Tesis Psicológica
ISSN: 2422-0450
Fundación Universitaria Los Libertadores

The role of previous visual experience in the acquisition of object permanence skills in bottlenose dolphins: a pilot study*

Pérez-Manrique, Ana; Gomila, Antoni
The role of previous visual experience in the acquisition of object permanence skills in bottlenose dolphins: a pilot study*
Tesis Psicológica, vol. 13, no. 2, 2018
Fundación Universitaria Los Libertadores
Available in: http://www.redalyc.org/articulo.oa?id=139061595006

Articulo de Investigación

The role of previous visual experience in the acquisition of object permanence skills in bottlenose dolphins: a pilot study*

El papel de la experiencia visual previa en la adquisición de habilidades de permanencia de objetos en delfines mulares: un estudio piloto

Ana Pérez-Manrique ** ana.perez@uib.cat
University of the Balearic Islands, España
ORCID: http://orcid.org/0000-0001-9211-0466
Antoni Gomila ***
University of the Balearic Islands, España

Tesis Psicológica, vol. 13, no. 2, 2018

Fundación Universitaria Los Libertadores

Received: 09 April 2018
Revised document received: 09 April 2018
Accepted: 10 December 2018

Funding
Funding source: Spanish Ministry of Economy and Competitiveness
Contract number: FFI2013-44007-P and FFI2017-86351-R

Abstract : Object permanence, the ability to represent hidden objects, has not been extensively assessed in cetaceans, and the available evidence is contradictory. Although bottlenose dolphins (*Tursiops truncatus*) are thought to be endowed with cognitive capacities required to pass complex object permanence tests, they have failed a series of tasks involving invisible displacements, which raises the question of whether they do master object permanence. Lack of understanding of containment or lack of experience tracking objects hidden from both sight and echolocation may explain such unexpected results. The goal of the current pilot study was to test these two hypotheses in a series of visible and invisible displacement tasks with bottlenose dolphins. Our results suggest that dolphins are indeed able to succeed in complex object permanence tasks but only if they have previous visual experience with the movements of objects inside other objects. Thus, these outcomes point to an important role of visual experience in the development of object permanence skills.

Keywords: object permanence development, bottlenose dolphins (Tursiops truncatus), invisible displacements, transpositions.

Resumen: La permanencia de los objetos o capacidad de representar objetos ocultos, no ha sido evaluada ampliamente en cetáceos, y la evidencia disponible es contradictoria. Aunque se piensa que los delfines de nariz de botella (*Tursiops truncatus*) están dotados de las capacidades cognitivas requeridas para pasar pruebas de permanencia de objetos complejos; fallan en una serie de tareas que involucran desplazamientos invisible, lo que conduce a plantear la cuestión sobre el dominio o no, de la permanencia del objeto. El objetivo del actual estudio piloto fue probar dos hipótesis: si se trata de la falta de comprensión de la contención, o la falta de experiencia en el seguimiento de objetos ocultos tanto a la vista como en ecolocación. Para tal fin se desarrollan una serie de tareas de desplazamientos visibles e invisibles con delfines mulares. Los resultados sugieren que los delfines son capaces de tener éxito en tareas complejas de permanencia de objetos, pero solo si tienen experiencia visual previa con los movimientos de objetos dentro de otros objetos, por tanto, se concluye que la experiencia visual juega un papel importante en el desarrollo de habilidades de permanencia de objetos en delfines mulares.

Palabras clave: permanencia del objeto, delfines mulares (Tursiops truncatus), desplazamientos invisibles, transposiciones.

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). Piaget (1953) assessed this capacity in children using visible and invisible displacement tasks. In the former, 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. Piaget (1953) concluded that the development of object permanence proceeds through six stages. It is at Stage 6 that children (around 18 months of age) are able to solve these complex invisible displacement tasks, understanding, thus, that the object placed inside a container moves with the container.

Several cognitive skills are required to perform object permanence tasks (Cacchione & Rakoczy, 2017). Succeeding at visible displacement tests requires not only a basic understanding of continuously existing objects but also dealing with several executive demands (visually track the object movements, planning behavior, memory, and inhibitory capacities) (Cacchione & Rakoczy, 2017).

Paradigms involving invisible displacements are more complicated. These tasks require not only understanding that a hidden object still exists and moves with the moving container but also visually tracking its movements in the 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 ...) (Cacchione & Rakoczy, 2017). Children perform invisible displacement tasks at around 18-24 months of age (Piaget, 1955). It is at this age when they also acquire other cognitive abilities related to the capacity to coordinate multiple representations of reality (language, instrumental problem-solving or self-recognition) (Cacchione & Rakoczy, 2017; Perner, 1991). 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).

Object permanence has also been a subject of interest in animal cognition. Many studies of visible and invisible displacements have been conducted in non-human animals. Although these studies have shown that some animal species (e.g. primates, dogs, corvids, parrots) could succeed in invisible displacement tests, many of these findings are controversial (reviewed by Jaakkola, 2014). Most of the criticisms focus on methodological issues such as the number of trials, training, lack of blinding protocols or control conditions, and number and disposition of containers (Cacchione & Rakoczy, 2017; Jaakkola, 2014). Due to these procedural differences across tasks, results on different species are not usually directly comparable (Cacchione & Rakoczy, 2017). Overall, there is a consensus that great apes and parrots are able to reliably perform invisible displacement tasks (e.g. Pepperberg *et al*., 1997; Barth & Call, 2006; Collier-Baker *et al*., 2006; Auersperg *et al*., 2014). For example, whereas two-year-old children found transposition tasks harder than the Piaget's stage-6 invisible displacement task, great apes performed equally well in both paradigms tracking and finding the hidden food (Barth & Call, 2006; Beran & Minahan, 2000; Josep Call, 2003). In turn, 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. On the one hand, bottlenose dolphins (*T. truncatus*) succeeded at visible displacements tasks but failed a series of invisible displacements tests (e.g. transposition tasks) in which dolphins were rewarded if they found an object hidden in one of three opaque buckets (Jaakkola, Guarino, Rodriguez, Erb, & Trone, 2010). In addition, another study in which fish was hidden in floating containers also failed to find complex object permanence understanding in bottlenose dolphins and beluga whales (*Delphinapterus leucas*) (Mitchel & Hoba, 2010). Dolphins' failure in invisible displacement tests was puzzling due to their previous success in tasks assumed to require cognitive capacities involved in object permanence (Mercado & DeLong 2010; Marino *et al.* 2007). On the other hand, bottlenose dolphins followed the invisible movements of a disc in a visual display which involved object occlusion rather than containment, suggesting that they could succeed at invisible displacement tasks (Johnson *et al.* 2015). In this study, the authors used an anticipatory looking protocol and videotaped the dolphins' head movements to assess whether dolphins anticipate the movements of a disk passing behind occluders. That is, dolphins succeeded at invisible displacement tasks involving occlusion of the target object but failed to pass tests in which the target object was hidden inside an opaque recipient; these conflicting pieces of 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 displacement tasks involving containment:

(1) Lack of understanding of containment: Infants seem to learn separately how occlusion and containment operate (Hespos & Baillargeon, 2001, 2006), and likewise, lack of understanding

of containment could explain dolphins' failure at tasks involving containment and their success on tasks involving occlusion.

(2) Lack of experience tracking objects hidden from both sight and echolocation. Dolphins live in aquatic environments in which objects often move differently than out of the water. Given this aquatic environment and their reliance on echolocation, it is 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 example, dolphins could be biased to infer which things will sink or float (Johnson *et al*. 2015; Mitchell & Hoban, 2010). Therefore, they may not have gained the necessary empirical experience to develop the capacity to track invisible displacements of objects inside other objects.

The developmental origins of object knowledge, including object permanence, have been a heavily debated topic. In general, we can distinguish three main views (Bremner, Slater, & Johnson, 2015; Johnson, Amso, & Slemmer, 2003). 1) 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. 2) Subsequent evidence challenged this Piagetian account by showing that many younger infants may have an understanding of some elements of the object concept long before they can move and manipulate objects (Baillargeon & Renée, 1987; Baillargeon, Spelke, & Wasserman, 1985; 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 and which try to infer what the individual understands on the grounds of their expectations. Four-month-old infants' success in these paradigms has led to postulates of innate object knowledge (Spelke, Breinlinger, Macomber, & Jacobson, 1992). 3) 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). In fact, two different experiments with infants and chicks (*Gallus gallus domesticus*) highlighted the crucial role of this early experience for the development of object permanence skills (Johnson, Amso, & Slemmer 2003; Prasad 2015). 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 behavior 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. Furthermore, Gagnon and Doré (1992) showed that dogs (*Canis familiaris*) were more successful in invisible displacements tests if they were tested before in visible displacement ones. This result suggests that previous experience with object permanence tasks may have an influence on the performance in invisible displacement tasks.

For the above-mentioned reasons, dolphins are an ideal model to assess the role of previous visual experience in the acquisition of object permanence abilities. In this pilot study, we aimed to test the two main hypotheses proposed by Jaakkola *et al.* (2010). Thus, our first objective was testing bottlenose dolphin's spontaneous ability to track simple visible and invisible displacements, giving them some experience with "containment" before the testing. If dolphins failed to spontaneously perform 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.

Material and methods

Subjects and apparatus

In this study participated two female Atlantic bottlenose dolphins housed at Marineland Mallorca. The dolphins lived in an outdoor pool conjoined to a medical pool, with a total volume of 1846.75 m^3 of water. The age of the study subjects was 8 years old (*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 experiment was conducted during the first training session of the day before the park opened to the public. Dolphins were fed according to their normal daily routine, which included a variety of fish (capelin, mackerel, and herring) and gelatin, six times per day. This daily routine was structured through several training sessions. In their free time, dolphins were usually offered enrichment items (e.g. floating toys). The dolphins were never deprived of food in any way.

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 were used as rewards. All sessions were videotaped using a waterproof camera SJCAM SJ4000.

Ethics statement

This study was approved by the UIB Committee of Research Ethics and Marineland Mallorca. This research was conducted in compliance with the standards of the European Association of Zoos and Aquaria (EAZA). All subjects tested in this study were housed in Marineland Mallorca in accordance with the Directive 1999/22/EC on the keeping of animals in zoos. The subjects participated in the experiments voluntarily.

Procedure

We used a simple protocol similar to that used by Call (2003) with great apes, but, in this pilot study, dolphins were rewarded for finding a target object (rubber frog). This protocol includes different spatial transposition tasks with only two containers. The experimenter sat behind the sliding platform facing the dolphin, who stayed at the edge of the pool in front of the platform (see Fig. 1). 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 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 Fig. 1).

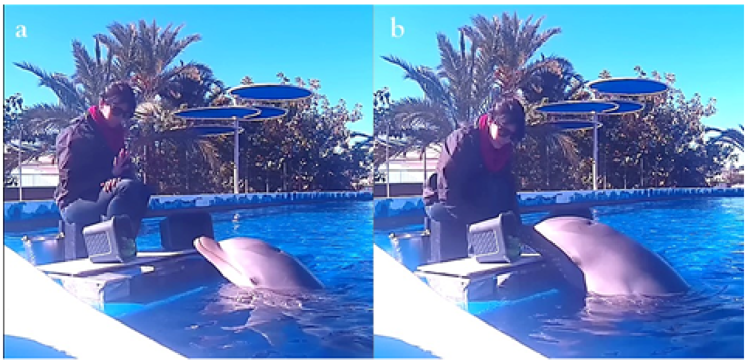


Fig. 1
Photographs depicting a testing session. (a) The object is located inside the right box, and the dolphin waits to make a choice; (b) the dolphin makes a correct choice
Source: Authors

If the subject chose the correct location (that in which the object was), it 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 experimenter slid the platform, the trial was repeated. If the subject performed any of these behaviors more than once for the same trial, the trial was coded as incorrect. 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. This phase had three aims: (1) familiarize the dolphin with the apparatus: 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; (2) train the dolphins to always choose the object's location: the sliding platform was divided into three areas (left, right, middle) in which the object and boxes could be placed (9 different dispositions); 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. 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. To avoid that the dolphins always chose the location in which the experimenter's hand was the time before, the experimenter moved the object in a standardized manner. In half of the trials, the right hand holding the object moved from left to right, and in the other half, from right to left. The experimenter's hand always passed in front of all three locations irrespective of where the object was placed. Our criterion for moving from training to testing was that the dolphin had succeeded on at least 8 out of 9 trials in two consecutive sessions.

2. Test. This phase consisted of several tasks that were administered in a specific order. The dolphin had to succeed at one task to move to 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.

2.1. *Visible displacement task:* This task tested dolphins' spontaneous ability to track the location of the object when both boxes were turned, hiding the object. At the beginning of each trial, the boxes' 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. 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.

2.2. *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. 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. Before each testing session, the dolphin received three warming up trials (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.

2.3. *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 criterion for moving from the visible transposition task to the second transposition task was 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.

2.4. *Second 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.

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. During the visible transposition tasks, dolphins could have learned some of these strategies. For example, to follow the hand that touched the box in which the object was seen last, or to use the crossing movement of the experimenter's hands as a cue indicating that they must select the box located opposite to the area in which the object had been 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:

3.1. *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.

3.2. *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.

3.3. *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. 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.

Data scoring and analysis

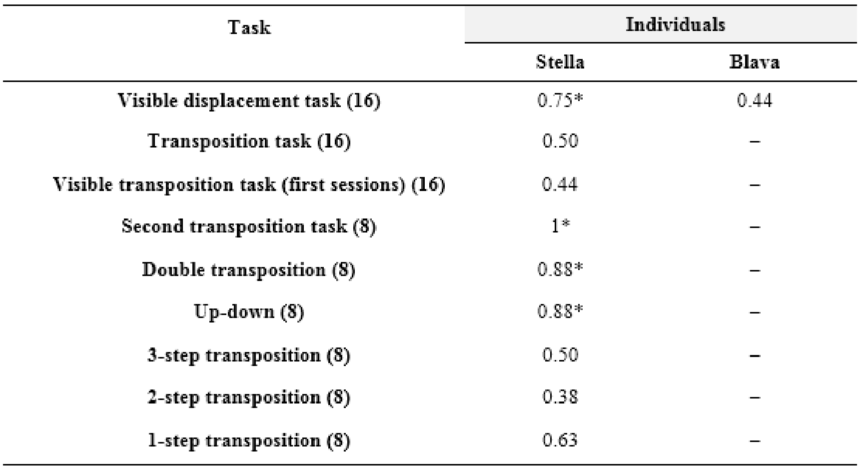
A dolphin was coded as making a choice when its rostrum contacted a box or the object. All trials were videotaped, and the dolphin's choices were scored by reviewing the video recordings. The dolphins' choice was unambiguous; therefore, no reliability coding was conducted. To assess dolphins' individual performance, we conducted binomial tests. The analyses were run using R 3.4.1. statistical software (R Core Team, 2017).

Results

Blava reached the testing criterion after receiving 305 training trials and *Stella* after 240. *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. 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 1 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).

Table 1

Proportion of correct choices per task for each individual (the total number of trials is indicated inside of parentheses).



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	–

* P < 0.05
Source: Authors

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).

Discussion

Both dolphins had difficulties with visible and invisible displacement tests even when they were tested in tasks involving the displacement of only two containers. Only one of the dolphins, *Stella*, succeeded at the visible displacement task without previous training. Our findings in this task replicated those of Jaakkola *et al.* (2010). In their study, only three out of six dolphins succeeded at the single visible displacement task, and only one out of six dolphins passed the double visible displacement test. These results suggest that previous learning and experience with the procedure are necessary to solve simple object permanence 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 succeed at the first transposition task, after receiving visual experience with visible transpositions, she passed 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 (Johnson *et al*., 2003; Prasad, 2015). 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, Crével, Böye, & Lemasson, 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 as well.

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 (Cacchione & Rakoczy, 2017; Jaakkola, 2014). In our study, the experimenter wore sunglasses to avoid giving eye-gaze cues to the dolphin. Furthermore, 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 such as "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 up and down and the double transposition task. If she had been following the first rule, she could not have passed either of these two controls; and if she followed the second rule, she could not have succeeded in the up and down control. However, *Stella* did not pass any of the controls involving sequential movements. In these tests, she chose the favoured box in almost all trials. Although negative results are always hard to interpret, three main hypotheses may explain these outcomes:

(1) Greater difficulty: It has been proposed that success in object permanence tasks is directly dependent on the number of elements that change locations (Barth & Call, 2006). Container crossing and substitution also affect performance in invisible displacement tasks (Rooijakkers, Kaminski, & Call, 2009). Furthermore, multiple displacements seem to be more challenging than single displacements in terms of visual tracking, memory, and inhibition capacities (Cacchione & Rakoczy, 2017). Therefore, some of these factors could have added extra difficulty to the sequential transpositions. In addition, while the boxes were always about 23.5 cm apart in the rest of the tasks, in some steps of the three sequential 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.

(2) 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.

(3) 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.

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 succeed at 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. Given that the same object has totally different movement dynamics in and out of the water, previous visual experience might be crucial for animals living in aquatic environments to solve transpositions. 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. Furthermore, dolphins early failure in some visible displacement tasks (Jaakkola *et al*., 2010) also points to the necessity of previous experience with the procedures of the tasks to succeed in such 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. Unfortunately, with our data, we were unable to clearly identify the critical factors influencing the dolphin's pattern of responses. Thus, 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.

Acknowledgements

This research has received the support of the Spanish Ministry of Economy and Competitiveness through project FFI 2013-44007-P. Ana Pérez-Manrique was supported by an FPU PhD scholarship from the Spanish Ministry of Education, Culture and Sport (AP2012-3501).

References

Auersperg, A. M. I., Szabo, B., von Bayern, A. M. P., & Bugnyar, T. (2014). Object permanence in the Goffin cockatoo (Cacatua goffini). Journal of Comparative Psychology, 128(1), 88-98. https://doi.org/10.1037/a0033272

Baillargeon, R., & Renée. (1987). Object permanence in 3½- and 4½-month-old infants. Developmental Psychology, 23(5), 655-664. https://doi.org/10.1037/0012-1649.23.5.655

Baillargeon, R., Spelke, E. S., & Wasserman, S. (1985). Object permanence in five-month-old infants. Cognition, 20(3), 191-208. https://doi.org/10.1016/0010-0277(85)90008-3

Barth, J., & Call, J. (2006). Tracking the displacement of objects: a series of tasks with great apes (Pan troglodytes, Pan paniscus, Gorilla gorilla, and Pongo pygmaeus) and young children (Homo sapiens). Journal of Experimental Psychology. Animal Behavior Processes, 32(3), 239-252. https://doi.org/10.1037/0097-7403.32.3.239

Beran, M. J., & Minahan, M. F. (2000). Monitoring Spatial Transpositions by Bonobos (Pan paniscus) and Chimpanzees (P. troglodytes). International Journal of Comparative Psychology, 13, 1.

Blois-Heulin, C., Crével, M., Böye, M., & Lemasson, A. (2012). Visual laterality in dolphins: importance of the familiarity of stimuli. BMC Neuroscience, 13(1), 9. https://doi.org/10.1186/1471-2202-13-9

Bremner, J. G., Slater, A. M., & Johnson, S. P. (2015). Perception of Object Persistence: The Origins of Object Permanence in Infancy. Child Development Perspectives, 9(1), 7-13. https://doi.org/10.1111/cdep.12098

Cacchione, T., & Rakoczy, H. (2017). Comparative metaphysics: Thinking about objects in space and time. In J. Call (Ed.), Handbook of Comparative Psychology (pp. 579-599). Washington: American Psychological Association. https://doi.org/10.1037/0000012-026

Call, J. (2003). Spatial rotations and transpositions in orangutans (Pongo pygmaeus) and chimpanzees (Pan troglodytes). Primates, 44(4), 347-357. https://doi.org/10.1007/s10329-003-0048-6

Collier-Baker, E., Davis, J. M., Nielsen, M., & Suddendorf, T. (2006). Do chimpanzees (Pan troglodytes) understand single invisible displacement? Animal Cognition, 9(1), 55-61. https://doi.org/10.1007/s10071-005-0004-5

Gagnon, S., & Doré, F. Y. (1992). Search behavior in various breeds of adult dogs (Canis familiaris): object permanence and olfactory cues. Journal of Comparative Psychology, 106(1), 58.

Hespos, S. J., & Baillargeon, R. (2001). Infants' Knowledge About Occlusion and Containment Events: A Surprising Discrepancy. Psychological Science, 12(2), 141-147. https://doi.org/10.1111/1467-9280.00324

Hespos, S. J., & Baillargeon, R. (2006). Décalage in infants' knowledge about occlusion and containment events: Converging evidence from action tasks. Cognition, 99(2), B31-B41. https://doi.org/10.1016/j.cognition.2005.01.010

Jaakkola, K. (2014). Do Animals Understand Invisible Displacement? A Critical Review. Journal of Comparative Psychology, 128(2), 1-15. https://doi.org/10.1037/a0035675

Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., & Trone, M. (2010). What do dolphins (Tursiops truncatus) understand about hidden objects? Animal Cognition, 13(1), 103-120. https://doi.org/10.1007/s10071-009-0250-z

Johnson, C. M., Sullivan, J., Buck, C. L., Trexel, J., & Scarpuzzi, M. (2015). Visible and invisible displacement with dynamic visual occlusion in bottlenose dolphins (Tursiops spp). Animal Cognition, 18(1), 179-193. https://doi.org/10.1007/s10071-014-0788-2

Johnson, S. P., Amso, D., & Slemmer, J. A. (2003). Development of object concepts in infancy: Evidence for early learning in an eye-tracking paradigm. Proceedings of the National Academy of Sciences of the United States of America, 100(18), 10568-10573. https://doi.org/10.1073/pnas.1630655100

Marino, L., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., ... Whitehead, H. (2007). Cetaceans Have Complex Brains for Complex Cognition. PLoS Biology, 5(5), e139. https://doi.org/10.1371/journal.pbio.0050139

Mercado III, E., & DeLong, C. M. (2010). Dolphin Cognition : Representations and Processes in Memory and Perception. International Journal of Comparative Psychology, 23, 344-378.

Mitchell, R.W., & Hoban, E. (2010). Does echolocation make understanding object permanence unnecessary? Failure to find object permanence understanding in dolphins and beluga whales. In: Dolins FL, Mitchell RW (eds) Spatial cognition, spatial perception: mapping the self and space. Cambridge University Press, Cambridge, pp 258-280

Pepperberg, I. M., Willner, M. R., & Gravitz, L. B. (1997). Development of Piagetian object permanence in a grey parrot (Psittacus erithacus). Journal of Comparative Psychology, 111(1), 63-75.

Perner, J. (1991). Understanding the representational mind (Vol. xiv). The MIT Press. https://doi.org/10.1016/S0191-6599(96)90063-7

Piaget, J. (1953). The origins of intelligence in children. Journal of Consulting Psychology, 17(6), 467-467. https://doi.org/10.1037/h0051916

Piaget, J. (1955). The construction of reality in the child. Psychological Bulletin, 52(1955), 526-528. https://doi.org/10.1037/h0039645

Prasad, A. (2015). Development of object permanence in a newborn visual system. University of Southern California.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Https://www.r-project.org/.

Rooijakkers, E. F., Kaminski, J., & Call, J. (2009). Comparing dogs and great apes in their ability to visually track object transpositions. Animal Cognition, 12(6), 789-96. https://doi.org/10.1007/s10071-009-0238-8

Spelke, E. S., Breinlinger, K., Macomber, J., & Jacobson, K. (1992). Origins of knowledge. Psychological Review, 99(4), 605-32.

Notes

* This research has received the support of the Spanish Ministry of Economy and Competitiveness through project FFI2013-44007-P and FFI2017-86351-R. Ana Pérez-Manrique was supported by an FPU PhD scholarship from the Spanish Ministry of Education, Culture and Sport (AP2012-3501).