other groups of dolphins (44% (Weaver, 2003), 18% (Holobinko & Waring, 2010) and 15% (Yamamoto *et al.*, 2015)). In our study group, we did not find evidence of appeasement or solicited bystander affiliation by winners. Although Yamamoto *et al.* (2015) found positive evidence of the presence of appeasement, solicited bystander affiliation by winners was also absent in their study group. TCT levels for appeasement in this group of dolphins (12%), were similar to those found by Yamamoto *et al.* (2015) (11%) but TCT levels for solicited bystander affiliation by winners (5%) were higher than those reported by them (0.3%). In this study, the absence of reconciliation, appeasement and solicited bystander affiliation by winners could be due to the observed high rates of winners' post-conflict aggression towards victims or bystanders (74%). The high risk of being the target of renewed or redirected aggression suggests that the costs of affiliating with winners may outweigh its benefits and thus victims and bystanders may avoid approaching winners after the conflict. Group composition and sample size may also explain the disparities found in these different groups of captive dolphins.

In the wild, the most stable and long-lasting bonds in bottlenose dolphins are those between same-sex members, while associations between males and females are generally weak and related to the reproductive state of females (Smolker *et al.*, 1992; Connor *et al.*, 2000; Lusseau *et al.*, 2003). Data on the association levels in this group of captive bottlenose dolphins was consistent with the association patterns observed in the wild, showing that affiliation was higher among members of the same sex. The main function of reconciliation could be to repair the opponents' relationship mitigating the costs of aggressive events (Aureli & Waal, 2000; Aureli *et al.*, 2002; Fraser & Bugnyar, 2010). Therefore, it is expected to occur when the loss of a more valuable relationship entails larger costs for both individuals (Aureli *et al.*, 2002). According to this view, reconciliation should be more likely to occur between opponents that are mutually valued social partners. Since our study group only consisted of two males and two females, and most of the conflicts involved male-female aggression (77%), it is reasonable to expect lower rates of reconciliation since aggressive events occurred between less valuable partners. Therefore, in this group of captive dolphins, the costs associated with the high risk of renewed aggression may outweigh the benefits of reconciliation.

On the other hand, both solicited and unsolicited bystander affiliation with victims were found in this group of dolphins. Concurrently with Yamamoto *et al.*'s (2015) results, we found that victims of aggression solicited affiliation to bystanders after an aggressive event. In addition, the TCT for solicited bystander affiliation by victims in this group of dolphins (16%) was similar to that reported by Yamamoto *et al.* (14%) but lower than those reported for ravens (21% (Fraser & Bugnyar, 2010)) and bonobos (23-35% (Palagi *et al.*, 2004; Clay & de Waal, 2013)). Although a previous study found no evidence of unsolicited bystander affiliation in a group of captive bottlenose dolphins (Holobinko

& Waring, 2010), other two studies reported the presence of such contacts in captive dolphins (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015). Our data thus confirmed the occurrence of unsolicited bystander affiliation in another group of dolphins in captivity. TCT for unsolicited bystander affiliation in the study group was higher (19%) than that reported in other groups of dolphins (11% (Yamamoto *et al.*, 2015)) and some groups of chimpanzees (13% (Koski & Sterck, 2007)), but closer to those reported in ravens (21% (Fraser & Bugnyar, 2010)) and other groups of chimpanzees (17% (Romero & de Waal, 2010)).

We found that the strongest predictor of unsolicited bystander affiliation was the relationship between bystanders and victims. Bystanders who provided unsolicited post-conflict affiliation were likely to share a valuable relationship with the victim of the conflict, result consistent with the “Valuable Relationship Hypothesis” (Aureli *et al.*, 2002). Given that such partners should be more sensitive to each other’s distress, this result also supports the hypothesis that unsolicited post-conflict interactions have a distress-alleviating function (Aureli & Schaffner, 2001; Fraser & Bugnyar, 2010). Our results are in line with previous evidence in other primate and bird species showing that unsolicited post-conflict affiliation is provided by valuable partners (de Waal & Yoshihara, 1983; de Waal & Ren, 1988; Arnold & Whiten, 2001; Aureli *et al.*, 2002; Fraser *et al.*, 2008, 2011; Fraser & Bugnyar, 2010; Romero *et al.*, 2010; Clay & de Waal, 2013; Palagi & Norscia, 2013).

Our model revealed that the intensity of the conflict was also a determinant factor predicting the occurrence of unsolicited bystander affiliation. Bystanders were more likely to provide affiliation to victims after more intense conflicts, that is, when victims experience a higher degree of distress, suggesting that these contacts may indeed serve a distress-alleviating function. Although this factor was included in the best fitting model, its effect was not significant, maybe due to the scarce number of registered conflicts characterized by low levels of aggression. In addition, our results showed that bystanders shared a more valuable relationship with the victim of aggression than with the aggressor, contradicting the theory that unsolicited bystander affiliation serves as a substitute for reconciliation on behalf of the aggressor (Fraser *et al.*, 2009; Wittig, 2010). Thus, in this group of dolphins, bystanders did not act as proxies for the aggressor repairing opponents’ relationship.

We found that winners were significantly more likely to engage in subsequent aggression either with victims or bystanders during PC periods in which they received no post-conflict affiliation. Therefore, in this group of captive dolphins, post-conflict affiliation with winners served to reduce winners’ aggressive tendencies irrespective of the target of aggression. The fact that post-conflict affiliation with winners but not with victims reduced the general aggressive tendencies of winners, suggests that this type of affiliative contacts may have a distress-alleviation function as well. These results are consistent with Yamamoto *et al.*’s (2015) findings showing that bystander affiliation with winners reduced renewed aggressions by winners in bottlenose dolphins. Post-conflict affiliation with victims of aggression (solicited or unsolicited) did not reduce the probability of being the target of winners’ aggression. Conversely, Yamamoto *et al.* found that post-conflict affiliation initiated by victims to bystanders or vice versa also reduced the probability of winners’ renewed attacks. Furthermore, in this study, we only observed one PC in which a bystander was subsequently attacked by the conflict victim. Thus, in this group of dolphins, unsolicited bystander affiliation was not provided by individuals more likely to be targets of redirected aggression by victims. Our results thus do not support the hypothesis that bystanders may engage in post-conflict affiliation to protect themselves from subsequent attacks (Romero *et al.*, 2009, 2011; Koski & Sterck, 2009; Yamamoto *et al.*, 2015).

In brief, bystanders were more likely to provide unsolicited post-conflict affiliation towards victims with whom they share a close relationship, and after more intense conflicts, thus when victims were

expected to experience more distress. Bystanders were not more closely bonded with the aggressor than with the victim, suggesting that it was unlikely that they affiliated with losers as a way to restore former opponents' relationships. Furthermore, bystanders were not at risk of being the target of victims' redirected attacks, and post-conflict affiliation with victims did not protect them from winners' further aggression, so it does not seem that the main function of these affiliative contacts is self-protection. Therefore, according to the theoretical framework proposed by Fraser *et al.* (2009), our findings are congruent with a distress-alleviating function and with an empathy-based explanation for unsolicited bystander affiliation. When unsolicited bystander affiliation implies the alleviation of the victim's distress, this post-conflict interaction is also termed as consolation. Given that consolation is the most representative example of sympathetic concern, this behaviour has been related to empathy (de Waal, 2008). According to the literature, familiarity has robust effects in processes facilitating empathy in several contexts (Preston & de Waal, 2002), and thus consolation is also characterized by the directionality of the bystanders' affiliations, directed mostly towards familiar individuals. Although our results showed that unsolicited bystander affiliation was directed mostly toward valuable partners, and suggested that these affiliative contacts may have a reassuring effect in the victim, since we did not record levels of arousal, nor empirically assessed whether victims' distress was lower after affiliation than without bystander affiliation, we should use the term "consolation" with caution. Future studies should try to examine the effect of affiliative post-conflict contacts on victims and winners' distress level. Although assessing emotional responses in cetaceans is not an easy task (Simmonds, 2006), some behavioural and physiological responses such as changes in respiratory rate, dive and surfacing patterns may serve as indicators of short-term responses to stress in these species (Peddemors, 1990; Waples & Gales, 2002; Esch *et al.*, 2009; Eskesen *et al.*, 2009; Jensen, Delfour, & Carter, 2013). These indicators can be easily observed in captivity or in the wild, thus allowing researchers to measure changes in distress levels after or without post-conflict affiliative contacts in cetaceans. Moreover, given that consolation behaviour requires an emotional reaction towards the distressed party (Pérez-Manrique & Gomila, 2017), and may involve emotional contagion processes, it is possible that bystanders provide unsolicited affiliative contacts to victims to reduce their own negative arousal. Thus, it is also crucial to determine the effect of affiliative post-conflict contacts on the stress responses of bystanders to better understand the nature and mechanisms underlying unsolicited bystander affiliation (Fraser & Bugnyar, 2010).

Consolation behaviour requires that the bystander spontaneously realize that the victim of aggression needs reassurance and provide it (Fraser *et al.*, 2011). Thus, this process apart from involving some degree of sensitivity to the emotional needs of other individuals may require a basic cognitive evaluation of the situation and an effective level of emotional regulation to distinguish between personal and vicarious emotions. This emotional regulation allows individuals to respond differently depending on the source of the emotion (de Waal, 2008). On the other hand, although solicited bystander affiliation could be functionally similar to unsolicited bystander affiliation also reducing victims' post-conflict distress, its underlying mechanism could be different from that of consolation. Solicited affiliative contacts may only require that bystanders tolerate victim's approaches or recognize specific signals emitted by the victim that automatically trigger affiliative responses, irrespective of whether the victim is distressed or not. Therefore, it is crucial to distinguish whether the initiator of post-conflict affiliation is the bystander or the victim (Fraser & Bugnyar, 2010). Given that we were unable to record dolphins' calls during post-conflict periods, we must also be cautious about the initiator of an interaction, since calls prior to the first affiliative contact may have gone undetected. In bottlenose dolphins, certain vocalizations could have an important role in the facilitation of affiliative contacts; however, no study has yet explored their occurrence and their role during post-conflict periods. It has been shown that in periods of distress or when facing potential threats, bottlenose dolphins emit what it seems to be alarm calls (Lilly, 1963;

Esch *et al.*, 2009). Future studies thus should take into account the possible emission of those vocalizations during post-conflict periods.

Overall, the literature points to a great flexibility in the functions of unsolicited bystander affiliative contacts towards victims of aggression, varying depending on the species, context and the social conditions (Clay & de Waal, 2013). Although our findings are most consistent with a distress-alleviation function and an empathy-based hypothesis, other alternative explanations may also partially explain these outcomes and need not be mutually exclusive (e.g. associative learning, automatic reactions to aversive stimuli...) (Clay & de Waal, 2013). Post-conflict strategies have been observed to match the social system of the species and depend on the level of association between individuals (Seed *et al.*, 2007; Fraser & Bugnyar, 2010; Clay & de Waal, 2013). Therefore, it is possible that the variability observed in post-conflict strategies within groups of the same species are due to differences in the structure of relationships within the population. For example, in the wild, dolphins' social organization varies depending on the habitat, the ecological constraints, developmental state and sex, giving rise to different social structures ranging from stable and closely associated groups to populations characterized by unstable and temporal associations (Weaver, 2003; Lusseau *et al.*, 2003). In captivity, the specific social structure of the group might have also a great influence on the post-conflict strategies displayed by the individuals. So, the preferential conflict resolution strategy may vary depending on the group's sex ratio and the strength of the bond between individuals.

In summary, as reported in previous studies (Tamaki *et al.*, 2006; Yamamoto *et al.*, 2015), bottlenose dolphins in this study group provided unsolicited bystander affiliation to victims with whom they shared a close relationship, confirming the presence of such contacts in this cetacean species. It so seems that bottlenose dolphins display post-conflict strategies similar to those described in primate and bird species to alleviate distress and reduce the costs of aggressive encounters, and of group living in general. Moreover, the features of these affiliative contacts point to an empathy-based mechanism of unsolicited bystander affiliation in these animals. More studies are needed to assess the occurrence of such contacts across captive and wild populations and its distress alleviation function. Finally, future research should try to address the influence of sex, age, group structure, and context on dolphins' post-conflict strategies.

### 3. Study 3: Theory of mind and false belief attribution in bottlenose dolphins

#### 3.1. Introduction

According to the empathy model proposed by Frans de Waal, more sophisticated forms of empathy such as empathic targeted helping require perspective-taking, the capacity to adopt another's point of view (de Waal, 2007). This capacity is related to Theory of mind (ToM), the ability to attribute mental states to oneself and other beings. One of the most important achievements in the development of ToM is the ability to attribute false beliefs. Attributing a false belief state to another individual is considered to be the crucial element indicating the understanding of another's mental state (Dennett, 1978; Suddendorf, 1999; Tschudin, 2006). This is so since the attribution of false beliefs requires a real understanding that mental states represent the world by entailing an appreciation of the possibility that misrepresentations can occur (Suddendorf & Whiten, 2001). Therefore, the false belief task is considered to be one of the most important indicators of ToM, and thus the key task for assessing ToM capacities in infants and non-human species (Wimmer & Perner, 1983; Baron-Cohen, Leslie, & Frith, 1985; Call & Tomasello, 1999; Onishi & Baillargeon, 2005).

The extent to which the ability to attribute false beliefs appears in young children is a matter of a renewed debate, after the new evidence regarding false belief attribution in the second year of life (or even earlier) (Southgate, Senju, & Csibra, 2007; Surian, Caldi, & Sperber, 2007; Buttelmann, Carpenter, & Tomasello, 2009; Baillargeon, Scott, & He, 2010; Surian & Geraci, 2012; Rubio-Fernández & Geurts, 2013). These studies resort to methods such as Violation of Expectation and Anticipatory Looking, which try to infer what the individual understands on the grounds of her expectations. In infants, the results obtained in these types of implicit tests contrast with those observed in the standard, explicit, false belief task. In this classic test, children are asked to predict where an agent will look for a hidden object that was transferred to another location while the agent was absent (Perner & Lang, 1999). Children pass this test at around 4 years of age. One possible explanation for the dissociation holds that, due to performance limitations, the standard test masks existing knowledge at the earlier age. An alternative hypothesis argues that success in the two types of tasks depends on different cognitive bases (Perner & Roessler, 2012). The first explanation postulates an early available basic understanding of belief in infancy, the second one opts for a simple mechanism which not requires belief attribution. Perner and Roessler (2012) chose the second explanation and argued that early sensitivity to false beliefs shown in these recent experiments (implicit online tasks) reflects implicit/unconscious social knowledge of lawful regularities. That is, infants keep track of what agents perceive; in particular, the state of the world last seen by the agents (e.g. initial location of a hidden object). Focus on the agent activates these records when he/she reappears and makes the infants to think of what the agent had experienced, thus influencing their looking behaviour. Given that what the agent experienced corresponds to the content of his or her false belief, infants are able to anticipate the agent's future actions (e.g. looking for the object in the initial location and not in the actual one). This process, therefore, does not involve belief or knowledge attribution, only requires keeping track of the agent actions and remember that record later. If the success in the false belief implicit tasks relies on such a simple mechanism, it is reasonable to expect that young children and some non-human animals such as great apes or cetaceans could pass the online task anticipating the agent's behaviour.

In fact, two recent studies have shown that great apes (chimpanzees, bonobos and orangutans) can pass a false belief implicit test (Krupenye *et al.*, 2016; Buttelmann *et al.*, 2017). In an anticipatory-

looking test, great apes anticipated where an actor would search for an object based on the actor's false belief about the object's location (Krupenye *et al.*, 2016). These three ape species also distinguished true from false beliefs in an interactive helping paradigm, predicting which box an experimenter wanted and helping her to open it (Buttelmann *et al.*, 2017). These results are surprising given that, since the seminal paper in which Premack & Woodruff (1978) asked "Does the chimpanzee have a theory of mind?", no convincing evidence of false-belief attribution has been found in nonhuman primates (Call & Tomasello, 1999; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; Krachun *et al.*, 2009, 2010). However, as the infants' studies, this recent evidence in great apes have been called into question. For example, it has been argued that great apes could succeed in Krupenye *et al.*'s false belief task without computing mental states, simply by predicting behaviour or associating the actor with a particular location (Ben-Yami, 2016; Scarf & Ruffman, 2017). In addition, in the study of Buttelman *et al.* (2017), great apes did not pass the true-belief task casting doubt on whether their success in the false belief task was really due to belief attribution.

Apart from the evidence provided by studies on great apes, there is a lack of data on ToM and false-belief attribution in most animal species. It is particularly surprising the lack of studies on cetaceans, given how similar these animals and primates are in terms of cognitive abilities (Marino, 2002). Research on bottlenose dolphins, for example, has shown that they display abilities considered to be precursors of ToM what makes them ideal candidates for passing belief attribution tasks (Tschudin, 2001).

For instance, bottlenose dolphins are endowed with very sophisticated and complex cognitive abilities such as a robust joint attention capacity, considered to be a precursor of ToM (Gómez, 2005, 2007, 2010). Examples of this proficiency in joint attention tasks are dolphins' understanding and production of indicative pointing, that was linked to the attentional behaviour of the receiver (Xitco *et al.*, 2004), and the understanding of the focus of another's gaze (Pack & Herman, 2006). It has been suggested that they might be capable of producing referential gestures (Xitco *et al.*, 2001) as well. Dolphins also possess several abilities relevant to secondary representation such as imitation (Herman, 2002, 2010), mirror self-recognition (Reiss & Marino, 2001), means-end reasoning (Kuczaj & Thames Walker, 2006), and the ability to understand external representations (Herman, Richards, & Wolz, 1984; Herman *et al.*, 2001; Herman & Forestell, 1985). These are abilities required for an understanding of the self/other distinction and a precursor to understanding others as mental agents (ToM). Based on the great amount of reports describing helping behaviour in dolphins, it has been proposed that these animals could have some degree of empathic perspective-taking (see **Chapter 4, section 3.2.**). Empathic perspective-taking, defined as the capacity to understand another's specific situation, emotions or needs separate from one's own (de Waal, 2008), might thus require some ToM capacities. This ensemble of findings highlights the remarkable capacity and flexibility of dolphin social cognition and points out that dolphins are endowed with cognitive capacities that are required for passing a belief attribution test.

To date, however, there is only one pilot study on false-belief attribution in bottlenose dolphins (Tschudin, Call, & Dunbar, (1999) described in Tschudin, (2006)). In this study, four captive bottlenose dolphins were tested using a modified version of Call & Tomasello (1999) false belief task. Dolphins were first trained to associate a tap signal from an experimenter ("the communicator") on a box with the location of a fish reward. After the training, dolphins received a series of pre-test control trials and finally, they were tested in several false-belief trials. In these trials, an experimenter ("the hider") hid the reward in one of two boxes while the communicator observed. The boxes were behind a screen, and thus the dolphin could not see directly the baiting process. Then, the screen was removed and the communicator left the experimental area. The hider switched the boxes in full

view of the dolphin. The communicator returned and tapped the box in which she falsely believed that the reward was hidden. Finally, the dolphin was allowed to choose a box. Unlike great apes (Call & Tomasello, 1999), all four dolphins passed this false-belief test. However, it might also happen that during the previous training and the pre-test controls, dolphins could have learned a conditional discrimination rule that allowed them to solve the task without understanding or attributing false beliefs to the communicator (Tschudin, 2006). Therefore, dolphins were retested in a subsequent experiment to rule out alternative explanations not based on false-belief attribution (Tschudin, 2006). In this second experiment, three of the dolphins previously tested received a task including interspersed false and true belief trials. On true belief trials, the boxes were switched after the return of the communicator so that, this time, the communicator tapped the box containing the fish. Although a significant interaction between the belief state of the communicator and dolphins' responses were found, none of the dolphin's performances was significant (Tschudin, 2006). Furthermore, inadvertent cueing by the experimenter could not be ruled out (Tschudin, 2006). Another source of potential confound was that the dolphins that previously succeeded in the false belief trials were the same tested in this experiment. Thus, it was also possible that they used the previously learned conditional discrimination rule during the test (Tschudin, 2006). Tschudin tried to address these issues conducting a third experiment with a naïve dolphin at a different facility (Tschudin, 2006). The new task included three types of trials: false belief trials, true belief trials and "dud" belief trials (the boxes did not switch locations). However, the dolphin continuously failed during the training trials and thus testing was terminated at this point.

Regarding bottlenose dolphins' complex social cognition abilities and the non-conclusive results of Tschudin's experiments, it would be of great interest to assess false belief attribution in bottlenose dolphins using a different paradigm.

With this aim, in this study, we examined dolphin's ability to attribute false-beliefs using a variation of the anticipatory looking task, "the anticipatory pointing task". In this test, dolphins first interact with their trainer while he or she hides and recovers an object inside one of two boxes. During this interactive situation, dolphins are able to develop expectations about their trainers' future behaviour. Then, to get a reward, dolphins must anticipate in which of the two available boxes the trainer is going to look for the hidden object by pointing one of the boxes. To choose the correct box, dolphins need to consider the trainers' true or false belief about the location of the hidden object. This protocol, thus, takes advantage of the special attention that captive dolphins pay to their trainers. Dolphins were tested in three conditions similar to those of Tschudin *et al.* (2006): a false belief condition, a true belief condition and a baseline condition. Unlike Tschudin *et al.*'s paradigm, this protocol only included object's visible displacements due to dolphins' previous failure on invisible displacement tasks (Jaakkola *et al.*, 2010).

The first objective of this study, thus, was to create an interactive situation between dolphins and their trainers that allow dolphins to develop expectations about their trainers' future actions. The second aim was to design a new false-belief task adapted to this interactive situation and based on anticipatory pointing. If dolphins passed the task, the third aim of the study was to clarify the mechanism by which dolphins have succeeded in the task. For this purpose, dolphins were tested in several control conditions. We hypothesize that the only way to be successful in all the control conditions is by relying on intentional attribution. Therefore, these control tests served to assess whether dolphins passed the task by attributing knowledge or false-beliefs to their trainers or if, instead, they succeed by other means like keeping track of what the trainer had perceived and recalling that record later (epistemic tracking) as suggested by Perner & Roessler (2012).

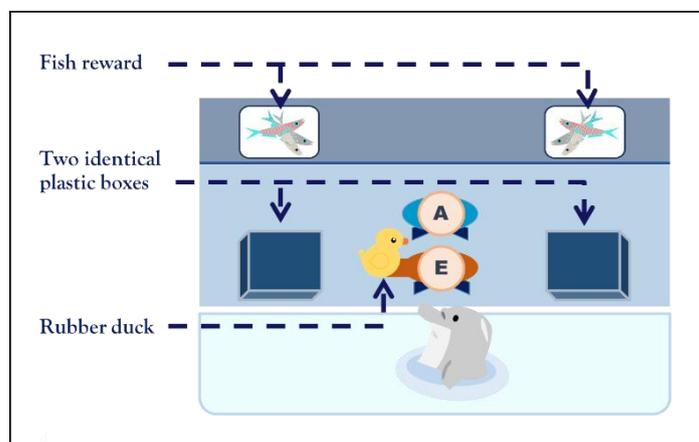
### 3.2. Method

#### *Subjects and facility*

In this study participated four female Atlantic bottlenose dolphins (*Tursiops truncatus*), housed at Marineland Mallorca. Two of the dolphins, *Stella* (7 years-old) and *Blava* (12-years-old), lived in an outdoor pool conjoined to a medical pool, with a total volume of 1846.75 m<sup>3</sup> of water. They shared the pool with a juvenile male. The other two participating females, *Estel* (12-years-old) and *Sacha* (11-years-old), lived in the show outdoor pool conjoined to two small pools with a total volume of 2296.82 m<sup>3</sup> of water. They shared the pool with two adult males. All the dolphins were captive born. They were fed according to their normal daily routine, which included a variety of fish (capelin, mackerel and herring) and gelatine. The experiment was generally conducted during the first training session of the day. During non-experimental sessions, the dolphins continued to participate in other training sessions including interactions with trainers and guests (*Blava* and *Stella*) and performing twice a day in the show (*Estel* and *Sacha*). None of the dolphins had participated before in cognitive tasks.

#### *Apparatus*

Material for this study were two identical black plastic boxes (39 x 28 x 28 cm). The boxes were positioned about 196 cm apart, at the edge of the pool and were covered by two black lids (39 x 28 cm). A rubber duck (18 x 14 x 16 cm) served as the target object. Two identical transparent plastic boxes (39 x 28 x 28 cm) covered by two transparent lids (39 x 28 cm) were used in the control conditions. During control conditions, a circular white buoy (35 cm diameter) also served as the distracting object. Fish (capelin, mackerel and herring) were used as rewards. The fish was placed in two identical plastic trays, one behind each box. Figure 14 shows the basic apparatus and testing setup. All sessions were videotaped using a waterproof camera SJCAM SJ4000.



**Figure 14.** Experimental setup and basic apparatus used in this study. **A:** actor, **E:** experimenter.

#### *Design and Procedure*

An experimenter and a trainer (“the actor”) participated in the study. The experimenter stood between the two boxes facing the dolphin, which stayed at the edge of the pool. In this initial position, the dolphin could not reach for the boxes. In turn, the actor (A) stood behind the experimenter (E) (see **Figure 15**). During the study, several trainers played the role of the actor, while the experimenter was always the same person. Each trial began with (E) showing the object (rubber duck) to the dolphin and handling it to (A). Then, (A) opened the lid of one of the boxes (counterbalanced order), put the object into it in full view of the dolphin and placed the lid on the box. What followed differed between conditions, but in all of them, the dolphin was rewarded by (A) if it anticipated where (A) would look for the object. The study consisted of four phases:

**1. Familiarization.** The boxes, the lids and the rubber duck were presented to the dolphins. All these objects were put in the pool and the dolphins could inspect them with echolocation and touch before testing. This procedure was repeated for several days.

**2. Pre-test.** The pre-test phase had two goals:

(1) Familiarize the dolphin with the apparatus, and (2) introduce the “choose signal”. The signal served to indicate the dolphin to choose one of the boxes anticipating the (A)’s movements. The pre-test phase consisted of three intermediate steps:

- a. *Introducing the object and signal:* (A) placed the object in different locations along the edge of the pool and returned to her position behind (E). Then, (E) gave the hand signal to the dolphin while (A) approached the object with an extended arm. The dolphin was rewarded if it touched the object at the same time that (A). In the first trials, (E) pointed to the object after giving the signal and (A) encouraged the dolphin to touch the rubber duck.
- b. *Introducing the boxes and the lids:* The boxes were placed on the edge of the pool at different locations. (A) placed the object on the edge of the pool or on top of one of the boxes and returned to her position behind (E). (E) gave the signal to the dolphin while (A) approached the object, the dolphin was rewarded for touching the object or the box in which the object was placed at the same time that (A).
- c. *Baseline trials:* Once the dolphin evidenced success with the previous procedure, pre-test composition was standardized and randomized. In this step, the dolphin generally received three sessions of 6 baseline trials per day. Baseline trials started with (E) showing the object to the dolphin. Then, (E) gave the object to (A) who opened the lid of one of the boxes and put the object inside it. (A) returned to her position behind (E). (E) gave the signal to the dolphin and once the dolphin has made its choice, (A) approached the box containing the object. If the dolphin chose the correct box, that in which the object was, (A) rewarded the dolphin with the fish placed on the tray behind the box. Then, (A) retrieved the object from the box and showed it to the dolphin. To avoid inadvertently giving cues to the dolphin, (A) stood behind (E) avoiding any visual contact with the dolphin. (E) always faced the dolphin during the test. The object’s location was counterbalanced across trials with the constraints that it was never placed more than two consecutive trials in the same box.

The main aim was that by the end of the pre-test phase the dolphin could anticipate (A)’s movement choosing the box that contained the object. Our criterion for moving from pre-test to testing was that the dolphin was correct in at least 5 out of 6 baseline trials in two consecutive sessions.

**3. Test.** Three different conditions were tested:

- a. *Baseline condition (B):* Baseline trials were identical to those of the pre-test phase.
- b. *True-belief condition (TB):* (E) showed the object to the dolphin and gave it to (A). (A) opened the lid of one of the boxes, put the object inside and returned to her position behind (E). (E) opened the lid of the box containing the object and transferred it to the other box in full view of (A) and the dolphin. Then, (E) closed the lid and returned to her position. (E) gave the signal to the



**Figure 15.** Photograph depicting the positions of the subject, the experimenter and the actor during the trials.

dolphin and (A) rewarded the dolphin if it chose the correct box, the one containing the object. Then, (A) opened the box and retrieved the object.

- c. *False-belief condition (FB)*: The procedure of the FB condition was similar to that of the TB condition with the exception that (A) left the scene after having hidden the object. (E) transferred the object to the other box in full view of the dolphin while (A) was absent. (E) gave the signal to the dolphin while (A) approached the scene. (A) rewarded the dolphin if it chose the correct box (the one in which (A) falsely believed the object was). (A) opened the empty box and waited until (E) approached the other box, retrieved the object and gave it to her.

The dolphin made its choice by swimming towards a box, pointing it with its rostrum and waiting until (A) approached the correct box. If the subject chose the correct box, that in which (A) believed that the object was hidden, the dolphin received positive reinforcements of fish and social interaction. If the dolphin chose the incorrect location, (A) or (E) (depending on the condition) retrieved the object and showed it to the dolphin. If during a trial the subject did not respond, swam away, or chose a box before the signal, the trial was repeated. During the experimental sessions, any other dolphins present in the pool were kept busy by the trainers. If one of those dolphins approached the experimental subject, the trial was aborted and resumed when the dolphin had returned to its trainer. In all conditions (E) ensured that the dolphin witnessed all the procedure and stopped if the subject became distracted.

During the first days of testing the FB and TB trials were introduced. Dolphins received several sessions of 7 trials per day (5 B trials, 1 FB trial, 1 TB trial). When dolphins were used to the new procedure, they received two sessions of 6 trials per day (three trials per condition: B, FB, TB). Order of trials was semi-randomized, with the constraints that the object was never placed more than two consecutive trials in any particular location. The object's location was counterbalanced across trials. Our criterion for moving from the testing phase to the control tests was that the dolphin was correct in at least 11 out of 12 trials (4 B, 4 TB, 4, FB) in two consecutive days.

**4. Control tests.** If dolphins succeeded in the testing phase, they were tested in three sessions of control tests. The purpose of the first two sessions was to control for the possibility that the dolphins were simply following learned conditioned rules to solve the task. The third session controlled for the possibility that dolphins passed the task following social cues unconsciously given by (E).

*Associative learning control tests*: Dolphins could have learned several low-level rules to pass the test such as:

- (1) If (A) stays, choose the box containing the object; if (A) leaves, choose the empty box.
- (2) If (A) stays and (E) retrieves the object, choose the box not touched by (A); if (A) leaves and (E) retrieves the object, choose the box touched by (A).
- (3) Always choose the last box (A) touched or paid attention to (Perner & Roessler, 2012).

To check the possibility that the dolphins followed any of these rules, dolphins were tested in several control trials (see **Table 12**):

- A. *FB-back turned*: Dolphins were tested in one FB trial in which (E) transferred the object hidden by (A) to the other box. (A) was present but stood with her back turned. In this case, although (A) stayed in the scene, she chose the empty box in which she falsely believed the object was. If the dolphin followed the first or the second rule, it should choose the box containing the object.
- B. *TB-same box-(A) absent*: Dolphins were tested in one TB trial in which, while (A) was absent, (E) retrieved the object hidden by (A) and put it back in the same box. (A) chose the box containing the object. If the dolphin followed the first or the second rule, it should choose the empty box.

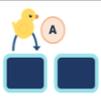
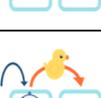
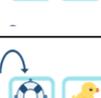
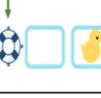
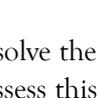
- C. *TB-same box*: (A) placed the object in one of the boxes. (E) retrieved the object and put it back again in the same box in full view of (A). If the dolphin followed the second rule, it should choose the empty box.
- D. *TB-empty box*: (A) placed the object in one of the boxes. (E) opened and closed the lid of the empty box in full view of (A). If the dolphin followed the second or the third rule, it should choose the empty box.
- E. *Baseline trial- (A) absent*: Identical to the baseline trial except that (A) left the scene and returned. If the dolphin followed the first rule, it should choose the empty box.
- F. *FB-transparent boxes*: Dolphins were tested in one FB trial with transparent boxes instead opaque ones. When (A) returned to the scene, he could see through the boxes and chose the box in which the object was. If the dolphin followed the first, second or third rule, it should choose the empty box.
- G. *FB-new object*: This trial served to control for the possibility that, in the previous trial, the dolphin chose the transparent box containing the object just because it was attracted by the object. Thus, the dolphin was tested in a trial in which, while (A) was absent, (E) transferred the object to the other box and introduced a new object (white buoy) in the initial box. If the dolphin followed the first rule, it should choose the box containing the new object.
- H. *TB-(A) absent- new object*: (E) put a new object in the empty box while (A) was absent. This trial controlled for the possibility that in the previous trial the dolphin chose the transparent box containing the object, not because it attributed knowledge to (A) but since it was attracted by the object.
- I. *FB-object out*: (E) retrieved the object while (A) was absent and put the object at the edge of the pool. When (A) returned, he could see the duck outside the boxes. If the dolphin followed the three mentioned rules it should choose an empty box.
- J. *FB-new object out*: To control for the possibility that in the previous trial the dolphin chose the object, not because it attributed knowledge to (A) but since it was attracted by the object, the dolphin was tested in a trial in which, while (A) was absent, (E) put a new object (white buoy) at the edge of the pool. If the dolphin followed the first rule, it should choose the empty box and if it is attracted by a new object located outside the boxes it should choose the new object.

The controls D, F and I also served to assess Perner & Roessler's (2012) account. In these trials, the dolphin's record of the (A)'s actions did not match the (A)'s updated belief about the current location of the object. Thus, the dolphin could not correctly anticipate the (A)'s behaviour only tracking her actions and recalling them later.

Dolphins were tested in these control trials in two consecutive days. During the first day, they were tested with the opaque boxes. The testing consisted in one session of 6 testing trials (2B, 2FB, 2TB) and one session of 6 control trials (one trial of the controls A, B, C, D; two trials of the control E (one per box)). During the second day, they were tested with the transparent boxes. The testing consisted in one session of 4 testing trials (2B, 2TB) and one session of 6 control trials (one trial of controls G, H, I, J and two trials of the control F (one per box)). The object's location was counterbalanced across trials with the constraints that it was never placed more than two consecutive trials in the same box. To avoid the possibility of cueing, the trainer who played the role of the (A) in

the control tests remained unaware of the objective of the study and thus, she did not know which box was the correct one. Once the dolphin had chosen a box, (E) verbally told (A) which was the correct box.

**Table 12.** Expected responses in each control condition depending on dolphins’ response strategy.

Control	Actor	Correct response	Response following rule 1	Response following rule 2	Response following rule 3	Attraction to the object	Example
<b>A</b>	Present Back turned	<b>Empty box</b>	Box containing the object	Box containing the object	Empty box	-	
<b>B</b>	Absent	<b>Box containing the object</b>	Empty box	Empty box	Box containing the object	-	
<b>C</b>	Present	<b>Box containing the object</b>	Box containing the object	Empty box	Box containing the object	-	
<b>D</b>	Present	<b>Box containing the object</b>	Box containing the object	Empty box	Empty box	-	
<b>E</b>	Absent	<b>Box containing the object</b>	Empty box	Box containing the object	Box containing the object	-	
<b>F</b>	Absent	<b>Box containing the object</b>	Empty box	Empty box	Empty box	Box containing the object	
<b>G</b>	Absent	<b>Box containing the object</b>	Empty box	Box containing the new object	Box containing the new object	Box containing the new object	
<b>H</b>	Absent	<b>Box containing the object</b>	Empty box	Box containing the object	Box containing the object	Box containing the new object	
<b>I</b>	Absent	<b>Object</b>	Empty box	Empty box	Empty box	Object	
<b>J</b>	Absent	<b>Box containing the object</b>	Empty box	Box containing the object	Box containing the object	New object/Object	

(E) always knew which was the correct box, thus it could be possible that the dolphins solve the tasks by reading unintentional body language or following another type of social cue. To assess this possibility, dolphins were tested in a third session of control tests:

*Social cues control test:* Dolphins received one session of 6 testing trials (2 FB, 2 TB, 2 B). In this session, both boxes were located to the right of (E) and (A). In this manner, (E) could not unconsciously indicate the side in which the correct box was located when giving the signal to the dolphin.

### Coding

A dolphin was coded as making a choice when it was positioned in front of a box, pointing at it with its rostrum. The dolphin must wait in front of the chosen box until the trainer approached one of the boxes. All trials were videotaped and the dolphin's choices were scored by reviewing the video-recordings. Dolphins' choice was unambiguous; therefore, no reliability coding was conducted.

### 3.3. Results

#### Pre-test

All dolphins learned to choose the box in which the trainer was to search for the object, in this case, it was also the box containing the object. Dolphins attained the criterion of at least five correct trials within the same session in two consecutive sessions in an average of 29.75 trials (SE = 6.18; range = 18–47). Dolphins selected the correct box on an average of 89.6% of the trials (SE = 3.99) in their last two sessions, a performance that is well above chance (one-sample *t*-test, one-tailed:  $t(3) = 9.92$ ,  $p < 0.01$ ).

#### Test

Only *Stella* attained the criterion of at least eleven correct trials in the test on two consecutive days (binomial test,  $p < 0.001$ ). Two of the dolphins (*Sacha* and *Estel*) became uncooperative during testing, swimming away repeatedly and were dropped from the study at the beginning of the testing phase. Even so, all the dolphins were tested at least in two testing sessions. *Stella*, *Sacha* and *Blava* succeeded in the first two trials of the FB condition. On the other hand, *Estel* failed the first two FB trials. All four dolphins succeeded in their first trial of the TB condition, while *Sacha* also succeeded in the second trial of this condition.

Considering all the testing sessions, *Blava* performed above chance in the B and the TB condition (binomial test,  $p < 0.001$  in both cases) but not in the FB condition. In turn, *Stella* performed above chance in all three conditions (binomial test,  $p < 0.05$  for B condition,  $p < 0.01$  for TB and FB conditions) (see **Figure 16** for individual performances).

In the two last days of testing, *Blava* and *Stella*'s individual performance was above chance levels (binomial test,  $p < 0.05$ ) with *Blava* scoring 0.71 and *Sacha* 0.96 success rate. *Blava* performed significantly above chance levels only in the B condition (binomial test,  $p < 0.05$ ). *Stella*'s performance was above chance levels in all three conditions (binomial test,  $p < 0.05$  for B condition,  $p < 0.01$  for TB and FB conditions).

*Blava* failed to reach criterion in the test. She received a total of 343 testing trials during 25 days (see **Figure 17**). To avoid causing any distress to the animal and following her lack of success we terminated her testing. We examined *Blava*'s strategies across the testing phase. We could identify three distinct periods based on the strategy used by *Blava* (see **Table 13**). During the first days of testing (days 1–9), *Blava* chose the correct box in the B condition above chance levels (binomial test,  $p < 0.001$ ) while in the other two conditions she did not follow a fixed strategy but chose the right box in most of the trials. In the second period (days 10–21), she performed above chance levels in the B and TB condition (binomial test,  $p < 0.001$  in both cases) and she chose the right box above chance levels in the FB condition (binomial test,  $p < 0.001$ ). Finally, in the third period (days 21–25) she also performed above chance levels in the B and TB conditions (binomial test,  $p < 0.05$  in both cases) and she chose the left box significantly above chance in the FB condition (binomial test,  $p < 0.05$ ).

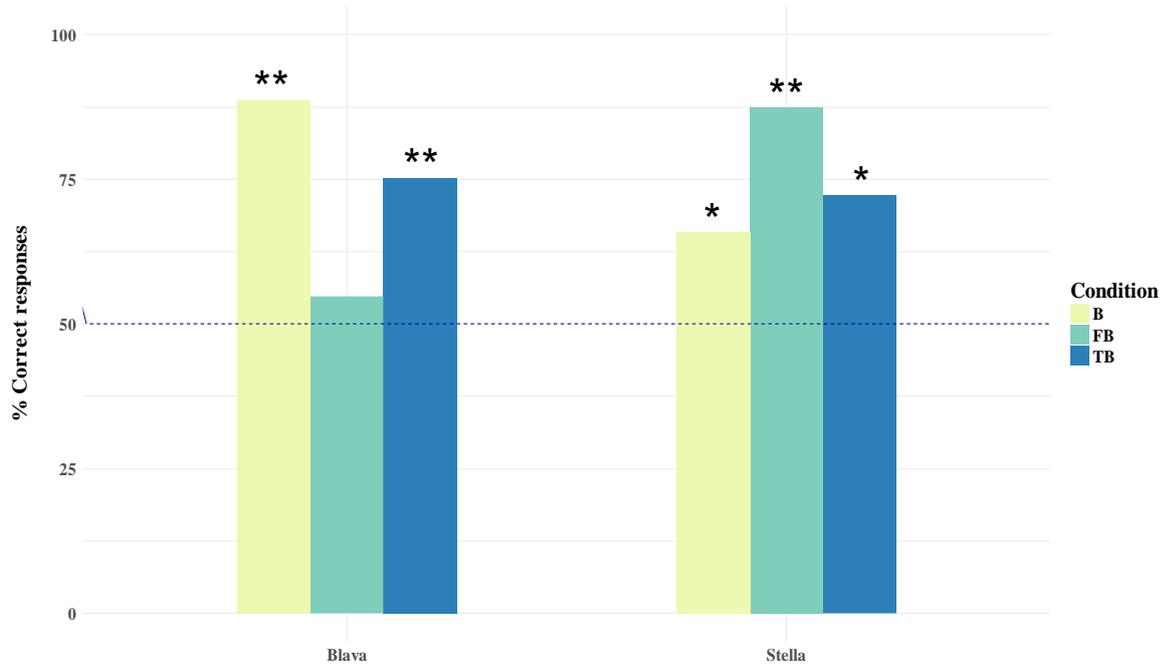


Figure 16. Proportion of total correct responses per condition in all testing sessions for each individual \*\*  $p < 0.01$ , \*  $p < 0.05$ .

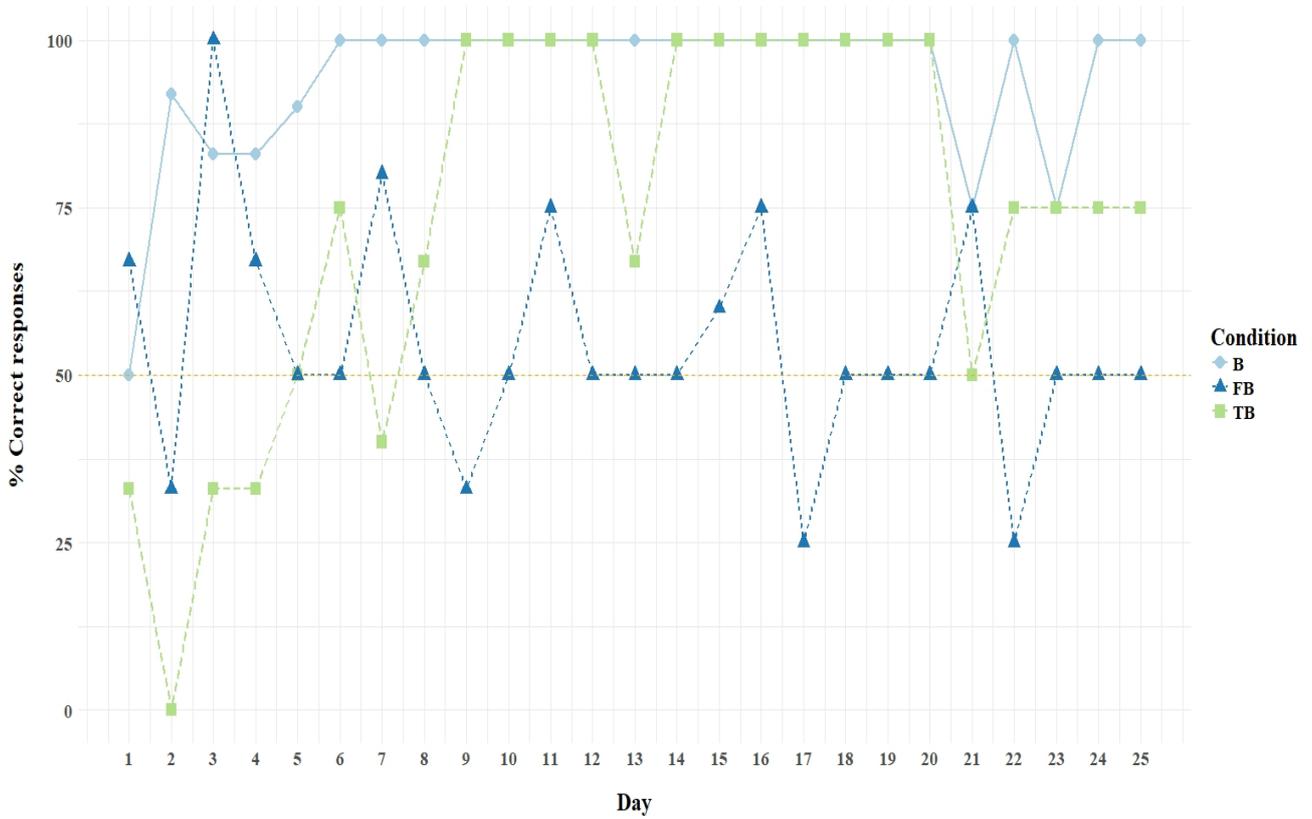


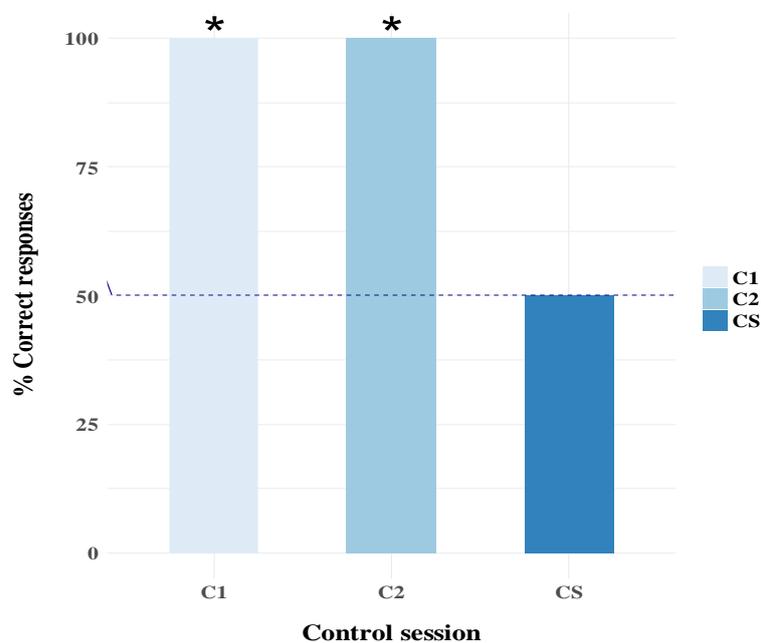
Figure 17. Blava's performance in the testing phase.

**Table 13.** Response strategies for *Blava* in the testing phase. C = correct box, R = right box, L = left box. \*\*  $p < 0.01$ , \*  $p < 0.05$ .

Condition				Strategy
Period	B	TB	FB	
Days 1-9	C**	R	R	In the B condition choose the box with the object or the last touched box, in the new conditions (TB and FB) choose the favoured box (R).
Days 20-21	C**	C**	R**	If the (A) stays choose the box with the object or the last touched box, if the (A) leaves choose the favoured box (R).
Days 22-25	C**	C*	L*	If the (A) stays choose the box with the object or the last touched box, if the (A) leaves choose the left box (L).

### Control tests

*Stella*'s performance in the two associative learning control sessions was above chance (binomial test,  $p < 0.05$ ). She passed all the control trials with both the opaque and transparent boxes. Conversely, *Stella* did not perform significantly above chance in the social cue control test (binomial test,  $p > 0.05$ ), choosing in all the trials the right box (binomial test,  $p < 0.05$ ) (see **Figure 18**).



**Figure 18.** Proportion of correct responses per control session for *Stella*. **C1**: associative learning control (opaque boxes), first session; **C2**: associative learning control (transparent boxes), second session; **CS**: social cues control, third session. \*  $p < 0.05$ .

### 3.4. Discussion

Only one of the dolphins, *Stella*, attained criterion in the testing phase, and thus she was tested in two types of controls, associative learning and social cues control tests. The dolphin succeeded in the associative learning control tests but not in the social cues control condition. This result suggests that *Stella* passed the test and the subsequent control trials by following inadvertent social cues given by the experimenter. Further analysis of the videos of the two last testing sessions and the two associative learning control sessions using “Kinovea” free software (<http://www.kinovea.org>) revealed a correct side-bias of the hand signal given by the experimenter in about 90% of the trials. In most of the trials thus the experimenter gave the signal with a slight deviation towards the correct box. Although the experimenter’s movements were fast, making this bias subtle and difficult to see, the dolphin may have been able to detect it and use it to correctly solve the task. Therefore, *Stella* could have guided its responses all along by noticing the slightly lateralized “choose” signal of the experimenter, who might have been cueing the box that counted as the right response given the condition.

Conversely, the other dolphin, *Blava*, did not seem to notice the experimenter’s unintentional biased signal and did not use it as a clue to choose the correct box. Its differential success across the three different conditions did not point in that direction. *Blava* did not attain criterion in the test, she only performed correctly in the B and TB conditions. Despite the long learning phase, *Blava* was unable to succeed in the FB condition. She followed different strategies in the testing phase. During the first days of testing, she only succeeded in the B condition, the one that she had learned in the pre-test. She seemed to treat equally the new TB and FB conditions, generally choosing the same box (right or left) in both conditions across sessions. In the period between day 10 and day 21, she succeeded in the B and TB conditions but not in the FB condition, choosing the box located on the right in most of the FB trials. In this period, she seemed to follow a conditional rule such as: if the trainer stays, choose the box containing the object or the last box the trainer or the experimenter had touched or paid attention to; if the trainer leaves, always choose the box located on the right. This was a very effective strategy. Using this rule, the dolphin attained an 83.3% of correct responses in a session, failing only the FB trial in which the experimenter transferred the object from the left box to the right box. During the last days of testing, she used a similar strategy performing correctly in the B and TB conditions but choosing the left box in most of the FB trials. This pattern of responses indicates that, although the dolphin seemed to differentiate between conditions, she did not solve the task attributing knowledge or beliefs to the trainer. If the dolphin had considered the trainer’s goal of retrieving the object, even if she was unable to attribute false beliefs to her, it should have chosen the box containing the object in all the conditions. But this was not the case. This suggests instead that *Blava* likely used simple conditional discrimination rules. She seemed to distinguish between two categories of trials, the ones in which the trainer stayed and those in which she left, applying a different rule to each category and thus responding differently in each case.

In Tschudin’s (2006) study, the dolphins also seemed to pass the task by using simple conditional rules. In fact, follow-up controls indicated that in the only task in which dolphins apparently succeeded, they likely used learned local rules. Further support for this hypothesis comes from evidence suggesting that dolphins are unable to pass invisible displacement tasks such as transpositions (Jaakkola *et al.*, 2010). In Tschudin’s experiment, false and true belief trials included a transposition procedure in which both boxes switched locations, so the hidden reward was invisibly displaced inside one of the boxes. Thus, dolphins needed to master object permanence to succeed in these trials by means of attributing beliefs to the communicator. However, according to Jaakkola *et al.*’s findings, dolphins cannot track this type of invisible displacements casting doubt on dolphins’ success in this task. So, although in Tschudin’s study dolphins were able to pass the pre-test controls

assessing their understanding of visible and invisible displacements, they likely succeed in those controls using a conditional discrimination rule. Furthermore, dolphins also seemed to have difficulties to pass visible displacement tasks. In Jaakkola *et al.*'s study, only three out of six dolphins passed the single visible displacement task and only one out of six dolphins passed the double visible displacement test. Thus, dolphins' difficulties to track the visible displacements of objects could have also influenced their performance in our study and it is a factor that we will examine in the following study.

Dolphins' prior training in the aquatic park may have also interfered in their performance in this test. These dolphins associate a specific trainer's hand signal with a specific behavioural response. Any change in this signal implies a change in the dolphin's response. Thus, trained dolphins seem to have fixed expectations of what they must do in response to a signal, and these responses have always been motor actions such as "jump", "swim", "go", "wait" ... In fact, during the first sessions of the pre-test, we observed that some dolphins responded to the "choose" signal performing a previously trained trick that consisted in swimming to one of the boxes and staying in that box until the trainer signalled the end of the trial. In our study, however, the experimenter's "choose" signal required moving to one or the other box, depending on the condition. Furthermore, the dolphins must consider another individual's actions and beliefs to decide how to respond to the same signal. It is possible that, due to their prior training history, this change in the procedure of the task was too demanding for the dolphins. Interestingly, we observed that *Blava* did anticipate the movements of the experimenter during the experimental procedure. Given that *Blava* could move freely while the experimenter transferred the object in the TB and FB conditions, she started anticipating the next movement of the experimenter, spontaneously swimming to the box in which she will retrieve or hide the object. However, *Blava* did not anticipate the trainer's subsequent movements after receiving the signal, as if she was unable to connect her action to her previous vision and the current position of the object. Therefore, although *Blava* seemed to anticipate the experimenter's movements prior the signal, once she received the signal, she responded as she used to do: performing a fixed motor action (swimming to the right or to the left) without considering the trainer's knowledge or beliefs. So, it is possible that the signal disrupted the dolphin's process of keeping track of the trainer's actions in a similar way that verbal designs of classical false-belief tasks tend to disrupt the infant's perspective-taking process (Rubio-Fernández & Geurts, 2013).

All dolphins were tested at least in two sessions of the test. Three dolphins succeeded in the first two trials of the FB condition and four in the first trial of the TB condition. Furthermore, one dolphin succeeded in the two first trials of both conditions. This result is suggestive, even though group and individual performances on different test conditions did not reach significance, probably due to the small number of trials run with each individual. Dolphins' success in the first trials of the FB condition could be explained by a simple mechanism such as the one proposed by Perner and Roessler (2012), which does not require belief attribution. The dolphin may have kept track of the trainer's actions and her reappearance in the FB condition reactivated the record of her last actions (hiding the duck in the currently empty box), driving the dolphins' attention to the correct box and thus influencing their responses. In general, it is possible that the actor's reappearance in the FB condition makes this record more salient than the record of the actor's actions in the TB condition, in which the actor is always present. In fact, some studies have shown that infants and chimpanzees passed FB tasks but not TB tasks (Tschudin, 2006; Buttelman *et al.*, 2009, 2017). Finally, as the test phase progressed and the dolphins received more trials, this effect may have been obscured by retroactive or proactive interference.

Although dolphins seemed to respond well in the first trials of the false and true belief conditions, only one dolphin passed the test performing correctly in the three experimental conditions. However,

this dolphin succeeded in the test not by attributing false beliefs to the actor, but by following inadvertent social cues given by the experimenter. The other dolphin tested in more than two testing sessions seemed to follow conditional discrimination rules rather than considering the trainer's beliefs during the testing phase. Overall, these results show that, while the dolphins clearly form expectations about the actions the humans with which they interact are going to perform, these expectations do not keep track of the humans' informational states, but are rather related to available locations or objects. Thus, neither our study nor that of Tschudin provided convincing evidence of the ability of dolphins to attribute false beliefs. Future studies should examine dolphins' ability to attribute false beliefs using paradigms that control for social cueing, associative learning strategies and with procedures that do not require object permanence abilities or trained signals.

## 4. Study 4: Object permanence and secondary representation in bottlenose dolphins

### 4.1. Introduction

Object permanence, the understanding that objects continue to exist even when they are out of sight, is considered to be a fundamental element of spatial cognition (Piaget, 1953, 1955). According to Piaget (1954), the development of object permanence proceeds through six stages. He assessed this capacity in children using both visible and invisible displacement tasks. In visible displacement tasks, an object is usually hidden in one of several containers in full view of the child. In invisible displacement tasks, the target object is placed inside one container that, in turn, is placed inside another recipient. The object is invisibly transferred from the first container into the second, and the former –now empty–, is shown to the child. It is at Stage 6 that children (around 18 months of age) are able to solve these complex invisible displacement tasks. In other words, they understand that the object placed inside a container moves with the container. Piaget (1954) suggested that Stage 6 signals the emergence of a new representational capacity. In Piaget's view, at Stage 6 the child would already acquire the capacity to use mental representations to track and reconstruct the invisible movements of hidden objects. In its turn, Perner (1991) suggested that the emergence of this new representational capacity, that he called secondary representation, is marked by a cluster of abilities including means-end reasoning, pretence, empathy, mirror self-recognition, interpretation of external representations, and understanding of invisible displacements. Thus, the ability to track invisible displacements is generally considered as an indicator of secondary representation (Piaget, 1955; Perner, 1991; Suddendorf & Whiten, 2001).

The developmental origins of object knowledge, including object permanence, is fundamental to cognitive science and has been a heavily debated topic. In general, we can distinguish three main views (Johnson, Amso, & Slemmer, 2003; Bremner, Slater, & Johnson, 2015). The first one is based on Piaget's constructionist account, according to which infants develop object permanence through active manual exploration of objects (Piaget, 1953, 1955). Thus, the emergence of object representations is linked to children's motor development. Subsequent evidence challenged this Piagetian account by showing that much younger infants, and long before they can move and manipulate objects, may have an understanding of some elements of the object concept (Baillargeon, Spelke, & Wasserman, 1985; Baillargeon & Renée, 1987; Hespos & Baillargeon, 2001). This evidence comes from studies using methods such as anticipatory looking or violation of expectation, that do not rely on active searching for objects. Four months old infants' success in these paradigms have led to postulates of innate object knowledge (Spelke *et al.*, 1992). An alternative view posits that theories based on innate knowledge may neglect the potential contributions of learning and previous visual experience to guide the acquisition of object knowledge (Johnson *et al.*, 2003). This account suggests that initial object concepts are learned from experience early in postnatal life (Johnson *et al.*, 2003).

Object permanence has also been a subject of interest in animal cognition. Although many studies of visible and invisible displacements have been conducted in non-human animals, findings on most animal species are controversial (reviewed by Jaakkola, 2014). Most of the criticisms focus on methodological issues such as number of trials, training, lack of blinding protocols or control conditions, and number and disposition of containers (Jaakkola, 2014; Cacchione & Rakoczy, 2017). Due to these procedural differences across tasks, results on different species are not usually directly comparable (Cacchione & Rakoczy, 2017). Furthermore, several cognitive skills are

required to succeed in object permanence tasks, thus proper interpretation of results is often difficult (Cacchione & Rakoczy, 2017).

To succeed in visible displacement tasks not only requires a basic understanding of continuously existing objects but also to deal with several executive demands (visually track the object movements, planning behaviour, memory and inhibitory capacities) (Cacchione & Rakoczy, 2017). Children about 12 months of age succeed at this task (Piaget, 1955). In turn, many studies have demonstrated that most primates (Vaughter, Smotherman, & Ordy, 1972; Natale *et al.*, 1986; Spinozzi & Natale, 1989; Schino, Spinozzi, & Berlinguer, 1990; Dumas & Brunet, 1994; de Blois, Novak, & Bond, 1998; Call, 2001; Hauser, 2001; Neiworth *et al.*, 2003), cats (*Felis silvestris catus*) (Dore, 1986; Dumas & Doré, 1991; Goulet *et al.*, 1994), dogs (Triana & Pasnak, 1981; Gagnon & Doré, 1992, 1993, 1994; Collier-Baker, Davis, & Suddendorf, 2004) and several species of birds (Pepperberg & Kozak, 1986; Dumas & Wilkie, 1995; Pepperberg, Willner, & Gravitz, 1997; Auersperg *et al.*, 2014) also succeed in visible displacement tasks.

Paradigms involving invisible displacements are further complicated. These tasks not only require understanding that a hidden object still exists and moves with the moving container but also visually tracking its movements in presence of several distractors (Barth & Call, 2006). This implies that the spatial representations and positions of the hidden object must be updated constantly (Barth & Call, 2006).

Mastering invisible displacement tasks involves a conglomerate of: (1) executive demands (advanced inhibitory and memory capacities); (2) reasoning demands (advanced spatial reasoning skills, logical reasoning or coordinate representation), and (3) sensitivity to context factors (disposition of containers and objects, number of trials etc.) (Cacchione & Rakoczy, 2017). Children pass invisible displacement tasks around 18–24 months of age (Piaget, 1955). It is at this age when children also acquire other cognitive abilities related to the capacity to coordinate multiple representations of reality (language, instrumental problem-solving or self-recognition) (Perner, 1991; Cacchione & Rakoczy, 2017). Non-human animals have been tested in invisible displacement tasks using different paradigms. Some of these paradigms have been called into question for not being properly blinded or for not including control conditions (Jaakkola, 2014). Therefore, positive findings on most species are still controversial. Overall, there is a consensus that only great apes and parrots are able to reliably pass invisible displacement tasks (e.g. Pepperberg *et al.*, 1997; Barth & Call, 2006; Collier-Baker *et al.*, 2006; Auersperg *et al.*, 2014).

One of the experimental paradigms used to assess invisible displacement tracking abilities is the transposition task. In this task, the object is visibly placed inside one of several containers, and then the container is moved to another location. In the most demanding version of this task, the container in which the object is hidden switches locations with another container (Barth & Call, 2006). Spatial transpositions usually imply that multiple elements move at one time thus eliminating any potential bias toward particular containers that moved (Beran & Minahan, 2000). Two-year-olds found transposition tasks harder than the Piaget's stage-6 invisible displacement task, whereas great apes performed equally well in both paradigms (Beran & Minahan, 2000; Call, 2003; Barth & Call, 2006). Unlike children, Goffin cockatoos (*Cacatua goffini*) found transposition tasks easier than Stage 6 tasks (Auersperg *et al.*, 2014).

Object permanence has not been extensively assessed in cetaceans and the few existing studies have provided contradictory data. Bottlenose dolphins succeeded at visible displacements tasks but failed a series of experiments involving invisible displacements like transposition tasks (Jaakkola *et al.*, 2010). Conversely, they seemed to follow the invisible movements of a disc in a visual display

which involved object occlusion rather than containment (Johnson *et al.*, 2015). These are totally unexpected results due to the previous success of dolphins in tasks assumed to require secondary representation and other cognitive capacities involved in object permanence (Marino *et al.*, 2007; Mercado III & DeLong, 2010). Thus, these conflicting evidence raise the question of whether dolphins do indeed master object permanence.

Jaakkola *et al.* (2010) proposed two main hypotheses to explain dolphins' general failure in invisible displacements tasks:

(1) *Lack of understanding of containment*: Infants, for example, seem to learn separately how occlusion and containment operate (Hespos & Baillargeon, 2001; HESPOS & BAILLARGEON, 2006). In two experiments, they were able to reason about height in occlusion but not in containment events; suggesting that understanding of containment is acquired later in infancy (Hespos & Baillargeon, 2001; HESPOS & BAILLARGEON, 2006). Likewise, lack of understanding of containment could explain dolphins' failure on tasks involving containment and their success on tasks involving occlusion.

(2) *Lack of experience tracking objects hidden from both sight and echolocation*: It could be that, due to dolphins' reliance on echolocation, they may not have gained the necessary empirical experience to develop the capacity to track invisible displacements (Jaakkola *et al.*, 2010). In fact, two different experiments with infants and chicks highlighted the crucial role of early experience viewing objects undergoing different events for the development of object permanence skills (Johnson *et al.*, 2003; Prasad, 2015).

Dolphins live in aquatic environments in which objects often move differently than out of the water. Given this particular aquatic environment and their reliance on echolocation, it is very likely that dolphins lack previous visual experience with the invisible movements of objects hidden inside other objects. Furthermore, due to the different physical properties of air and aquatic environments, dolphins' early experience with moving objects underwater could not apply to what they observe out of the water. For these reasons, dolphins are an ideal model to assess the role of previous visual experience in the acquisition of object permanence abilities.

Due to dolphins' successes across a variety of tasks requiring advanced cognitive abilities related to secondary representation (reviewed in Pack & Herman, 2006; Jaakkola *et al.*, 2010), it seems unlikely that a general incapacity for secondary representation explains their previous failure in invisible displacement tasks (Jaakkola *et al.*, 2010). Therefore, we hypothesized that this failure was due to their lack of visual experience with "containment" and with the movement of objects hidden inside other objects out of the water. Due to this lack of experience, it is reasonable that, even the simplest object permanence task poses a greater challenge for dolphins than for terrestrial animals like primates. Thus, the first aim of this study was testing bottlenose dolphin's spontaneous ability to track simple visible and invisible displacements. In doing so, we used a simpler protocol than that of Jaakkola *et al.* (2010), by adapting to dolphins the one used by Call (2003) with great apes. This protocol includes different spatial transposition tasks with only two containers. As dolphins are not used to manipulate containers, we allowed dolphins to inspect them with echolocation and touch before the testing. In fact, it seems that dolphins need to manipulate an object to construct a global representation of that object as if they were Piagetian creatures (Blois-Heulin *et al.*, 2012). In addition, to give them more experience with "containment", during the training we placed the boxes on their side so that the open sides were facing the subject and the object was still visible inside them. If dolphins failed to spontaneously pass simple visible or invisible displacement tasks, the second aim of the study was to assess the role of previous visual experience in dolphin's acquisition of object

permanence skills. For this purpose, the dolphin received visual experience with an object visibly moving inside a container before being retested in an invisible displacement task. With this procedure, we aimed to see if previous visual experience influences the performance of dolphins in this type of tasks.

## 4.2. Method

### *Subjects and facility*

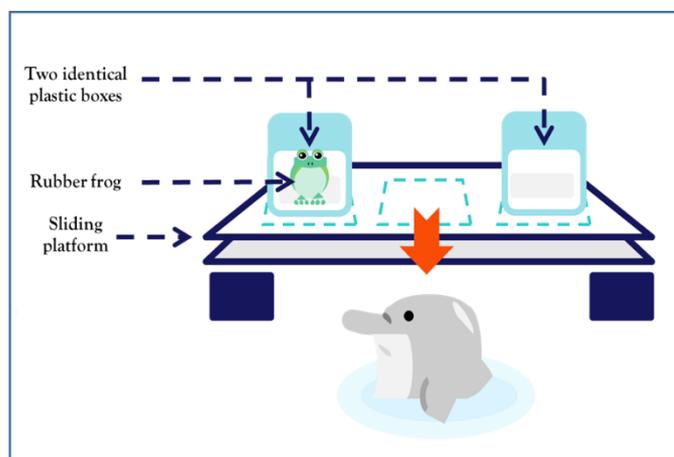
Two female Atlantic bottlenose dolphins (*Tursiops truncatus*) housed at Marineland Mallorca participated in this study. The dolphins lived in an outdoor pool conjoined to a medical pool, with a total volume of 1846.75 m<sup>3</sup> of water. The age of the study subjects was 8 years (*Stella*) and 13-years-old (*Blava*). Both dolphins were captive born and shared the pool with a juvenile male. At the end of the study, they also shared the pool with two adult females and a calf. The dolphins were fed according to their normal daily routine, which included a variety of fish (capelin, mackerel and herring) and gelatin. The experiment was conducted during the first training session of the day before the park opened to the public. During non-experimental sessions, the dolphins continued to participate in other training sessions including interactions with trainers and guests.

### *Apparatus*

Two identical opaque grey plastic boxes (27.6 x 22 x 17 cm) were used as hiding devices. During the trials, the boxes were positioned about 23.5 cm apart on a wooden sliding platform (123 x 34 x 9 cm) located at the edge of the pool. A rubber frog (17 x 12.5 x 9.5 cm) served as the target object and fish (capelin, mackerel and herring) were used as rewards. All sessions were videotaped using a waterproof camera SJCAM SJ4000. **Figure 19** shows the experimental setup and apparatus.

### *Design and Procedure*

The experimenter sat behind the sliding platform facing the dolphin, who stayed at the edge of the pool in front of the platform (see Figure 20). During testing, the experimenter wore sunglasses to avoid giving gaze cues. At the beginning of each trial, the platform was in a slid-back position. Each trial started when the experimenter showed the object (rubber frog) to the dolphin and placed it on the platform (inside or outside the boxes, depending on the experimental condition). Then, the experimenter pushed the platform towards the subject allowing it to make a choice. The dolphin made its choice by touching a box or the object with its rostrum (see Figure 20). If the subject chose the correct location (that in which the object was), the dolphin received positive reinforcements of fish and social interaction. If the dolphin chose the incorrect location, the experimenter retrieved the object and showed it to the dolphin. If during a trial, the subject did not respond, swam away, or chose a location before the



**Figure 19. Experimental setup.** In this study, two plastic boxes located on a sliding platform were used as hiding devices and a rubber frog was used as the target object. The sliding platform was divided in three areas in which the boxes or the object could be placed.

experimenter slid the platform, the trial was repeated. During the experimental sessions, any other dolphins present in the pool were kept busy by the trainers. If one of those dolphins approached the experimental subject, the trial was aborted and resumed when the dolphin had returned to its trainer. The study consisted of three phases:

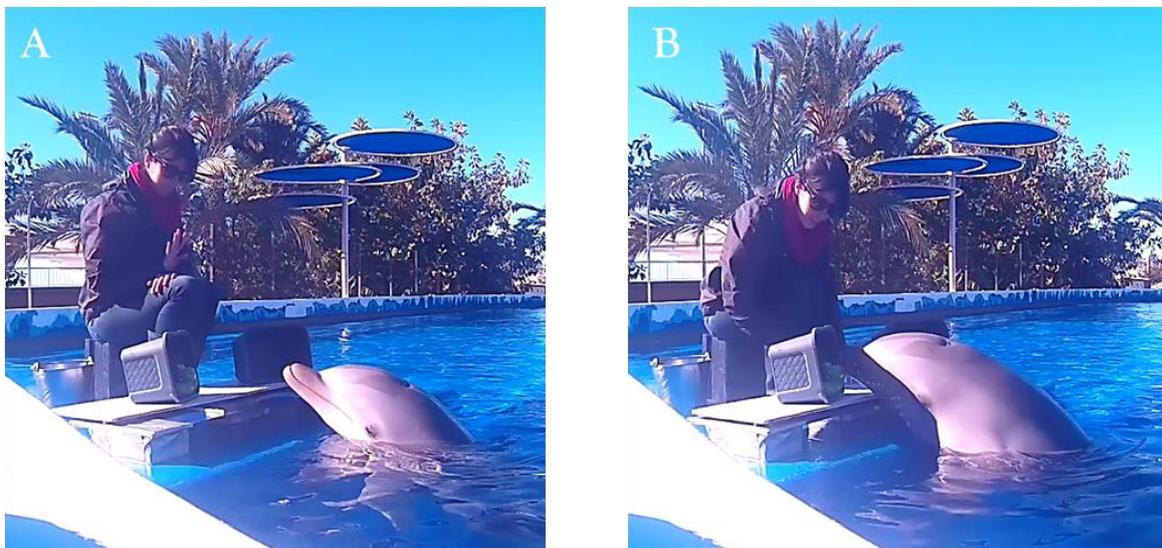
**1. Training.** The training sessions had three aims: (1) familiarize the dolphin with the apparatus; (2) train the dolphins to choose the object's location; and (3) give the dolphins some experience with "containment". During the training, the boxes were always placed on their side so that the open sides were facing the subject and the object was still visible inside them. Furthermore, during the first session of training, the object and the boxes were put in the pool so dolphins had ample opportunity to inspect them with echolocation and touch. The training phase consisted of several intermediate steps:

- a. *Introducing the object:* The experimenter showed the object to the dolphin and approached it to its rostrum. The dolphin was rewarded for touching the object.
- b. *Introducing the sliding platform:* The experimenter showed the object to the dolphin and placed it on the platform. The sliding platform was divided into three areas (left, right, middle; see **Figure 19**) in which the object and boxes could be placed. During this procedure, the experimenter used a signal to train the dolphin to wait before making a choice. Then, the experimenter slid the platform and pointed to the object. The dolphin was rewarded for touching the object.
- c. *Introducing the boxes:* The experimenter placed one box on the platform (three possible locations) and then placed the object inside the box or directly on the platform (9 possible dispositions). The dolphin was rewarded for touching the object. Once the dolphin evidenced success with this procedure, the second box was introduced. There were 9 possible dispositions of the two boxes and the object on the three available locations on the platform. The experimenter placed the object inside one of the boxes or on the empty location on the platform (9 possible dispositions). To avoid that the dolphins always chose the location in which the experimenter's hand was for the last time, the experimenter moved the object in a standardized manner. In some trials, the right hand holding the object moved from left to right, and in others, from right to left. The experimenter's hand always passed in front of all three locations irrespective of where the object was placed.

Each dolphin's training included each of these steps. However, there was some flexibility between subjects with respect to the rigidity with which the steps were incorporated. By the end of the training phase, training composition was standardized and randomized. Each training session consisted of some warming up trials in which the object was directly placed on the platform (at least one per location) followed by 9 training trials (one per disposition) including the object and the two boxes. Order of trials was semi-randomized, with the constraints that the object was never placed more than two consecutive trials in any particular location. The object's location was counterbalanced across trials. The aim was that by the end of the training phase, each dolphin could indicate the object's location (1) irrespective of whether it was inside a box or placed directly on the platform; (2) regardless of the experimenter's hand movement; and (3) whatever the disposition of boxes and the object on the platform. Our criteria for moving from training to testing were that the dolphin was correct on at least 8 out of 9 trials on two consecutive sessions.

**2. Test.** The testing phase consisted of several tasks that were administered in a specific order. The dolphin had to succeed in one task to move onto the next one. The reason for this experimental design is that each task assesses a prerequisite for the ability tested in the following task. Thus, all subjects underwent the tasks in the same order.

- a. *Visible displacement task*: This task tested dolphins' spontaneous ability to track the location of the object when both boxes were turned, hiding the object. This test was equivalent to the "no movement" condition in Call (2003). The boxes were separated 23.5 cm from each other and the open ends faced the dolphin thus, the object was still visible inside them. The experimenter placed the object inside one box and simultaneously turned both boxes in full view of the dolphin. Testing was divided into two sessions that took place over two consecutive days in the week. Before each testing session, the dolphin received three warming up trials (object placed directly on the platform, one per location) and two training trials (object still visible inside the box, one per box). If the dolphin missed one of these trials, testing was postponed to the next day. Each session consisted of two training trials (one per box) and eight visible displacement trials. The object's location was counterbalanced across trials. Order of trials was semi-randomized, with the constraints that the object was never placed more than two consecutive trials in any particular location. In one session, the experimenter's hand moved from right to left, and in the other, from left to right.



**Figure 20.** Photographs depicting a testing session. **A:** The object is located inside one of the boxes and the dolphin waits to make a choice; **B:** Dolphin makes a correct a choice.

- b. *Transposition task*: This task tested dolphins' ability to track the invisible displacement of the hidden object when both boxes substituted each other's starting locations, crossing each other's path. This task was equivalent to the "one-step swap" of Call's (2003) protocol. The procedure was identical to that of the visible displacement task but, once the boxes were turned, the experimenter grabbed both boxes (the right box with the right hand and the left box with the left hand) and switched their positions simultaneously. Testing was divided into two sessions that took place over two consecutive days. Before each testing session, the dolphin received three warming up trials (object placed directly on the platform, one per location) and two visible displacement trials (one per box). If the dolphin missed one of these trials, testing was postponed to the next day. Each testing session consisted of eight transposition trials. Order of trials was semi-randomized, with the constraints that the object was never placed more than two consecutive trials in any particular location.

- c. *Visible transposition task*: If a dolphin failed the transposition task, it received several sessions of a transposition task in which the object was still visible inside the box. The aim of this task was to give the dolphins visual experience with the movement of objects inside of other objects. This task was identical to the transposition task except that both boxes were not turned. By the end of this phase, the dolphin received sessions that consisted of two training trials, six visible displacement trials and six visible transposition trials. The object's location was counterbalanced across trials. Order of trials was semi-randomized, with the constraints that the object was never placed more than two consecutive trials in any particular location. Our criteria for moving from the visible transposition task to the second transposition task were that the dolphin was correct on at least 11 out of 12 visible displacement trials and 11 out of 12 visible transpositions trials in two consecutive sessions.
- d. *Transposition task*: Dolphins were retested in one session of the transposition task.

No more than 6 days elapsed between the session in which the dolphin reached the criterion on a particular task and the first testing session of the next one. **Table 14** presents a detailed description of each task.

**3. Control tests.** If a dolphin passed the second transposition task it received 5 control tests. The aim of these control tests was to rule out associative learning strategies such as following the hand that touched the box in which the object was seen last, rather than tracking the object displacements. As the dolphins are used to pay attention to the trainers' hand movements as signals, it is also possible that, during the visible transpositions tasks, they learned to use the crossing movement of the experimenter's hands as a cue. With these tests, thus we controlled for the possibility that the dolphin used this cue as a signal indicating that they must select the box located on the opposite side of the area in which the object was last seen. Before each control test session, dolphins received two visible displacement trials and two visible transposition trials.

Dolphins were tested in the following control tests (see **Table 14** for order and detailed description of each task):

- a. *Up and down (1 test)*: The procedure was identical to the transposition task except that, instead of switching the boxes' location, the experimenter crossed her arms and moved the boxes up and down. Thus, the boxes remained in the same position.
- b. *Double transposition (1 test)*: The double transposition test involved two consecutive transpositions. Boxes switched positions twice, thus the object ended up at the same side to which it was initially located. This control test was equivalent to the "reverse swap" of Call's (2003) protocol.
- c. *Sequential transpositions (3 tests)*: In these three control tests, the hidden object was displaced using new sequential movements rather than simultaneous movements. The experimenter always used her right hand to move the boxes after turning them with both hands. In the 3-step transposition, both boxes switched positions in three sequential displacements. The location of the boxes at the beginning of each trial was the same as in the previous conditions. This control was similar to the "3-step swap" condition of Call (2003). In the 2-step transposition, both boxes were moved from their initial positions to new locations in two sequential displacements. In this control, the location of the boxes at the beginning of the trials was different from that of previous conditions. Boxes crossed each other's path. In the 1-step transposition, one of the boxes was moved to a new location. In this control, the location of the boxes at the beginning of each trial was different from that of previous conditions. The object's start and final location changed. The box crossed the other's path.

**Table 14.** Type of displacement and movement, and detailed description of each of the experimental conditions. (E): experimenter; 1: first movement, 2: second movement, 3: third movement.

Condition	Type of displacement	Type of movement	Definition	Example
Training	Visible	-	(E) puts the object in one of three possible locations: directly on the sliding platform or inside one of two boxes (the object is still visible inside the box).	
Visible displacement	Visible	Simultaneous	(E) puts the object inside one of two boxes and then turns both boxes hiding the object while the dolphin observes.	
Transposition	Invisible	Simultaneous	(E) puts the object inside one of two boxes, turns both boxes hiding the object and switches both boxes positions simultaneously.	
Visible Transposition	Visible	Simultaneous	(E) puts the object inside one of two boxes and switches both boxes positions simultaneously.	
3-step transposition (C1)	Invisible	Sequential	(E) puts the object inside one of two boxes, turns both boxes hiding the object and displaces both boxes sequentially in three movements until each box is located in the other's initial location.	
Up and down (C2)	Invisible	Simultaneous	(E) puts the object inside one of two boxes, turns both boxes hiding the object, crosses her arms and moves the boxes up and down.	
2-step transposition (C3)	Invisible	Sequential	(E) puts the object inside one of two boxes, turns both boxes hiding the object and displaces both boxes sequentially to new locations.	
Double transposition (C4)	Invisible	Simultaneous	(E) puts the object inside one of two boxes, turns both boxes hiding the object and switches both boxes positions simultaneously two times.	
1-step transposition (C5)	Invisible	Sequential	(E) puts the object inside one of two boxes, turns both boxes hiding the object and displaces one of the boxes to a new location.	

*Coding*

A dolphin was coded as making a choice when its rostrum contacted a box or the object. All trials were videotaped and the dolphin's choices were scored by reviewing the video recordings. Dolphins' choice was unambiguous; therefore, no reliability coding was conducted.

### 4.3. Results

One of the two dolphins (*Blava*) was only tested in the visible displacement task since it was moved to the show pool and we were forced to terminate her testing. Thus, only one dolphin was tested in all the tasks. Training duration and maintenance trials between experiments for individual dolphins are presented in **Table 15**.

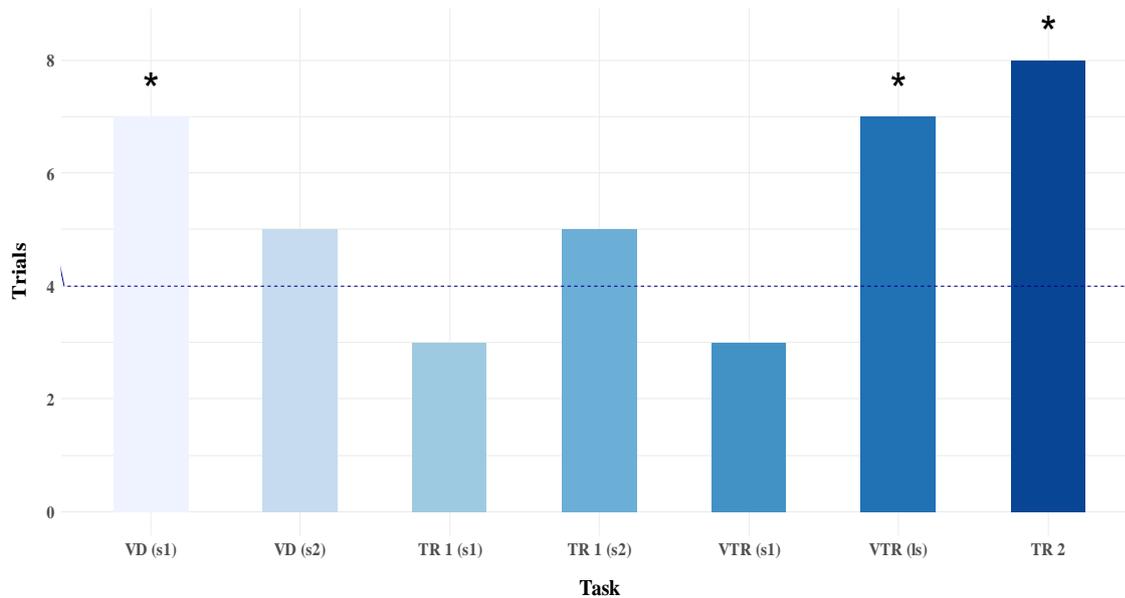
**Table 15.** The total number of training/maintenance trials between experiments per individual.

Task	Individuals	
	Stella	Blava
Training	240	305
Pre-transposition task	41	-
Pre-visible transposition task	13	-
Pre-second transposition task	133	-
Pre-C1 (3-step transposition)	0	-
Pre-C2 (Up and down)	0	-
Pre-C3 (2-step transposition)	0	-
Pre-C4 (Double transposition)	0	-
Pre-C5 (1-step transposition)	0	-

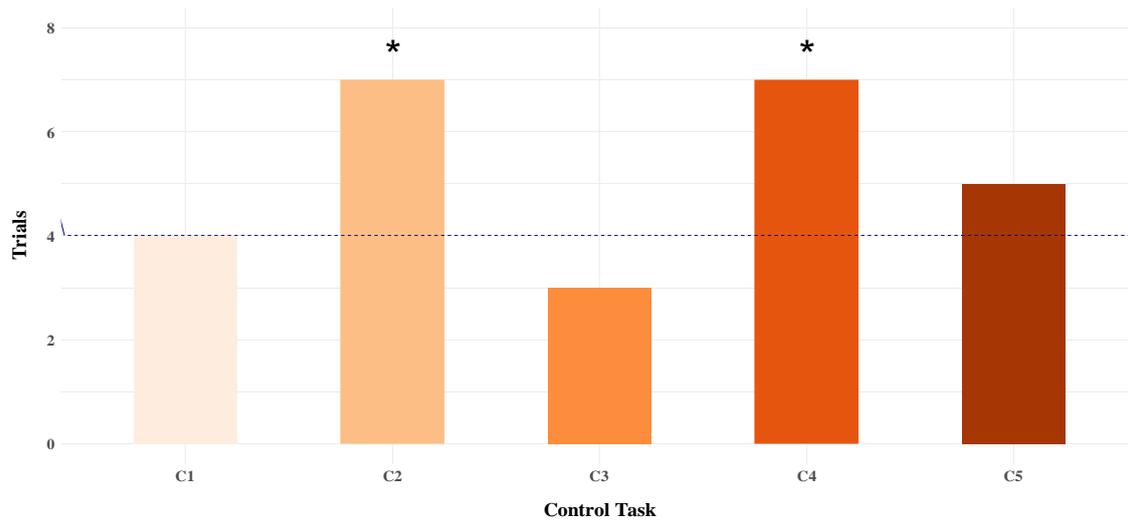
Overall, dolphins did not perform above chance in the visible displacement task (one-sample  $t$ -test, one-tailed:  $t_1 = 0.6$ ,  $p = 0.328$ ). Only *Stella* performed above chance for visible displacements (binomial test,  $p < 0.05$ ). *Stella* did not perform significantly above chance either in the transposition task or within the first two sessions of the visible transposition task (binomial test,  $p > 0.05$ ). It took about four sessions to reach criterion in this task (last two sessions, binomial test,  $p < 0.001$ ). After receiving the visible transposition sessions, *Stella's* performance in the second transposition task was above chance levels (binomial test,  $p < 0.01$ ). **Table 16** presents the proportion of correct responses per task for each dolphin. *Stella* performed above chance in the up and down control test and in the double transposition test (binomial test,  $p < 0.05$ ) but not in any of the controls involving sequential movements (binomial test,  $p > 0.05$ ). **Figures 21** and **22** show the total number of correct trials per task for *Stella*.

**Table 16.** Proportion of correct choices per task for each individual (the number of trials is indicated inside of parentheses) \*  $p < 0.05$ .

Task	Individuals	
	Stella	Blava
Visible displacement task (16)	0.75*	0.44
Transposition task (16)	0.50	-
Visible transposition task (first sessions) (16)	0.44	-
Second transposition task (8)	1*	-
Double transposition (8)	0.88*	-
Up-down (8)	0.88*	-
3-step transposition (8)	0.50	-
2-step transposition (8)	0.38	-
1-step transposition (8)	0.63	-



**Figure 21.** Total number of correct trials per task for Stella. **VD:** visible displacement task; **TR1:** first transposition task; **VTR:** visible transposition task; **TR2:** second transposition; **(s1):** first session; **(s2):** second session; **(ls):** last session. \*  $p < 0.05$ .



**Figure 22.** Total number of correct trials per control task for Stella. \*  $p < 0.05$ .

Finally, we examined the dolphins' individual strategies for responding. We only identified two strategies: (1) correct responding, and (2) selecting a favoured location (left or right). In the visible displacement task, *Blava* selected 13 times out of 16 the left box (binomial test,  $p < 0.01$ ). In turn, *Stella* significantly selected the favored location (right) in the two first sessions of the visible transposition task (binomial test,  $p < 0.01$ ) and in the three control tests involving sequential movements (3-step transposition: binomial test,  $p < 0.01$ ; 2-step and 1-step transposition: binomial test,  $p < 0.05$ ). **Table 17** shows the response strategies identified for each dolphin.

**Table 17.** Response strategies per task for each dolphin. **Ok:** Correct responding; **Fav:** significantly selecting a favoured box (right or left); **-:** no identifiable response strategy.

Task	Individuals	
	Stella	Blava
Visible displacement task	Ok	Fav (left)
Transposition task	-	-
Visible transposition task (first sessions)	Fav (right)	-
Second transposition task	Ok	-
3-step transposition (C1)	Fav (right)	-
Up-down (C2)	Ok	-
2-step transposition (C3)	Fav (right)	-
Double transposition (C4)	Ok	-
1-step transposition (C5)	Fav (right)	-

#### 4.4. Discussion

In the present study, we tested dolphins' spontaneous ability to track simple visible and invisible displacements. We also assessed the role of previous visual experience in the development of this capacity. Overall, dolphins had difficulties with both tests even when they were tested in tasks involving the displacement of only two containers. Only one of the dolphins, *Stella*, succeed in the visible displacement task without previous training. However, this dolphin did not spontaneously pass the transposition task. On the other hand, after receiving further visual experience with containment and the object visibly moving inside the boxes, it succeeded when retested in this task. This result suggests that, if dolphins receive enough visual experience with containment and moving objects, they can pass invisible displacements tasks. This outcome supports the hypothesis that dolphins' previous failure in invisible displacement tasks were not due to a lack of secondary representation capacities.

Our findings in the visible displacement task replicated those of Jaakkola *et al.* (2010). In their study, only three out of six dolphins passed the single visible displacement task and only one out of six dolphins passed the double visible displacement test. Goffin cockatoos, which succeed in several invisible displacement tasks, also had difficulties to pass the single visible displacement task (Auersperg *et al.*, 2014). Only one out of eight birds reached criterion in the first session. For all other birds, acquisition was extremely slow, needing a minimum of seven sessions to reach criterion in this task. These results suggest that previous learning and experience with the procedure are necessary to solve simple object permanence tasks. Some animals may need time to understand the dynamics of these procedures. Once they have had enough experience with the new elements and how they operate, they can solve more difficult tasks. Thus, some of the traditional object permanence tasks that seem intuitive and easy to solve from the human perspective, might not be as simple as previously thought.

Although *Stella* failed to spontaneously pass the first transposition task, after receiving visual experience with visible transpositions she succeeded in this test. Furthermore, she passed two control tests including a more complex double transposition task. These results support the hypothesis that learning and previous visual experience are crucial for the development of object permanence abilities. This effect of previous visual experience in the performance of object permanence tasks was also reported in infants and chicks. Four-month-old infants that received an initial period of experience viewing an un-occluded trajectory were able to better anticipate occluded trajectory displays than infants who did not receive this experience (Johnson *et al.*, 2003). In turn, Prasad (2015) compared object permanence abilities of newborn chicks raised in natural worlds and chicks raised in impossible visual worlds (worlds in which objects exhibit behaviour not consistent with the laws of physics). The results of this study showed that chicks raised in impossible visual worlds failed to develop object permanence abilities, suggesting that some types of visual inputs are necessary for the emergence of this ability.

Most of the criticisms made on possible successes of animal species in invisible displacements tasks focus on methodological issues such as lack of controls for sensory and associative cues or social cueing (Jaakkola, 2014; Cacchione & Rakoczy, 2017). In our study, the experimenter wore sunglasses to avoid giving eye-gaze cues to the dolphin. However, she always knew the correct location of the object, thus, it could be possible that the dolphin deduced the correct answer by reading unintentional body language. Nevertheless, due to *Stella's* differential success across tasks, it seems unlikely that her successes were based on inadvertent social or sensory cues.

Another possibility for *Stella*'s success in the second transposition task is that, during the visible transposition sessions, she could have learned some simple associational rules. These rules could be something like "whenever the experimenter crosses her hands, choose the opposite location to where the object was last seen" or "follow the hand that last touched the box containing the object". To rule out these associative learning explanations we tested the dolphin in five different control tests. *Stella* succeeded in two of these control tests, the ones that involved synchronous movements. If she was following the second rule, she could have succeeded in the visible transposition task, in the second transposition task and in the double transposition control but not in the up and down control. In this test, after turning the boxes, the hand that last touched the box in which the object was last seen grabbed the opposite box. Thus, if the dolphin had been following this rule, in this test it should have chosen the incorrect box. In turn, if *Stella* was using the experimenter's hand crossing movement as a cue for choosing the opposite location to where the object was last seen, she could have succeeded in the visible transposition and in the second transposition task but not in the up and down task or in the double transposition task. In these two controls, the experimenter crossed her hands but the object remained in the same location. Therefore, if the dolphin had been following this rule, it should have chosen the incorrect box.

In the study of Call (2003), great apes passed all the spatial transposition tasks regardless of the type of movement used (synchronous or sequential). Conversely, in this study, *Stella* did not pass any of the controls involving sequential movements. In these tests, she chose the favoured box (the one located on the right) in almost all trials. Thus, the dolphin did not make initial location errors (choosing the box where the object was initially hidden) or moved box errors (choosing the box that was last moved during the transposition). Negative results are always hard to interpret. Four hypotheses may explain the dolphin's success in the tests involving simultaneous movements but not in those involving sequential movements:

1. *Greater difficulty*: The three sequential controls include some elements that could make them more difficult to solve. In fact, one of the orangutans in the study of Call (2003) passed all the transposition tasks except the 3-step swap. Thus, it could be the case that the dolphin succeeded in the transposition tasks involving synchronous movements simply because these tasks were easier than the sequential ones. It has been proposed that success in object permanence tasks is directly dependent on the number of elements that change locations (Barth & Call, 2006). That is, the more elements change locations, the more difficult the task becomes (Barth & Call, 2006). Also, memory load and certain object-container configurations determine success in invisible displacement tasks (Barth & Call, 2006). It has been shown that container crossing and substitution affects performance in invisible displacement tasks (Rooijackers, Kaminski, & Call, 2009). For example, dogs only succeeded in tasks in which the containers did not cross and ended up in new locations (Rooijackers *et al.*, 2009). Furthermore, multiple displacements seem to be more challenging than single displacements in terms of visual tracking, memory and inhibition capacities (Cacchione & Rakoczy, 2017). In the 3-step transposition task, the dolphin had to track three more invisible sequential displacements of the object besides tracking the visible displacements of the object (the object was located inside one box and then both boxes turned simultaneously hiding the object). Furthermore, the boxes crossed each other's path and substituted the other's initial location. Tracking all the displacements of the object and the boxes through all this procedure clearly implied a higher memory load than the rest of tasks.

However, memory load and container crossing and substitution do not fully explain dolphin's failure in the three sequential transpositions. The 1-step and the 2-step control conditions did not require a higher memory load than the double transposition task and in these two tasks, the containers did not substitute the other's initial location. Furthermore, visible, single and double

transposition tasks also implied box crossing and substitution and the dolphin succeeded in all these tasks. One factor that might have had a great influence on the dolphin's performance in the three sequential control conditions is the distance between boxes. While in the rest of the tasks the boxes were always about 23.5 cm apart, in some steps of the three sequential transpositions (especially in 2 and 3-step transpositions) the boxes were separated from each other only by a few centimetres. This disposition may have caused that the dolphin could not visually discriminate one box from the other, losing track of the object's subsequent movements and opting for always choosing the favoured box. Unlike in the other two controls in which the dolphin always chose the right box, in one trial of the 1-step transposition task the dolphin correctly chose the left box and in another trial, after having chosen the incorrect box it quickly rectified and, again, correctly selected the left box. This pattern of responses may be indicative that this task was easier than the other two sequential controls and that dolphin's failure in this test could be due to an inhibition problem rather than an inability to track invisible displacements. It is also possible that the dolphin's lack of success in this task was an artefact of the small number of trials administered (n=8).

2. *Inhibition problems:* Stella's failure in the three sequential transpositions may be due to an inhibition problem. In these tasks, she consistently chose the right box that, in turn, was the one that always crossed the other's path. Thus, the movement of the right box could be more salient and the dolphin could be unable to refrain from systematically choosing this box. However, in the other transposition tasks, the right box was also the one that always crossed over the left box and even so the dolphin passed these tasks. Another possibility is that the dolphin may have been influenced by the position of the right hand, that was the one that moved the object and the boxes in these three controls. The dolphin thus could have selected the right box in most trials since it was always the closest box to the right hand. A similar pattern of response has been observed in dogs, which showed a preference for the location closest to the experimenter (Fiset & LeBlanc, 2007; Rooijackers *et al.*, 2009). However, the experimenter always used the right hand to place the object inside the boxes across all the tasks of the study, from the training phase to the control conditions. And even so, the dolphin could override this tendency selecting the correct box in several tasks.
3. *Interference of previous training:* An alternative hypothesis is that dolphins' might be able to track invisible displacements but their previous training in the aquatic park could have influenced their performance across tasks. Trained dolphins associate each specific trainer's signal with a specific behavioural response. Any change in this signal implies a change in the dolphin's response. Thus, it is possible that the dolphins interpreted any significant change of the elements or movements during the procedure as a change of task, and responded differently every time a new modification was added to the paradigm. This hypothesis may explain their failure in almost every task that involved new elements. For example, *Blava* failed to pass the visible displacement task that included new procedures such as turning the boxes and choosing a box instead of the object. Although *Stella*'s failure in the first transposition task could be due to a lack of the ability to track invisible displacements, this hypothesis does not fully explain why she also failed the visible transposition task, in which the object was still visible inside the box. An influence of previous training, however, could explain *Stella*'s results in both tasks. She might have failed the first transposition task and the subsequent visible transposition tasks since these tests included new movements of the hands and the boxes. Unlike the two controls involving synchronous movements, the three sequential transpositions did include new elements such as extra displacements of the containers and new initial and final locations of the boxes. Due to these modifications of the experimental procedure, the dolphin could have treated these controls as new tasks, changing its response strategy. In fact, *Stella* used the same strategy for the visible

transposition task and the three sequential transpositions: choosing the right box in almost all the trials.

4. *Lack of the ability to track invisible displacements:* Finally, it could be possible that the dolphin's failure in the three new sequential transposition tasks was due to a lack of the ability to track invisible displacements. If this were the case, the dolphin should have succeeded in the second transposition task and in the two other controls by following some undetected lower-level strategies learned during the visible transposition sessions. One could also argue that success on the second and double transpositions tasks may be explained by a simple attentional mechanism rather than by a conceptual understanding of object permanence (Jaakkola, 2014). The fact that in these tasks both boxes moved simultaneously could have helped to draw the dolphin's attention to a single box, and subsequently tracking that box. However, if the dolphin's successes are due to a simpler attentional mechanism it should have also passed the 1-step transposition task or the first transposition task. In the 1-step transposition, for example, only one of the boxes was moved to a new location, thus it could be easier to track the object's displacements in this task than in the double transposition task. *Stella*, however, did not pass this task and passed the double transposition test. Furthermore, it has been shown that spatial transpositions are especially challenging for some species. Dogs have special difficulties tracking the reward during transpositions (Dore *et al.*, 1996; Rooijakkers *et al.*, 2009) and even children have trouble with spatial transpositions (Sophian & Sage, 1983; Sophian, 1984, 1986) performing worse than apes in this type of task (Barth & Call, 2006). Spatial transpositions require to cope with the movement of several objects moving at once, monitoring the movement of relevant objects while disregarding other irrelevant object displacements (Beran & Minahan, 2000). This procedure may also require inference capacities to deduce where objects are located after they move when the animal does not see them in their new locations (Beran & Minahan, 2000). Therefore, transposition tasks do not seem to be one of the easiest tasks within the range of tests used to assess object permanence skills.

In any case, previous experience with the visible displacements of the object inside the box improved the dolphin's performance in the subsequent transposition tasks. This visual experience allowed the dolphin to pass a spatial transposition task and a more difficult version of this test, the double transposition. Spatial transpositions require an understanding of the physical nature of objects and containers and how they relate through movement when the container moves holding the object (Beran & Minahan, 2000). Thus, it is reasonable that previous visual experience with this type of visual stimulus is necessary to understand the dynamics of objects' invisible displacements and apply this knowledge to solve spatial transpositions. This previous visual experience might be crucial to the success of animals living in aquatic environments in invisible displacement tasks since the same object has totally different movement dynamics in and out of the water. If so, dolphins' previous failure in invisible displacement tasks could be due to their lack of empirical experience with the movement dynamics of the elements used in these tasks rather than a lack of secondary representation capacities. Furthermore, dolphins and cockatoos' early failure in some visible displacement tasks (Jaakkola *et al.*, 2010; Auersperg *et al.*, 2014) also points to the necessity of previous experience with the procedures of the tasks to succeed in such tasks.

In addition to the integration of visual and echoic information, dolphins might need to manipulate an object to construct a global representation of that object (Blois-Heulin *et al.*, 2012). Thus, dolphins may have difficulties in constructing a spatial mental representation of never manipulated objects (Blois-Heulin *et al.*, 2012). In this study, dolphins were allowed to manipulate both the object and the containers, procedure that could have also influenced the dolphin's subsequent performance in the transposition tasks.

The dolphin's success in the control tests involving synchronous movements and its failure in the sequential ones, especially in the 1-step transposition, is puzzling. Interference with the dolphin's previous training, an inhibition control problem, a greater cognitive demand, the small number of trials or some combination of the previous factors might explain the dolphin's failure in those controls. With our data, however, we were unable to clearly identify the critical factors influencing the dolphin's pattern of responses. This fact highlights the importance of including better controls to try to identify the factors influencing dolphins' performance when they are confronted with new tasks. Another interpretation for dolphin's failure in the sequential controls is that the dolphin lacked the ability to track the displacements of hidden objects and it passed the other transposition tasks by learning not identified simple associational rules. Unfortunately, with our data, we cannot rule out completely this possibility. As Pepperberg (2015) pointed out almost any behaviour pattern can be explained in associative terms and completely eliminating arguments for associative learning is not possible.

Finally, these outcomes could partially explain the results obtained in the Study 3 of the present thesis. In this way, dolphins' failure in the false belief task could be due in part to their lack of experience with "containment" and with objects moving inside other objects, which could have added an extra difficulty to the false belief task.

Overall, more studies including a larger number of subjects are desirable to confirm the role of previous visual experience in the development of invisible displacement tracking abilities in dolphins and other species. This, ultimately, may shed light on the debate of whether object permanence is a hardwired property of the visual system or learned during development through previous visual experience with moving objects.

## 5. Study 5: Prosocial behaviour, other-regarding preferences and instrumental helping in bottlenose dolphins

### 5.1. Introduction

Prosociality has been defined as the behavioural tendency to benefit one or more individuals other than oneself (Batson & Powell, 2003; Yamamoto, 2017). Helping behaviour is considered to be an example of prosocial, altruistic, behaviour (Batson & Powell, 2003). Helping involves promoting the wellbeing of another individual with no immediate benefit to oneself. This helping behaviour is costly and evolutionarily rare when directed toward non-kin (Warneken & Tomasello, 2006). For this reason, the evolution of altruism has been the focus of much debate (Wilson, 2005; Foster, Wenseleers, & Ratnieks, 2006; de Waal, 2008; Yamamoto & Tanaka, 2009).

A big part of the debate has concerned its proximate mechanisms. In particular, whether or not altruistic behaviour is the outcome of altruistic motivations. On the one hand, some authors argue that selfish motivations best explain most prosocial behaviour like helping in non-human species (Stevens *et al.*, 2004), which is seen in fact as a form of delayed reciprocity. On the other hand, though, there are researchers who contend that there exist genuine altruistic motivations. The idea behind this approach is to conceive of the evolution of altruism in terms of the evolution of psychological mechanisms that give rise to other-regarding preferences. Thus, for instance, helping behaviour may be the consequence of being empathic (de Waal, 2008), or of a basic disposition to cooperate with others (Warneken & Tomasello, 2006). More precisely, it could stem from an emotional response triggered by the understanding of another's emotional state or situation (de Waal, 2008; Yamamoto, 2017). From this point of view, empathic targeted helping is considered to be one of the most complex forms of empathy (de Waal, 2008). This type of helping response is cognitively demanding, requiring the understanding of the other's situation and knowing something about the goal the other is attempting to achieve (Warneken & Tomasello, 2006). Furthermore, empathic targeted helping may also require other-regarding preferences or concern for the welfare of others, which refers to whether an individual is sensitive to the other's payoffs (Yamamoto & Tanaka, 2010). These two dimensions –perspective taking and other-regarding preferences– jointly support the notion of genuine altruistic motivations because both dimensions characterize flexible and context-dependent abilities, which call for a psychological explanation.

Research on other-regarding preferences in non-human animals has failed to provide clear-cut results (see **Chapter 3, section 3.2.**). The findings vary depending on context and paradigm used (Silk *et al.*, 2005; Jensen *et al.*, 2006; de Waal, 2008; Lakshminarayanan & Santos, 2008; Brosnan *et al.*, 2010; Melis *et al.*, 2011; Victoria Horner *et al.*, 2011; Silk, 2012; Schwab *et al.*, 2012; Suchak & de Waal, 2012; Burkart & van Schaik, 2013; Drayton & Santos, 2014; Hernandez-Lallement *et al.*, 2015; Claidière *et al.*, 2015). There are just a few experimental studies on helping behaviour in non-human species. Due to ethical reasons, it is a difficult task to experimentally assess animals' empathic helping responses towards distressed conspecifics in species such as primates or cetaceans. Therefore, instrumental or targeted helping paradigms seem to be a good alternative to examine some of the factors and situations that favour helping responses in animals, because it does not require eliciting distress in the experimental subjects. Instrumental helping is a behaviour performed by an individual that enables another to reach a goal that cannot be achieved otherwise (Greenberg *et al.*, 2010). As empathic targeted helping, instrumental helping also requires a cognitive evaluation of the other's situation and seems also to involve other-regarding preferences (de Waal, 2008; Yamamoto *et al.*, 2012). Importantly, instrumental helping paradigms allow to vary motivational factors, such as the identity of the recipient or the cost of the helping responses, as well as cognitive

factors, like the difficulty of the instrumental context (Skerry *et al.*, 2011). Both, motivational and cognitive variables have proved to be the main factors influencing animals' prosocial responses (Skerry *et al.*, 2011).

Studies on instrumental helping in chimpanzees showed that these animals provide flexible targeted helping according to other individual's situation (Yamamoto *et al.*, 2009, 2012). But, although they seemed to understand their partner's need, chimpanzees rarely helped proactively (Yamamoto, 2017). That is, chimpanzees provided helping responses only upon a partner's request (Yamamoto & Tanaka, 2009). Conversely, two studies with capuchin monkeys reported that these monkeys do not exhibit strong prosocial preferences in instrumental helping tasks (Barnes *et al.*, 2008; Skerry *et al.*, 2011). Capuchins failed to consider the perspective of others when they could obtain food for themselves, their helping responses were limited by the cost of helping (Barnes *et al.*, 2008), and they did not spontaneously help a conspecific to achieve a specific goal in a minimal-cost instrumental helping task (Skerry *et al.*, 2011).

Studies on instrumental helping in species other than primates are scarce and inconclusive and need further research. Bottlenose dolphins are ideal candidates for this endeavour since they are a highly social species endowed with sophisticated cognitive abilities (Pack & Herman, 2006; Herman, 2010). In the wild, bottlenose dolphins engage in several prosocial behaviours such as epimeletic care (Caldwell & Caldwell, 1966; Cockcroft, 1990; Kuczaj *et al.*, 2001), rescue behaviour (Siebenaler & Caldwell, 1956; Caldwell & Caldwell, 1966), cooperative feeding and hunting behaviours (Duffy-Echevarria, Connor, & St. Aubin, 2008; Torres & Read, 2009), and alliance formation for protection and mate acquisition (Connor *et al.*, 2011; Connor & Krützen, 2015). However, only a few studies have examined the underlying mechanisms of these prosocial behaviours in this cetacean. One of such studies showed that a pair of captive bottlenose dolphins seemed to cooperate to solve a task requiring them to coordinate their actions to get a reward (Kuczaj *et al.*, 2015b). But it has been argued that dolphins' success in this task was due to competitive rather than cooperative interactions (King *et al.*, 2016). Nakahara *et al.*, (2017) examined whether bottlenose dolphins behave prosocially in two different paradigms. In both experiments, water shower devices (enrichment items) were used instead of food rewards. The first experiment was a prosocial choice task in which the subject could choose between two options: (1) the prosocial option that provided a reward (take a shower) to both individuals, and (2) the selfish option in which only the subject received the reward. The second experiment consisted in a giving assistance task in which the subject could either instrumentally help its partner to take a shower or do nothing. In the prosocial choice task, dolphins significantly chose the prosocial option without partner's request. Conversely, dolphins did not help their partner in the giving assistance task. Therefore, it remains to be further clarified the extent to which bottlenose dolphins show other-regarding preferences and provide instrumental helping to others.

In order to contribute to this objective, in this study we examined whether bottlenose dolphins would spontaneously behave prosocially in a minimal-cost instrumental helping task. For this purpose, we adapted to dolphins the protocol used by Skerry *et al.* (2011) with capuchin monkeys. Dolphins were first trained to exchange tokens for their favoured toy (a ball) with an experimenter. Once the dolphins mastered the exchange schema, dolphins were divided into two groups. One group had access to the tokens but could not exchange them because the experimenter was out of reach (helper group), whereas the other group could interact with the experimenter but did not have access to the tokens (recipient group). Thus, dolphins in the helper group had the opportunity to share the tokens that would allow their partners to obtain a preferred toy or do nothing. And dolphins in the recipient group could request their partners in the first group for the tokens, or do nothing. Dolphins

were tested in their free time and were given a large number of tokens so that their helping responses only involved a minimum cost. In this way, even if a dolphin shared a token with a partner it still had some tokens left. The number of balls was also in excess, to allow for the remote possibility that receiver group individuals could keep exchanging the tokens received from helper group so that the balls could be obtained for all members of the group. Therefore, this paradigm also served to examine possible cooperative or reciprocal responses across sessions. The composition of the groups varied across testing sessions in order to test the influence of the quality of dolphins' relationships in their helping responses. As in the study of Skerry *et al.*'s (2011), we included two control conditions to assess whether the dolphins' helping responses might be due to factors other than other-regarding preferences.

## 5.2. Method

### *Subjects and facility*

Four Atlantic bottlenose dolphins housed at Marineland Mallorca participated in this study (see **Table 18**, for subjects' sex and age). The dolphins lived in a social group in an outdoor main pool conjoined to two small pools with a total volume of 2296.82 m<sup>3</sup> of water. The dolphins shared the pool with an adult male (25-years-old) that was excluded from the experiment since it was born almost blind of the right eye. All the dolphins were captive born. They were fed according to their normal daily routine, which included a variety of fish (capelin, mackerel and herring) and gelatine. The experiment was conducted during their free time before the first training session of the day, without any food reinforcement. The park was closed to the public for the duration of the experiment.

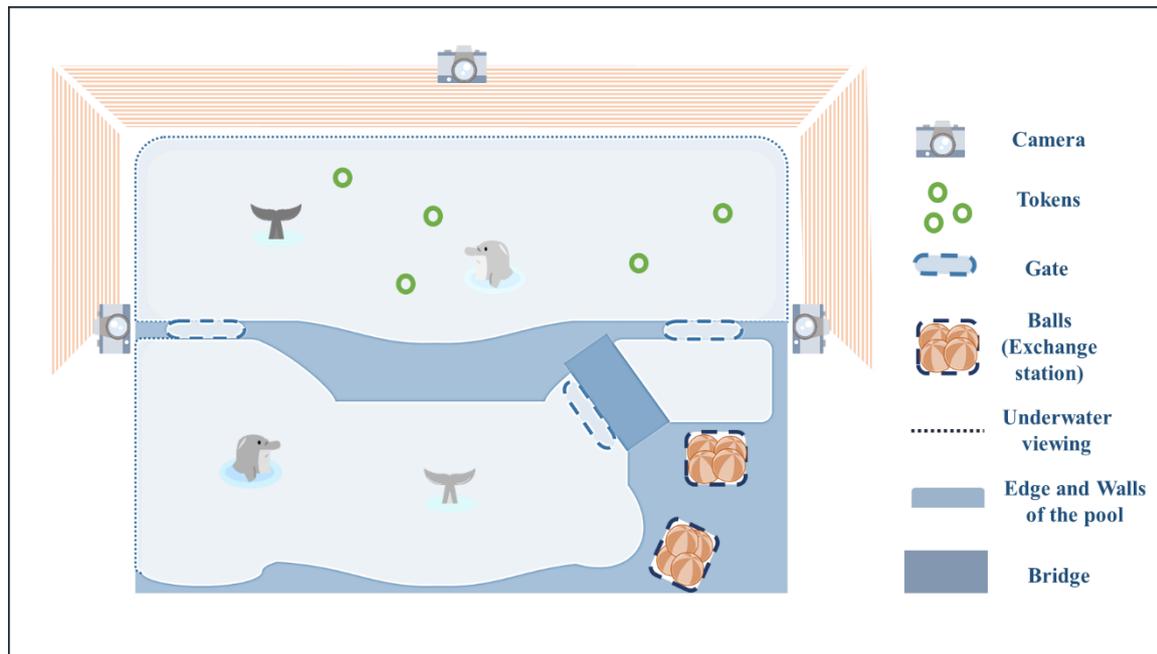
**Table 18.** Age and sex of the experimental subjects. M: male; F: female.

Subject	Sex	Age (years)
Blue	M	25
Mateo	M	13
Blava	F	13
Stella	F	8
Aytami	M	7

### *Apparatus*

**Figure 23** shows the basic apparatus and testing setup. In this study, several plastic hoops (20 cm diameter) served as tokens that could be exchanged for dolphins' preferred toy, a rubber ball (70 cm circumference). Rubber balls were stored in a transparent plastic box near the pool for the dolphins to have visual access to them. The main pool could be separated from the other two pools by two vertical sliding gates made of canvas or mesh and mounted on a stainless-steel frame that made it impossible for dolphins to pass from one pool to the other. Dolphins on opposite sides of the canvas gate had acoustical contact when the gate was closed, but limited underwater visual and physical contact. On the other hand, the mesh gate allowed acoustical and underwater visual contact between

dolphins. All sessions were videotaped using three waterproof cameras SJCAM SJ4000 located in three different areas of the enclosure.



**Figure 23.** Facility, basic apparatus, testing-up and camera placement in this study.

### *Design and Procedure*

**Training.** During the training sessions, the gates were open and dolphins had free access to all the pools. Dolphins were trained in their free time to exchange tokens (plastic hoops) for their preferred toy (rubber ball) with an experimenter. At the beginning of each training session, the experimenter threw the tokens to the pool and waited until a dolphin approached with a hoop (see **Figure 23**). The experimenter sometimes pointed to a token to motivate the dolphins to pick the hoop and give it to her. At the end of the training phase, the procedure was standardized. First, the experimenter carrying both the tokens and the balls approached the edge of the main pool. Then, she threw the tokens into the main pool (one per individual) and she moved with the box to the medical pool. She placed the box out of dolphins' reach but still visible from the dolphins' perspective. At this point, the dolphins had to collect a token from the main pool, took it to the medical pool where the experimenter was and gave the hoop to her to get the ball (see **Figure 24**). The experimenter only exchanged balls for tokens in this specific location of the pool or in the other interconnected small pool if the box was located there, but never in the main pool. When all dolphins evidence success with this procedure, exchanging the tokens with the trainer in at least three separate days, we passed to the testing phase.

**Testing.** The testing sessions were conducted during dolphins' free time, before the first training session of the day. During the testing sessions two gates were closed and the main pool was separated from the other two pools. In this aquatic park, separating one individual from the rest of the group would have caused undue stress; for this reason, dolphins were tested in groups. Dolphins were divided into two groups: the helper group and the recipient group. The helper group stayed in the main pool and had access to the tokens but could not exchange them with the experimenter. Conversely, the recipient group stayed in the small pools and had the opportunity to interact with the experimenter but no access to the tokens.



**Figure 24.** Photographs depicting different moments of a training session. **A:** Exchange station; **B:** dolphin bringing a token to the exchange station; **C:** dolphin exchanging a token; **D:** dolphin getting the ball.

Before each experimental session, the trainers divided the dolphins into two groups closing the sliding gates and rewarding the dolphins with fish at the end of the procedure. To control for motivational factors such as the influence of the identity of the recipient in dolphins' helping responses, it would have been desirable that each individual had had the opportunity to help or receive help from the other three individuals. However, the juvenile male had previously refused to be alone with the two adult males so only five of the six possible combinations of interacting individuals could be tested (see **Table 19** for the combination and composition of the groups). In addition, some of the dolphins displayed preferences for one of the pools. Therefore, if a dolphin transferred a token to a specific partner, in the consecutive session we tried to reverse the situation to assess reciprocity. If there were no transfers, the composition and the distribution of the group were left to the trainers' decision to cause the minimum stress possible to the animals.

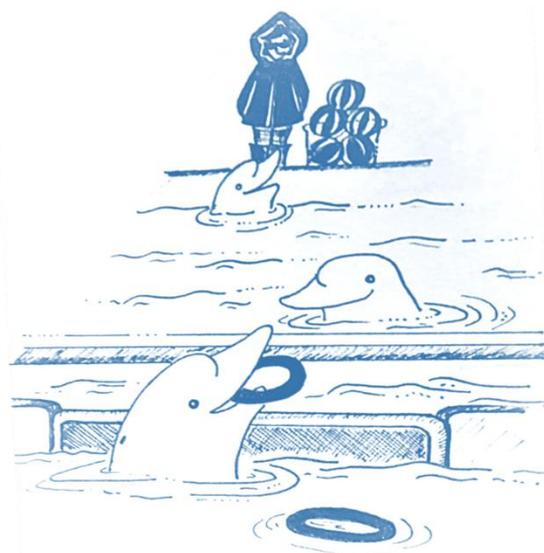
**Table 19.** Experimental conditions, composition of the groups and type of gate used per day and testing session. **Mt:** Mateo; **Bl:** Blue; **St:** Stella; **Bla:** Blava; **Ay:** Aytami; **-:** none.

Day	Session	Condition	Main pool	Small pool	Gate
1	1	Goal	Mt+Bl	St+Bla+Ay	Canvas
	2	No-Goal			
2	1	Goal	St+Bla+Ay	Mt+Bl	Canvas
	2	No-Goal			

3	1	Goal	Mt+Bl+St	Bla+Ay	Canvas
	2	No-Goal			
4	1	Goal	Mt+Bl+St	Bla+Ay	Canvas
	2	No-Goal			
5	1	Goal	Bla+Ay	Mt+Bl+St	Canvas-Mesh
	2	No-Goal			
6	1	Goal	Mt+Bl+St	Bla+Ay	Canvas-Mesh
	2	No-Goal			
7	1	No-recipient	Mt+Bl+St+Bla+Ay	-	Canvas-Mesh

Dolphins were tested in the same three experimental conditions as the capuchin monkeys in Skerry, Sheskin, & Santos's (2011) study (see Figure 26):

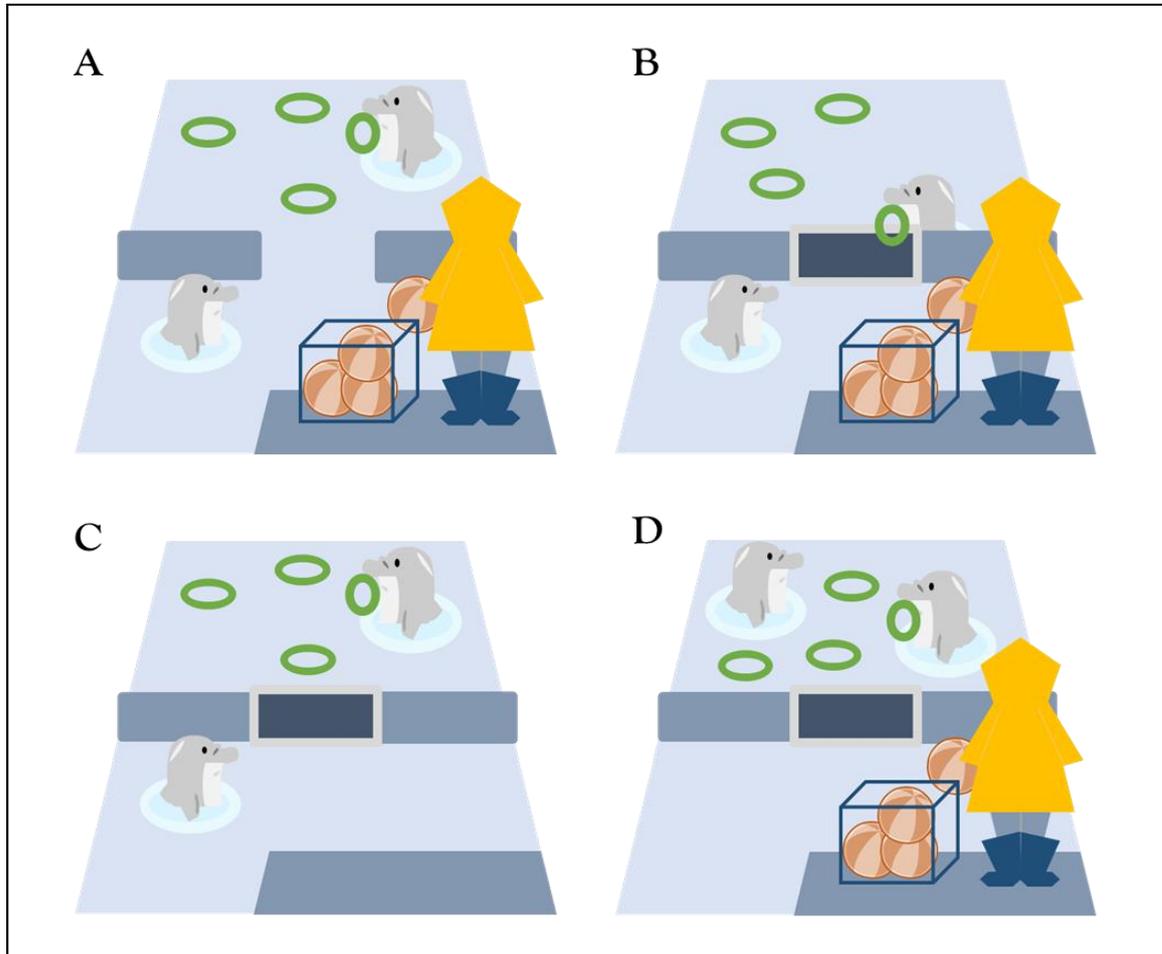
1. *Goal condition:* The helper group received the tokens (3 per individual) but could not exchange them with the experimenter, whereas the recipient group could interact with the experimenter but had no access to the tokens. The subjects in the helper group had the opportunity to help the recipients by passing the tokens above the gate (see **Figure 25**), through a hole in the canvas of one of the gates or throwing them over the wall of the main pool, as they used to do with other toys in their free time. The experimenter recorded how many tokens were transferred to the adjacent pool and the identity of the helper and the receiver.



2. *No-goal condition (control 1):* This condition was identical to the goal condition except that the experimenter and the balls were absent. Thus, the recipients did not have the opportunity to interact with the experimenter. The aim of this control condition was to rule out the possibility that the dolphins transferred tokens simply because they preferred to pass tokens through holes or over walls or passing toys to a conspecific. It is expected that if the transfers were motivated by the welfare of their partners, helpers would pass the tokens less often in this condition than in the goal condition in which the recipients had the opportunity to get the preferred toy. The experimenter recorded how many tokens were transferred to the adjacent pool and the identity of the helper and the receiver.

**Figure 25.** View of the testing-set up in the Goal-condition. Drawing by APM

3. *No-recipient condition (control 2)*: In this control condition, the experimenter and the balls were present but all the dolphins remained in the main pool with the tokens. Thus, there were no recipients to exchange tokens with the experimenter. The aim of this control condition was to rule out the possibility that the presence of the experimenter with the balls elicited somehow the token transfer. If the dolphins behave prosocially, helpers would pass the tokens less often in this condition than in the goal condition in which the recipients could get the ball. The experimenter recorded how many tokens were transferred to the adjacent pool and the identity of the individual who transferred the token.



**Figure 26.** Diagram depicting the different experimental conditions. **A:** Training; **B:** Goal condition; **C:** No-goal condition; and **D:** No-recipient condition.

The frequency of token transfer in the goal condition was compared to the frequency of transfers in the two control conditions. The frequency of token transfer to other sides of the pool was also recorded and compared to the three experimental conditions.

Dolphins received 13 experimental sessions. Every subject underwent six sessions (10 min each) of the goal condition, six sessions of the no-goal conditions (10 min each) and one session (10 min) of the no-recipient condition. Each dolphin received at least two sessions in the role of the helper and two sessions in the role of the recipient in the goal and no-goal conditions (see **Table 19**). Testing sessions were divided into blocks of 2 sessions per day (one session of the goal condition followed by one session of the no-goal condition) except for the last day in which they only received one session of the no-recipient condition. Dolphins were tested on two consecutive days per week for a total of seven days of testing distributed in four weeks. In the day following the two consecutive testing days,

they received a remainder training session to avoid frustration (three remainder testing sessions, one per week). The remainder training sessions and the next testing session were separated by three days.

*Index of affiliation relationships (IA):* To examine the effect of valuable relationships on dolphins' possible helping responses, we calculated the index of affiliation relationships between the four dolphins following the procedure described in Yamamoto *et al.* (2016). Relative frequencies of synchronous swimming between dolphins were recorded using 0–1 sampling (3-minute intervals) (Altmann, 1974). The behavioural observations (39–54-minute periods of 0–1 sampling) were conducted during dolphins' "free-time" on three days in which the dolphins received no training or testing sessions. Observations were all carried out by the same person (APM) and occurred for approximately 135 min between 8:00 and 11:00 in March 2017. For calculating the index of affiliation relationships for each couple, the number of 1–0 sampling periods in which synchronous swimming between individuals A and B occurred ( $X_{AB}$ ) was divided by the number of 1–0 sampling periods in which the individuals A and B were observed ( $Y_{AB}$ ) (Whitehead & James, 2015; Yamamoto *et al.*, 2016). Behavioural data were collected using both direct observation and video recordings.

### 5.3. Results

None of the dolphins shared the tokens in the goal condition or in the no-recipient condition. Only one dolphin accidentally transferred one of the tokens in one session of the no-goal condition (Mean transfers  $\pm$  SE =  $0.17 \pm 0.16$ ). During experimental sessions, some dolphins passed the tokens to other sides of the enclosure through the glass walls of the pools (Mean transfers  $\pm$  SE =  $0.83 \pm 0.47$ ). No differences in the transfer rate were observed depending on the composition of the experimental groups. **Table 20** shows the index of affiliation relationships for each dyad.

**Table 20.** Affiliation indexes for each dyad.

Dyad	IA	Dyad	IA
Mateo–Stella	0.61	Blue–Aytami	0.05
Mateo–Blue	0.32	Mateo–Aytami	0.05
Blava–Stella	0.27	Stella–Aytami	0.05
Blava–Aytami	0.25	Mateo–Blava	0
Blue–Stella	0.09	Blava–Blue	0

### 5.4. Discussion

In this minimal-cost instrumental helping task, dolphins did not spontaneously share tokens with other conspecifics, irrespective of the level of affiliation with the potential partners. Our results are consistent with those of the study of Nakahara *et al.*, (2017), in which dolphins also did not behave prosocially towards their partners in a giving assistance task. Importantly, in our study dolphins did not differentiate between conditions, not transferring tokens in any of the conditions tested, independently of whether the experimenter was present or not, and irrespectively of whether there was a recipient in the other pool or not.

Several methodological problems have been proposed as the main factors behind failure in tasks assessing prosocial and cooperative behaviours in non-human animals (Albiach-Serrano, 2015). These methodological problems are related to both, social and physical elements of the tasks (Skerry *et al.*, 2011; Albiach-Serrano, 2015). Thus, it is possible that, in this experiment, the lack of helping responses of dolphins could be related to some of these aspects of the study design:

1. *Social and motivational aspects of the task*: The subjects' motivation to behave prosocially or cooperate in instrumental tasks could be affected by social aspects such as tolerance or relative dominance between participants (Albiach-Serrano, 2015). For example, a dominant animal can monopolize the apparatus, the tokens or the obtained rewards in the test, and thus subordinates could not be motivated to help or cooperate in the task (Albiach-Serrano, 2015). In this paradigm, however, we provided a large number of tokens and observed that none of the dolphins monopolized them. Indeed, we observed that, during the experimental period, there were generally several available tokens floating in the pool. Moreover, dolphins could transfer the tokens through several areas of the pool (passing them over the two gates or throwing them over the walls of the pool). This disposition allowed that the presence of a specific individual in a particular zone did not prevent that other individuals transfer the tokens through other areas of the pool.

The identity of the recipient could also influence subjects' motivation to help. In fact, it has been shown that prosocial or empathic behaviours seem to follow a familiarity gradient, offered mostly to familiar individuals (Preston & de Waal, 2002). But, although in this experiment dolphins could provide help to several familiar conspecifics towards whom they should be motivated to behave prosocially (in-group members with whom they shared different levels of affiliative relationships), they did not transfer any token. Furthermore, the quality of the relationship with the recipients did not affect their performance across sessions.

The cost of helping and the presence of motivating rewards for the helper are other motivational factors that could have affected dolphins' behaviour in the task. For example, in an instrumental helping task, capuchin monkeys' helping responses were limited by the cost of helping, and if they could obtain rewards for themselves, they failed to consider the perspective of the recipient (Barnes *et al.*, 2008). During the familiarization phase, it was observed that, although dolphins preferred the balls over the tokens, in occasions some of them also played with the tokens in absence of the balls. Therefore, to minimize the cost associated with sharing the tokens, dolphins were given many of them. So, even if they shared a token with a partner they still had some tokens left to play with. Nevertheless, the action of transferring a token to a partner had other associated costs. To voluntarily pass the hoop to the other side of the pool, the dolphin had to pick up the token, approach one of the gates and pass it over the frame of the gate, located a few centimetres above the dolphin's snout. Dolphins could also transfer the tokens throwing them above the walls of the pool or above the frame of the gates (**Figure 24**). Throwing objects through the air or pass toys from a pool to another are part of the repertoire of actions observed during play in this group of dolphins. These dolphins also used to play by throwing balls or buoys to humans located at the other side of the glass tank walls of the enclosure. In fact, during the experimental sessions, some of the dolphins played with the tokens throwing them in the air and over the glass tank walls. Thus, the action of transferring a token to the other pools did not seem to require a great amount of effort. However, only one of the dolphins accidentally threw one of the tokens into the other pool.

On the other hand, it is also possible that the dolphins did not share tokens with their partners since they were motivated to obtain later the reward for themselves. As the experimenter could move through the enclosure, the dolphins could have saved the tokens expecting that she would

approach their side of the pool to exchange the balls with them. However, dolphins were tested in several experimental sessions, so they had the opportunity to learn that, even though they kept the tokens until the end of the session, they could not exchange them with the experimenter. Even so, they did not share the tokens either during the first or during the last sessions of the experiment.

2. *Physical and cognitive aspects of the task:* In general, instrumental helping tasks are cognitively demanding and some of them might be too difficult to solve (Albiach-Serrano, 2015). This type of tasks requires simultaneously representing the physical context of the task and another individual's goal state and using these representations for a prosocial motivation (Skerry *et al.*, 2011). Thus, providing prosocial responses in instrumental tasks may also depend on the ability of the subject to infer another's goals and the salience and ease with which the subject can infer this goal from the situation (Vonk *et al.*, 2008; Skerry *et al.*, 2011). Furthermore, the physical aspects of some apparatuses used in these tasks could hinder subjects' understanding of the experimental procedure (Albiach-Serrano, 2015).

We tried to keep the task as simple as possible, reducing the number of elements used in the experimental procedure to three: the tokens, the experimenter and the reward. Despite the simplicity of the task, it could be possible that the dolphins had problems understanding some aspects of the procedure or they were unable to attribute or infer the recipients' goal or integrating relevant representations to successfully help their partners.

Chimpanzees seemed to behave prosocially in tasks where goals are made salient or as long as the partner requested help, suggesting that the salience of the end goal and partner's request are critical factors constraining the expression of prosocial behaviour in some species (Warneken & Tomasello, 2006; Warneken *et al.*, 2007; Yamamoto *et al.*, 2009; Melis *et al.*, 2011; Skerry *et al.*, 2011). Conversely, in a prosocial choice task, dolphins chose the prosocial option spontaneously, without requests from the partner (Nakahara *et al.*, 2017). In our experiment, subjects were familiar with the specific goal of the recipients not only because they have been previously trained to exchange tokens for rewards but also since the roles were reversed across sessions. With this procedure, dolphins had the opportunity to appreciate and experience both perspectives, that of the recipient and that of the helper and learn about the dynamics of the task. Even so, it could be possible that they failed to help their partners since it was difficult to infer their partners' goal in this context, or simply because their partners were not interested in the task and need no help. For example, it might be possible that the rewards did not elicit sufficient motivation in the recipients. However, during the familiarization, most of the dolphins were highly motivated to obtain balls for themselves, exchanging tokens almost immediately after the start of the session. Sometimes, when they lost the ball they immediately searched for a token and exchanged it again to obtain a new one.

Furthermore, we observed that during the experimental sessions the recipient dolphins approached the experimenter and performed attention-getting behaviours. Such behaviours consisted in emitting audible sounds while looking at the experimenter, splashing water with the snout, performing trained tricks (e.g. swimming backwards), or in one occasion one of the dolphins seemed to alternate pointing to the balls and gazing the experimenter. These behaviours suggest that the dolphins were highly interested in the balls, attempting to get the experimenter's attention and trying to get the balls in several ways. Moreover, during the experimental sessions recipient dolphins usually rammed, pushed or displaced the gate closest to the experimenter. Sometimes, they did so after having tried to get the balls from the experimenter. During these episodes, it was likely that, while pushing the gate, dolphins also

emitted vocalizations, but we could not record these calls. These pushing and ramming behaviours could be an attempt of the recipients to get the attention of other dolphins and request for tokens. However, these dolphins have been observed to push and ram closed gates in other contexts, so it was difficult to determine whether these behaviours were requests for help, attempts to open the gate to get the tokens or signs of frustration or aggression derived from the situation. The fact that the canvas gate limited visual and physical contact between dolphins could have made the recipients' request behaviours less salient. However, one of the canvas gates broke and was replaced by a mesh gate during the last two weeks of testing. The mesh gate allowed more visual contact between dolphins during the experimental sessions but even so the dolphins did not transfer any token in these days. So, in any case, the recipients' pushing and ramming behaviours did not elicit any prosocial response in their partners in none of the experimental conditions. Finally, it is also possible that dolphins did not behave prosocially towards their partners because they lack the ability to attribute goals to others. Although it has been shown that dolphins are endowed with well-developed cognitive skills such as robust joint attention skills (Xitco *et al.*, 2001; Xitco, Gory, & Kuczaj, 2004; Pack & Herman, 2006), to date there is no positive evidence of goal attribution in dolphins.

Given that this experiment was conceived as an initial attempt to assess spontaneous helping responses in dolphins, we kept the task as simple as possible, not training the dolphins to transfer the tokens from one pool to another, and not reinforcing them for doing so. During their free time, this group of dolphins used to play throwing toys through the air and passing balls from one pool to another and recovering them later. It was therefore plausible that dolphins spontaneously used this knowledge for devising a way to transfer the tokens during the experimental sessions. However, dolphins did not transfer any token under any of the conditions tested, not even in the no-recipient condition when they could have tried to get the reward for themselves, as capuchins in Skerry *et al.*'s study. So, it could be possible that the lack of prosocial responses was due to dolphins' inability to find a way to transfer the tokens rather than due to a lack of prosocial preferences. In fact, in some experiments, chimpanzees were unable to solve simple cooperative instrumental tasks if they do not receive enough experience with the apparatuses or procedures of the task (Albiach-Serrano, 2015). Furthermore, instrumental helping tasks require integrating relevant representations of both, the physical and social context to help effectively (Skerry *et al.*, 2011). This process is cognitively challenging and thus, despite its apparent simplicity, this task may require integrating relevant socio-cognitive representations in a flexible way that could be too demanding for dolphins.

Apart from the social and physical constraints of the task, another explanatory alternative might be that dolphins were indifferent to the opportunity to help others. In other words, dolphins may not have shared the tokens with their partners simply because they lack other-regarding preferences. If this were true, dolphins understood the procedure of the task but they did not transfer any token in any condition because they realized that they could not get rewards for themselves. This hypothesis might partially explain why dolphins only voluntarily passed the tokens through the glass tank walls, out of reach of their partners but within reach of the experimenter or the trainers that could pass through that area after the end of the experiment. However, this behaviour could also be explained by the fact that dolphins often play to throw toys above these walls expecting a human to throw them back.

Overall, our results showed that dolphins did not spontaneously help their partners in a minimal-cost instrumental helping task. This lack of prosocial responses might be due to some of the motivational and socio-cognitive constraints of the task that could have made the experimental procedure too demanding for dolphins or have hindered their understanding of the task. Especially

the lack of previous experience transferring tokens from one pool to another could have affected dolphins' performance in this task. Another possible interpretation of the data is that dolphins did not behave prosocially since they lack other-regarding preferences. Further studies are needed to distinguish between these interpretations of our results and other possible hypotheses. As previously reported, this experimental design controlled for several factors that may constrain prosocial responses in instrumental helping tasks such as the identity of the recipient, the simplicity of the task, the familiarity of the subjects with the end goal, the opportunity of subjects to gain for themselves or the influence of the presence or absence of a goal and a recipient. We conceived this experiment as a first approach to assess spontaneous helping responses in dolphins. For this reason, we kept the procedure as simple as possible, expecting that dolphins would be able to integrate the physical and social constraints of the task without intensive training. The experimental design thus did not control for dolphins' knowledge about how to transfer tokens to the other pool. As previously mentioned, this factor may have affected dolphins' performance in this task. Therefore, to assess the influence of this factor in dolphins' helping responses, it would be of great interest to give the dolphins enough experience passing tokens through the gates and retest them in a subsequent experiment. Moreover, the fact that the experimenter could move across the enclosure might have made the subjects to expect gain rewards for themselves and fail to take into account the recipients' perspective. To control for this constraint, in addition to testing each individual in several sessions, it would be interesting to retest dolphins using an exchange machine similar to that used in Skerry *et al.*'s paradigm and counterbalancing the order of presentation of the different experimental conditions. These subsequent experiments would allow us to better assess the crucial factors constraining prosocial behaviour in dolphins.

Wild and captive dolphins have been reported to perform several prosocial behaviours such as rescuing or caring for other individuals. Little is known however about the factors and mechanisms underlying such behaviours. In particular, it is not known whether these behaviours are addressed towards kin. The extent to which dolphins display other-regarding preferences or helping behaviours towards non-kin conspecifics in a flexible way and in different contexts deserves further research. Due to both its simplicity and the ease of controlling motivational and cognitive factors, the experimental paradigm used in this study represents a powerful tool for this purpose. In addition, this protocol also allows us to examine reciprocal and cooperative behaviours across sessions. Thus, this experimental paradigm could serve to examine prosocial behaviours and related processes in dolphins and other animal species. Identifying the main factors influencing prosocial and helping responses in non-human animals would help us to expand our knowledge on the evolution of prosociality and its phylogenetic continuity across the animal kingdom.



## CHAPTER 6

### GENERAL DISCUSSION AND CONCLUSIONS

While empathy is a century-old psychological concept, its study in non-human animals has become the focus of much recent scientific interest, as it promises to provide the clues to understand the evolutionary origins of our social and moral nature. However, the study of animal empathy has developed using different paradigms, different concepts of the phenomena involved, and the absence of a systematic program. The first Section of this thesis aimed to overcome some of these issues, complementing and constraining anthropocentric views of empathy. In this way, the present thesis has tried to clarify the terminology and taxonomy of basic and complex forms of empathy, providing operative criteria for these phenomena that could be applicable to both human and non-human species. In Chapter 2 and 3 a comprehensive review of the literature on basic and complex forms of empathy in non-human animals is provided. This review integrated current findings in this field and served to clarify the challenges and conditions to satisfy. Furthermore, these chapters included extensive discussions on whether the available evidence really offers examples of empathic behaviours similar to those described in humans. These discussions also highlighted the importance of the comparative study of these processes for elucidating the evolutionary history and adaptive function of empathy across the animal kingdom. The ultimate goal of this Section was to build a robust theoretical framework that serves as a guideline to carry out future studies on animal empathy.

In the second Section of the present dissertation, this theoretical framework is applied to the particular case of bottlenose dolphins. In this section, five studies on empathy-related behaviours in dolphins are described. Overall, these studies showed that dolphins seem to be affected by the emotional state of conspecifics, especially from that of close affiliated partners. Furthermore, in certain contexts, the perception of distress in a partner seemed to elicit empathy-like behaviours in witness dolphins. These behaviours could have led to the improvement of the situation of the distressed dolphin, supporting the hypothesis that these responses are empathy based. These results thus consolidate dolphins as ideal animal models for the study of empathic phenomena and posit the necessity of more systematic research on the field.

#### *Basic forms of empathy in non-human animals*

One of the specific aims of the present thesis was to clarify and describe basic forms of empathy in non-human animals, focusing, in particular, on why these processes have been proposed to function as primitive forms of empathy and why they have been linked to more complex empathic behaviours. This objective is addressed in Chapter 2, and the main conclusions are the following:

(1) Most empathy models have traditionally considered emotional contagion, motor mimicry or social synchrony as the most basic elements of human emotional empathy. In this regard, these processes may represent basic forms of empathy *per se* and/or be linked to more complex empathic behaviours. However, in other species, little is known about the nature and mechanisms of these

processes or whether they underlie complex forms of empathy. The available evidence suggests that, indeed, emotional contagion, mimicry and social synchrony may allow non-human animals to be attuned to the affective state of their partners in a simple and automatic way. Given that it is generally considered that the core feature of empathy is to share, match or be affected by the emotional experiences of another, these basic motor and emotional processes could thus function as rudimentary forms of empathy in many social animals.

(2) These processes could be related to the ecological circumstances and socio-behavioural traits of the species and thus present a great variability across the animal kingdom. These phenomena thus could be far more complex and flexible than previously thought, and we should be cautious when generalizing about their functions and mechanisms between species. Nevertheless, all these processes seem to allow individuals to “feel into” another’s affective state, highlighting the important adaptive advantages that this capacity might provide to social animals. In this manner, emotional contagion, mimicry and social synchrony could be important evolutionary adaptations for animals that need to interact and cooperate with others. These processes may serve to ease affiliative behaviours, promote social bonds, restore relationships after agonistic interactions, enhance social acceptance, and mark others as similar to self in a simple manner. Moreover, animals that are more prone to mimicry, social synchrony or emotional contagion may experience significant social benefits, which in turn would increase their probability of reproduction (Sullivan & Rickers, 2013). These adaptations thus may be crucial for animals living in pairs or social groups or even for species that only interact with others in short periods of time (e.g. breeding season).

(3) Ultimately, emotional contagion, mimicry and social synchrony could also lead to an increase in the probability of cooperation and prosociality between conspecifics. For group or pair-living species, this assistance as well as social coordination, interaction and effective communication are essential for breeding success and survival. Through these automatic and simple processes, many social animals may maintain social relationships and elicit conspecifics’ assistance without requiring the involvement of complex cognitive processes. Therefore, emotional contagion, mimicry and synchrony might function as primitive forms of empathy providing important adaptive advantages to group or pair-living species. In addition, in animals endowed with well-developed cognitive capacities, these phenomena and related prosocial behaviours might not always be purely reflex-like and underlie some complex empathic behaviours, as proposed by current views of empathy.

(4) Overall, more research is needed in order to expand our knowledge of the functions and mechanisms of emotional contagion, mimicry and social synchrony, and whether these processes are present in a wide variety of species. The use of systematized paradigms including both behavioural and physiological measures and reliable controls would be very helpful in this endeavour. Simultaneously registering physiological and behavioural responses in both individuals (observer and distressed party) would allow us to reliably establish the occurrence of an emotional state-matching between individuals. Furthermore, examining the spread of positive emotions emerges as a useful way to overcome the impediments linked to the study of emotional responding in species such as primates or cetaceans. Future studies should try to assess whether there is a causal relationship between mimicry or social synchrony processes and emotional contagion in non-human animals, and the directionality of this link. It is also important to establish how social learning takes place during emotional situations, and if there are differences between species. In this regard, it is necessary to address whether this process really involves the contagion of emotions from one individual to another or if it works through the detection of previously learned signals without involving the sharing of emotional cues. A broader understanding of these phenomena could allow us to establish the neurobiological substrates underlying basic empathic processes that may be involved in more complex ones. Furthermore, comparative studies in this field could serve for building a robust framework for

the study of the evolutionary roots of empathy and its phylogenetic continuity across a great number of species.

### *Complex forms of empathy in non-human animals*

The Chapter 3 of this dissertation focused on complex forms of empathy: sympathetic concern and empathic perspective-taking. One of the objectives of this chapter was to provide operative criteria that represent the best available approach for reviewing the existing evidence. Given that most of the current evidence on complex forms of empathy does not provide data on the motivations underlying the observed or measured responses, we left aside the behavioural motives in defining those operative criteria and focused on the available data (reactions, responses and outcomes/effects). These criteria were used in this chapter and in section 3 of Chapter 6 to distinguish between empathic behaviours and similar behaviours that are not empathy-based in non-human animals. The main conclusions derived from these chapters are the following:

(1) Sympathetic concern, empathic perspective-taking and the two major behaviours in these categories, consolation and empathic targeted helping, have been traditionally defined in terms of their underlying motivations. This approach cannot be easily applied to the available data on empathic behaviours in non-human animals. Thus, in this thesis, we operationalize these behaviours in terms of the type of reaction and response triggered by the perception of distress in others and its main effect or outcome. Separating the underlying motivations of the behaviours and focusing instead on the set of behavioural and physiological features of animals' reactions and responses towards distressed individuals allows us to distinguish empathic from non-empathic behaviours better in non-human animals. We note that this method may still not be sufficient in ambiguous cases.

(2) A wide range of social species can perform sophisticated behaviours that calm, help or rescue other group members from distressing situations. These behaviours are related to the species' behavioural ecology and may be simple, not involving empathy-based mechanisms, such as rescue behaviour in ants, or more complex behaviours requiring an emotional component and which, in turn, can be graded into different levels of complexity (de Waal, 2008). The combination of emotional and cognitive elements allows animals to respond effectively even in new situations, which is presumably an important adaptation for animals living in unpredictable environments.

(3) In general, empathic behaviours seem to follow a familiarity gradient, offered mostly to familiar individuals but, for animals living in fission-fusion groups like some primates and cetaceans, responses to others' needs irrespective of their identity may also be an important adaptation. For these species, the involvement of emotion may provide a more generalized response to others' emotional states. Humans regularly help strangers (Raihani & Bshary, 2015) and some studies reviewed herein record cases in which primates, cetaceans or dogs helped non-familiar individuals or even members of other species. Thus, whereas familiarity could facilitate empathy in several contexts, expanding these emotional responses towards a wider range of individuals including strangers might indicate an increased empathic capacity as in humans.

(4) Compliance with all three requirements defined in **Table 1** is essential to distinguish empathic from non-empathic processes. Only some reports involving primates, cetaceans and elephants seem to meet all three criteria (**Table 2**). More research is needed to characterize these behaviours better. For primates and cetaceans obtaining physiological measures could be extremely difficult due to methodological and ethical issues and we must, therefore, rely on behavioural parameters. Interpreting behaviour is contentious but by combining such information with data on the level of effective emotional regulation for each species and with features of the two other requirements (response and outcome) we could develop a more complete picture of the observed phenomena.

Although in this dissertation we have not extensively discussed evidence for neural mechanisms of empathy in non-human animals (most of the available data comes from rodent studies, and there are several reviews available: Panksepp & Lahvis, 2011; Panksepp & Panksepp, 2013; Keum & Shin, 2016; Meyza *et al.*, 2016; Sivaselvachandran *et al.*, 2016), the study of the neural basis of empathy is very promising for assessing continuity between empathy in humans and other species. Finally, future studies assessing the motives underlying possible empathic behaviours (e.g. using tests of conditioned place preference/aversion) will provide useful information to clarify the nature and features of empathic behaviours in non-human animals and their phylogenetic continuity across the animal kingdom.

### *Empathic capacities of bottlenose dolphins*

The second Section of this thesis is devoted to the study of cetacean empathy. In particular, Chapter 5 presents a series of experimental and observational studies investigating cognitive and emotional processes that have been related to empathy in bottlenose dolphins. Due to the scarcity of empirical studies assessing the empathic capacities of cetaceans, these experiments were conceived as an initial attempt to establish useful paradigms that allow us to expand our knowledge in this field. Furthermore, another objective of these studies was to examine whether bottlenose dolphins display empathic-like responses towards conspecifics applying the theoretical framework developed in the first Section of this dissertation. This theoretical framework served to classify as empathic or not the dolphins' responses based on the requirements defined in **Table 1**. The main conclusions drawn from these five studies are the following:

(1) Many anecdotal reports have suggested that cetaceans could be affected by the emotional state of others and that, in certain situations, dolphins and whales are able to help, care or protect conspecifics in need. Most of the evidence provided by the studies detailed in this thesis are consistent with these anecdotal reports, suggesting that bottlenose dolphins are indeed affected by the emotional or arousal state of their conspecifics. Moreover, these studies also suggest that, in some contexts, dolphins direct affiliative and prosocial behaviours towards others in distress. Some of those observed behaviours could be attempts to comfort or help the distressed party and thus may be indicative that dolphins are aware of the needs and situation of the other and act to alleviate its suffering. Therefore, some of these behaviours could be considered as empathic.

(2) As pointed out above, the compliance with all three requirements defined in **Table 1** is crucial to distinguish empathic from non-empathic processes, and some of the dolphins' responses described in the previous studies could meet some of these criteria. In the first study, dolphins' behaviours seemed to involve a moderate emotional reaction in response to another's distress and other-oriented responses including attempts to ameliorate the other's state. These are two of the three requirements established in Chapter 3 for a behaviour to be considered as an example of sympathetic concern (consolation). Furthermore, in the second study, bystanders' unsolicited affiliative responses towards conflict victims also seemed to meet the second and third established components of sympathetic concern (consolation). That is, bystanders' behaviour included other-oriented responses such as approaches and attempts to comfort the distressed party and these responses likely lead to the alleviation of the distressed individual. Furthermore, in both studies, the affiliative relationship with the distressed party was a strong modulator of dolphins' responses. This factor also has robust effects on processes facilitating empathy (Preston & de Waal, 2002), and is considered to be one of the main features characterizing consolation behaviour. Overall, although it was not possible to assess the compliance of all three requirements of sympathetic concern, the behavioural responses registered in these studies met some of the main factors defining consolatory responses and may have involved emotional contagion processes.

(3) Furthermore, some of the behaviours performed by dolphins in the first study were suggestive of flexible targeted helping and thus could meet the second requirement of empathic perspective-taking. However, this hypothesis could not be confirmed with the available data. Dolphins' failure in Studies 3 and 5 neither allowed to confirm the presence of targeted helping or sophisticated ToM capacities in this group of captive bottlenose dolphins. Nevertheless, the results provided by the fourth study suggest that, after receiving enough visual experience with objects moving inside other objects, dolphins are able to pass object permanence tasks. Object permanence is an indicator of secondary representation, which is considered to be a precursor of ToM and perspective-taking, abilities that are thought to be necessary to display complex forms of empathy such as empathic perspective taking.

(4) The paradigms used in studies 1 and 5 of the present thesis have proved to be very useful methods for assessing different processes and factors related to both basic and complex forms of empathy in cetaceans. The protocol developed in the first study proposes to take advantage of common management procedures in zoos such as animals transfers that represent a source of short-term stress for the animals. This protocol thus allows the study of observers' emotional reactions and empathy-like behaviours towards a distressed conspecific, avoiding some of the general problems associated with research on emotions in certain species like primates or cetaceans. In turn, the paradigm used in Study 5 allows the assessment of flexible targeted helping in animals without eliciting distress in the subjects. This experimental design also serves for controlling the main factors influencing animals' prosocial responses in helping tasks such as motivational and cognitive variables. On the other hand, our results in some of these studies have highlighted the importance of taking into account the species' socio-behavioural traits and the life history of the experimental subjects (e.g. previous training) at the time of designing an appropriate experimental paradigm. It is also important to consider the cognitive requisites that the protocol poses to the animal since these cognitive aspects might hinder subject understanding of the tests. For example, given the difficulty that dolphins seem to have with tasks requiring object permanence, experimental designs aiming to test other cognitive capacities should try to avoid the use of procedures that imply visually tracking visible or invisible displacements.

(5) Overall, more research is needed to expand our knowledge on the empathic capacities of cetaceans. Nevertheless, the studies described in the present thesis have highlighted the extent to which dolphins are affected by the emotional state of their partners, and suggest that, in those situations, they provide other-oriented behaviours that are likely to improve the situation of the distressed animal. Thus, these results consolidate bottlenose dolphins as an ideal animal model for the comparative study of empathy. Furthermore, although it was not the main aim of this dissertation, the fourth study has pointed out that previous visual experience with movement dynamics of objects could be crucial for the normal development of object permanence skills. The fact that dolphins are highly auditory animals that use echolocation extensively in their aquatic habitat but they also perform well in air thanks to good vision (Griebel, 2002), makes them very interesting experimental subjects for the study of the role of previous visual experience in the development of object permanence.

(6) Further studies in captivity and in the wild are needed to confirm some of the evidence provided in this thesis. Future works including auditory recordings and physiological measures could serve to better characterize the nature and mechanisms underlying dolphins' responses to the perception of conspecifics' distress. In general, registering physiological parameters in cetaceans is not an easy task but some physiological responses to stressors such as changes in the respiratory rate or breath-hold capability (Peddemors, 1990) could be easier to register. These parameters could be a useful tool to determine stress levels in cetaceans since they are observable from the surface and do

not require any procedure that could evoke an emotional reaction in the subjects. Carrying out more controlled studies on dolphins' instrumental helping behaviour, perspective taking abilities and other-regarding preferences would also help to assess some of the main factors involved in complex forms of empathy such as empathic targeted helping. These works could provide valuable data to fulfil all the established criteria for a behaviour to be considered as empathic, allowing us to better characterize the empathic capacities of cetaceans.

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