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PHYLOGENETICALLY ANCIENT MECHANISMS INVOLVED IN VISUAL AESTHETIC EXPERIENCE: VISUAL PREFERENCE FOR CURVED CONTOURS IN PRIMATES

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Doctoral Programme of Human Evolution and Cognition

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Dr Enric Munar, of the University of the Balearic Islands

I DECLARE:

That the thesis entitled *Phylogenetically Ancient Mechanisms Involved in Visual Aesthetic Experiences: Visual Preference for Curved Contours in Primates*, presented by Gerardo Gómez Puerto to obtain a doctoral degree, has been completed under my supervision and meets the requirements to opt for an International Doctorate.

For all intents and purposes, I hereby sign this document.

Signature

Palma de Mallorca, 21st May 2017

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This research would have not been possible without access to the resources and equipment from the University of the Balearic Islands.

DEDICATORY

To all the living beings that, by sheer will for survival or mere luck, created the world in which this dissertation could come to be.

More precisely:

To Mati, the best school teacher any child could dream of. And to all those in the education system who taught me and knew how to pique my curiosity.

To my parents, thanks to whom I could keep studying, learning, making mistakes and finding answers.

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LIST OF PUBLISHED CONTENT

This Doctoral Dissertation consists of a collection of papers published in a series of books and peer reviewed journals. The following publications are presented under Chapter 4 and discussed and contextualized through the remaining chapters:

Nadal, M., & Gómez-Puerto, G. (2014). Evolutionary approaches to art and aesthetics. In P. P. L. Tinio & J. K. Smith (Eds.), *The Cambridge Handbook of the Psychology of Aesthetics and the Arts* (pp. 167–194). Cambridge: Cambridge University Press. http://doi.org/10.1017/CBO9781139207058.010

Munar, E., Gómez-Puerto, G., & Gomila, A. (2014). The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference. In A. Scarinzi (Ed.), *Embodied Aesthetics: Proceedings of the 1st International Conference on Aesthetics and the Embodied Mind*. Leiden: Brill Academic Publishers. https://doi.org/10.1163/9789004281516_003

Munar, E., Gómez-Puerto, G., Call, J., & Nadal, M. (2015). Common Visual Preference for Curved Contours in Humans and Great Apes. *PloS One*. https://doi.org/10.1371/journal.pone.0141106 – JIF: 3.057

Gómez-Puerto, G., Munar, E., & Nadal, M. (2016). Preference for curvature: A historical and conceptual framework. *Frontiers in Human Neuroscience*, 9(712). http://doi.org/10.3389/fnhum.2015.00712 – JIF[1]: 3.634

Gómez-Puerto, G., Rosselló, J., Corradi, G., Acedo-Carmona, C., Munar, E., & Nadal, M. (2017). Preference for curved contours across cultures. *Psychology of Aesthetics, Creativity, and the Arts, in press*. – JIF: 2.24

To this day, these publications have resulted in an *h*-index = 3, as calculated by Google Scholar: https://scholar.google.es/citations?user=yQ8KRvQAAAAJ&hl=en

[1] Journal Impact Factor

PHYLOGENETICALLY ANCIENT MECHANISMS INVOLVED IN VISUAL AESTHETIC EXPERIENCE: VISUAL PREFERENCE FOR CURVED CONTOURS IN PRIMATES

RESUM

De forma general, l'estètica pot ser entesa com una capacitat cognitiva de baix nivell que té la funció de guiar el comportament animal en base a estímuls sensorials rellevants presents en el medi. En aquesta tesi doctoral es recullen una sèrie de publicacions, resultat de les meves tasques de recerca doctoral, en què aquesta perspectiva és desenvolupada i explorada de forma tant teòrica com empírica.

En *Evolutionary approaches to art and aesthetics* es fa un repàs dels diferents intents realitzats fins al moment per entendre les implicacions de la teoria evolutiva en l'estudi de l'activitat estètica humana; explicant com la històrica confusió entre els conceptes d'art i estètica ha dificultat considerablement l'avanç de la disciplina.

The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference adopta un enfocament més constructiu que descriptiu, proposant un mètode d'estudi *encarnat*, naturalista i evolucionista de l'estètica. Aquí s'introdueix el concepte de primitiu estètic com la unitat sensorial menor amb contingut informatiu significatiu; i, a manera d'exemple, es planteja un programa d'estudi pràctic centrat en l'estudi de la curvatura.

Les connotacions epistemològiques de la curvatura són explorades a *Preference for curvature: A historical and conceptual framework*, a la qual s'informa de com l'evidència empírica sembla indicar una tendència generalitzada en l'ésser humà a preferir les formes corbes; així com a relacionar sensacions d'estrès i amenaça amb les formes anguloses. No obstant això, la heterodòxia dels enfocaments, l'absència de rèpliques experimentals i d'una definició unívoca de curvatura exigeixen precaució a l'hora d'interpretar l'evidència acumulada.

A *Preference for curved Contours across cultures* i *Common Visual Preference for Curved Contours in Humans and Great Apes* presentem les nostres propis troballes fruit de la investigació experimental; duta a terme tant amb poblacions humanes de diferents cultures, com amb grups captius de ximpanzés i goril·les. En tots els casos, observem una tendència significativa a preferir els contorns corbs enfront dels angulosos; la qual cosa resulta coherent amb la literatura prèviament revisada i podria ser indici que la curvatura actua com a primitiu estètic per als primats o, almenys, a la majoria dels membres de la família *Hominidae*.

Aquestes publicacions, que formen el nucli de la present tesi doctoral, són contextualitzades i analitzades en una sèrie de capítols introductoris i de discussió en els quals s'argumenta a favor d'una concepció epistemològica de l'estètica que la situï en el seu context natural.

RESUMEN

De forma general, la estética puede ser entendida como una capacidad cognitiva de bajo nivel cuya función es guiar el comportamiento animal en base a estímulos sensoriales relevantes presentes en el medio. En esta tesis doctoral se recogen una serie de publicaciones, resultado de mis labores de investigación doctoral, en las que esta perspectiva es desarrollada y explorada de forma tanto teórica como empírica.

En *Evolutionary approaches to art and aesthetics* se hace un repaso de los distintos intentos realizados hasta el momento por entender las implicaciones de la teoría evolutiva en el estudio de la actividad estética humana; explicando cómo la histórica confusión entre los conceptos de arte y estética ha dificultado considerablemente el avance de la disciplina.

The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference adopta un enfoque más constructivo que descriptivo, proponiendo un método de estudio *encarnado*, naturalista y evolucionista de la estética. Aquí se introduce el concepto de *primitivo estético* como la unidad sensorial menor con contenido informativo significativo; y, a modo de ejemplo, se plantea un programa de estudio práctico centrado en el estudio de la curvatura.

Las connotaciones epistemológicas de la curvatura son exploradas en *Preference for curvature: A historical and conceptual framework*, donde se da cuenta de cómo la evidencia empírica parece indicar una tendencia generalizada en el ser humano a preferir las formas curvas; así como a relacionar sensaciones de estrés y amenaza con las formas angulosas. Sin embargo, lo heterodoxo de los enfoques, la ausencia de réplicas experimentales y de una definición unívoca de curvatura exigen precaución a la hora de interpretar la evidencia acumulada.

En *Preference for curved contours across cultures* y *Common Visual Preference for Curved Contours in Humans and Great Apes* presentamos nuestros propios hallazgos fruto de la investigación experimental; llevada a cabo tanto con poblaciones humanas de diferentes culturas, como con grupos cautivos de chimpancés y gorilas. En todos los casos, observamos una tendencia significativa a preferir los contornos curvos frente a los angulosos; lo cual resulta coherente con la literatura previamente revisada y podría ser indicio de que la curvatura actúa como primitivo estético para los primates o, al menos, la mayoría de los miembros de la familia *Hominidae*.

Estas publicaciones, que forman el núcleo de la presente tesis doctoral, son contextualizadas y analizadas en una serie de capítulos introductorios y de discusión en los que se argumenta a favor de una concepción epistemológica de la estética que la sitúe en su contexto natural.

SUMMARY

This dissertation collects a series of papers produced as part of my doctoral research activities. In them, I approach aesthetics as a broad, low-level cognitive capacity guiding animal behaviour in accord with environmentally relevant sensory stimuli.

In *Evolutionary approaches to art and aesthetics* we discuss the different attempts at understanding human aesthetic experience in light of evolutionary theory; pointing at how the historical confusion between the concepts of art and aesthetics has severely hindered the development of this area of study.

The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference takes a more constructive –as opposed to descriptive– stance, by arguing for an embodied, naturalistic and evolutionary approach to aesthetics. Here we introduce the *aesthetic primitive* concept: a minimal sensory unit carrying meaningful information. We then propose a research program concerning for the study of curvature as a practical demonstration

Preference for curvature: A historical and conceptual framework explores the epistemological value of curvature. Here we present empirical evidence that hints at a general tendency among humans to prefer curved shapes, while relating stressful and threatening feelings to sharp ones. Nevertheless, the heterogeneity of the different approaches, together with a certain lack of replication, and the absence of an unambiguous definition of curvature claim for a cautious interpretation of the evidence.

Preference for curved contours across cultures and *Common Visual Preference for Curved Contours in Humans and Great Apes* feature our very own findings resulting from empirical experimentation. Human populations of varied cultural backgrounds, but also groups of captive chimpanzees and gorillas were presented with similar tasks. In every case, a significant tendency to prefer curved contours to sharp ones was observed. This is consistent with the literature and hints at curvature serving as an aesthetic primitive for primates –or, at least, for most of the *Hominidae* family.

These papers, which constitute the core of my dissertation, are further analysed and put into context through various introductory and discussion chapters; in which I argue for an epistemological understanding of aesthetic that gives it its pace in nature.

PHYLOGENETICALLY ANCIENT MECHANISMS INVOLVED IN VISUAL AESTHETIC EXPERIENCE: VISUAL PREFERENCE FOR CURVED CONTOURS IN PRIMATES

1. INTRODUCTION

The thesis work here presented collects years of research exploring the possible evolutionary origins of aesthetic experience, as exemplified by the factual preference for curved contours apparently shared among the members of the different extant genera of *Hominidae* primates (*Gorilla*, *Homo*, *Pan*, *Pongo*). The empirical nature of this research has resulted in a series of peer reviewed publications, book chapters, and contributions to congresses. Among them, I have selected and arranged those that form a coherent narrative; which goes from the general, abstract theoretical considerations, to the concrete gathering of empirical data through behavioral experimentation (*Fig. 1*).

After reviewing the extant literature regarding the naturalistic study of aesthetics in *Evolutionary Approaches to Art and Aesthetics*, *The evolutionary Roots of Aesthetics* introduces a new framework rooted in embodied cognition and approach-avoidance theory; proposing its empirical realization in the form of a research program for curvature, understood as an aesthetic primitive.

Preference for Curvature further explores evidence regarding the aesthetics of curvature, in an attempt to properly define and understand the chosen object of study. Finally, the different findings resulting from our own empirical research are collected and discussed throughout *Preference for Curved Contours Across Cultures* and *Common Visual Preference for Curved Contours in Humans and Great Apes*.

This neat presentation is, of course, a fiction. Research rarely follows a linear pattern, with new findings iteratively requiring a continuous reflection and shift in the theoretical framework. Articles take time to be written, and more to be reviewed. Moreover, the spread among different journals and books requires answering to a set of distinct editorial needs and audiences, which impedes –to a point– the development of a cohesive and concise theoretical discussion.

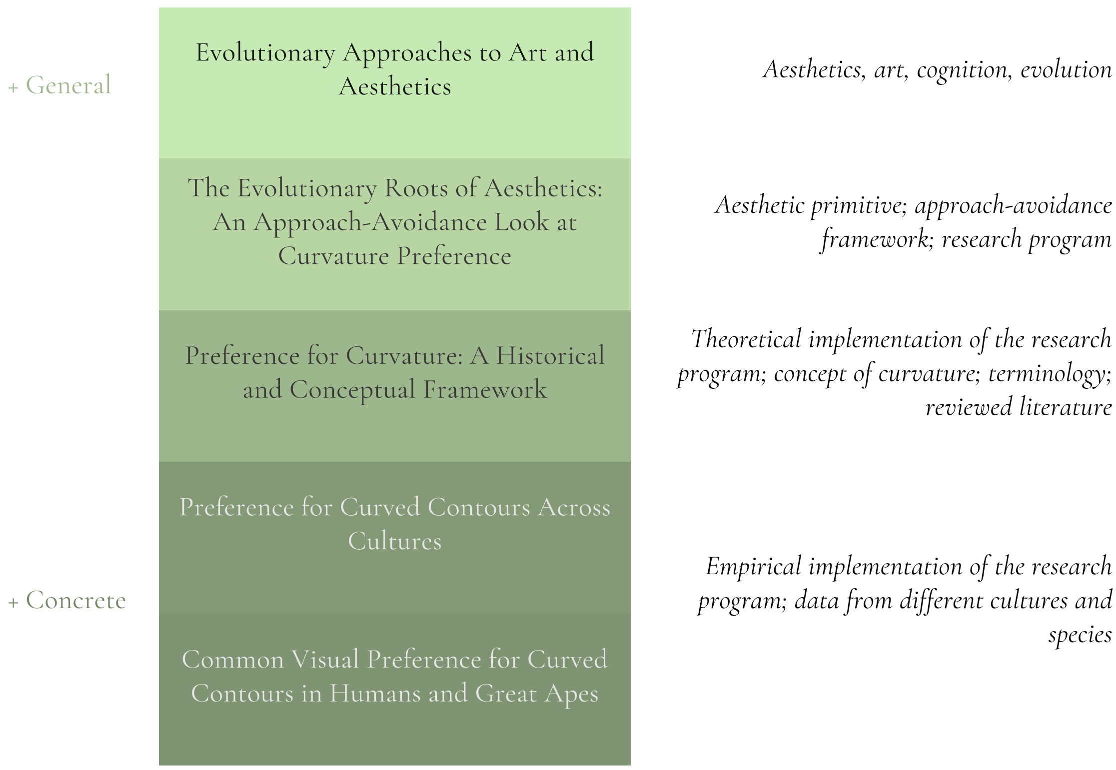

Fig. 1: Published work narrative

Therefore, this dissertation offers a perfect environment to finally gather together these different pieces of research; so that, presented under a unified and clarified theoretical framework, they shed light on one another, helping to cement what I believe to be a promising way of understanding aesthetics and its scientific study.

In what follows, I will briefly introduce each paper, signaling and explaining whatever conceptual inconsistencies they might incur in. I will also direct the reader's attention towards those matters that I find particularly deserving of further discussion, which will be addressed in later chapters.

Evolutionary Approaches to Art and Aesthetics

It is difficult not to start each of these sections by thanking the many people that contributed to the work in it discussed. But, in this particular case, most of the praise and blame –if any!– is due to Marcos Nadal. He was too kind to invite me to collaborate in what I consider a very important and needed piece of literature; but I am not completely sure his encyclopaedic knowledge ever required of my limited skills as reviewer and consultant.

Having said this, I am very happy with the way the text came out. It is a comprehensive and fair review of the scientific study of arts and aesthetics as viewed under the light of natural selection. Due to its nature as a handbook chapter, the content has a strong descriptive tone, in which disagreement with the different approaches to the study of aesthetics from an evolutionary perspective is expressed constructively in the manner of a parsimonious sketch of a framework.

Still, we make the important point of distinguishing Art from art; and both from aesthetics itself. By doing so, we expose the confusion of these concepts as the underlying cause of most failed attempts at understanding aesthetics as a natural phenomenon.

On account of its introductory –but comprehensive– nature, I could not have hoped for a better foundation from which to build the narrative of my work. But it is also true that, when the piece was written, I was at the earlier stages of my research; and my views about the matter have inevitably changed since then. If I were to write the same chapter now, I would address some topics differently –especially the distinction between art and aesthetics.

Because of this, and because I consider a collected thesis to be a better environment in which to discuss bolder ideas, this entry will be complemented by a brief account of my current understanding of aesthetics in chapter 3 and further theoretical discussion in chapter 5.

The Evolutionary Roots of Aesthetics: An Approach-Avoidance Look at Curvature Preference

This chapter was published in the *Proceedings of the 1st International Conference on Aesthetics and the Embodied Mind*, and in it we laid the foundations of the research program that I would be implementing in the following years.

As luck would have it, the call for papers came to our attention at the precise moment I was testing my latest experimental design; which Enric Munar had cleverly conceptualized in an approach-avoidance framework. Intrigued by the emphasis the organizer, Alfonsina Scarinzi, put on the work of Mark Johnson, we did some reading and soon understood that his reasoning agreed well with our own understanding of human aesthetics.

While it is a rather short piece, directed at a specialized public, and in which three contributing authors had to soften their theoretical inklings for the sake of consensus, I find it to be a fair summary of the main ideas that drove our research. Specifically, I would like to direct the attention of the reader to points 1, 4 and 6; as they reflect our early views on the study of aesthetics. Although chronologically relevant, I think points 3 and 5 are better developed in their own monographic articles[2].

The presentation of our research program in point 4 includes two key aspects that illustrate the approach to the science of aesthetics I would like to discuss here. In line with the naturalized tradition of Dewey (1922), we explain that

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[2] Cf. *Preference for Curvature: A Historical and Conceptual Framework* for point 3 and *Preference for Curved Contours Across Cultures* for point 5

> we should see aesthetics or morals as a set of complex problem-solving systems that, by directing our interaction with the environment in a certain way, makes it meaningful. It is only *a posteriori*, when higher cognitive processes have mediated the experience, that we call a particular experience as aesthetic or moral. (Munar, Gómez-puerto, & Gomila, 2014, p. 7)

It is also the first time we introduce the concept of *aesthetic primitive* as defined by Latto (1995, p. 68): "a property of a stimulus that is intrinsically interesting, even in the absence of narrative meaning."

These two core ideas underlie my theoretical and empirical work, and I will expand them on upcoming chapters. Nevertheless, I want to make a point to emphasize that the aesthetic primitive concept should not be understood in an *ontological* manner, but in a *methodological* one. I could not care less whether aesthetic experience results indeed from the sum of aesthetic primitives; or whether humans possess modular adaptations instead of general problem-solving systems. But I do think that conceptualizing aesthetics as an abstraction that represents a defined set of cognitive processes, which can be further divided into aesthetic primitive units, is a useful and promising way of studying human cognition. And this is what I seek to illustrate with the contents of this dissertation.

Preference for Curvature: A Historical and Conceptual Framework

After introducing the evolutionary study of aesthetics, and laying out the foundations of our research program, I proceed to explore the topic to which said program was to be applied: a possible tendency, shown by humans, to prefer curved contours, which was hypothesized to be phylogenetically ancient.

Prior to this publication, there was little to none explicit discussion of what was meant by the term *preference for curvature*. Henceforth, the article was given a deliberately ambiguous title with the intention of attracting readers interested in this poorly defined topic. The fact that I often receive ill-informed invitations to contribute to monographs on unrelated fields –such as the physics or mathematics of curvature– goes to show that the terminology used so far when addressing this kind of preference is far from unequivocal or well-stablished.

The goal of this article was to set a starting point from which a more precise and useful conceptualization of visual preference for curvature could be achieved[3]. Whether this was

[3] Unfortunately, I have yet to find a better umbrella term for the broad range of phenomena described as preference for curvature.

accomplished, only time can tell. But, in regards to my own research, this investigation served as a fair improvement of our conceptual tool belt.

More than the heterogeneous terms used through the literature to refer to the same phenomenon, I was surprised by the fact that different phenomena –which had not been proved to be linked– were usually understood as being exemplars of the same one. It is the case of curved lines, curved shapes and curved contours. While it can be argued that there is no reason to consider shapes and contour to be different types of stimuli, the same cannot be said for simple lines (Bertamini, Palumbo, Nicoleta, & Galatsidas, 2015).

Curiously, it was the study of lines that first draw attention to the emotional implications of curvature (Hogarth, 1753). Early research was concerned with zig-zags (Uher, 1991), wavy lines, curves and angles (Hevner, 1935; Lundholm, 1921; Poffenberger & Barrows, 1924); but at some point, during the second half of the 20th century, interest shifted towards shapes –first– and objects (Guthrie & Wiener, 1966; Kastl & Child, 1968).

Not only the nature of the stimuli studied has been often disregarded, but the sensory system involved in its perception has been too. It has been common to refer to a general *preference for curvature* when, strictly speaking, most studies are limited to the *visual* domain. An in deep exploration of other sensory dimensions is yet to be conducted[4].

But the most glaring omission is a proper operationalization of the term *curvature* itself. Through the literature, it is not clear whether curvature is to be understood as the absence of sharp, angular interjections; the presence of rounded corners; or a specific degree of curvature. I must admit I have been unable to find any paper in which a physical characterization of the kind of curvature underlying the studied phenomenon is presented.

In the light of this, we have taken measures to warranty a certain degree of precision and clarity in our later published works; such as employing *visual preference for curved contours* to refer to our object of study. Nevertheless, we cannot presume to be blameless.

It would have been desirable to unequivocally describe the degree and kind of curvature present in the stimuli employed during our research. Alas, the contemporary requirements of academic production do not agree well with the apparent idleness of philosophical reflection; so it was not after the research had been ongoing for more than a year that I had a chance to come upon these thoughts.

Therefore, it must be noted that the field remains in need of a proper psychophysical definition of curvature, which is out of the scope of this work. The reader should understand any reference to curvature as a general absence of sharp angles, paying special attention to the actual descriptions and illustrations depicting the stimuli employed.

[4] There are remarkable exceptions. For instance, Jakesch & Carbon (2011) give account of a similar phenomenon of preference for curved shapes in the haptic domain. Similarly, Hess, Gryc, and Hareli (2013) describe an experiment which involves interacting with sharp and round contoured puzzle pieces.

Preference for Curved Contours Across Cultures and Common Visual Preference for Curved Contours in Humans and Great Apes

Being a practical realization of the theoretical building so far discussed, these articles are fairly self-explanatory. They are also the result of the combined efforts of different individuals, to whom I am deeply indebted[5]. But, more importantly, these papers constitute my main factual contribution to the ever-growing corpus of human knowledge –as limited in scope as they might be.

Further sections of this work will be devoted to discuss and asses the relevance of the findings presented on these two publications. I will also defend a naturalized approach to the study of aesthetics that builds in its epistemological nature and the concept of primitive aesthetic.

[5] I must give due credit to Cristina Acedo-Carmona, who was responsible for running the experiments in Ghana and Mexico; and to Matthias Allritz, who taught me most of what I know about working with great apes employing touch enabled devices.

2. OBJECTIVES

My doctoral work sought to explore the possible evolutionary origins of human aesthetic experience. This initial goal, inscribed in the broader research program of the Human Evolution and Cognition Research Group (EVOCOG) at the University of the Balearic Islands, was tentatively phrased as *Phylogenetically Ancient Mechanisms Involved in Visual Aesthetic Experience*, which was the working title under which my studies took form.

The idea was to focus on a concrete unit conforming aesthetic experience, that was hypothesized to increase fitness, and to devise a method with which it would be possible to test such assumption. Because of recent findings showing promise, and because of its study being still in its infancy, visual preference for curvature was chosen to be that unit of study.

During the first years of my research, I focused on the experimental recollection and analysis of data. But, as my activity grew more theoretical, I realized that both the study of preference for curvature and that of evolutionary aesthetics were in need of a more precise conceptualization.

Thus, the main goals of my work could be summarised as: to produce comparative and cross-cultural data about the occurrence of a given aesthetic phenomenon; and to produce a theoretical framework of aesthetics as a biological feature. In a more detailed fashion, this could be expressed as:

a) To define the subject of study of aesthetics as a science, signaling its relevance for the understanding of human cognition
b) To naturalize the concept of aesthetics by placing it in a biological and evolutionary context
c) To develop a set of conceptual tools that permit the empirical study of aesthetics as per *a)* and *b)*
d) To implement such tools in a concrete research program that illustrate *a)* and *b)* by
    - finding a suitable research topic in the literature available –in this case, a possible preference for curvature
    - clearly defining the chosen topic in a manner both coherent with previous research and the framework developed in *c)*
    - designing the best suited set of experiments
e) To realize the empirical investigation derived from *d)*
f) To analyze the data obtained and to interpret in the light of the theoretical framework previously developed
g) To integrate the knowledge thus achieved in the existing *corpus* by considering its implications and proposing future research
h) To divulgate said knowledge so that is available to the scientific community

3. A NATURALISTIC APPROACH TO AESTHETICS

Most books on the psychology of aesthetics or of art begin by saying what is meant, or is going to be meant in the book, by "aesthetics" or by "art." –Daniel Berlyne

There is today still a pervasive cultural misunderstanding of, and consequent prejudice against, aesthetics –Mark Johnson

Why should science bother with aesthetics at all? Is it not a mere matter of taste, of subjective opinion? Why try to make sense of some outdated notion, that even contemporary artists seem to have thrown out of the window?

For starters, aesthetics might be, together with moral and language, one of the few functional apomorphies characterising our species. We may not know what goes through the mind of an orang-utan when he covers himself with a stylish leaf or a zoo blanket. We might wonder at the structures created by mound-building termites. We could –and should– argue whether male peacocks are using their natural beauty to impress a possible mating partner. But we are *almost* certain that no species –besides ours– builds museums or tries to find meaning and enlightenment in a collection of strange forms and colours.

Unfortunately, this line of thought –as promising as it seems– showcases the main problem with aesthetics: its ambiguity. As anyone familiar with the field must have noticed, the previous paragraph confounds *art*, *beauty*, *consciousness* and *communication* in an unclear concept that, from the get-go, sets its nebulous boundaries around a varied array of *strictly human* behaviours and thoughts.

This problem is not uncommon among the Human Sciences, where many ill-defined concepts –such as *consciousness* itself– are the cause of endless debates and the seemingly slow development of these disciplines when compared with other, more easily conceptualized, fields of study.

But this should not be a valid reason to give up any attempt to understand human nature, nor to avoid delving in the complexities of aesthetics. For, if there is a phenomenon –or set of phenomena–, as ill-defined as it might be, that we as species have considered to be worth of our attention for centuries, the complexity of its study should not stop us from trying to gain a better understanding of it.

Instead, we should strive to define and model it in a meaningful, useful manner. Not with the intention of discovering some sort of unifying, ultimate concept; but to clearly present the object of our study so that a serious and constructive discussion can take place.

Despite the number of findings provided by empirical aesthetics in the last decades –of which this work hopes to be a good exemplar–, it is somewhat frustrating to see how the same theoretical problems discussed by Berlyne in his seminal Aesthetics and

Psychobiology are brought, once and again, to light –to the point that one comes to fear that the field has been shaped in the image of an ever-devouring ouroboros.

While writing this introduction, I often could not help but feel that my words were no more than a poor echo of Berlyne's. If this was the case, I would have no option but to warn the reader that he or she would do better by consulting the original. But I *do* hope my work has something more to offer; something that goes beyond the factual data we have already published. It is my intent that the reflections here presented, together with the different theoretical discussions contained in our published work, might shed some light in the complex task that is to study human cognition –and, especially, aesthetics.

Understanding aesthetics

Aesthetics is commonly misunderstood as the study of the arts. I believe this frequent misconception is likely rooted in its own etymology. Funnily enough, αἰσθητικός can be –roughly– translated as "pertaining to sense perception". Therefore, the term *aesthetics* could be seen like a useful shorthand for "the study of the arts" –which, most certainly, pertain to sense perception. Furthermore, Western art traditions have usually concerned themselves with beauty. And so it happens that, in 1750, German philosopher Alexander Baumgarten had this ingenious notion to entitle his treaty about beauty and taste with this ponderous little word: *Aesthetica*. Since then, *aesthetics*, *beauty* and *arts* have been used interchangeably in a confusing manner not suited for constructive debate.

But, while we are not in need of a misleading synonym for *arts* or *beauty*, we certainly lack a concise term to describe the way in which "our bodies are inhabiting, and interacting meaningfully with, the environment beneath the level of conscious awareness" (Johnson 2008, 24); or to address "the origins and structures of meaning in the organic activities of embodied creatures in interaction with their changing environments." (*ibid.*, 11).

In his book –aptly subtitled *Aesthetics of Human Understading*– Mark Johson goes to great lengths to argue that meaning-making is an embodied, bottom-up process common to all living organisms. I believe this is a perfect way of understanding aesthetics from a naturalistic point of view.

Naturalizing aesthetics means looking at aesthetic experiences in their biological context. Mainly, we have two different ways to accomplish this: by considering aesthetics to be a unique feature of human beings, steaming from our idiosyncratic evolutionary history; or by defining it as a common –if graded– capacity to most living organisms. While some might disagree, I consider the latter to be a more parsimonious and useful approach.

Having reached this point, I would like to attempt a provisional definition of aesthetics as

> *the field of knowledge concerned with the production of meaning during the interaction of an embodied organism with its ever-changing environment.*

I *think* I would agree with such a definition. And I say I think, because I am not really sure. How could I be? Do plants or beetles produce meaning? Do bacteria have bodies? It depends. It always depends. We could define meaning in such a way that could be applied to all kinds of living organisms. But my stated goal when defining aesthetics was to clearly conceptualize the object of study in a useful way, not to hide it beneath a multilayered definition.

As influential as Mark Johnson's work has been to my research, I do not care that much about bodies or meaning. I see each living organism as a whole system, in which the so-called *mind* is but an expression of the inner workings that make that organism fit for survival.

From a scientific point of view, it is not useful to worry about the nature of abstract concepts such as *consciousness*, *mind*, *meaning* or even *body*. These concepts are unavoidable in everyday life, and might be useful in certain areas of research; but they often confound communication due to their ambiguity. *Most* of the times, we could do without them when studying cognition.

Therefore, I would prefer to rework my previous definition so that it can be stated in a clearer, philosophically agnostic manner. Such as,

> *aesthetics is the field of knowledge concerned with sensorimotor reactions to, and internal state changes prompted by, external stimuli informing pre-rational behaviour.*

Now, this is a definition I can be comfortable with. Once stripped of most of it ambiguities, this definition's features can be further explored.

For starters, there is no mention of beauty, art, cultural phenomena or tradition. As I have been discussing, this is a good thing. But, at the same time, it is broad enough to include non-scientific practices –such as art itself– in the set of tools that could attain such knowledge. It also underlines the affective, directed and communicative nature of aesthetic phenomena, which usually involves one or more receptors and one or more external stimuli[6]. It also takes a stance by explicitly acknowledging that aesthetics has a biological function non-exclusive to human beings. Finally, it characterises such function by defining it as pre-rational –that is, primary, immediate and prior to rational thought– and stating its use: to quickly guide behaviour.

I present this definition with the sole intent of clearly defining those matters that concern my work as presented in this thesis. While our published research can be understood and appreciated on its own merits, I deem it to be good practice to explicitly state in a non-ambivalent manner the way the subject of study is modelled and understood. This information is extremely useful for the reader to better understand the different decisions taken during the design and analysis of the experiments; and to comprehend –be it to question or to agree with– the reasoning behind their interpretation.

I *do* think that an embodied understanding of human –or, in a broader sense, animal– cognition is more interesting and accurate than a dualist or emergent one. I also believe

[6] It could be argued that these stimuli do not need to be external, but that discussion is mostly semantical and out of the scope of this work.

that, when studying aesthetics scientifically, it is way more fruitful and true to nature to consider its biological function over a historically and culturally given interpretation. When view in this manner, aesthetics becomes a foundational aspect of animal behavior that no cognitive scientist should overlook.

The aesthetic primitive

Still, giving aesthetics a place in the natural world is not enough. While I have expressed an intent –to consider aesthetic experience in its biological context–, I am yet to define a unit of study that can be modelled and operationalized.

At the earlier stages of our research, we faced the problem of lacking a simple term to address our object of study. We knew we wanted to explore the evolutionary origins of human aesthetics; and, to do so, we had chosen to focus on reports of visual preference for curved contours among Western psychology students. 'Phylogenetically ancient mechanisms involved in visual aesthetic experience' might be a technically correct description of such occurrences; but it is such a mouthful that we never came to use it. For ill or good, the term that stuck was *aesthetic primitive*.

We first came across this expression in Latto's The Brain of the Beholder (1995), where it is defined first as "a stimulus or property of a stimulus that is intrinsically interesting, even in the absence of narrative meaning, because it resonates with the mechanisms of the visual system processing it" (68) and later, in a more generalized manner, as "a stimulus that stirs the emotions because it has an exceptional ability to excite our visual neurones" (90).

We appropriated the aesthetic primitive concept by expanding it into a more flexible one that could be applied to different sensory domains disregarding any presupposition about its actual implementation. Per this extended use, an *aesthetic primitive* could be defined as

> *a concrete cue to which our perceptive system is pre-programmed to quickly respond, be it because of a specific need of our organism, or as an accidental effect derived from its configuration.*

In a broader sense, an aesthetic primitive is a well-defined unit of study that produces a primary aesthetic response in an organism. It is primitive in the sense of ancient –that is, of having been shaped by evolutionary processes– and in the sense of immediacy –by causing a bottom-up response that might conduct to higher cognitive processes.

While this definition is especially suited for an embodied and naturalistic approach to aesthetics, it is a tool that might prove useful for anyone interested in the evolutionary study of art, aesthetics or human behaviour.

There is a fair number of stimuli, traditionally studied in empirical aesthetics, that could be conceptualized as *aesthetic primitives*. Just in the domain of visual perception, we could consider symmetry, contrast, colour, complexity and curvature, to name a few. As it has already been explained, among all of them, we turned our attention towards curvature, a topic that will be more thoroughly explored in upcoming chapters.

Scientific reductionism

There is a last matter to discuss before finally giving voice to our published research. When a naturalized approach to any aspect of contemporary human nature or behaviour is proposed, it is often followed by an echo of lamentations decrying its reductive scientism. These fears are ill founded and usually arise from a fundamental misunderstanding of science itself.

The conception of aesthetics I have defended *is* indeed reductionist. That is a feature, not a fault; for this is how scientific knowledge is build: by reducing the unfathomable complexity of the natural world to a simple model which can be operated, tested, and discussed. Accusing such an approach of reductionism is akin to complaining that a map was drawn using a scale.

This does not mean that we should give up on art or other humanistic approaches to aesthetics at all. *Au contraire*! I believe artistic experimentation, phenomenology, cultural studies, art critic and many other distinct disciplines are especially suited to explore and give us a better understanding of the world that surrounds us.

Science happens to be an incomparable epistemological tool. It is clearly defined, versatile, empirically informed, and has given us the best practical results any other way of knowledge has ever given us. That does not make it the be-all and end-all of our relation with the natural world.

Bridging the infamous gap between the *Two Cultures* (Snow 1959) does not consist in slaving all kinds of knowledge to scientific rigour. It is understanding that such practice can –and should– be applied to any aspect of human nature, as humans are but part of the natural world. It is the fact that knowledge thus produced cannot be disdained, nor ignored, by anyone concerned with such nature. But it is also the fact that humans possess a wide –if limited– array of epistemological capacities, shaped by our evolutionary history, that gives access to –and understanding of– the natural world. And aesthetics, I believe, is one of them.

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4. COLLECTED PAPERS

Evolutionary approaches to art and and aesthetics

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8 Evolutionary approaches to art and aesthetics

Marcos Nadal and Gerardo Gómez-Puerto

Evolution provides the key to understanding why living organisms are the way they are, and natural selection constitutes the fundamental principle for explanation in biology (Ayala, 1970). Darwin's (1859) theory of evolution by means of natural selection revolutionized biology because it provided a unified explanation for centuries-old observations of the living world. For all our peculiarities and uniqueness, human beings are the result of evolution, just like bacteria and fungi, and our lineage has been shaped by the very same mechanisms of natural selection. A meaningful understanding of human beings – of our anatomy, physiology and behavior – is not possible unless we consider ourselves in the light of evolution (Dobzhansky, 1973). Why do we have color vision? Why do things taste the way they do? Why do we feel pain? Why do we feel attachment toward our kin? Why does it feel nice to be accepted and popular? The answers to such questions reside, in part at least, in our evolutionary history, in the fact that our species evolved from primitive hominins that evolved from primitive primates that evolved from primitive mammals, and so on.

Darwin (1859) believed that natural selection was not only responsible for the evolution of physical traits, but for mental traits as well. Our capacity for perceiving, for attending, for remembering and recognizing, for making decisions and for feeling emotions, together with all other mental capacities, should be understood as products of a long evolutionary history. Contemporary American psychologists received Darwin's proposal with enthusiasm. Prominent voices argued that the mind could not be comprehended without reference to the world it evolved in, and that the main purpose of mental processes was to organize adaptive behavior. Herbert Spencer (1870, 1873), for instance, showed how cognition and memory were the products of evolution. In his view, they originated from simple forms of association, which came to be heritable with repetition. As they accumulated over time, these heritable associations became instincts, which in turn evolved into higher forms of cognition. James (1890, 1892) was a firm proponent of this "psychology of adaptation and survival-value" (Boring, 1950, p. 507). He wrote that "our inner faculties are adapted in advance to the features of the world in which we dwell, adapted, I mean, so as to secure our safety and prosperity in its midst" (James, 1892, p. 3). His thorough and influential *Principles* (James, 1890) remains, still today, the epitome of psychology in the light of evolution.

It might seem surprising to learn, thus, that art and aesthetics, apparently so distinctively human, were not systematically studied in the same light. At the time, in fact, very few psychologists approached art and aesthetics from an evolutionary perspective, and the whole topic has remained largely out of the mainstream of experimental psychology. There are two main reasons for this. First, the prevailing view during the nineteenth century considered that art and aesthetics had no purpose beyond themselves. The notions of art for art's sake and of detached aesthetic contemplation were the antithesis of the kind of mental processes whose purpose was adaptive and preservative action. The few that realized the adaptive value of aesthetic responses tended to restrict its scope to mate choice or habitat selection. The second reason is that, although the importance of aesthetics was acknowledged by evolutionary-minded American psychologists, most – including James (1890) himself – did not seriously deal with the topic. Psychological aesthetics was born in Europe (Fechner, 1876), where evolutionary thought had impregnated psychology to a lesser extent. There, it thrived into a consolidated research program, mostly in Germany and the United Kingdom, where it remained largely out of reach from evolutionary thinking. Psychological aesthetics became a topic of interest in the United States only at the turn of the century, where it was soon absorbed into behaviorism as the study of pleasant and unpleasant responses to external stimuli. Aesthetic experiences were no longer conceived as mental processes; they became behavioral reactions to the environment. Only in the wake of the cognitive revolution did experimental aesthetics reemerge as a proper domain of experimental psychology (Berlyne, 1971). Berlyne's new experimental aesthetics was set on biological foundations, though with little reference to evolution. It was not until the burgeoning of evolutionary psychology in the early 1990s (Barkow *et al*., 1992) that a community of researchers interested in the evolution of art and aesthetics emerged.

This chapter revises attempts to understand the evolution of art and aesthetics. How and when did the capacities for art and aesthetics appear? This is a legitimate evolutionary question. It is not, however, an easy one. Although plausible hypotheses abound, not much has been actually proven since the earliest proposals based on Darwin's (1859; 1871) principles of natural and sexual selection. At least three reasons explain such meager progress. First, whereas the locomotion and habitat of our ancestors, for instance, can be studied from their fossil remains and the fossils of plants and other animals found at the same archaeological sites, there is relatively little material evidence for the evolution of art and aesthetics. Even the evidence of pigment processing, engraving or painting is evidence only of the results of cognition and behavior. We can only infer the cognitive and affective processes that led to such manifestations, as well as their personal and social meanings and roles. Second, the fact that our closest primate relatives produce nothing like art, and appear to lack aesthetic appreciation, reveals a discontinuity that is difficult to reconcile with the slow and gradual process of natural selection. Such a divide poses difficult challenges for potential comparative studies. Third, the notions of art and aesthetics lack clear-cut definitions. It has even been argued that attempting to define art is a futile endeavor (e.g., Weitz, 1956) because the concept "art" is an open concept: new exemplars of artworks, styles and art forms have emerged throughout history, and will foreseeably continue to do so, constantly forcing new definitions that can accommodate them. Can we really learn anything about the evolution of a human capacity we have trouble defining? Would there be any hope of understanding the evolution of human locomotion or diet if researchers did not agree on the crucial features that define them?

Such difficulties not only hamper our understanding of the evolution of art and aesthetics. They also encumber research on the evolution of other mental traits, like language or morality, to the point that in the opening paragraphs of an essay on the evolution of cognition, Lewontin (1990, p. 229) wrote, with unvarnished skepticism: "If …it were our purpose in this chapter to say what is actually known about the evolution of human cognition, we could stop at the end of this sentence." Lewontin's (1990) chapter aimed to question the usefulness of hypotheses about the evolution of mental traits in the absence of direct evidence to test them, and to caution against mistaking plausible scenarios for demonstrated truth about the evolution of cognition in general.

Lewontin (1990), nevertheless, went on to write a whole chapter after that sentence, hinting that there might be some hope after all, if we proceed cautiously. And there are at least three reasons to proceed. First, the capacity for art and aesthetics has traditionally been considered one of the features that identify the human species, distinguishing it from its closest living and extinct relatives (Dobzhansky, 1962). The appreciation of aesthetics and art seems to be "unique to the human species in its essentials and a common part of our shared biological endowment," a "true species property" in the terms Chomsky (1988) used to refer to language. To understand the nature of the appreciation of aesthetics and art is, thus, to understand a part of what makes our species unique. Second, not only are art and aesthetics related to the creation and admiration of some of the most extraordinary manifestations of human culture, such as music or architecture. They are also part of many of our ordinary activities, such as choosing what clothes to wear, which car to buy, how to decorate our homes and who to approach or avoid in the street depending on the context (Leder *et al*., 2010). Finally, our understanding of the capacities to make and appreciate art and aesthetics will be incomplete unless we know about their evolution (Tinbergen, 1963).

Approaches to the evolution of art and aesthetics

The reconstruction of the evolutionary history of biological traits – including the capacities for art and aesthetics – tends to begin with questions "which ask what is or might have been the selective advantage that is responsible for the presence of a particular feature" (Mayr, 1983, p. 325). Huron (2001), for instance, asked "What advantage is conferred on those individuals who exhibit musical behaviors over those who do not?" (2001, p. 43). Most hypotheses about the evolution of art or aesthetics are grounded on the assumption that they are adaptations. An adaptation is usually defined as a trait that endows an organism with a specific selective advantage. However, fortuitous benefits are also adaptive, but they should probably not be regarded as adaptations (Williams, 1966). Thus, researchers agree that the term should be restricted to traits that provide selective benefits and that emerged through natural selection owing to those benefits (Lauder *et al*., 1993). What benefits might have art and aesthetics provided humans? Different possibilities, examined below, have been set forth. Most were initially proposed during the late nineteenth or early twentieth centuries, and have been repeated in slightly different forms at later times. The majority of these adaptive hypotheses postulate individual selective advantages, though some researchers have argued that art and aesthetics also confer group-level advantages (Brown, 2000).

Some authors, however, believe that art and aesthetics do not qualify as adaptations, that they should be regarded as exaptations, or "features that now enhance fitness but were not built by natural selection for their current role" (Gould and Vrba, 1982, p. 4). Thus, exaptations include traits that did not originate owing to the direct effects of natural selection but that have subsequently been put to new advantageous uses, and traits molded by natural selection to perform specific functions – that is to say, adaptations – that were later coopted to perform different functions and provided new benefits.

Table 8.1 summarizes some of the most popular hypotheses about the evolution of art and aesthetics. It classifies them according to the main postulated evolutionary mechanism (adaptation or exaptation) and according to the level of selection in the case of adaptive scenarios (individual or group). Some of these proposals, such as habitat selection and mate choice, were intended mainly to explain the origin of humans' capacity for aesthetic appreciation. Others, such as group selection theories, aimed to account for the evolution of our capacity to produce and appreciate art. Because some authors believe there is an intimate connection

Table 8.1. *Main hypotheses on the evolution of art and aesthetics in terms of the posited adaptive function and level of selection*

	Level of selection	
Evolutionary status	Individual	Group
Adaptation	Habitat selection Mate selection Acquisition of knowledge Imagination, pretense and fiction Influence over others Relief of tension and anxiety	Enhancement of group cohesion and cooperation

between art and aesthetic qualities, especially beauty, they have postulated that art and aesthetic appreciation were driven by a common selective advantage, such as mate choice.

Habitat selection

Clay (1908) was among the first to propose that the adaptive value of aesthetic appreciation derived from our ancestors' perceptual and affective responses to environments. Specifically, the main selective advantage conferred by aesthetic responses – he believed – was the possibility of distinguishing favorable from unfavorable environments.

Evolutionary psychologists updated and expanded this line of reasoning later in the twentieth century. The basic assumption grounding their hypotheses is that habitat selection was especially important to our Pleistocene ancestors because they lived in hunter-gatherer groups that roved across, and frequently resettled in, savannah-like environments. Natural selection molded aesthetic experience through the adaptive advantages conferred by emotional responses when making decisions and solving problems related with such a way of life (Orians, 2001): "Our aesthetic reactions to landscapes may have derived, in part, from an evolved psychology that functioned to help hunter-gatherers make better decisions about where to move, where to settle, and what activities to follow in various localities" (Orians and Heerwagen, 1992, p. 557). Natural selection would have endowed humans with a series of specific adaptations to quickly and unconsciously assess the suitability of certain landscape features, animals, fruits or natural indications that certain behaviors need to be modified (Kaplan, 1987, 1992).

In sum, our aesthetic appreciation originated in emotional responses shaped for generations because of the advantages they conferred in determining which elements in the environment required attention and the appropriate responses to them. From this perspective, humans' preference for natural sceneries, environments and landscapes is not just a special case of aesthetics; it is the foundation of some of the more traditional aesthetic domains (Kaplan, 1987, p. 25).

Mate choice

The association between aesthetic appreciation and mate choice has a long tradition in philosophical thinking. Joseph Addison (1712), for instance, believed animals' particular sensitivity to the beautiful qualities of their own kind served the purpose of attracting them toward potential mates of the same species. Thomas Reid (1785) conjectured that the varied ways in which animals instinctively respond to beauty has a fundamental biological function: "There seem likewise to be varieties in the sense of beauty in the individuals of the same species, by which they are directed in the choice of a mate, and in the love and care of their offspring" (p. 744).

Darwin (1871), however, was the first to elaborate a proper theoretical framework capable of explaining the role of aesthetic appreciation in mate choice: the theory of sexual selection. This theory originated from the observation that certain individual organisms have better access to reproduction than others of the same species and sex. One of its main accomplishments was to explain the existence of sexually dimorphic traits, especially those that have evolved to be so conspicuous and exaggerated that they seem to counter the logic of natural selection. He identified two major categories of sexual selection (Jones and Ratterman, 2009): intra-sexual and intersexual. Intra-sexual selection refers to the competition among members of the same sex to access potential mates. It can take the form of staying reproductively active longer than rivals, developing strategies to find mates faster, eliminating the competition through display or combat, sperm competition, suppression of competitors' gonadal function or elaborating alternative mating strategies, such as female mimicry or inconspicuous mating behavior, among others. Intersexual selection, conversely, occurs when the preferences of one sex restrict access to mating. Examples include: limiting the chance of fertile mating with specific individuals, female selection of sperm from different males in her reproductive tract or selection among zygotes, embryos or offspring. Intra-sexual selection leads to traits related with aggression and intimidation, such as large size, horns, sharp teeth and claws; intersexual selection leads to advertisement and enhancement of secondary sexual traits (Paul, 2002).

The capacity to derive pleasure from sounds, colors and forms was, in Darwin's (1871) view, an important element of intersexual selection. In fact, he believed that the appreciation of beauty was common to many animal species whose evolution has been driven by sexual selection. He noted, as Reid (1785) had, that the appreciation of beauty in other species was confined to opposite-sex conspecifics. Even though our species is peculiar in the open-endedness of the category of objects we appreciate aesthetically, Darwin (1871) believed that human ornaments, body decoration, art and music originally performed a similar role in many animal courtship songs and signaling calls. Aesthetics and art, thus, are the result of sexual selection.

Building on the foundation Darwin (1871) laid down, Allen (1880) conjectured that the earliest humans possessed only an elementary sensibility for the beauty of form, symmetry and color. The fully conscious manifestation of this capacity would occur solely in relation to physical features of opposite-sex conspecifics. The expression of this sensibility in relation to objects, such as flowers, fruits and feathers, would have been very limited. As human beings continued to evolve, this primitive appreciation of beauty broadened to include the sensibility for natural and cultural elements (Allen, 1880). The emergence of a flexible intelligence in humans decisively influenced this process of continuing evolution. Whereas the human production and appreciation of symmetry, for instance, are flexible, learned and consciously appreciated and valued for themselves, in other animals they emerge from stereotyped innate behavior patterns.

Miller (2000, 2001) updated Darwin's (1871) and Allen's (1880) views on the role of mate choice in the evolution of art and aesthetics and placed them within the framework of modern evolutionary psychology. He argues that our aesthetic preferences evolved favoring works of art that could only have been created by high-fitness artists. Evolution shaped our aesthetic preference as a domain-specific adaptive mechanism to distinguish difficult from easy, rare from common, skillful from careless and costly from cheap. Thus, we are inclined to consider people who are able to produce high-qualitative work as attractive due to our evolved preferences for what is difficult, rare, skillful and costly. Such qualities serve as indicators of health, energy, creativity, access to rare materials, good learning abilities, intelligence and coordination (Miller, 2001).

Acquisition of knowledge

A different line of reasoning suggests that art's main advantage is that it stimulates knowledge acquisition and improves perceptual and cognitive problem solving. Allott (1994), for instance, suggested that artists are driven to create by a biological impulse to explore the world and the motivation to reproduce it in some lasting manner. He is not alone in suggesting that the selective advantage of art is related to knowledge acquisition. Some of the pioneers of neuroaesthetics have argued that art's main function is to acquire knowledge about the world. In this sense, art constitutes a sort of continuation of the brain's main function (Zeki, 2004). Given that art is the product of the human brain, its creation and appreciation are necessarily constrained by its properties. Zeki (2001) believes that art cannot be understood without reference to two main "laws" of the brain. The first of these is the *law of constancy*: Just as one of the main functions of the visual brain is to gather information about the constant and essential qualities of the objects around us despite their continually changing appearance due to local conditions, great works of art constitute refined renderings of fundamental and constant features. The second law, the *law of abstraction*, is based on the fact that efficient organizing of knowledge requires moving beyond the particular, creating representations that are applicable to many instances. This also allows overcoming working memory limitations and the need for recalling all the details of encountered instances. Abstracting and conveying general ideas and concepts are important features of art. The ambiguity of great art affords spectators the possibility of many different matches with conceptual networks stored in their minds, and of picking the alternative that suits their own concepts better, thus enabling multiple individual interpretations and meanings (Zeki, 2002).

Like Zeki, Ramachandran and Hirstein (1999) argue that art is based on the neural mechanisms that allow us to understand the world and create our internal representations of it. They, however, believe that the work of artists not only reflects the essence of things, ideas or feelings. Rather, artists distort them by magnifying their distinctive features. As a result, artworks engage the same neural mechanisms involved in processing the real entity, though in a more powerful way. Artists, in Ramachandran and Hirstein's (1999) view, use nine strategies to exploit the neural mechanisms that enable us to make sense of the world. Importantly, in the context of art, these mechanisms lead to pleasant feelings. First, they hypothesize that artists' enhancement of certain shapes produces an increase of activity in the brain regions that process form, a phenomenon akin to the *peak shift effect*. Second, artists' work draws on the mechanisms of *perceptual grouping* and *binding* of features. Third, by *isolating a single area*, they also emphasize a given feature, focusing attention to a particular source of information and directing the viewer to the artists' enhancements. Fourth, artists also manipulate *contrast*, which engages neurons in specific brain regions that are sensitive to color or motion contrasts. Fifth, artists might challenge spectators with *perceptual problems* they can solve, which leads to satisfaction. The sixth and seventh resources grounded in information processing mechanisms used by artists are s*ymmetry* and *order*. Eighth, to avoid unlikely coincidences and one-of-a-kind images, artists tend to portray content from a *generic point of view*. Ninth, artists will often make use of *visual metaphors*, produced as a result of abstraction and the formation of concepts (Ramachandran and Hirstein, 1999).

Imagination, pretense and fiction

Some have argued that art's adaptive role throughout human evolution was intrinsically linked to play. Grosse (1914) believed that art and play emerged from a common tendency to engage in mental or physical activities lacking any specific purpose, often involving diverse forms of imitation. He thought this tendency had been part of human nature since the origin of humanity, and cultural evolutionary processes shaped and molded it into its different manifestations, past and present. Groos (1919) agreed with Grosse (1914) that art's main evolutionary foundation is play, and noted the common features binding art and play: Enjoyment of regularity, rhythm, imitation, illusion and attraction toward intensity and difficulty.

Influenced by the tight relation Schiller (1895) wove between play, art and beauty, Groos (1919) regarded art as a form of adult play. And just as play is fundamental for children's healthy development, he viewed art as biologically and socially decisive for adults' development. Art – he thought, following Schiller (1895) – is an essential means for the improvement of human capacities. Art allows cultivating and exercising perceptual, cognitive and affective processes that would otherwise wither with the monotonous routine of everyday human life. There are two main aspects that distinguish art from play, however. First, in art, imitation is not an end in itself, but a means to create an effect on spectators. The production of art is inseparable from the fact that it is destined to be appreciated. Second, and probably more importantly, art provides a moral elevation and insight into life that play does not (Groos, 1919).

Almost a century later, Carroll (2007) suggested that this second property of art is its main adaptive value. He postulated that literature, as well as other art forms, foster the elaboration of imaginary experiences. Although these images can serve as practical guides for action, this is not their main function. Their fundamental purpose is to allow people to make sense of the world around them, and of their reactions to it. It lets them assess and organize their own principles and motivations, and to value important aspects of their lives, giving personal and social meaning to their existence (Carroll, 2006)

Tooby and Cosmides (2001) elaborated the notion that the playful use of illusion is at the root of art within the framework of evolutionary psychology. They argued that natural selection endowed our species with specialized cognitive systems for art, and that fiction provides the key to understanding its adaptive value. The main selective advantage of this capacity for fiction is that it stimulates and helps organize the development of the ability to reason about conjectural situations. Furthermore, fiction allows practicing certain skills and responses to situations that could be dangerous, infrequent or uninformative in real life. Through fiction we can safely explore situations and events, improving the skills and knowledge required to deal with real-world situations.

Influence over others

Boyd (2005) shares with the proposals in the previous section the conviction that the fundamental evolutionary building block of art is the ability to imagine alternative realities, to think beyond the immediate present, testing and examining ideas. He believes, however, that this is only one of the two cognitive building blocks of art. The second one is the fundamental human drive to seek and direct the attention of others, which developed out of primates' social attention. He argues that art emerged as these two capacities became intertwined throughout human evolution. Natural selection made it pleasurable to engage in unbounded exploration of imagined scenarios, and increased the importance of social attention, endowing us with a great ability to share and guide others' attention. At some point, "the ability to share and shape the attention of others by appeals to common cognitive preferences led to the development of art: to behaviors that focus not on the immediate needs of the here and now but on directing attention and engaging emotion for its own sake, even toward distant realities and new possibilities" (Boyd, 2005, p. 10). Art would confer two adaptive advantages: At an individual level, it would foster commanding and following others' attention; at a social level, it would increase a group's coordination and cohesion, improving its chances of outcompeting others.

Taking this view a step further, Aiken (1998) argued that art's main adaptive value resides in the control of behavior. Although art can use cultural associations and techniques to move us, she believes that it also makes use of core automatic emotional response to certain elementary perceptual configurations. In her view, humans are predisposed to react in reliable and consistent ways to specific combinations of lines, colors, shades, angles, sounds and so on, which are often used in artworks around the world. Artworks function, thus, almost as complexes of fixed action pattern releasers. Such complexes can elicit a broad spectrum of behaviors and emotional responses, though to make her case she focuses mostly on defensive responses to threatening cues in art, such as sharp edges, or pointy angles.

In Aiken's (1998) view, art initially emerged from these automatic emotional responses. The original function of our emotional responses to such kinds of stimuli configurations was to guide our behavior in a complex environment, avoiding dangers and finding resources and safety. At some point, artists realized that they could exploit these reactions, related to environmental dangers and human desire, to control others' fears and pleasures. At this point, art became a means to acquire and perpetuate power. Leading figures in the community would have realized the value of this instrument to produce common emotional reactions in their groups, increasing their unity by focusing on the same goals or problems. Furthermore, they would have recognized that art, as a means of harnessing power, had the advantage of avoiding the use of force.

Relief of tension and anxiety

Humans are no different from other animals in their inclination to seek pleasure and avoid pain. Hirn (1900) argued that such a basic natural tendency was the key to understanding art production and appreciation. Specifically, he believed that the external expression of feelings had the effect of heightening pleasure or relieving pain. He also believed that art was primarily a means for expressing and conveying emotions. Such premises led him to conclude that, at an individual level, art was an intrinsically pleasurable experience. However, in Hirn's (1900) view, art is fundamentally social. The expression of emotions, through art or otherwise, elicits similar emotions in other people. In turn, others' sympathetic emotional responses feed back to the original individual, heightening the initial emotion he or she expressed. Artists, thus, are able to go beyond the automatic increase of pleasure and reduction of pain through emotional expression, common to all people. They can heighten pleasure and relieve pain by eliciting similar emotions in others. Although Hirn (1900) believed that every aspect of artistic creation is aimed toward emotional expression and contagion, he noted that the primitive pleasure-seeking/pain- avoiding impulse provided only the raw artistic drive. Artists devised the complex and varied artistic forms and mediums to express their feelings throughout evolution, probably based on elaborate gesture and vocal expressions of emotion.

Hirn's (1900) line of reasoning was picked up by contemporary researchers interested in the evolution of music and art in general. Fukui's (2001) hypothesis about the evolution of music, for instance, is grounded on the idea that, at some point during the evolution of our lineage, new tensions arose because of competition for resources and mates. The adoption of a new lifestyle, including monogamy, biparental families and group living would have led to an excess of testosterone, fueling aggression and sexual conflict. Based on the finding that music alters testosterone levels in men and women, Fukui (2001) believes that music appeared as a means to control this hormone's levels, suppressing the problematic aggressive and sexual behaviors it promoted.

Dissanayake (2007) also considers that one of art's essential functions is to relieve tension and anxiety. However, there is a crucial issue that distinguishes her views from those reviewed up to this point. She believes that, together with its relieving effects, art fosters a sense of coping with uncertainty by leading individuals to feel that they belong to a larger community. Thus, Dissanayake's (1992, 2000) evolutionary scenario combines selective advantages for the individual, but also for the group, a topic to which we now turn.

Enhancement of group cohesion and cooperation

Grosse (1914) was among the first to realize that during human evolution art had an important role in developing and strengthening social bonds within groups. This view contrasts with many of the previous hypotheses, based mostly on competition for resources or mates. Grosse (1914) contended that art was eminently a group activity during the early stages of human evolution. The individual relevance of art became apparent only recently, after the gradual specialization of certain people in artistic activities, allowing them to achieve highly valued creations. Dissanayake (1992) also emphasized that human arts did not emerge as autonomous activities; they were originally intertwined with rituals and ceremonies. Art's main evolutionary contribution was to reinforce social cooperation and group cohesion. The way she views the nature of art is fundamental to the articulation of her evolutionary proposal:

> [I view] art itself as being not an entity or a quality *but a way of doing or treating something*; that is, a behavior of art, or "ratification." When "artifying," I suggest, *one intentionally makes ordinary reality extra-ordinary through certain operations: formalization, elaboration, repetition, exaggeration, and (sometimes) manipulation of expectation, or surprise*. (Dissanayake, 2007, p. 9; emphasis in original)

By making our ancestors feel they belonged to a social group, the shared experiences of making special or "artifying" through temporal and rhythmic coordination of behavior provided, in Dissanayake's view, a way to mitigate apprehension and nervousness, encouraging a sense of coping with uncertainty, as noted in the preceding section. Dissanayake (2000) traces the origin of such "artification" behaviors and their soothing consequences back to early evolutionary stages of the genus *Homo*. This genus' commitment to strict bipedalism required the narrowing of the pelvis in large-brain-sized erectus-grade hominins, about 1.8 million years ago. Natural selection favored a shorter gestation period and the appearance of maternal strategies to provide the additional care for extremely immature offspring. Those ancestral adults communicated with infants using simplified or stereotyped, repetitive, exaggerated and elaborated visual, vocal and kinaesthetic signals, which must have caught infants' attention and generated states of anticipation and expectation. Such behaviors served as a pool from which later hominins could draw when they began to engage in artistic and ritual activities (Dissanayake, 2000). In fact, these are the attributes that constitute the essential components of ritualization and artification observed in the art of all human societies.

Brown (2000) has argued along similar lines regarding music, making the case that music is a group-level adaptation that increased group fitness. Like Dissanayake (1992), Brown (2000) believes that music did not evolve in isolation. In fact, he argues that its evolutionary history is linked with human rituals, which constitute a means of highlighting an event or time, of making it special. By inducing pleasurable emotions in the participants, music plays the crucial role of reinforcing ritual activities, which serve many important and diverse functions in human groups. The main advantage conferred by music and dance is to boost and affirm human groupishness, understood as a complex set of emotional and motivational traits that promote coordination, the formation of coalitions, in-group preferences and out-group hostilities. Brown argues that "Music's fitness advantages come about from its ability to promote group-wide cooperation, coordination, cohesion and catharsis, and this operates to increase both the absolute and relative fitness of groups. It functions to promote both group welfare and group warfare" (Brown, 2000, p. 257).

Art as an exaptation

Darwin (1871) tried hard to understand the mystery of how natural selection had produced the human ability for, and interest in, music given the absence of decisive advantages it afforded. In his solution to this mystery, Pinker (1997) excluded all adaptive function from music. He famously likened music to cheesecake, conceiving it as a non-adaptive pleasure-seeking mechanism. In his view, most features of other art forms also lack adaptive value. Music, and maybe art in general, did not directly promote survival, it just exploited some of the pleasure mechanisms that appeared as a way to reinforce some sort of adaptive behavior.

Pinker (1997) is not alone. De Smedt and De Cruz (2010) revised various lines of evidence relevant to the origin and evolution of art, and concluded that the production and appreciation of most instances of art emerged as by-products of common perceptual and motivational cognitive processes that evolved because they solved problems that were originally unrelated to art, including the perception and discrimination of salient features of the visual world and speech. Davies also believes that art is closer to being an exaptation than an adaptation:

> When I review the theories and the evidence, I am doubtful that the arts, either together or singly, are selected to serve an adaptive function. If I had to bet,
>
> I would say that the adaptations that give rise to art behaviors are intelligence, imagination, humor, sociality, emotionality, inventiveness, curiosity. Though art is mediated by culture, it gives direct and immediate expression to these traits and dispositions, so I would identify it as a by-product rather than as a technology. Art gives vivid and powerful expression to these qualities, which are central to our human nature and indicate our humanity. (Davies, 2012, p. 185)

In view of the fruitless discussions about the adaptive advantages conferred by music, or lack of them, McDermott (2009; McDermott and Hauser, 2005) advocated an experimental approach to determine the adaptive status of several musical processing components. Their basic assumption is that any perceptual or cognitive processes involved in music that are shared with other closely related primates cannot be considered to be part of an adaptation for music. Rather, they should be viewed as pre-existing cognitive traits that have been recruited by music at a later evolutionary stage, that is to say, as exaptations. Musical adaptations should be exclusively human, as well as exclusive to the domain of music. For instance, it has been argued that the capacity to process pitch contours, and recognize versions that have been shifted up or down in overall pitch, are a uniquely human trait and specific to music. However, the fact that people can also recognize brightness and loudness contours, even when the relations are replicated in a different range, led McDermott (2009) to argue that contour processing relies on general mechanisms of the auditory system, and that other animals' difficulties with recognizing transposed melodies might be related with limitations in their abilities to cope with relations among stimuli. Thus, "There is, as yet, no compelling evidence that any of these represent traits that are specific to music, consistent with the notion that music is a side effect of traits that evolved for other functions" (McDermott, 2009, p. 168).

Combinations

Although the different explanations for the origin of art and aesthetics have been offered as alternatives, these need not be mutually exclusive. In fact, some researchers have offered elaborated hypotheses that include different combinations of those. Dutton's (2009) account of the origins of art synthesizes a number of the scenarios noted above. Although art is practiced and appreciated in many different ways across cultures, Dutton (2009) believed that it exhibits a cluster of common features. Some of these are characteristics of the works themselves, and others refer to the way we experience them. Not all artworks, art forms or cultural art practices need to exhibit all of these features, but they will certainly show most of them. His cluster is composed of twelve items:

1. Artworks are valued as sources of pleasure, aesthetic pleasure.
2. Producing artworks requires skill and virtuosity.
3. Artworks are produced according to recognizable styles, and following specified rules and norms.
4. Artworks are treasured for their creativity and their novelty.
5. All art is accompanied by a system of criticism, which includes terminology that structures judgment and appreciation of the works.
6. To different degrees, art is about representation: it represents or imitates real or imaginary experiences or objects.
7. Artworks are conceived as separate entities from ordinary life, people create special places, moments or manners in which to engage with art.
8. Artworks are endowed with expressive individuality, reflecting the personality or identity of the maker.
9. The experience of art is ~~a~~ fundamentally an emotional one.
10. Artworks are created to be perceptually and cognitively stimulating, to pose an intellectual challenge.

1. Art is performed, understood and valued within specific traditions and institutions.
2. Artworks foster imaginary experiences in the artist and the audience: "All art, in this way, happens in a make-believe world." (Dutton, 2009, p. 58)

Because these features are common to art in all human cultures, Dutton (2009) believed that they stem from a biological drive, an innate predisposition, which he called the art instinct. Thus, he aimed to explain the evolutionary origin of the human universal capacity to create and value artworks, understood as the kind of objects and experiences that exhibit most of the features listed above. He framed his evolutionary argument within the parameters established by evolutionary psychology, in a narrow sense (Tooby and Cosmides, 1992). For instance, he believed that the crucial aspects of our human makeup appeared during the Pleistocene, owing mainly to our ancestors' adaptation to environmental features and challenges. He also committed to a strong version of mental modularity, which assumes that the human mind is constituted by a certain number of specific mechanisms adapted to solve specific environmental and social problems.

Dutton's (2009) position is clearly adaptionist: art practices appeared and evolved because they increased our ancestors' well-being and chances of survival and reproduction. He articulated his account based on three main adaptive pillars: storytelling, social cohesion and mate choice. The event that set the evolution of art into motion was the appearance of the capacity to create and understand invented stories and fictions. Fashioning hypothetical scenarios, future possibilities or alternatives to past events allowed our ancestors to plan and rehearse their responses to physical or social situations that in real life would be menacing or compromising. The capacity to imagine rich stories would benefit individuals by increasing their competence when actually encountering those situations. It would also benefit the community because storytelling allows communicating advice and enhances empathy toward others, strengthening the group's bonds. Those who were better at storytelling would have had better chances of survival and transmitting this capacity to their offspring. Also, groups with good storytellers would have had better chances of survival than groups with fewer or worse storytellers (Dutton, 2009). In addition, individuals who were more proficient at creating engaging stories or objects would have been more successful than others in attracting mates for reproduction, who presumably appreciated such features as indicators of the creator's fitness, much in the line of Miller's (2000, 2001) argument. At some point during human evolution, the capacity to imagine and embellish stories to capture others' attention would have generalized to other forms of creation, such as sculpture or dance.

A new framework for the evolution of art and aesthetics

The options reviewed above certainly do not exhaust the range of possibilities. Many more explanations for the origin of aesthetics, art and the particular arts have been presented. Because art and aesthetics perform so many functions in our cultures, any of them could have been their fundamental adaptive advantage. Among this large number of alternatives, some might seem very appealing. Some are logically sound, and well argued. However, in the absence of suitable evidence to test, or at least constrain these hypotheses, any of them could be right. They could also all be wrong. Unfortunately, however, we have no way of knowing, because these hypotheses are seldom accompanied by an appropriate description of the kind of facts that could falsify them. They thus run the risk of becoming little more than “Just-So” stories (Fitch, 2006; McDermott, 2009). Many of the facts required to determine whether art or aesthetics are adaptations or exaptations, or ascertaining the selective advantage they conferred, are simply out of our reach at the moment. Furthermore, we have to consider the possibility that they might never be within our grasp (Fitch, 2006).

Hence, we might as well accept that there is a good chance we will never really know how art and aesthetics evolved, and turn to more productive fields of inquiry. On the other hand, we might devise new approaches that attempt to overcome this obstacle. Fitch (2006), for instance, suggested that the kind of scenarios reviewed above can have a useful heuristic role: They can be used to motivate hypotheses that could be experimentally tested with humans or other animals, in line with the work of Fink, Grammer and Matts (2006) and Schaefer and colleagues (2006) on human attractiveness. In this section, we present a general framework that can serve to guide such kinds of hypotheses and delimit an appropriate theoretical space. This framework, first, defines the kinds of features of art and aesthetics that are amenable to evolutionary explanation, or the sense in which we should conceive *art* and *aesthetics* within an evolutionary cognitive neuroscience of art and aesthetics. Second, it assembles the relevant evidence from neuroscience, comparative neuro-anatomy and archaeology.

Defining the object of study

Any evolutionary approach to art and aesthetics should make clear the sense in which the terms “art” and “aesthetics” are used. In doing so, at least three crucial facts should be taken into account: (1) Art, as a distinct and autonomous domain of human experience is a recent Western notion. (2) The kind of activities that we recognize as art nowadays do not constitute a natural kind, and have not always been considered to be art forms. (3) Art and aesthetics are practiced and experienced in countless different ways around the world. Unfortunately, the implications of these points are not always fully appreciated.

Art, as a separate domain from craft and other human activities, is a very recent cultural phenomenon. It was only since the eighteenth century that artworks became autonomous objects free from all functional purpose, which could be fully appreciated without reference to context, and which were intended solely for aesthetic and intellectual contemplation. Artworks had previously been an integral part of a community’s events or locations, serving diverse purposes and promoting social values, beliefs and interaction. However, since the eighteenth century, they were increasingly accumulated in museums or private collections, where they were turned into purposeless objects for contemplation, and their condition as artworks was underscored and exalted (Carroll, 2008; O'Doherty, 1986). Whereas art became inextricably identified with the production of beauty, and regarded as the product of inspiration and genius (Tatarkiewicz, 1971), crafts were relegated to a secondary position, and were thought of as merely requiring skill, following conventions and destined for use or entertainment (Shiner, 2001). This breach was accompanied by a distinction between the gratifications that people were expected to obtain from art and craft. Art, the fine art, was supposed to be enjoyed with a refined and elevated sort of contemplative pleasure, an aesthetic pleasure. Crafts, on the other hand, could produce ordinary functional pleasure derived from the useful or amusing (Shiner, 2001). Thus, the separation of art from other spheres of human experience was paralleled by the tearing of aesthetic interests away from all-purpose and common pleasure (Carroll, 2008).

Our second point was that, although most of the hypotheses reviewed in the sections above attempt to explain the origin and evolution of the class of activities that we regard as artistic nowadays, such as painting, music, sculpture, architecture and so on, the category of arts is not a natural category, it is a cultural construction. The kind of activities we refer to as art in the twenty-first century were not recognized as constituting a common set until recently. Toward the end of the seventeenth century and beginning of the eighteenth, the classification of the arts was widely discussed within European cultured circles. Even Kant (1892) dealt with this issue, dividing the fine arts into speaking arts (poetry and eloquence), plastic arts (painting, sculpture, architecture and gardening) and arts of the beautiful play of sentiments (music and the art of color). But Batteux's *Les beaux-arts reduits à un même principe* (1746) turned out to be the most influential classification, and it is regarded as the decisive step toward the modern system of arts (Kristeller, 1952; Shiner, 2001). Batteux separated the fine arts from the mechanical arts because he believed that fine arts sought to imitate nature, though choosing only that which was beautiful, and that their purpose was pleasure. The fine arts included music, poetry, painting, sculpture and dance. Eloquence and architecture were placed in a separate group that combined pleasure and usefulness (Kristeller, 1952). Such a system could obviously only have appeared at a place and time when imitation and purposelessness were regarded as the essence of art, and it turned out to be very appealing.

Although the notion of a common essence to all arts that justifies their inclusion in a common category has endured the passage of time, the modern system of the arts is more a reflection of the spirit of a past time than of the nature of art. The category "art" is a conventional division of objects or of human activities or capacities. There is nothing in the nature of painting that makes it more an art than gardening or eloquence. It is precisely because we have lost sight of the idea that there is no essential quality binding our cherished arts together that we have been searching for a single explanation for the evolutionary origin of the human capacity to produce and enjoy art. We have been trying to determine *the* fundamental selective advantage that art conferred our ancestors. Stating, for instance, that "The purpose of art, surely, is not merely to depict or represent reality – for that can be accomplished very easily with a camera – but to enhance, transcend, or even to distort reality" (Ramachandran and Hirstein, 1999, p. 16) is a gross overgeneralization: "Even a fleeting visit to one of the great museums might serve to convince the authors that few of the exhibits conform to the laws of art they postulate" (Gombrich, 2000, p. 17). Contrary to what Ramachandran and Hirstein (1999) state, the purpose of art is manifold. Art performs and has performed many functions, some of which might have been beneficial for individuals, some might have been beneficial for groups of people and some might have had no immediate benefits. Moreover, these benefits might have changed dramatically throughout history.

Our third point is extremely relevant, because most of the evolutionary work we have reviewed has taken Western art and aesthetics as a point of departure. They have mostly tried to explain art as we understand it, as we have learnt it and as we appreciate it. Western art and aesthetics, however, are not the best representatives of art and aesthetics as they are practiced and understood around the world. They are most familiar and comprehensible to Western researchers, but they are the result of just one of the many particular traditions in the world, the European one. It is fruitless to attempt to explain the biological evolution of art understood as an autonomous domain of human experience related with the purposeless contemplation of the fine arts for their own sake. These qualities of Western art are already adequately explained by art history. If we wish to understand the biological bases of art and aesthetic experience, a particular form of experience afforded by our human nature, then we need to be able to account for varieties of such activities across many human cultures. Anderson's (1989) study of art around the world can help us home in on the special features exhibited by art in different cultures: (1) it conveys culturally significant meaning; (2) it shows a characteristic style; (3) it is produced using a sensuous, affective medium; (4) it involves the recognition of special skill. He has, accordingly, defined art as "culturally significant meaning, skillfully encoded in an affecting, sensuous medium" (Anderson, 2004, p. 277).

In sum, from an evolutionary perspective, it only makes sense to explain the origin and evolution of art/craft, or popular art, or art with lowercase "a." By this we mean a sort of activity that can be deeply embedded within ritual and ceremony, that can serve many individual and social purposes (many of which have nothing to do with beauty), that is practiced in innumerable manners and that elicits many different responses. From this perspective, the study of the evolution of art should aim to ascertain how natural selection endowed *Homo sapiens* with the capacity to create and appreciate affective and sensuous media skillfully used to convey important cultural meaning.

The notion of aesthetics also requires careful consideration. Like in the case of art, non-Western aesthetics generally permeates a broader range of activities and objects than Western aesthetics, and, unlike the European tradition, it is related to the communication of spiritual, ethical and philosophical meaning (Anderson, 1989). For instance, writing about Huichol aesthetics, Shelton remarked that "Aesthetics as a discourse does not exist, but aesthetics as an ethical codification of the use, significance, and purpose behind sacred and ritual arts pervades metaphysics and ontology" (Shelton, 1992, p. 235). Beauty, for the Huichol, is a measure of the extent to which something incarnates the character of the deity it is meant to represent. Thus, Huichol aesthetics and ethics are inextricably bound together. In this sense, the notion of aesthetics cannot "be regarded as pertaining to the study of the visual perception of the beauty of a material object" (Van Damme, 1996, p. 56). We require an evolutionary framework to account not only for visual and auditory aesthetic experiences, but also for olfactory, gustatory, tactile and kinaesthetic experiences, as well as multiple and dynamic combinations of them. Moreover, we need to account for aesthetic experiences that are unrelated to beauty, such as those that arise from human engagement with the ugly, the comic, religious symbolism, identity markers and so on (Van Damme, 1996).

The recognition of the inadequacy of the traditional notion of aesthetic experience has led some philosophers to search for better ways of conceiving it. Carroll, for instance, proposed a content-oriented notion: "An experience is an aesthetic one if it involves informed attention to the formal, expressive or otherwise aesthetic properties of the artwork in ways that are consistent with the norms and strategies of detection proscribed for that type of work by its conventions, genre, and tradition" (Carroll, 2008, p. 159). Shusterman (1997; Shusterman and Tomlin, 2008) and Bergeron and Lopes (2012) presented a similar view, though they unpacked it into three main features: An aesthetic experience has an evaluative dimension, in the sense that it involves the valuation of an object; it has a phenomenological or affective dimension, in that it is subjectively felt and savored and it draws our attention; and, finally, it has a semantic dimension, in that an aesthetic experience is a meaningful experience, it is not mere sensation. Thus, in our evolutionary framework, the question about the origin and evolution of aesthetics is answered by determining the conditions under which, and by virtue of what evolutionary processes, did human experiences become evaluable, affectively absorbing and individually and socially meaningful.

Assembling the evidence: neuroscience

There are two lines of research that have advanced our understanding of the neural mechanisms underlying the creation and appreciation of art and aesthetics: The study of the effects of neurological disorders and neuroimaging. The first of these has shown that artists are vulnerable to the same visual, motor, auditory and cognitive neuropsychological deficits that affect other people, despite their proficient perceptual and motor skills. The difference, in Chatterjee's (2004) words, is that artists manifest these deficits in strikingly eloquent ways. Most artists suffering from neurological disorders continue to be artistically motivated, productive and expressive after the onset of their condition (Zaidel, 2005). There usually is, however, a noticeable change in the work of most artists who have suffered a stroke.

Neurological conditions can thus have diverse effects on artistic production. But what about their influence on appreciation, the other side of the artistic coin? What can similar cases tell us about the biological underpinnings of aesthetic enjoyment? Overall, they argue against the existence of specialized brain mechanisms underlying the experience of art (Zaidel, 2005). Several studies suggest that the perception, recognition and emotional impact of artworks can be affected. Most patients, however, are still able to recognize and experience art in a meaningful and consistent way, even in the face of extensive brain damage or disabling neurodegenerative diseases (Halpern *et al*., 2008; Halpern, and O'Connor, 2013).

Neuroimaging techniques have allowed researchers to address similar and new issues in healthy subjects in controlled situations, and to correlate appreciation and enjoyment of music, painting, architecture or sculpture, among other forms of art, with the activity of several brain structures. A number of recent neuroimaging studies have revealed that aesthetic appreciation of different artistic manifestations involves at least three different kinds of measurable brain activity (Nadal and Pearce, 2011): (1) an engagement of the reward circuit, including cortical and subcortical regions, as well as some of the regulators of this circuit; (2) an enhancement of cortical sensory processing; (3) high-level top-down processing and activation of cortical areas involved in evaluative judgment. It is clear from neuroimaging studies that these brain regions, described in three functional clusters, interact in complex ways to produce our experiences of art and aesthetics. Processing is performed in parallel along highly interrelated brain networks, relying heavily on information feedback, making it impossible to describe any meaningful sequence of events. One cannot even say that an art experience begins with perception, given the strong biasing influences that context, expectations and prior knowledge have even on very early perceptual processes (Cupchik *et al*., 2009; Kirk *et al*., 2009; Leder *et al*., 2004).

Neurological and neuroimaging evidence, thus, leads to a series of conclusions that should be taken into account by evolutionary explanations of art and aesthetics. First, there is no localized seat for art or aesthetics in the brain. Such experiences are the result of complex feedforward and feedback interactions among the nodes of a broadly distributed network of cortical and subcortical brain regions. This distributed and unspecific quality of the neural underpinnings of art and aesthetics might explain why the production and enjoyment of art are generally resilient to neurological disorders. In spite of the different effects that these disorders seem to have on the experience of art, patients continue to engage with art in personally meaningful ways, even though perceptual, memorable or affective qualities might escape them. Crucially, none of the brain regions identified in neuroimaging studies is specialized in responding to art alone, or specifically suited to aesthetic experiences. Not even in the sense that one could think of Broca and Wernicke's regions as specialized for language processing. All of the relevant brain regions are involved in other domains of human experience, from perceiving small details in the world or making trivial decisions to abstract reasoning or establishing social relationships.

Assembling the evidence: comparative neuroanatomy

Let us assume, as neuroimaging and neurological evidence suggests, that the network of brain regions described above, divided into three functional components, constitutes the neural underpinnings of aesthetic experiences. It seems reasonable to suppose that the evolution of art and aesthetics was made possible because natural selection molded and integrated the elements of this network. To what extent have this network's components changed throughout human evolution? Has the whole network changed, or did evolution target specific components? Comparative neuroanatomy can, to a point, inform about this process. Although our knowledge of the evolution of the brain regions involved in aesthetic and artistic appreciation is very incomplete, a number of conclusions can be drawn from the review of this evidence (see Table 8.2 for a summary). First, some features of these regions are largely conserved, suggesting that they have undergone little change throughout human evolution. Second, some features are derived, meaning that they appeared at some point during human evolution, after our lineage split from that of chimpanzees.

Trivial as these two points might seem, theories on the evolution of art and aesthetics have not fully accommodated their implications. Human evolution did not begin from scratch. The brain and cognitive system of the common ancestor of humans and chimpanzees provided the starting point. Based on living non-human primate cognition, it can be assumed that this hominoid had highly developed physical and social cognition (Tomasello and Call, 1997; Zentall and Wasserman, 2012) that relied on the complex primate brain organization (Dehaene *et al*., 2005; Hofman and Falk, 2012). Thus, a considerable portion of the neural architecture that was later recruited for the appreciation of art and aesthetics was already in place between 6 and 8 million years ago, when hominins first appeared (Cela-Conde and Ayala, 2007), and long before the first archaeological indicators of artistic and aesthetic activities. Natural selection did not build art and aesthetics *de novo*. It used certain aspects of pre-existent primate brain regions and networks involved in several perceptual, affective and cognitive processes, and modified others, to assemble the neural mechanisms to support art and aesthetics. This sort of tinkering is common in evolution (Jacob, 1977). Thus, we can narrow the general question, "How did art and aesthetics evolve?", to "How and why did natural selection modify certain aspects of the underlying neural circuitry (e.g., reducing neuron density in prefrontal regions or increasing the complexity of processing within the ventral striatum) and integrate these innovations with primitive features (e.g., the basic architecture of the prefrontal cortex or the connectivity of the frontal poles)?" In light of the comparative evidence, it is also fair to wonder to what extent were these broadly distributed changes, which no doubt had far-reaching effects on cognition and brain function, the result of natural

Table 8.2. *Summary of the evidence provided by comparative neuroanatomy of the evolution of brain regions involved in the appreciation of art and aesthetics*

		Evolutionary status	
Function in appreciation of art and aesthetics		*Conserved*	*Derived*
Affect	Orbitofrontal cortex Anterior cingulate cortex	Function	Low cellular density High connectivity New cytoarchitectonic areas High number and clustering of spindle cells
	Ventral striatum	Function	Greater internal regulation Enhanced and differentiated processing
Perceptual enhancement	Visual cortex	Retinotopic organization of V1, V2	Reduction in relative size Expansion of dorsal visual processing stream
Evaluative judgment	Lateral prefrontal cortex	Cytoarchitectonic organization Functional divisions	Multisensory input Relative increase in size Low cellular density High connectivity
	Anterior medial prefrontal cortex		Relative increase in size Low cellular density High connectivity
	Temporal pole	Functions Connectivity	
	Precuneus	Functions Connectivity	Relative increase in size Complex organization

selection strictly for art or aesthetics. It is plausible that the evolution of at least some of the brain regions we considered above was driven by domain-general advantages that had effects in diverse spheres of human life (Justus and Hutsler, 2005).

Assembling the evidence: archaeology

Palaeoanthropologists commonly consider early artistic and aesthetic activities, such as the decorative use of pigment or engraving, to be part of a suite of indicators of modern symbolic human behavior, together with evidence for transcendent thinking, such as burying the deceased with tools, decorations and ornaments. Human symbolic cognition, however, appeared together with other indicators of modern human cognition (McBrearty and Brooks, 2000), including those related to ecology (e.g., broad diet), technology (e.g., microblades, hafting, use of bone and antler to craft tools) and economy and social organization (e.g., exchange networks across long distances, reoccupation of habitation sites, specialized hunting of large and dangerous animals). Several explanations for the origin of human modern behavior have been put forward, but they lie between two extreme perspectives: the revolution and the gradualist hypotheses. The revolution hypothesis sees evidence in the archaeological record for a recent and rapid appearance of modern human behavior in Europe between 50,000 and 40,000 years ago. The richness of the archaeological remains unearthed at European Upper Palaeolithic sites is regarded as proof of a substantial change in human cognition (Mellars, 1991) and its neural substrates (Klein, 1995). This contrasts with Middle Palaeolithic sites, which indicate lower effectiveness of resource exploitation, and yield a simpler and less varied lithic technology, as well as virtually no evidence for symbolic behavior. This view, popular during the twentieth century, has recently been questioned by authors favoring the gradualist perspective, which argues that the set of behaviors regarded as indicators of human cognitive modernity did not appear at a single time and place. The use of ocher, engraving, bone working, complex subsistence strategies and other similar activities appeared much earlier than posited by the revolution hypothesis (McBrearty and Brooks, 2000). In fact, there is now ample evidence supporting the notion of a gradual and prolonged emergence of the cognitive underpinnings of art, including early use of pigments, engraving traditions, the elaboration of personal ornaments, the production of music and early evidence from Asia and Australia. Thus, the archaeological record tells the story of a slow and gradual accumulation of behaviors related to art and aesthetics. The capacities to create and appreciate art emerged together with new and complex forms of social, technological and environmental cognition that characterize our species. Although some of these aesthetic or artistic behaviors have their roots in the behavior of earlier hominins, nothing like the pervasiveness of ornaments, pigment use, engraving and musical instruments is associated with any other prior or contemporary hominin species. Since the earliest artistic or aesthetic manifestations, humans have expressed this capacity in many different ways, creating traditions that appeared, disappeared and reappeared. These patterns of artistic flourishing and withering, including the Upper Palaeolithic creative explosion in Europe, seem to be the result of geographic, climatic and demographic factors (Mellars, 2009), rather than biological adaptations.

Sketching a framework for the evolutionary cognitive neuroscience of art and aesthetics

We have argued that it makes little sense for evolutionary approaches to art and aesthetics to focus on the practice and appreciation of High Art in the European tradition. Trying to understand how evolution gave us Impressionism, Picasso or Warhol's *Brillo Boxes* is like trying to understand how it gave us French or Swahili. Obviously French and Swahili speakers and listeners are able to engage in conversation due to brain systems that evolved for millions of years. But such systems evolved because of the adaptive advantages conferred by the capacity for language. French and Swahili are the result of particular cultural and historical processes that are the subject of historical linguistics. Just as the field of language evolution attempts to understand how the capacity for language evolved, our framework aims to accommodate hypotheses about the evolution of the capacities for art and aesthetics and of their neural underpinnings. Based on the common features of art in different small-scale societies (Anderson, 1989), we have tentatively defined the capacity for art as the capacity to create and appreciate the skillful use of affective and sensuous media to convey important cultural meaning. Variations in media, required skills and the meaning conveyed have allowed the flourishing of art's wonderful and distinct cultural and historical manifestations, styles, schools and movements. Attempting to capture the enormous variety of aesthetics as experienced around the world, we have defined an aesthetic experience as one that is evaluable, affectively absorbing and individually and socially meaningful.

In this framework, thus, we aim to ascertain the evolutionary processes that led to the appearance of the capacity to create and appreciate the skillful use of affective and sensuous media to convey important cultural meaning, and the conditions under which, and by virtue of what evolutionary processes, human experiences became evaluable, affectively absorbing and individually and socially meaningful. The domains of art and aesthetics overlap somewhat, in the sense that artworks can be created and appreciated for their aesthetic qualities. On the other hand, we can enjoy the aesthetics of non-artistic objects or events and we can enjoy art for non-aesthetic reasons. Unfortunately, at this moment it is difficult to say whether art and aesthetics evolved as independent capacities, or whether they have common evolutionary roots. Furthermore, it is virtually impossible to distinguish the archaeological and neuroscientific evidence for the evolution of art from evidence for the evolution of aesthetics. Most neuroimaging studies of the aesthetic experience have used artworks as materials, and most archaeological finds lack a sufficiently rich context to be able to make the distinction.

The second aspect of our framework refers to neuroscientific and archaeological facts that should be acknowledged by hypotheses about the evolution of art and aesthetics. First, there is no specialized brain region or mental process that makes us capable of engaging with art and aesthetics. Our experiences of art and aesthetics rely on a complex network of brain regions, none of which is specific to this domain of human experience. Our appreciation of art and aesthetics is the result of neural interactions throughout a network of at least three functionally distinct sets of brain regions, related to affective and emotional processing, evaluative judgment and attention-driven enhanced perceptual processing.

Second, we share many of the features of these brain regions with our primate relatives, suggesting we inherited them from distant ancestors. Other features of these brain regions have been subjected to significant modifications throughout the hominin lineage. The challenge for the evolutionary cognitive neuroscience of art and aesthetics is to explain why and how natural selection preserved some of the features of the brain regions that constitute the network underlying the appreciation of art and aesthetics and favored changes to others. Because such brain regions are involved in many other domains, it is likely that some of the changes were not driven specifically due to the advantages conferred in the domains of art or aesthetics.

Third, the archaeological evidence indicates that different artistic and aesthetic activities appeared gradually at different moments and places of our species' evolution. The creative explosion evident in the European Upper Palaeolithic record is the result of an accumulation of behaviors and traditions that had emerged much earlier, some maybe even before the appearance of our own species. Engraving, coloring and beading traditions appeared and disappeared owing to the impact of environmental and demographic factors.

Evidently, there are many gaps – major voids, one could say – in the general framework we have just sketched. In fact, it merely highlights the kinds of questions and evidence that hold the greatest promise for increasing our understanding of the evolution of art and aesthetics. Answering these questions, and finding new kinds of evidence, will require further research that can fill in many details and even major aspects of the framework. For instance, we need to explore the potential of experimental approaches, especially the comparative method, to unlock the answers to some of those questions. The only way to accomplish this is through truly interdisciplinary work. The picture of the evolution of art and aesthetics will not come into focus unless psychologists, neuroscientists, evolutionary anthropologists, archaeologists, anthropologists, art historians, art theorists and philosophers overcome traditional disciplinary boundaries and work together to move the field beyond its mostly conjectural and provisional state. However, if we agree with James when he wrote that "the best mark of health that a science can show is this unfinished-seeming front" (James, 1890, vii), there is good reason for optimism.

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The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference

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The evolutionary roots of aesthetics: an approach-avoidance look at curvature preference

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1. The evolution of aesthetics

From an evolutionary point of view, aesthetics can be regarded as one of the functional –as opposed to anatomical– apomorphies[7] that characterise our species. However, this does not mean that the capacity of aesthetics is unique to *Homo sapiens*. There is no *a priori* reason to consider that perhaps other members of the *Hominin* tribe didn't possess this trait. It is still an open question how such a capacity evolved.

Unfortunately, it is not an easy task to understand the evolutionary process that gave rise to aesthetics, both in terms of the reconstruction of the milestones in said process, and in terms of the selective pressures that may have provided functional value to such a capacity. As regards the reconstruction of the process, we need to rely on the archaeological and fossil evidence, but they are both incomplete and partial, given that at most they provide evidence of the results, not of the psychological capacities. Thus, marks in lithic tools or different materials may reveal the effect of anthropic actions with no apparent utility, or uncertain symbolic meaning; while the anatomical correlates of a particular functional trait are to be determined before they can be found in the fossil record.

[7] An apomorphy, or derived state, is a trait present in a group of organisms, but absent in the last common ancestor group and near-contemporary groups.

In the case of aesthetics, this becomes especially problematic, as there is no particular anatomical trait to be considered, beyond specific aspects of brain organization. To make things more complicated, aesthetic appreciation seems not to be a single psychological function, but the outcome of a mosaic evolutionary process (Nadal et al. 2009) that involved the assemblage of different, emotional and cognitive, components. Research about such different components is gaining momentum, giving us some insight about (1) which brain areas are involved in the capacity of aesthetics (Cela-Conde et al. 2004; Cela-Conde et al. 2009; Kawabata and Zeki 2004; Vartanian and Goel 2004; Munar et al. 2012a); and (2) how do these areas work together in different aesthetic tasks (Munar et al. 2012b; Cela-Conde et al. 2013). From this standpoint, it makes sense to start small: looking for the roots of aesthetics in the most simple and basic processes which already exhibits the marks of aesthetic appreciation. Basic perceptual preferences constitute, in our view, such a minimal stage of aesthetics.

Preferences also seem the right place to look when considering the functional dimension of the evolutionary process that gave rise to aesthetics, as they relate to the ecological background and primal behaviours underlying it. It is possible to investigate whether they are universal, and whether they are exclusively human, or also present in our closest relatives. While this might result in just so stories depicting dubious adaptive scenarios, an empirically sound evolutionary approach would be invaluable when attempting to make sense of our aesthetic capacity.

In this chapter, after reviewing some of the most well known preferences, we will focus our attention on the case of the visual preference for curvature. This preference has been hypothesised to result from a primitive perception of sharp transitions in contour as conveying a sense of threat.[8] We introduce a new approach- avoidance paradigm, inspired by the embodied mind framework, as a better suited method to study such preferences while presenting some of the most important results obtained in our comparative and cross-cultural studies so far.

2. Basic perceptual preferences

A general feature of our perceptive systems is that they are not neutral, but preferentially oriented. That is, some stimuli are preferred over others, and this can be seen as a basic form of aesthetic preference. This preference seems to be sustained at the neuronal level by the reward system, among others, which makes some stimuli more appealing, or positively arousing; while driving us to avoid or dislike others –even if the liking judgment may result from a longer, more cognitive, process (Cela-Conde et al. 2013). Although it is perfectly possible that some of these preferences are the outcome of an individual process of reinforcement learning, such possibility is still dependent on the existence of intrinsic preferences and unconditioned stimuli, which can be expected to be universal and innate.

[8] Were this hypothesis true, 'avoidance of sharpness' would be a more precise term to describe the phenomenon. Yet, while there is no definitive proof of this proposed origin, we'll see that empirical evidence shows that curvature is, usually, better evaluated than sharpness. Hence the reason we have decided to use 'preference for curvature' throughout the text.

Therefore, we propose a research programme that identifies these basic preferences, testing whether they are, in effect, innate –and not the result of an idiosyncratic reinforcement story, or culture-specific preference depending on its cognitive acquisition. This programme also addresses the question of the evolution of such preferences: how did our species come to acquire such preferences? Was there any kind of evolutionary advantage in having them? In other words, were they selected at some point? Which functional advantages did they provide? And, in particular, are they human specific, or do we share these preferences with our primate relatives?

Several examples of perceptual preferences, which can be viewed as the possible building blocks of human aesthetics, have already been singled out in the literature. In the last decades several features have been proposed as universal determinants of visual aesthetic preference, such as vertical symmetry, regularity, colour, brightness, or complexity. We are not trying to create an all-encompassing endless list that would include every single element that may constitute our aesthetic capacity, but to simply illustrate the sort of approach that we have in mind. Accordingly, we focus only on symmetry and colour preferences, in order to place the preference for curvature in a broader context.

a) Symmetry: It has been stated from different sources that humans prefer more symmetrical patterns than non-symmetrical ones (Bornstein, Ferdinandsen, and Gross 1981; Enquist and Arak 1994). While most empirical evidence comes from experiments with faces (Rhodes et al. 1998), we can find studies focusing on bodies (Tovée, Tasker, and Benson 2000) and other kinds of stimuli such as drawings (Humphrey 1997) and meaningless patterns (Bertamini, Makin, and Pecchinenda 2013). Moreover, it could be argued that bifaces –with Acheulean handaxes dating up to 500,000 years ago– might be one of the first manifestations in the human lineage towards the preference for a lateral symmetry (Hodgson 2011).

Magnus Enquist and Anthony Arak suggested that the preference for symmetry could result from the need to recognise objects regardless of its position and orientation in the visual field. Thus, symmetry would be preferred for facilitating mental transformations needed in order to recognise specific objects. A later proposal by Rolf Reber (2002), while still relating preference and ease of cognition, switched the emphasis to perceptual fluency. Yet, on a different note, several authors coming from a more evolutionary perspective have proposed that sexual selection –in particular, the signalling of mate health as indicated by developmental stability– could be the explanation of the preference for symmetry (Møller and Thornhill 1998; Tovée, Tasker, and Benson 2000; Jones et al. 2001).

b) Colour preference: Among all the colours, blue is the most preferred by men and women (Winch 1909; McManus, Jones, and Cottrell 1981; Hurlbert and Ling 2007). However, when focusing on the red-green mechanism, it has been found that females show a greater preference for reddish hues than males (Bimler, Kirkland, and Jameson 2004; Hurlbert and Ling 2007).[9] Anya Hurlbert and Yazhu Ling suggested that this sex

[9] While this seems congruent with current trends of girls' preference for pink as pointed out by Greene and Gynther (1995), said preference has not been historically constant, so we would suggest caution while trying to extrapolate those findings to the understanding of sexual differences.

difference arose from sex-specific functional specializations in the evolutionary division of labour. With trichromacy and the red-green opponent channel being modern adaptations in primate evolution that facilitate the identification of edible ripe red fruits embedded in green foliage; female preference for red would be explained by the fact that they, as gatherers, would have required a higher degree of awareness of colour information than males did as hunters.

3. The preference for curvature

During the last century, different sources have been slowly providing a sparse but ever growing amount of evidence that seems to point to a generalised innate preference for curvature in human beings. As early as 1924, A.T. Poffenberger and B.E. Barrows reported a tendency to relate sharp angled lines with feelings of agitation and violence, while rounded angled lines were related with feelings of quietness; results that would later be replicated by Kate Hevner (1935). Consistently, Gerald Guthrie and Morton Wiener (1966) found that it was the sharpness of the lines used to close the angles in an image depicting a man, and not the presence of a gun, that made participants describe an image presented subliminally as portraying negative connotations. More recently, Moshe Bar and Maital Neta (2006) employed a like/dislike forced-choice task with everyday objects, letters, and meaningless patterns to find a significant preference for curvature as opposed to neutral and sharp contours. They would later hypothesise that said preference results from a primitive perception of sharp transitions in contour as conveying a sense of threat (Bar and Neta 2007). By using fMRI, they found higher levels of activation of the amygdala, a brain structure involved in fear processing, when participants looked at the sharp version of the stimuli, a result that seemed to support their original claim.

Unfortunately, this hypothesis is not exempt of problems. For starters, it predicts avoidance of sharp angles, rather than preference for rounded shapes. It is not clear that it would be advantageous to have such an avoidance mechanism, nor which kind of environmental pressure would make advantageous to possess the capacity to quickly detect and avoid sharp shapes. Furthermore, all the studies mentioned were carried out among Western educated individuals, which weakens its claims of universality. As a matter of fact, Claus-Christian Carbon (2010) has reported that appreciation for curvature changes dynamically over time, proposing adaptation effects as plausible candidates for triggering such changes. That is, preference for curvature would be mediated by fashion or trends, in what he calls a *Zeitgeist* effect. This proposal is sustained by his empirical research, in which, after presenting images of car exteriors spanning different decades to participants, he found that their preference for curvature in cars through time followed an U shape; being at its peak for models produced during the middle and the end of the 20th century, and at its lowest during the 1970s.

Furthermore, Helmut Leder, Pablo Tinio, and Moshe Bar (2011) while replicating Bar and Neta's findings about preference for curvature when using the same stimuli, found that it disappeared when employing stimuli of negative valence. That is, participants did still prefer the curved version when the object depicted had positive connotations; but there was no effect of shape when using negative stimuli, such as a bomb or a coffin. While the authors' interpretation of these results doesn't confront the adaptive hypothesis, simply stating that valence is prioritised over contour –so that once an object has been identified as negative, there is no need for the contour to be taken in account– it brings into question once more the kind of scenario that would have created such an environmental pressure for the avoidance of sharp non-negative contours to be adaptively relevant. In this case, it could be argued that, if the hypothesis were true, the sharp-avoidance system would have to be more ancient than the valence-evaluation one.

4. The approach-avoidance research programme

To address these issues, we propose a theoretical framework inspired by the embodiment thesis, especially as portrayed by Mark Johnson (2008), according to which cognition is action, and aesthetics a primary tool of meaning-making. For Johnson (2012), who follows John Dewey (1922), neither our experiences nor our judgments are neatly pre-categorised into different types: aesthetic, moral, political, scientific, or religious. Instead, we should see aesthetics or morals as a set of complex problem-solving systems that, by directing our interaction with the environment in a certain way, makes it meaningful. It is only *a posteriori*, when higher cognitive processes have mediated the experience, that we call a particular experience as aesthetic or moral.

Thus, if humans were to prefer curved contours because of sharpness being perceived as a threat, such behaviour could easily be modelled as a basic drive under an approach-avoidance framework. It could also be a clear case of meaning making as described by Johnson, as this avoidance of sharpness would be a way in which

> our bodies are inhabiting, and interacting meaningfully with, the environment beneath the level of conscious awareness [...], forming the basis for both the meaning of our movements and, at the same time, the meaning of the world that we move within. (Johnson 2008, 24)

Hence, the meaning of curvature and sharpness, of roundness and angularity, would arise from this original avoidance of a threat making contour fit the definition of aesthetic primitive as proposed by Richard Latto (1995, 68): "a property of a stimulus that is intrinsically interesting, even in the absence of narrative meaning."

In other words, it is our contention that verbal reporting is not the best way to assess perceptual preferences, which have to show up as a kind of sensory-motor loop. Therefore, we propose an experimental approach-avoidance paradigm, as one markedly suited for this task due to its naturalistic nature and its emphasis on primal interactions between an organism and its environment. This approach brings experimental aesthetics closer to the most basic and elemental behaviours, while averting, as much as possible, complicated cognitive interpretations from both participants and researchers.

It is common for investigators in the fields of experimental aesthetics and neuroaesthetics to ask questions regarding liking, wanting, preference or appreciation in a given task. Sometimes, participants require conceptual clarifications about these terms, which adds an extra layer of alienation from the original task. Committing ourselves to the immediacy of the approach-avoidance paradigm and the idea that aesthetic traits arise from specific problem-solving situations in which human beings are driven to a pattern of action, we believe that the experimental design must follow these principles of specificity and conceptual simplicity.

In addition, as Andrew Elliot and Martin Covington (2001) put it, the distinction between approach and avoidance motivations is basic for the understanding of human behaviour. They justify this position with the following five arguments, which we have also adopted as the basis of our framework.

1) This distinction has a long and rich history in intellectual thought. We can find it being used in psychology, in different forms, since its beginnings as a scientific discipline: pursuit of pleasure or avoidance of pain; movements of interest towards or away from social objects; orienting response towards the stimulus or a defensive response away from the stimulus; reference to the end towards or away from which the organism is moving; positive valences that attract and negative ones that repel; conditioned appetitive and aversive drives; and deficit needs to reduce a negative state of tension and growth needs to increase positive stimulation. That is, it is present in each of the major theoretical traditions in psychology: functionalism, psychoanalysis, reflexology, behaviourism, humanism, cognitivism, and psychobiology.

2) It can be applied to different forms of animated life: the distinction in behaviour and motivation can be found even in the lowest organisms of the phylogenetic scale. Theodore Schneirla (1965) stated that all organisms possess mechanisms that evoke approach reactions to facilitate food, shelter and mating, and mechanisms that evoke withdrawal reactions to facilitate defence, flight and protection in general. The sophistication of these mechanisms varies considerably across species: from rudimentary and rigid to advanced and flexible. These behavioural adjustments suppose a clearly significant adaptation to the environment. Moreover, John Tooby and Leda Cosmides (1990) argue that the behaviour of approach or withdrawal has been the fundamental adaptive decision that organisms have had to make throughout their evolutionary history; so that its survival value has driven organisms towards potentially beneficial stimuli and away from potentially harmful ones. As Elliot and Covington (2001), paraphrasing Schneirla (1965), say

3)

> the high road of evolution has been littered with the remains of species that have failed to acquire one or more mechanisms for accurately determining the beneficial or harmful potential of environmental stimuli. (77)

Therefore, the approach-withdraw behaviour presents itself as a paradigm well suited to reproduce the most natural human reactions throughout evolutionary and embodied experiments. Moreover, it allows us to run the same task among different cultures and species with minimal instructions and maximal reproducibility.

4) The most basic mechanisms of approach and avoidance are fast and automatic. These attributes are also characteristic in unconditioned reflexes and likely have a special significance in the process of survival. The approach-avoidance mechanisms could be a small sophistication of these reflexes, allowing other mechanisms of the same organism to interact with them or even interrupt them. That is, they would be the first step to elude the rigidity of these reflexes and grant the organism more behavioural flexibility. Flexibility that some organisms would develop throughout their evolutive process. The ultimate expression of this flexibility would be the complex human cognition. However, as Johnson (2008) proposes and the general embodied approach argues, this complex cognition would have been built upon simpler sensorimotor mechanisms. In accordance with this argument, it would be appropriate to analyse the more sophisticated cognitive mechanisms based on these simpler sensorimotor behaviours such as the approach-avoidance one.

5) There is evidence of the existence of separate approach and avoidance systems in the brain. This evidence comes from research in subcortical (Cacioppo, Gardner, and Berntson 1999) along with cortical systems (Davidson 1995). This neurological division underlines and underlies the relevance of the two elemental behaviours in the cognitive system.

6) The distinction between approach and avoidance behaviour is highly intuitive. Using this framework in the experimental field, it is easy to design a scenario in which the participant has to decide between a response that will simulate approaching to the stimulus and another that will simulate withdrawing from it; thus, not requiring the understanding of complex cognitive concepts.

In summary, our approach-avoidance paradigm offers an original and well-motivated way to study perceptual preferences, in a way that makes possible comparative and cross-cultural research.

5. A cross-cultural study

With these procedural assumptions in mind, and seeking to test the universality of the phenomenon of preference for curvature, we designed an experimental procedure based on the approach-avoidance paradigm, so it could be applied in different cultures and species. In order to reduce instructions to the minimum possible, we devised a two- alternative forced choice (2AFC), so the participant –be it human or not– didn't have to evaluate, but to simply select one between two options. For this, we prepared pairs of stimuli, selected among those previously employed by Bar and Neta (2006), trying to include objects that wouldn't be too strange to non-western cultures (see Figure 1 as an example). These target pairs consisted of two images depicting the very same objects (baskets, buckets, cones, etc.), one of them of curved contour and the other of sharp one.


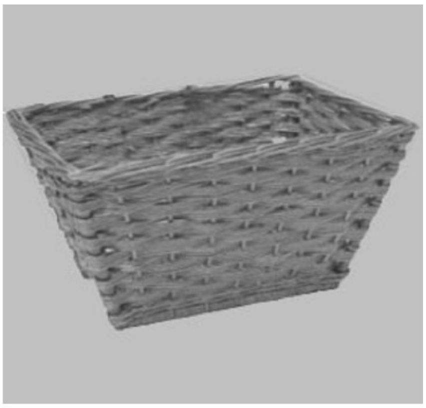

Figure 1. Pair of target stimuli employed in our research. These images of everyday real objects were first employed by Bar and Neta (2006).

This set was complemented with another one consisting of 36 pairs of distractor stimuli: objects matching in their overall contour, but conveying different semantic meanings. Furthermore, in order to avoid possible bias due to lateralization, two blocks consisting of the same pairs of images each were constructed: so in one of them half of the images would appear on one side of the screen, while in the other block they would be shown on the opposite side. The order of both blocks was randomised, as it was the order of the set of trials that conformed each of them.

So we could make the task fully comparable to the one that other primates would perform, human participants were given very simple instructions: they were informed that they would be shown pairs of images on screen, their task consisting in choosing one of them by using the keyboard arrows, so the selected image would be shown once again enlarged. In this way we tried to replicate the effect of choosing to approach the object. As stated, this design allowed us to replicate an almost similar experiment with apes; the main difference being they used a touch screen to select the images, and being randomly rewarded 50% of the trials, whatever their response, so that they would stay interested.

So far, we have run this experimental design with two human samples: one consisting of students from the University of the Balearic Islands, and the other comprising participants from Ghana. While the students carried out the task in an isolated laboratory, the Ghanaians did it in an enclosed space free from distracting stimuli. In both groups, curved objects were chosen with a higher proportion, in a manner that was significant among Spaniards, but only a strong trend among Ghanaians. However, when the results for the first and the second blocks were treated independently, we found that Ghanaians did indeed share the preference for curved contours in a very significant manner. Our experimenter in Ghana reported that the participants paid less attention during the latter part of the test, something that was confirmed by a high increase in the reaction time when the second block of stimuli was presented; a loss of attention that could be attributed to the lack of familiarity with this kind of tasks for the participants, among other cultural and environmental differences.

All in all, these preliminary results point out a universal effect that demands further research in different populations. Exploratory analysis of the data obtained in a recent work with chimpanzees and gorillas, together with our latest results from Mexico seem to support this idea, showing a strongly significant trend of preference for curvature across different human cultures and different primate species. While our work is still in progress, we feel confident to suggest that perceptual preferences, such as that of curvature can be seen as elements of phylogenetic continuity in the appearance of our aesthetic capacity, constituting the roots of aesthetics.

6. Conclusion

In this chapter, we have sought to present an experimental approach directed to untangle the roots of aesthetics that takes in account the embodied dimension of human cognition, and allows research into its evolutionary origin, given that it is well suited for cross-cultural and comparative research. We believe that aesthetics should be considered as a trait that emerged as a distinctive set of answers to specific environmental requirements; answers that cannot be understood without relating them to the stimuli and environments that favoured their appearance. As Johnson claims, aesthetics must not be narrowly construed as the study of the art, but the study of the human capacity to make and experience meaning, and basic preferences constitute its starting point. Thus, in accordance with Dewey's principle of continuity, our so-called higher cognitive faculties recruit cognitive resources that operate in our sensorimotor experience and our monitoring of emotions, at the same level that the most basic aesthetic processes are working, so that preconscious meaning underlies our higher- level faculties of thought and communication.

We have shown an example of how a research programme like this can be implemented. However, it could be argued that such a model should be improved in order to achieve a higher degree of ecological validity. This could be accomplished through the use of other kinds of stimuli that would better replicate a scenario of approach-avoidance, such as three-dimensional objects in movement, scenarios with a relevant context, simulations of the distance to the object, or the use of real objects. Similarly, other means of response input such as the use of a joystick, virtual reality, or simply allowing the participants to move freely, might also improve on ecological validity.

Such an increase in the ecological aspects of the task should result in an augment of the examined effect. Thus, by employing effect size statistics together with other well-suited procedures, we could test one of the principal premises of the embodied approach: that the particular effect is stronger in the actual situation that gave rise to its emergence and it is weakened in other situations, according to the influence magnitude of other factors. In this way, it would be possible to test a hypothesis about the evolutionary origin of a particular effect, while identifying the kind of situation in which it might trigger cognitive and behavioural responses.

Our proposal can be applied to the basic perceptual preferences as answers to specific environmental requirements that probably gave rise to what we have ended up calling aesthetics. We have started to apply it to the visual preference for rounded shapes against sharp-angled ones. We got results that indicate that this preference could be universal, and some data that the primates could also show this preference. After establishing the universality and ancient origin of the preference for curvature, we want to explore the different hypotheses that have been proposed to explain said preference. According to what we have discussed so far, this could be achieved by modifying the contextual cues of the test in an ecologically relevant manner. One way of doing this would be priming participants with threatening stimuli, before presenting them with a pair of images only varying in contour. We would expect them to seek the source of the menace, and therefore, if the threat hypothesis is correct, their pupils should first fixate on the sharp stimulus. In this manner, variations in the stimuli used and the cultures and species tested would help us shed light on the evolutionary origin of the preference.

A different line of research dealing with this basic visual preference would lead us to test whether it might be related to similar effects in other sensory systems, such as hearing and touch. While the preference for curvature has been usually addressed from a visual perspective, Martina Jakesch and Claus-Christian Carbon (2011) documented a clear preference for curved objects in the domain of haptics. It could be that these visual and haptic preferences have a common origin, maybe one being a consequence of the other; a matter that should be solved empirically. On the other hand and following Dewey's principle of continuity, it will also be interesting to study if these preferences could be recruited for higher cognitive consequences, as some instances in language could show: 'well rounded', 'sharp practice', 'come round', 'a short sharp shock', 'the sharp end', and sharp as quite not honest.

Finally, we would like to believe that, beyond its theoretical relevance, this program could lead to results in applied research. Finding the conditions in which this preference works and the factors that interact with it would be of great value for art, advertising and other applied fields. Good examples of this are the research of Westerman et al. (2012) in marketing and of Vartanian et al. (2013) in architecture; in both studies a preference for curvature was found. These studies show how an applied approach can be relevant to professionals and cognitive researchers alike.

In this way, and despite some limitations of our approach, we contend that it offers a promising way to understand the roots of aesthetics, and to uncover the elements of continuity and novelty that make aesthetics one of the most salient human apomorphies.

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Preference for curvature:
A historical and conceptual framework

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Preference for Curvature: A Historical and Conceptual Framework

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That people find curved contours and lines more pleasurable than straight ones is a recurrent observation in the aesthetic literature. Although such observation has been tested sporadically throughout the history of scientific psychology, only during the last decade has it been the object of systematic research. Recent studies lend support to the idea that human preference for curved contours is biologically determined. However, it has also been argued that this preference is a cultural phenomenon. In this article, we review the available evidence, together with different attempts to explain the nature of preference for curvature: sensoriomotor-based and valuation-based approaches. We also argue that the lack of a unifying framework and clearly defined concepts might be undermining our efforts towards a better understanding of the nature of preference for curvature. Finally, we point to a series of unresolved matters as the starting point to further develop a consistent research program.

Keywords: preference, curvature, angularity, empirical aesthetics, evolutionary aesthetics

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INTRODUCTION

Curved lines and forms occupy a special place in the Western traditions of philosophical, psychological, and evolutionary thought on aesthetics (e.g., Hogarth, 1753; Spencer, 1873; Allen, 1877; Santayana, 1896; Valentine, 1913). They have often been regarded as more harmonious, relaxing, or pleasant—and more in consonance with nature—than straight or broken lines. Only after the development of Fechner's (1876) empirical aesthetics, however, were such conjectures about curvature subjected to experimental scrutiny. Stratton's (1902) attempt to relate the pleasure derived from the observation of curved lines to the concurrent movements of the extraocular muscles constitutes one of the earliest empirical tests of the contribution of curvature to aesthetic experience. Like Spencer (1873) and Santayana (1896) before him, Stratton (1902) conjectured that eye movements required to follow sharp, broken lines must be more abrupt and, therefore, less pleasant than those required to follow curved lines. Using an early eye-tracking device, Stratton (1902) recorded the gaze patterns of two participants while viewing different kinds of curved stimuli and test this hypothesis.

The jerky and discontinuous nature of saccades, even when participants attempted to follow smooth curved lines, proved his original expectation wrong. Nevertheless, Stratton's (1902) study greatly influenced subsequent research on the aesthetic qualities of curvature (Valentine, 1913). In fact, his seminal work included reflections on the two issues that have been the central focus of research and discussion during the 20th and 21st centuries: (i) the mechanism underlying preference for curvature and (ii) the functional significance of such preference. On the one hand, he believed that curved lines provide observers with a continuous flow of information that is easy to process.

On the other hand, he noticed that experience, environment, and cultural cues might influence the appraisal of those lines. He pointed out that most movements in nature are curved, which makes us perceive the curved line as an indication of a functional, normal behavior. But it is not only in curved lines that we find meaning: while curved lines might be more appealing due to their complete and perfect nature, broken lines, though imperfect, convey a stronger sense of power.

Although research on preference for curvature was conducted only sporadically during most of the 20th century, interest in the cognitive and neural mechanisms underpinning preference for curvature, as well as in its psychological and biological functions, resurged in the last decade (e.g., Bar and Neta, 2006, 2007; Leder et al., 2011; Vartanian et al., 2013; Bertamini et al., 2015). Nevertheless, the mere accumulation of behavioral and neuroimaging data does not ensure the progress of scientific research. Explaining the cognitive and biological mechanisms underlying preference for curvature requires, just like in other domains of the cognitive sciences (Block, 2014)—and science in general–, substantive theories resting on clear concepts.

In this article, we develop a framework for research on the psychological and neural mechanisms involved in preference for curvature. We follow the history of this research and the conceptual unfolding of the two main issues raised in Stratton's (1902) discussion. First, regarding the mechanisms underlying humans' preference for curvature, we distinguish approaches that base their explanation on features of the sensorimotor systems from those that base it on appraisal processes. Second, regarding the origin of this preference, we distinguish approaches positing an evolutionary foundation from those postulating it is the result of learning processes.

PREFERENCE FOR CURVATURE: COGNITIVE AND NEURAL MECHANISMS

Sensorimotor-Based Explanations

A number of researchers have argued that human preference for curvature derives from the way in which physical properties of curved stimuli directly interact with specific characteristics of the sensorimotor system. Thus, from this perspective, preference for curved features owes to a sort of natural coupling between perceptual features and sensorimotor processes that are attuned to curved configurations. This general framework has been developed in three directions, differing in their central explanatory mechanism: movement, specific neural activity, and fluency/Gestalt principles.

Movement

Stratton's aforementioned studies attempted to explain the perceived beauty of curved stimuli as a consequence of sensorimotor activity, namely eye movements. This approach was inspired by Spencer's (1873) idea that the grace of curved lines is enjoyable because it gives a sense of economy in the expenditure of force, and by Wundt's notion that the pleasure provided by curves resulted from the ease of the eyes' motion as they glided over the curve. However, as noted above, Stratton's results did not support these conjectures. Whereas the line offered to the eyes for following was continuous and smooth, the gaze path itself was irregular, varying, and even sharp angled. Even when the eyes follow a curve, their movements are characterized by jerks and pauses, short rapid flights followed by sudden interruptions. Stratton finally concluded that it would be an error to regard the enjoyment of graceful forms as resulting from this muscular adjustment, and considered other alternatives beyond the simple sensuous impression, whether muscular or retinal.

A different possibility is that preference for curvature is not related to the movements of the eyes, but to the ease and comfort of certain movements when drawing, or simply moving our arms or hands. As stated by Hogarth (1753, p. 38) in his classical *Analysis of Beauty*: "It is to be observed [...] that the waving line, or line of beauty, varying still more, being composed of two curves contrasted, becomes still more ornamental and pleasing, insomuch that the hand takes a lively movement in making it with pen or pencil." There seems to be, however, little or no empirical research addressing the relation between preference for lines and the ease of movements required to produce them. For instance, although Martin (1906) considered Hogarth's observation as an alternative hypothesis to Stratton's initial conjecture, she did not fully explore those thoughts empirically.

Neural Activity

Preference for curvature has also been explained in terms of the neurophysiology of the visual system. Fantz and Miranda (1975), for instance, showed that 1-week-old neonates fixate longer on curved contour geometric forms than on sharp contour ones. They explained this very early preference for curvature based on Hubel and Wiesel's (1968) identification of a set of cortical cells whose activity is sensitive to deviations from continuous straight contours, such as curves and angles. Fantz and Miranda (1975) suggested that the differential fixation on curved and straight geometric forms might be related to these cells' responsiveness to shifts in line direction, with curved visual patterns inducing greater activity in these cells than straight patterns. Although it is not clear how this differential activity might translate into differences in looking time, the neural coding hypothesis has recently gained traction after it has been shown that preference for curvature is still found when participants are presented with stimuli consisting of the low spatial frequencies of images depicting real objects—but not when those stimuli contain only the high spatial frequencies of the original images (Bar and Neta, 2007). This is consistent with Vuilleumier et al.'s (2003) finding that high and low spatial frequency information in visual images is processed by distinct neural channels. They showed dissociable roles of these channels for processing emotional expressions. Low-frequency faces with fearful expressions elicit greater responses in specified subcortical pathways (amygdala, pulvinar and superior colliculus) than the same high-frequency faces.

Fluency and the Gestalt Principles

Quinn et al. (1997) showed that Gestalt organizational effects and preference for curvature are both involved in the initial parsing and subsequent organization of complex visual patterns. Using a familiarization-novelty preference procedure, the authors found that 3- and 4-month-old infants were able to segregate the contours of two intersecting visual forms, and that they did so relying on the Gestalt principle of good continuation. Moreover, they argued that spontaneous preference for curvature facilitated the Gestalt organization of complex configurations into coherent forms.

This explanation is related to the processing fluency theory of aesthetic pleasure (Reber et al., 2004): fluent processing of an object leads to positive aesthetic responses. From this perspective, preference for curved stimuli is greater than preference for non-curved stimuli because curvature facilitates processing fluency. Indeed, there are several studies that have reported that curvilinear features are easier to detect (Treisman and Gelade, 1980; Wolfe et al., 1992; Álvarez et al., 2002). However, Bar and Neta (2006, 2007) found no differences in the time it took participants to rate curved and sharp stimuli, even when curved ones were preferred. This led them to conclude that curved features did not facilitate the processing of the stimuli and therefore, the explanation for preference should lie elsewhere.

Nonetheless, the time participants take to respond in a preference task need not correspond to the speed of processing curves or sharp angles. Ruta et al. (2014) found that participants are faster in detecting intrinsic features of curved polygons compared to their angular version, which seems to indicate that efficient visual processing is affected by the presence of curved features in the contour. They also explored the relation between the global/local configuration of the stimulus and preference for curvature, finding that preference remained even with the local elements being orthogonal to the continuity of the global contour. This led them to conclude that preference for curvature is likely caused by intrinsic characteristics of the lines, which can be described as cases of good continuation or good Gestalt.

Appraisal-Based Explanations

A good amount of research on preference for curvature has focused on appraisal processes, whether implicit or explicit, and the way in which they impact aesthetic experience. In contrast to the different sensorimotor-based approaches noted above, appraisal approaches show strong consistency and thematic uniformity, motivated by early findings about the emotional evaluation of straight and curved lines. Even when these studies report slight differences in the qualities and connotations ascribed to angular features, they tend to agree that curvature is imbued with non-representational semantic meaning.

In Lundholm's (1921) early study, eight participants received a series of words describing different kinds of feelings and were asked to draw lines matching those words. Results showed that sharp lines were considered to be *agitating, hard*, or *furious*, whereas curved ones were perceived as *gentle* and *quiet*—but also *sad* or *lazy*. Extending this research line, Poffenberger and Barrows (1924) asked 500 adult participants to perform the inverse task: to match those lines drawn by Lundholm's participants to a given list of feelings. Their results confirmed Lundholm's (1921) earlier findings, as did Hevner's (1935), who used a more complex set of stimuli that included not only lines, but also abstract shapes.

Although this exploration of the links between feelings and different degrees of angularity was both relevant and promising, empirical interest in curvature seemed to fade somewhat in the following decades. Later work, including Guthrie and Wiener's (1966) and Kastl and Child's (1968) research, moved beyond the study of the effects of isolated lines, and analyzed the impact of the curvature of objects' contours.

Guthrie and Wiener (1966) sought to prove that the response to subliminal stimuli was not determined by observers' full discrimination and comprehension of the presented stimuli. They believed, rather, that observers relied mainly on primitive cues that elicited a predicable response. Their initial results showed that participants' responses varied when presented with lines differing in their angularity and thickness, with curved lines being linked to positive traits, and sharp ones to negative traits. In order to further explore the possibility that the feelings ascribed to isolated lines were responsible for differing reactions to more complex subliminal stimuli, they prepared two very similar drawings of a sitting man. In one of them, the man was pointing a gun to his head; in the other he was not. After making sure that participants were able to discriminate the valence of the image when presented subliminally, Guthrie and Wiener (1966) created two different versions of each image: one in which the overall contour was sharp, and another in which it was smooth. This allowed them to prove that, as predicted, it was the overall sharpness, and not the presence of a gun, that determined whether the image was perceived as threatening and negative.

Kastl and Child's (1968) study of the emotional meaning of different typographies lent additional support to the notion that the distinct feelings conveyed by isolated lines remains relevant when the stimuli presented consists of more complex shapes and contours. Still, it should be noted that some of their findings, such as angular types appearing to be *sadder*, contradict those of Lundholm's (1921) work.

Research on the effects of curvature on preference was reinvigorated by Bar and Neta's (2006) study, designed to test the hypothesis that curved stimuli are preferred because sharp contours evoke a sense of threat. They first presented a sample of 14 participants with images depicting abstract shapes and everyday objects varying in the curvature of their contour. Each image was shown for only 84 ms, and participants were asked to make a like/dislike choice. Their results revealed that curved stimuli were liked more than neutral or sharp ones (Bar and Neta, 2006). In a subsequent neuroimaging study, they again found higher liking for stimuli with curved contours, and that sharp contours were subjectively perceived as more threatening. Moreover, they observed a bilateral increase in amygdala activity when participants were presented with sharp stimuli, as was expected if such stimuli did elicit a sense of threat (Bar and Neta, 2007).

Leder et al. (2011) further explored this interaction between preference for curvature and threat perception.

They hypothesized that if the perception of threat produced by an object was related to preference, then the negative valence of an object could override other positive cues such as the curvature of its contour. In order to test this assumption, and after replicating the findings of preference using the same stimuli as Bar and Neta (2006), they presented participants with new stimuli depicting images of real objects that had been manipulated to create a round and a sharp contoured version of each of the 20 selected objects. These objects were selected according to their emotional valence, so that they could be evenly split into two groups depending on whether their valence was positive or negative. As predicted, they again found that curved stimuli were preferred to sharp ones, but only when the objects had a positive or neutral valence. They argued that this shows how threat and preference are interconnected, and that semantic evaluation takes precedence over the evaluation of contour, overriding the effects that curvature might have in preference.

In contrast to these studies, there is growing evidence questioning the notion that curvature is preferred because sharp angles are perceived as threatening. Bertamini et al. (2015), asked 36 participants to perform a manikin task in which they had to bring a stick figure closer or farther, as instructed, from a series of irregular polygons varying in their curvature. The study showed that participants moved the manikin faster when presented with sharp stimuli, independently of whether they were instructed to bring it closer or farther. But when presented with curved stimuli, participants reacted faster only when the task was to bring it closer to the polygons. This is the opposite behavior that would be expected if sharp angles were perceived as threatening. Thus, Bertamini et al. (2015) concluded that preference owes to the intrinsic characteristics of curvature, be it configurational or featural, and not to a rejection of sharp contours.

In the same line, Vartanian et al.'s (2013) fMRI study, in which participants were presented with images of interior architectural spaces, found no increase in amygdala activity when viewing photographs of rooms with sharp angled contours, and that curved spaces were subjectively preferred overall. The authors suggested that this finding could be explained by sharp cues in buildings having lost their threatening nature by learning and exposure. This raises the fundamental point of how much preference for curvature, if any, might be culturally determined.

PREFERENCE FOR CURVATURE: ORIGINS

A Learnt Preference

By being more familiarized with a certain kind of feature, or by having specific expectations regarding the shape of a given object, we can process it easier and faster, which in turn will cause that feature or shape to be preferred to others (Bornstein and D'Agostino, 1994). Familiarity and mere exposure are indeed the factors that Leder and Carbon (2005) used to explain the results from their research on car design. In their study, participants were presented with drawings of car interiors varying in a series of dimensions, such as innovation, complexity, or form. Whereas curved interiors were preferred to straight ones, the authors argued that, in this particular field of design, straight lines were innovative; and therefore, the mere exposure effect could be held accountable for effects of preference for curvature. Carbon (2010) sought to further explore this possibility by showing participants images of automobiles representing different epochs and styles in car design. His results showed that curved car exteriors were only preferred when the design itself belonged to a decade in which the trend was to build a more rounded chassis. This, he claimed, showed that preference for curvature was not static and uniform, but it was under the influence of the aesthetic *Zeitgeist* of a given time.

The unclear—but significant—link between expertise and liking of curved shapes reported by Silvia and Barona (2009) may be considered further proof of preference for curvature being mediated by cultural learning and experience. When participants with different artistic expertise were shown a series of stimuli that consisted of a differing number of hexagons and circles, only non-expert ones found circles to be more pleasant, with experts preferring even slightly more the stimuli depicting hexagons. In a second experiment, in which abstract shapes, varying in curvature, replaced hexagons and circles, Silvia and Barona (2009) found that only experts preferred curved stimuli to the angular ones. This latter result seems consistent with the data from Leder and Carbon (2005), who also found a higher preference for curvature among those participants characterized as experts in the arts—although, in that case, the difference was explained as an interaction between innovation and curvature, with expert participants being more conservative than non-experts.

All in all, these findings are a reminder that the influence of cultural factors in preference for curvature should not be overlooked. Whereas most published studies have had a tendency to tacitly assume that the observed results are indication of a universal phenomenon, the general lack of cross-cultural data begs for a cautious attitude towards such assumptions.

An Evolved Preference

A nativist explanation of preference for curvature should be fairly easy to defend from a sensorimotor point of view, as derived from biological constitution. Still, it has been precisely among the leading studies concerned with appraisal that a possible evolutionary origin has been more openly and widely discussed. The reason for this is twofold: on one hand, as previously shown, most research on curvature has focused on the different emotional connotations conveyed by round and sharp lines and contours. The strong and pervasive link between sharpness and negative, threatening, or agitated feelings has led researchers to regard this association as an adaptation. On the other hand, most of the sensorimotor approaches have avoided discussing the evolutionary origins of how we perceive curvature.

Allen (1877) argued for a biological origin of the appreciation of curved lines, and many other aesthetic features, before the publication of any of the experiments noted in the preceding sections. He did so, nonetheless, only in general terms. Specific arguments for the adaptive value of the affective responses to sharp and curved contours were not put forth until the late 20th century, after the restoration of evolutionary thinking in sociology, anthropology, and psychology. In this line, Uher (1991) explicitly linked the widespread use of zigzag motifs among different cultures of the world to ancient environmental pressures. She found this pattern to be usually present in aggressive and defensive contexts, often accompanied by the symbolic representation of eye motifs, which have been found to produce an aversive reaction due to their threatening nature (Coss, 1972; Ellsworth et al., 1972). To explore this possibility, she presented 1100 participants from Central Europe with different sets of wavy and zigzag lines, some of these accompanied by eye motifs. She then asked participants to classify the stimuli according to 24 pairs of opposed adjectives. Consistent with her hypothesis and previous findings, Uher (1991) found that zigzag lines were reliably and significantly associated with antagonistic adjectives, whereas wavy lines were associated with affiliative ones. She found this evidence to be in favor of the influence of our biological heritage in the use of zigzag motifs; an influence that, nonetheless, was susceptible to cultural modulation. These considerations would later provide the backbone for Aiken's (1998) argument that preference for curvature was actually motivated by a fear induced by sharp lines. This fear, she argued, had served an adaptive function in our distant past: to help us rapidly detect and avoid possible threats to our survival. Aiken (1998) believed this to be a canonical example of how primitive emotions, which originated initially as a fitness-increasing response to environmental pressures, have been repurposed, owing to their interaction with higher cognition, giving rise to the aesthetic experience of art.

But it was Bar and Neta (2007) who first tested the possible link between preference for curvature and the threatening nature of sharp lines. By taking in account subjective perceptions of preference and threat, as well as relative levels of amygdala activity, they found empirical support for the hypothesis that preference for curvature results from a primitive association between sharp transitions in contour and a sense of threat. Bar and Neta (2008), however, later interpreted their findings from a non-nativist point of view, as the result of developmental learning. Given the lack of cross-cultural data, and of a clearly defined evolutionary scenario in which environmental pressure would be sufficient to warrant such an adaptation, this is an equally plausible scenario.

Nevertheless, while these limitations invite us to be cautious, there are scattered data that support the idea of an evolutionary origin of preference for curvature, whether understood from a sensorimotor or an appraisal perspective. In particular, it has been found that not only children (Jadva et al., 2010), but even 1 week-old infants (Fantz and Miranda, 1975), have a tendency to look longer at curved stimuli than sharp ones. Furthermore, recent research has found that preference for curvature is also present in non-Western cultures, such as rural Ghana (Gómez-Puerto et al., 2013), and even among non-human primates (Munar et al., 2015).

Additionally, the idea that sharp angles are perceived as threatening due to evolutionary constraints has antecedents also in face research. Larson et al. (2007) showed that minimal geometric figures, resembling facial configurations of expressed anger and happiness, influence attentional processes and the attributed semantic meaning. Specifically, people associate angular V-shaped geometric figures—straight lines converging in an angle—to anger, and rounded shapes and figures to happiness (Aronoff et al., 1992; Aronoff, 2006). The authors posit that such configurations might be processed by Ekman's (2003) "auto-appraisers", a hypothesized set of feature detectors—innate appraisal mechanisms—that enable observers to quickly decode facial emotional expressions (Larson et al., 2007). Hence, the human preference for curvature might owe to a deep-rooted association between angular and curved geometric configurations and threatening and pleasant facial expressions, respectively. This, however, is not the only possible link between preference for curvature and facial features. Neotenic features—juvenile physical traits still present in adults—tend to result in salient curved configurations, such as a rounded head or large rounded eyes, and seem to have been favored by sexual selection. Neoteny and attraction toward neotenic traits, therefore, constitute plausible evolutionary foundations for preference for curvature (Bertamini et al., 2015).

In a different direction, LoBue (2014) has proposed that the widely studied Snake Detection Hypothesis—the idea that humans visually detect snakes faster than other stimuli—might be explained by the curvilinear body characteristic of those animals. By deconstructing snakes' anatomy into its very basic curved features, she was able to compare the detection time of these features to that of its rectilinear equivalents, showing that the faster detection times reported when employing photographs of real snakes remain even when participants are presented with its most basic, curvilinear features.

All in all, there is a certain amount of evidence supporting a possible evolutionary origin of preference for curvature, and several unexplored hypotheses that could explain it. Humans might avoid sharp contours because they are related to threats in nature, or because we are hardwired to detect threatening facial expressions. But we might also be faster and better at processing curved stimuli, and prefer them because of this very same reason. Solid answers will only be provided by developing these proposals into testable hypotheses, and gathering data from different cultures and species.

FURTHER RESEARCH

There is enough evidence to consider preference for curvature as a well-established phenomenon and yet, after more than a century of research, we are still far from a good explanation. This is due to a lack of a strong, unifying framework and a common perspective, but also to the fact that several fundamental and pressing issues have still to be appropriately addressed.

First of all, there is a matter of conceptual and terminological clarity. As can be seen in **Table 1**, whereas there is an overall consensus in the use of terms in the domain of *curvature* (i.e., *curves*, *curved lines*, *curvy*), the nomenclature usually employed is far from univocal, specially when addressing the lack of curvature itself: is it angularity? Sharpness? Straightness? Broken, zigzag lines? Is it all the same? This question is far from trivial. We have mentioned how a widespread hypothesis postulates that preference for curvature is a result of the threatening appearance of sharp-angled contours, due to developmental or evolutionary

TABLE 1 | Terminology used throughout relevant literature on curvature.

Term	Opposed to	Reference
Curved, curves	Straight	Hogarth (1753), Stratton (1902), Lundholm (1921), Poffenberger and Barrows (1924), Hevner (1935), Fantz and Miranda (1975), Quinn et al. (1997) and Leder and Carbon (2005)
	Straight, waving, ellipses, circles	Martin (1906)
	Angular	Allen (1877), Guthrie and Wiener (1966), Kastl and Child (1968), Carbon (2010) and Bertamini et al. (2015)
	Pointed/sharp, zigzag	Aiken (1998)
	Sharp, sharp-angled	Allen (1877), Bar and Neta (2006), Jakesch and Carbon (2011), Leder et al. (2011) and Gómez-Puerto et al. (2013)
Round	Sharp	Larson et al. (2007), Hess et al. (2013) and Gómez-Puerto et al. (2013)
	Angular	Silvia and Barona (2009), Jadva et al. (2010) and Westerman et al. (2012)
Wavy, waving	Straight	Hogarth (1753)
	Straight, curved, ellipses, circles	Martin (1906)
	Zigzag	Uher (1991)
Curvilinear	Rectilinear	Vartanian et al. (2013) and LoBue (2014)
Serpentine	Straight	Hogarth (1753)

While some authors make use of several terms as synonyms, we have only included those that appear in a consistent manner in a given work.

reasons. An illustration of what researchers have in mind when making such claims can be found when Carbon (2010) presents the images of shark teeth, the outline of a shark, and a rose thorn as paradigmatical examples of sharp transitions in nature signaling threat. In these three instances, it could be argued that the stimuli, while pointy, are curved in contour, not sharp-angled. As a matter of fact, it might not be easy to find examples of strictly sharp-angled contours present in the organic environment of primates. Defining central concepts in a clear and univocal manner should be the first step to build compelling and testable explanations of preference for curvature.

But in order to achieve this, we might need to delve into the psychophysics of curvature. When is an angle perceived as sharp? What is deemed to be curved? Do different features of the stimuli (size, extension, complexity, dimensions) affect the perceived curvature? Actually, it is not even clear whether the phenomenon we are dealing with consists of a preference for curvature or an avoidance or rejection of sharpness. There is enough evidence supporting both hypotheses, and future research should attempt to clarify this apparent contradiction.

Furthermore, it has usually been assumed that preference for curvature is a fundamentally visual phenomenon. And yet, it is no surprise that the same preference has been found in the haptic domain, employing three-dimensional, physical objects (Jakesch and Carbon, 2011). As we have seen, in the early days of the study of the perception of curvature, isolated lines were the main objects of study. It was in the second half of the 20th century that abstract and geometrical forms, and the contour of real objects, began to be studied. Still, there is a need of further evidence proving that preference for curved contours is the same phenomenon as preference for isolated curved lines. Researchers considering this possibility should also address the fact that most research has usually involved bi-dimensional objects, and should consider why we expect the principal domain of such preference to be visual.

So far, most research has implicitly assumed the universality of the phenomenon, with only a few papers daring to suggest an evolutionary explanation in a couple of sentences. The most serious approach was Carbon's (2010) attempt to prove the influence of culture in preference for curvature, which, in isolation, is incomplete. In this regard, research on curvature could benefit from following a theoretical development akin to that of the Snake Detection Hypothesis, a somewhat similar phenomenon that, as we have discussed, might even be related. A number of studies have shown over and over that humans of different ages are especially fast when detecting snake and snake-like stimuli. The use of standardized tests, together with strong and consistent findings, has led this theory to be widely accepted. But, as is still the case in research for curvature, the universality and evolutionary origin of snake detection was mostly taken for granted without further proof. It was not until recently that Isbell (2006) wrote a compelling case for its evolutionary implications, proposing up to 36 testable predictions derived from her hypothesis. These range from comparing speed differences in snake detection to the possibility of establishing datable paleotropical relationships through the study of retroviruses. Turning the hypothesis into a testable theory allowed for an enriching and strong debate that has benefited from the expertise of primatologists, evolutionary anthropologists, and other professionals with different interests other than the psychological aspects of the theory. We believe that further theoretical developments in preference for curvature should follow this example by expanding its current tentative explanations into full testable predictions, or by proposing new ones altogether. On a more basic level, delineating the evolutionary history of human preference for curvature requires gathering further relevant data from non-Western cultures, and other primates and mammals.

All these considerations form the foundations of a unified framework that aims to advance the understanding of preference for curvature. Future studies and theoretical work will undoubtedly shape it further. As a starting point, we recapitulate what we consider the most relevant conclusions that can be reached from published research:

- People tend to prefer curved stimuli to sharp-angled ones. This phenomenon has been studied mostly in Western populations, but it has also been found in newborn babies, non-Western cultures, and other primates. Thus, there is some evidence supporting the universality or innateness of this preference. Nevertheless, other evidence suggests that it is culturally influenced. The two options are not mutually exclusive, but they should be acknowledged and considered when designing and discussing further research.

- This phenomenon seems to encompass isolated lines as well as shapes and contours. Still, it is not proven whether the similarities imply the same underlying mechanism. Moreover, it is also unclear whether this is a unimodal or multimodal phenomenon.
- The term *curvature* is widely used throughout most published research. Deeming it wise to reach some terminological consensus in order to strengthen the field and avoid misunderstandings, we propose the use of the dichotomy *curvature/sharpness* to describe the object of study, and *curved/sharp-angled* to characterize the stimuli causing the effect. There is a case to be made for the use of *angular* as opposed to *curved*, but its polysemy might be misleading. The feature of interest is not the number of angles, but the degree of their curvature.
- These conceptual quandaries clearly show that the psychophysical nature of these features is yet to be explored. For now, any stimulus whose angles are evidently smooth, forming a continuous line that is perceived as such in plain view should be understood as curved.
- There is not enough evidence to ascertain whether we are indeed dealing with a preference for curvature or an avoidance or rejection of sharpness. So far, we consider it more parsimonious to speak of preference, but this issue requires further study. When proposing an evolutionary origin, it is not enough to suggest a plausible explanation. A detailed scenario with testable predictions is required for the hypothesis to be useful.

The study of preference for curvature is a promising endeavor. Not only because of its aesthetic, psychological, evolutionary, and epistemological implications, but also because of its practical consequences. One of humans' defining characteristics is the extent to which we create and shape our environment, and the freedom of choice we have in doing so. We surround ourselves with stimuli differing in curvature. And there is evidence showing how much this feature affects our perception, preference, and choice of—for instance—cars (Leder and Carbon, 2005), products' graphics and container designs (Westerman et al., 2012), and architectural interiors (Vartanian et al., 2013). Not only do we prefer curved-contoured objects, but we also find them more innovative, less aggressive, and we are more willing to purchase them. Moreover, curved and sharp elements in our environment might even influence decisions about cooperating and competing with others (Hess et al., 2013).

In sum, the contours of objects around us and with which we interact are not mere inconsequential design niceties. They have a tangible impact on our preferences and choices in consumer and social contexts. A better understanding of the mechanisms underlying preference for contour, and their evolutionary and cultural foundations, will therefore contribute to explaining human behavior in such contexts.

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Preference for curved contours across cultures

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Preference for curved contours across cultures

Gerardo Gómez-Puerto, Jaume Rosselló, Guido Corradi, Cristina Acedo-Carmona, Enric Munar, Marcos Nadal

The classic debate about the role of nature and nurture in human cognition dissipated with the realization that human nature and culture are inextricably intertwined. Our nature is cultural; our culture, natural (Kim & Sasaki, 2014; Laland, Odling-Smee, & Myles, 2010; Richerson & Boyd, 2005). Cognition is both biologically and culturally grounded. For instance, humans have a natural propensity to acquire and develop language, which is expressed culturally in myriad languages, dialects, jargons, and idiolects. This propensity is constituted by a set of perceptual and cognitive biases and abilities that orient human newborns and young infants towards certain physical and statistical properties of speech, facilitating language acquisition (Bijeljac-Babic, Bertoncini, & Mehler, 1993; Eimas, Siqueland, Jusczyk, & Vigorito, 1971; Mehler et al., 1988; Saffran, Aslin, & Newport, 1996). Thus, we are born perceptually and cognitively equipped to acquire language as we develop in a language-rich environment.

Like language, it is conceivable that our species is endowed with a natural propensity for aesthetics, which is expressed culturally and individually in the form of diverse traditions, canons, schools, and tastes. Unlike language, however, very little research has aimed to identify and characterize the constituents of humans' natural propensity for aesthetics. In fact, it is even unclear what to search for. In what terms should a natural propensity for aesthetics be understood? In a broad sense, we believe it makes sense to conceive it as a disposition to develop various forms of aesthetic experience, including those of aesthetic enjoyment, preference, judgment, production, and so on.

In this paper we focus on the propensity for aesthetic preference, conceived as a set of sensory-motor, perceptual, cognitive, and affective abilities and biases that orient humans towards the sort of sensory features—and arrangements thereof—that convey culturally relevant meaning. Color, symmetry, form, texture, speed, direction, angle, rhythm, tone, and many other sensory features, convey meaningful information about natural phenomena, resources, and threats. Moreover, these features, combined with affectively engaging media, are intentionally and skillfully exploited in large- and small-scale societies to imbue objects, movements, sounds, smells, people, places, times, occasions, and so on, with culturally relevant meaning (Anderson, 1989). These constitute the aesthetically enriched environments within which the putative propensity for aesthetics develops into fully-fledged aesthetic preferences.

Preference for curvature exhibits the sort of qualities expected from the product of a natural propensity for aesthetic preference, as defined above. Several converging lines of evidence support this remark. First, contour curvature is preferred in a broad range of visual stimuli: people prefer objects (Bar & Neta, 2006, 2007), rooms (Vartanian et al., 2013), designs (Westerman et al., 2012), and geometric figures (Bertamini, Palumbo, Gheorghes, & Galatsidas, 2016; Palumbo & Bertamini, 2016; Palumbo, Ruta, & Bertamini, 2015; Silvia & Barona, 2009) with curved contours to those with sharp-angled contours. Second, evidence for this preference has been obtained reliably using several different experimental paradigms (Gómez-Puerto, Munar, & Nadal, 2015; Palumbo & Bertamini, 2016). Third, people prefer curved contours even when stimuli are shown very briefly (Bar & Neta, 2006, 2007). Fourth, young infants (Jadva, Hines, & Golombok, 2010) and even newborns (Fantz & Miranda, 1975) prefer curved contours to sharp ones. Fifth, curves and angles convey distinct meanings: whereas curved lines are commonly regarded as gentle, quiet, sad or lazy, sharp lines are consistently regarded as agitating, hard or furious (Hevner, 1935; Lundholm, 1921; Poffenberger & Barrows, 1924). Finally, chimpanzees and gorillas also prefer curved contours to sharp-angled ones (Munar, Gómez-Puerto, Call, & Nadal, 2015) and, like humans, they tend to fixate on them first (Gómez-Puerto, Munar, Kano, & Call, 2015). The evidence, thus, suggests the existence of evolutionary ancient sensory-motor, perceptual, cognitive and/or affective mechanisms driving humans' preference for curved contours in many objects and under varying presentation conditions, even from early infancy, which are often associated with meanings, moods, and feelings.

Lacking in this catalog, however, is critical evidence for cross-cultural agreement in preference for curved contours. In general terms, if humans are, by their nature, endowed with a set of abilities and biases that orient them toward the aforementioned kind of sensory features, there should be evidence for such orientation and preference in cultures around the world. This has been successfully demonstrated for music. Several features of music structure and function are common across cultures, including the influence of processing constraints on music perception and memory (Stevens & Byron, 2009), the recognition of emotions carried by music (Fritz et al., 2009), and several features related to musical structure, such as pitch and rhythm, and function, such as performance style and social context (Savage, Brown, Sakai, & Currie, 2015). Thus, despite the wondrous variety of music around the world, a core of common features and functions are determined by our species' nature—by the features and limitations of our cognition and biology.

In sharp contrast, there is no evidence that people outside western industrialized countries prefer—or do not prefer, for that matter—curved contours to sharp-angled ones. The reason is that research on preference for curvature is remarkably "culture-blind" (Heine & Norenzayan, 2006): Findings from western samples—often college students—are uncritically assumed to generalize to all humans. Moreover, cross-cultural research on the psychological mechanisms involved in the aesthetic appreciation of visual features of any sort has been, at best, sporadic and unsystematic. The first wave of studies were mainly concerned with ascertaining whether there was agreement across cultures on the aesthetic value of specific geometric patterns or particular works (Lawlor, 1955; Lowie, 1921; McElroy, 1952). Later work shifted the emphasis to agreement among experts from different cultures on the artistic value of paintings and other visual materials (Anwar &

Child, 1972; Child & Siroto, 1965; Ford, Prothro, & Child, 1966; Iwao & Child, 1966; Iwao, Child, & García, 1969). The most recent trend attempted to determine whether certain visual features—mainly visual complexity and symmetry—drive aesthetic preference in different cultures (Berlyne, 1975, 1976; Berlyne, Robbins, & Thompson, 1974; Eysenck & Iwawaki, 1971, 1975; Farley & Ahn, 1973; Soueif & Eysenck, 1971, 1972).

Even when taken together, it is uncertain what these studies reveal about the commonalities and differences in aesthetic preference among cultures. In fact, from Child's search for agreement on artistic merit among experts from different cultures to Berlyne's search for common dimensions across cultures underlying preference for complexity, the aforementioned studies addressed different issues. The differences are subtle, but important. There can be agreement across cultures on the features that are relevant to aesthetics, but differences in the preferred values of those features, or in the meanings attributed to those features or values: "In the visual arts [...] certain formal categories are universally attended to. These include, at the very least, symmetry, proportion and balance, surface finish, and where pertinent, structural soundness.

Cultures may differ widely in terms of what exactly is valued in these categories, but the categories themselves are attended to by artist and audience alike." (Silver, 1979, p. 290). Thus, the examination of cross-cultural commonalities in aesthetic preference requires a precise specification of what it is that is common. Extending Silver's (1979) account, at least four sorts of commonalities could be expected in relation to aesthetic preference in the visual domain (table 1): (i) The formal categories or dimensions that are taken into account; (ii) The preferred level of those categories or dimensions; (iii) The values/meanings attributed to such categories and levels; and (iv) The semantic or symbolic content of aesthetic expressions.

In some cases, cultures exhibit several of these levels of commonalities simultaneously. McManus and Wu (2013) provide evidence for cross-cultural agreement for proportion on three of these levels. They showed that rectangle proportion (height vs. width) influenced British and Chinese participants' preference for the figures, that both groups had a bimodal preference distribution favoring squares and rectangles close to the golden section, and that both groups agreed on the meanings conveyed by rectangles of certain

Sort of cross-cultural commonality	**Examples**
Formal categories that are attended to	The simplicity-complexity is relevant to aesthetic preference (Berlyne *et al*., 1974; Berlyne, 1975)
Preferred level of formal category	Organized patterns are preferred to unorganized patterns (Berlyne et al., 1974; Berlyne, 1975)
Values/meanings attributed to formal category	Tall, thin, vertical rectangles are regarded as active, unstable, elegant and tense (McManus & Wu, 2013)
Content of aesthetic manifestations	Eye spots, bulging eyes, direct gaze in masks, paintings, etc. elicit defense reaction (Aiken, 1998)

Table 1. Levels of possible cross-cultural commonalities in aesthetic preference

proportions. Thus, across cultures, (i) people take proportion into consideration when asked to express their aesthetic preference for geometric figures, (ii) certain proportions are preferred to others, and (iii) certain proportions convey specific meanings. In other cases, however, cultures might show only one of these sorts of commonalities. Uduehi (1995), for instance, reported that although regularity influenced American and Nigerian participants' aesthetic judgments, Americans preferred regular forms and Nigerians tended to prefer irregular forms. Thus, Americans and Nigerians seemed to take the same formal category "regularity" into consideration, but they differed regarding the pole they preferred most.

With regards to these distinctions, we postulate that humans' propensity for aesthetic preference predisposes people (i) to orient towards the dimension of *curvature*, and (ii) to develop a preference for objects with curved contours rather than for those with sharp-angled contours. Accordingly, the study reported here aimed to answer two questions: (i) Are the visual preferences of people in small- and large-scale societies influenced by curvature? (ii) Do people in small- and large-scale societies prefer curved contours to sharp-angled ones? Positive answers to both of these questions would constitute cross-cultural evidence of a common orientation towards the formal dimension *curvature*, and of a common preference for one of the dimension's poles: curved contours.

Method

Participants

Twenty Spanish adults (18 females, age M = 20.75, SD = 4.60), 23 Mexican adults (11 females, age M = 46.17, SD = 13.15) and 13 Ghanaian adults (6

females, ages unknown) participated in the experiment. This research was approved by the Ethical Committee of the *Comunitat Autònoma de les Illes Balears* (Spain) and all participants were treated in accordance with the Declaration of Helsinki (2008). The Spanish sample was constituted by psychology students from the University of the Balearic Islands, thus pertaining to a large-scale industrialized European society, and similar to the samples used in previous studies on preference for curvature.

The Mexican and Ghanaian samples, in contrast, represent small-scale non- industrialized American and African societies (Anderson, 1989). The Mexican sample was conformed by indigenous *Chontal*, living in several small towns (aprox. 135-3,600 inhabitants) in the Tehuantepec district, located in the Isthmus region of Oaxaca, one of the Mexican federal states. Most people's livelyhood in this region depends on small- scale subsistence farming and agriculture, growing corn, sugar cane, rice, and fruits, and live in small nuclear families of parents and children. Despite growing homogenization among Mexican cultures, these indigenous people maintain their distinct identity, customs, clothing and dialects (Acedo-Carmona & Gomila, 2015).

The Ghanaian sample included participants from the town of Bawku (aprox. 69,500 inhabitants), an urban nucleus located in the Bawku Municipal District in the improverished Northen region of Ghana. People in this region, dominated by Savannah grasslands, are reliant on subsistence slash-and-burn agriculture and livestock. Ghanian participants' ethnic origins were diverse (*Kussasi*, *Sissala*, *Frafra*, *Ashanti*, *Bissa*, *Waala*, and *Mossi*). Since the country's independence in 1957 these groups have reaffirmed their own cultural identity, with their own languages, customs, and beliefs. Large extended monogamous or polygamous families are the most frequent form of cohabitation, and they are closely related to properties, identity, and status (Acedo- Carmona & Gomila, 2015).

Materials

One hundred and forty four grey-scale photographs of diverse real objects, lacking any inherent positive or negative valence, were chosen from a set used in previous studies (Bar & Neta, 2006, 2007; Munar, Gómez-Puerto, Call, & Nadal, 2015), and available on the Web at https://faculty.biu.ac.il/~barlab/stimuli.html. The stimuli were improved in resolution and combined to create two sets of 36 pairs: a contour set, in which both images in a pair depicted the same object and differed mainly in the curvature of its contour, such that one of the alternatives was curved and the other sharp-angled (Figure 1), and a content set, in which images in a pair depicted different objects with the same sort of contour (curved or

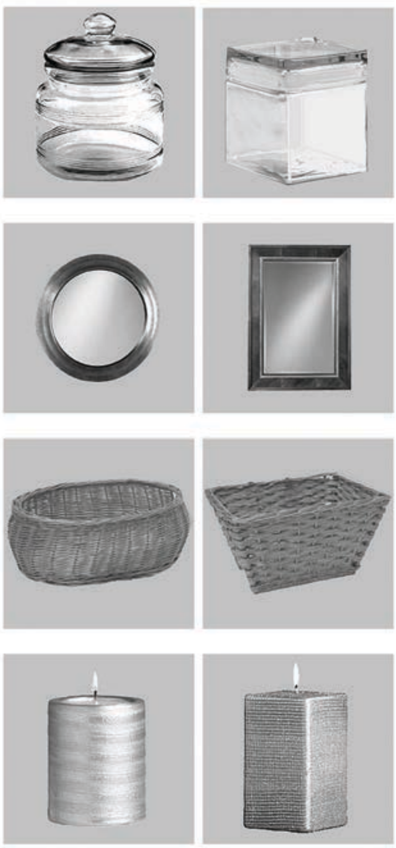

Figure 1. Four examples of *contour pairs*: The objects in each pair share a common semantic content but differ in contour. Here, the objects on the left have curved contours; the ones on the right, sharp-angled contours. From Bar & Neta (2006), used with their permission.

Figure 2. Four examples of *content pairs*: The objects in each pair share the same kind of contour but differ in semantic meaning. Objects in the two top pairs have curved contours; those in the two bottom pairs, sharp-angled contours. From Bar & Neta (2006), used with their permission

sharp-angled), thus differing in their semantic meaning (Figure 2). Content pairs were designed and included only as filler trials, in order to make the aims and main aesthetic dimension (contour curvature) of the study less apparent to participants. An additional 16 non-related images taken from the same set that combined distinct curved and sharp features were paired to create a set of 8 practice trials.

Each individual image was scaled to a resolution of 340 x 340 px. Due to the limitations derived from fieldwork, the size of the screens employed varied across locations, thus resulting in varying presentation sizes (Spain: 19" at 1440 × 900 px; Ghana: 10.1" at 1024x600 px; Mexico: 13.3" at 1366 x 768 px). Nevertheless, there is no indication that these differences might have affected the results obtained.

Procedure

We designed a 2-alternative forced choice (2-AFC) task that minimized verbal content, so that it would not be dependent on cognitive or linguistic skills, nor cultural differences in the understanding of verbal instructions. As discussed elsewhere (Munar, Gómez-Puerto, & Gomila, 2015), this was achieved based on an approach-avoidance framework, in which the forced choice was followed by displaying the selected image as being closer to the participant. In this way, the task was made self-evident, requiring minimal verbal instructuions, and allowing its use in very different cultural environments and even with other primate species (Munar, Gómez-Puerto, Call, et al., 2015).

In each trial of the task, participants were presented with a pair of images varying in their contour or semantic content and instructed to select one of the images in the presented pair by pressing a keyboard arrow (left or right). Instructions were simple, and specifically avoided the use of terms such as *wanting*, *liking* or *preferring*. The action of choosing was made meaningful in a non-semantically dependent way by implementing the effect of approaching the chosen image upon selection. This was achieved by immediately displaying the chosen image on its own, centered and enlarged. A trial consisted of a fixation cross shown for 500ms, followed by the paired stimuli displayed for 80ms. These images were then immediately replaced by a pair of light grey squares, which prompted the participant to make a choice, and reduced possible after-effects. As soon as one of the images was selected, it was shown again for 1 second, centered, and at twice it original size.

To avoid undesired familiarity effects, participants were tested in a single session. Each session consisted of two equivalent blocks of 72 trials performed in succession without interruption. Both blocks were identical, except each element of a pair appeared on different sides of the screen on each occasion. For simplicity, the stimuli pairs were assigned to two sub-blocks of 36, and all the pairs in each sub-block switched together from the first to the second block.

The order of both blocks was randomized, as was the order of the 72 trials within each block. This design enabled measuring lateralization effects and identifying other possible sources for preference, while at the same time increasing the number of trials. Eight additional training trials, comprising stimuli that combined both curved and sharp-angled features, were added at the beginning of the session, so participants could become familiar with the procedure before the actual test began.

The presentation and recording of the data was performed using the DirectRT software v.2006 and v. 2014 (Empirisoft Corporation, New York, NY, USA) in a controlled environment. In Spain, participants undertook the experiment in isolation, inside a soundproof laboratory with constant light. An effort was made so that conditions in Mexico and Ghana replicated this setting; but due to the lack of resources and cultural differences, full isolation was not possible. Still, participants in those countries were able to participate in an adequately lit environment devoid of distractions.

Data preparation

Given the cultural differences between participants from different countries and the lack of familiarity of a good part of them with computer-based tasks, data examination and data depuration were required prior to analysis. Only data from the contour trials were analyzed.

As both very short and very long response times can seriously affect choice processes, thus biasing the results and interpretation, the responses were first examined, in a trial by trial basis, with reference to the corresponding response times. This way, we conducted a preliminary exploratory analysis in order to detect outliers showing both very fast and very slow responses. Response times under 300ms were considered fast responses, and those falling above the Q3 + 1.5 IQR (Interquartile Range) for each country were regarded as slow outliers (Ghana: 2013ms; Mexico: 3474ms; Spain: 1384ms). These fast and slow trials were excluded from the analyses (9.51% of all responses). For six participants, this data depuration implied that more than a half of their trials were excluded, so we decided to remove those individuals from subsequent analyses (increasing the number of excluded responses to 13.26%).

Finally, to further ensure the integrity of the data, we removed all the trials from two additional participants whose response patterns were aberrant, suggesting either they performed choices in a careless way and/or they misunderstood the task: one participant always pressed the same key; the other systematically alternated, trial by trial, between the two options. By countries, the final percentages of excluded responses were 27.71% (Ghana), 19.43% (Mexico), and 6.73% (Spain). We then proceeded to restructure the remaining data (83.17%, 48 participants), setting the proportion of curved choices for the contour pairs as the dependent variable. From this point, results are based on this data array

Results

Data were analyzed with SPSS 20.0.0 (SPSS Inc., Chicago, IL, USA). An alpha level of .05 was used for all analyses. The dependent variable was checked both for normality and homogeneity of variances. Shapiro–Wilks test indicated normality could be assumed for each of the 3 samples, $W(10)=0.966$, $p=.848$ (Ghana); $W(19)=0.962$, $p=.606$ (Mexico); $W(19)=0.914$, $p=.089$ (Spain). However, Levene's test was significant, $F(2,45)=10.626$, $p<.001$, indicating that, for the country factor, the variances were statistically different, an outcome we must take into account in further analyses.

In order to contrast the hypothesis regarding general visual preferences for curved contours, we first conducted a one-sample t-test (two-tailed) for the overall mean (all samples taken together) of curved choices proportions (M=0.57, SD=0.08), which was above the chance level of 0.5, showing a statistically significant mean difference of 0.07, 95% CI[0.048, 0.094], $t(47)$=6.275, p<.001, d=0.905.

To test the hypothesis that the visual preference for curved contours occurs in every country, three additional one-sample t-tests were conducted to determine if a statistically significant difference existed between the mean proportion of curved choices for each country and the chance level. Results indicated that the proportion of curved choices from Ghana (M=0.58, SD=0.07), from Mexico (M=0.55, SD=0.05) and from Spain (M=0.59, SD=0.1) were all greater than 0.5. The statistically significant mean differences were, for Ghana m = 0.082, 95% CI[0.034, 0.129], $t(9)$=3.898, p=.004 d=1.23, for Mexico m = 0.047, 95% CI[0.026, 0.069], $t(18)$=4.537, p<.001, d=1.04, and for Spain m = 0.089, 95% CI[0.039, 0.14], $t(18)$=3.742, p=.001, d=0.858.

An additional analysis was conducted to compare the preference for curved contours between the three groups. Thus, we ran a one-way between-subjects ANOVA to test whether there were any statistically significant differences between the three countries regarding the proportion of curved choices. Since heteroscedasticity is commonly regarded to be a problem, especially when sample sizes are unequal in different levels of a factor, we decided to use the Welch's adjusted F ratio (1.94). The test did not reveal any significant effect of the country on the preference for curved contours, *Welch's F* (2, 21.682) =1.94, p=.167, *est.* ω_2=.038 (see Figure 3).

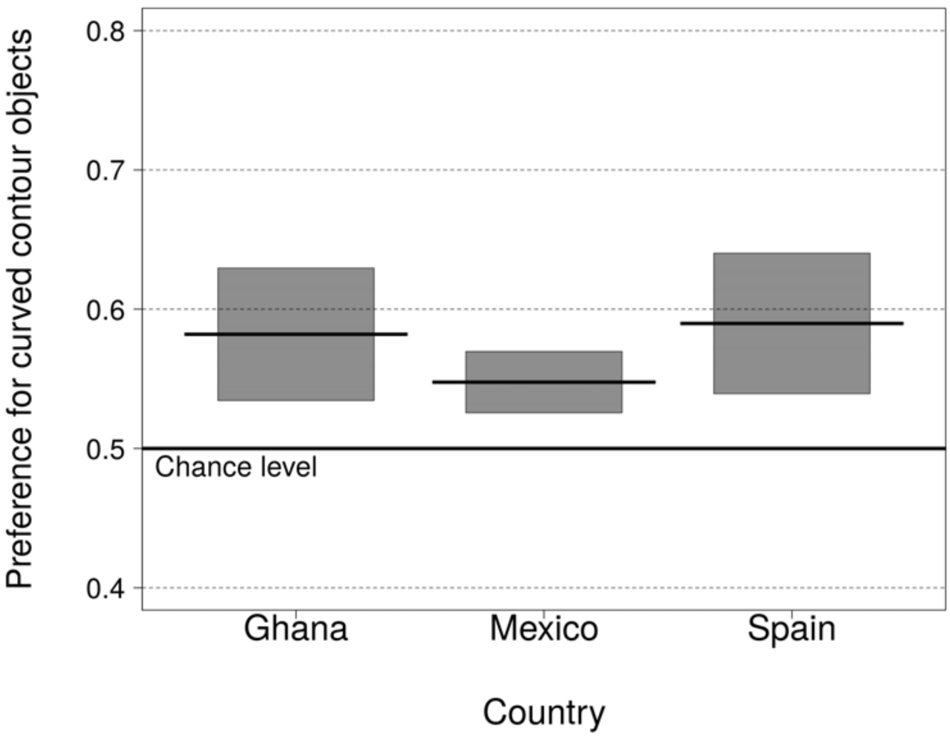

Figure 3. Preference for curved contours for each of the participant groups. Values over .5 reflect preference for curved contours; values below .5 reflect preference for sharp-angled contours. Lines indicate mean values; gray shading indicate 95% confidence intervals.

Therefore, since there were statistically significant differences between the mean of each country and the chance level, the results support the conclusion that people from Bawku (Ghana), from Oaxaca (Mexico) and from Mallorca (Spain), prefer curved contours to sharp-angled ones. Moreover, there were no significant differences among cultures in the extent of such preference, as indicated by the outcome of the Welch ANOVA.

We conducted additional by-stimulus and by-participant analyses to offer another angle on our results. First, we checked for object pairs that elicited extreme preference responses—either for the curved or the sharp-angled options—using the 1.5 IQR method for detecting extreme responses. This analysis revealed that there were no object pairs with extremely low (below Q1-1.5IQR) or extremely high (above Q3+1.5IQR) proportions of "curved" preference choices. This was the case when considering the three samples together, and when conducting this analysis separately for each of them. Second, we wished to determine the proportion of participants in each country who chose curved items most often (i.e. in over 50% of trials). The results showed that 90% of Ghanian, 85.22% of Mexican, and 79.85% of Spanish participants (83.34% overall) chose the curved alternative more often than not.

Discussion

In In this study we aimed to determine whether preference for curved contours is common across cultures from three different continents. Specifically, we wished to ascertain whether contour curvature-sharpness constitutes a relevant dimension for visual preferences of people in small- and large-scale societies, and whether curved contours are preferred to sharp-angled ones in small- and large-scale societies. Our results show that indeed this is the case. First, contour influenced the choices of participants in the Mexican, Ghanian, and Spanish samples: they were significantly different from the chance level in all groups, meaning that participants' choices were not indifferent to this dimension. Second, participants in the three samples preferred objects with curved contours significantly more than their sharp-angled equivalents. Moreover, we found no evidence of between-groups differences in the extent to which they preferred curved contours (there were no significant differences between preference levels). Taken together, these results suggest that orientation towards, and preference for, curvature are common across small- and large-scale societies sampled from different continents.

These results, thus, suggest that *curvature* is one of the aesthetic categories or dimensions that drive visual preference of people from different cultures around the world, together with *color hue*, *saturation* and *lightness*, *symmetry*, *complexity*, *regularity*, and *proportion* (Berlyne, 1976; Eysenck & Iwawaki, 1971; McManus & Wu, 2013; Palmer, Schloss, & Sammartino, 2013; Silver, 1979). Moreover, "curved" constitutes the preferred value (at least to "sharp-angled") across cultures for the *curvature* dimension, just as there seems to be cross-cultural agreement on preference for certain values along other dimensions: "square" and "near-golden section" are the preferred proportions in rectangles (McManus & Wu, 2013).

To argue for a general preference for curved contour objects, however, is not to claim that everyone prefers curves over angles all the time. In this study, almost 17% of participants chose the sharp-angled items most of the times. And other recent research shows that openness to experience and training in art history or architecture can attenuate—an even invert—preference for curved contour objects, shapes, and rooms (Belman et al., 2016; Cotter, Silvia, Bertamini, Palumbo, & Vartanian, subm.; Vartanian et al., subm.). Thus, everyday life experience and formal training, among other factors, contribte to shaping the outcome of the hypothesized propensity to develop preferences in relation to curvature: although general among people, preference for curvature is not uniform across people.

The full significance of the results presented in this paper is apparent when woven together with other strands of evidence. Curved contours are preferred to sharp- angled ones in many sorts of images (Bar & Neta, 2006, 2007; Bertamini et al., 2016; Palumbo & Bertamini, 2016; Palumbo et al., 2015; Silvia & Barona, 2009; Vartanian et al., 2013; Westerman et al., 2012), even when different methods are used (Palumbo & Bertamini, 2016), and under very short presentation times (Bar & Neta, 2006, 2007).

This preference arises early in infancy (Fantz & Miranda, 1975; Jadva et al., 2010), it is common across large- and small-scale societies from different continents, and present even in great apes (Munar, Gómez-Puerto, Call, & Nadal, 2015) (Gómez-Puerto, Munar, Kano, & Call, 2015). We believe that, together, these strands of evidence support the following conjectures:

1. Humans are endowed with a natural propensity to acquire aesthetic preferences as we develop in an aesthetically-rich environment, that functions to orient us fast and efficiently toward sensory features that, alone or in combination, carry culturally-relevant meanings.

2. This propensity is constituted by a set of sensory-motor, perceptual, affective and/or cognitive capacities and biases. Although characterizing these psychological processes is the object of current research, their precise nature remains still largely unknown.

3. The evidence to date, however, indicates that we share, at least in a large part, the psychological mechanisms underlying the human propensity for aesthetics with African great apes. This suggests that humans, gorillas and chimpanzees inherited such mechanisms from their common ancestor, which lived some 9-10 million years ago. It also suggests that although in humans these psychological mechanisms play a crucial role in aesthetic preference, they are best regarded as components of a primate—maybe even mammal—general valuation system.

4. This propensity is culturally and individually expressed in the form of historically and geographically distinct traditions, canons, schools, and tastes, and can be modulated by training, and experience in general.

Although these conjectures are in agreement with this study's results and those of the studies reviewed in the introduction, much more evidence is required to support them.

Indeed, the research presented in this paper corresponds to stage 1 of Heine and Norenzayan's (2006) research program for a culture-sensitive cognitive psychology: the documentation of similarities and differences in psychological processes across cultures. In the case of the present study's research line, stage 2—the explanation of these similarities and differences—will require additional experiments to determine the psychological processes underlying preference for curvature (Gómez-Puerto et al., 2015), the developmental processes involved in the expression of such putative propensity into full-fledged preferences, the differences and similarities in the cultural expression of aesthetic preference, and the differences and

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RESEARCH ARTICLE

Common Visual Preference for Curved Contours in Humans and Great Apes

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Abstract

Among the visual preferences that guide many everyday activities and decisions, from consumer choices to social judgment, preference for curved over sharp-angled contours is commonly thought to have played an adaptive role throughout human evolution, favoring the avoidance of potentially harmful objects. However, because nonhuman primates also exhibit preferences for certain visual qualities, it is conceivable that humans' preference for curved contours is grounded on perceptual and cognitive mechanisms shared with extant nonhuman primate species. Here we aimed to determine whether nonhuman great apes and humans share a visual preference for curved over sharp-angled contours using a 2-alternative forced choice experimental paradigm under comparable conditions. Our results revealed that the human group and the great ape group indeed share a common preference for curved over sharp-angled contours, but that they differ in the manner and magnitude with which this preference is expressed behaviorally. These results suggest that humans' visual preference for curved objects evolved from earlier primate species' visual preferences, and that during this process it became stronger, but also more susceptible to the influence of higher cognitive processes and preference for other visual features.

Introduction

Visual preference, that is to say, the choice of one item over others based on visual qualities, plays an important role in many human everyday activities and decisions [1]. For instance, visual preference guides consumer decisions [2,3], social judgment and behavior [4–6], or partner choice [7,8]. Although such preferences are sensitive to personal and contextual factors, most research has been aimed at understanding the perceptual features that drive them. These include color, combinations of colors, complexity, symmetry, as well as low-level properties, such as spatial frequency [1].

Among these attributes, one that has recently received attention is the quality of object contour; specifically, the distinction between curved and sharp-angled contours. A number of behavioral studies have shown that people prefer curved contours significantly more than sharp-angled ones [9–16]. Such a preference even seems to be present in newborns, as they preferentially fixate on curved contours, compared to sharp-angled ones [17,18].

Bar and Neta [11,12] suggested that sharp transitions in contour may convey a primitive sense of threat that triggers a primary negative response, which in turn leads to avoidance or rejection. Consistent with this hypothesis, activity in the amygdala, involved in processing information related to fear and high arousal [19], is significantly higher while viewing objects with sharp-angled contours than while viewing their curved contour counterparts [12]. Moreover, the difference in preference between curved and sharp-angled contours was more apparent with low spatial frequencies (LSFs) of the image than with high spatial frequencies (HSFs). Because the LSFs are processed faster than the HSFs [20,21], those results support the idea that the observed preference might be based on a fast extraction of information from the image at a low level of processing. In fact, several studies with adults have presented the stimuli very briefly (80–85 ms) and/or required quick responses from the participants [11,12,14], preventing top-down processing (enabled by long exposure times to the stimuli) from overriding the observed preferences. Other studies, however, have used longer presentation times, ranging from 2000 ms [13] to 3000 ms [16], or even free viewing times [10,15]. In fact, preference for curved over sharp-angled contours is not a constant that affects all our decisions about objects. There are several factors that modulate, reduce, or even eliminate such preference. Preferences for curved objects, for instance, can be partially modulated by fashion or trends, and adaptation effects are plausible candidates for triggering such changes in preference [22]. In addition, the preference for curved contours disappears when objects possess a negative emotional valence [14].

Visual preference is thought to have played an adaptive role during the evolution of the human lineage by directing our ancestors' attention to important aspects of their natural environments [23]. From this perspective, it is believed that humans are biologically predisposed to prefer certain landscapes [24] and environmental cues [25] that contain information relative to resources and threats [26,27]. Similarly to this sort of environmental preference, it is also believed that a preference for curved contours, or a predisposition to develop this preference [28], might also have been acquired at some point throughout human evolution [12]: "It is possible that our brains have evolved to detect sharp features rapidly, perhaps using low-level features such as spatial frequencies" [12]. This fast detection and avoidance mechanism would have allowed individuals to detect and keep clear of sharp objects like thorns and pointed branches.

Some authors have proposed that this kind of preference was acquired after the human lineage separated from that of chimpanzees [29]. However, there is currently no evidence to support the notion that preference for curved contours actually is a derived human trait. In fact, there is reason to believe that the opposite might be the case. Other nonhuman primates exhibit diverse visual preferences, including the preference for regularity and symmetry [30], certain colors and brightness levels [31], and particular kinds of social information [32,33]. This is especially relevant when considering snakes, a well-researched threat to primates with a conspicuously curved contour [34]. The need to quickly detect such a threat might have helped to shape primate visual system [35], while it has been recently claimed that the rapid detection of snakes might be driven by key curved features of its body [36]. Thus, it is conceivable that the human preference for curved over sharp-angled contours evolved from preexisting cognitive and neural mechanisms related to visual preference present in our primate ancestors. If this were the case, visual preference for curved contours might be shared, at least to a certain degree, with other extant primate species.

The main aim of the present study was to test this possibility by comparing, under similar testing conditions, humans and nonhuman great apes' (henceforth apes) preference for curved and sharp-angled contours. In the absence of an existing paradigm that allowed us to directly compare human and great ape visual preference, we designed an *ad hoc* experimental paradigm to test preference for contour curvature in humans (Experiments 1 & 2) and apes (Experiments 3 & 4). Our procedure was based on the approach-avoidance framework whose naturalistic essence and focus on primal interactions between organism and environment allowed us to minimize interpretative problems [37].

Participants were required to choose between two visual stimuli presented on a computer screen. The stimuli depicted objects that differed either only in their contour (thus, two versions of the same object, one with curved contour, the other with a sharp-angled contour) or in their content (both alternatives had the same sort of contour but depicted different objects). To simulate the effect of approaching the object, immediately after the choice had been made, the selected image was enlarged on the computer screen. Previous studies have established that two-alternative forced-choice paradigms are useful for detecting spontaneous preferences in primates [30,38,39]. Moreover, since humans and other primates share the same basic visual system and low-level visual processing [40], this paradigm was deemed particularly suitable to detect preferences for curved over sharp-angled contours.

Experiment 1 attempted to replicate previous results [11] using a 2-alternative forced choice (2AFC) with an 80-ms stimuli presentation time in humans. Based on the literature surveyed above, we predicted that humans would show a preference for curved objects by selecting the curved object above chance levels (50%). Given that previous studies using long or unrestricted viewing times have produced inconsistent results (e.g. [14], [16]), Experiment 2 was designed to study humans' preference for curvature under unrestricted time conditions, also using a 2AFC. We hypothesized that the aforementioned inconsistencies are a reflection of the attenuation of preference for curvature with longer presentations. Thus, we expected to find a reduction in participants' choices of the curved items in comparison to Experiment 1. Experiments 3 and 4 tested preferences in chimpanzees and gorillas using a touch screen with an 84 ms and unrestricted time stimuli exposure, respectively. We also expected apes to show a preference for curved objects, given the aforementioned evidence for other shared visual preferences. Nevertheless, we anticipated that the effects of longer exposure times would be different, owing to the weaker relevance of the semantic content of the presented items for apes.

We also analyzed response latency and choice consistency to attain a better understanding of the sources underlying participants' choices. In this context, choice consistency indicates the frequency with which participants select the same item in the pairs when presented in two different experimental blocks. Thus, whereas the preference value reflects the extent to which participants' choice is driven by contour, the consistency value reflects the extent to which this choice is linked to specific object pairs.

Materials and Methods

Experiment 1

Twenty psychology students from the University of the Balearic Islands (18 females, age $M = 20.75$, $SD = 4.60$, all adults) volunteered to take part. All of them were unaware of the goals of the experiment and had normal or corrected-to-normal vision. Experiments 1 and 2, and their consent procedure were approved by the Ethical Committee of the Comunitat

Fig 1. Example of contour pair. Same semantic meaning and different contour. From Bar & Neta (2006), used with their permission.

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Autònoma de les Illes Balears (Spain). Participants provided written informed consent to take part in the experiments.

One hundred and sixty gray-scale photographs of real objects, a subset of those used in previous studies [11,12], were selected as stimuli. Each image had a resolution of 340 x 340 pixels so, when being shown on a 19-inch screen at 1440 × 900px (89.37 PPI), its real size was of 9.66 × 9.66 cm. The images were paired in order to create two sorts of pairings. A set of 36 contour pairs was created, each consisting of two versions of the same object that differed only in the curvature of its contour (one of the alternatives was curved, the other sharp-angled) (Fig 1). Additionally, 36 content pairs were created, consisting of different objects with the same sort of contour (curved or sharp-angled), thus differing in their semantic meaning (Fig 2).

These 72 pairs of images were distributed into two equivalent blocks. The two blocks were identical, except that, for each, pair the alternatives appeared on the opposite side of the screen. The order of both blocks was randomized, as was the order of the 72 trials in each block. This design enabled measuring lateralization effects and identifying other possible sources for preference, while at the same time increasing the number of trials. Eight additional training trials, comprising neutral stimuli that portrayed both curved and sharp-angled features, were added at the beginning of each session, so participants could become familiar with the procedure before the actual test began.

Each participant undertook only one session, in order to avoid undesired familiarity effects. They sat 50 to 60 cm from the screen in an isolated room, and were shown a total of 152 pairs of stimuli, consisting of the aforementioned 8 training pairs, and 36 contour pairs and 36 content pairs in each of the two blocks. Participants were instructed to select one of the images shown in a 2-alternative forced choice task by means of pressing a keyboard arrow that indicated the position of the selected image. These instructions were given avoiding the use of words in the semantic fields of *liking*, *preferring* or *wanting*, so participants were not led in a particular direction, and to facilitate inter species comparisons.

Fig 2. Example of content pair. Same kind of contour and different semantic meaning. From Bar & Neta (2006), used with their permission.

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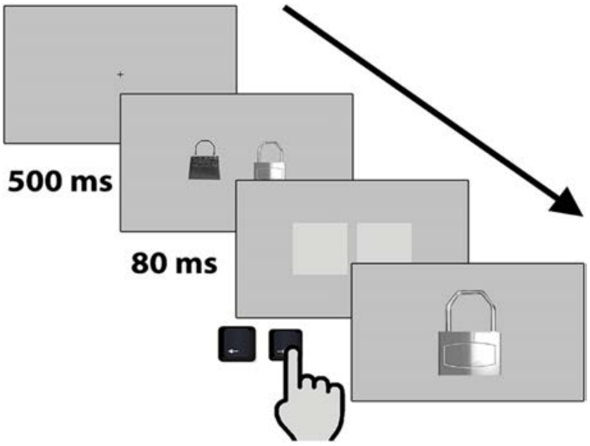

Fig 3. Trial sequence of Experiment 1. A fixation cross shown for 500 ms, followed by a pair of stimuli for 80 ms, immediately replaced by a pair of grey squares, and the chosen image was shown once again, centered, and enlarged.

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A trial consisted of a fixation cross, shown for 500 ms, followed by a pair of stimuli displayed for 80 ms (Fig 3). This pair was then immediately replaced by a pair of grey squares, which minimized possible after-effects and served as a non-verbal cue signaling participants to make a choice. Once one of the options had been selected, the chosen image was shown once again for 1 second, centered, at twice its original size. This manipulation was aimed at 1) simulating the act of approaching the preferred image (by enlarging it) and 2) minimizing the task's verbal requirements, thus enabling participants from different cultures and species to perform it [37].

Data were recorded by the computer and we measured three dependent variables: 1) choice preference, defined as the percentage of trials in which participants selected the curved contour alternative, 2) choice consistency, defined as the percentage of trials in which participants selected the same stimulus in the two experimental blocks and 3) latency, defined as the elapsed time between stimulus presentation and choice. Data were normally distributed and we used 2-tailed parametric statistical tests.

Experiment 2

Twenty-nine students from the University of the Balearic Islands (24 women, age *M* = 19.86 *SD* = 1.78, all adults) took part in a 2 alternative forced choice task similar to that described in Experiment 1. The only difference was that the stimuli remained on the screen until the participant made a choice. All participants were unaware of the goals of the experiment and had normal or corrected to normal vision. Data analysis was the same as in Experiment 1.

Experiment 3

Seven adolescent and adult chimpanzees (*Pan troglodytes;* 3 females) and two adult female western lowland gorillas (*Gorilla gorilla gorilla*) housed at the Wolfgang Köhler Primate Research Center (WKPRC) (age *M* = 14.22, *SD* = 5.21, Range: 8–20 years) took part in this experiment. One additional chimpanzee was removed from the study due to low performance during the training condition. In accordance with the recommendations of the Weatherall report "the use of non-human primates in research" groups of apes were housed in semi-natural indoor and outdoor enclosures with regular feedings, daily enrichment and water ad lib.

Apes at WKPRC live in groups housed in separated outdoor (1400–4000 m^2) and indoor enclosures (175–430 m^2) that contain climbing structures, such as ropes and platforms; natural features, such as vegetation, trees and streams; and a variety of permanent enrichment devices. They spend the night in a series of interconnected sleeping rooms (32–47 m^2), and receive regular feedings through the day consisting of a variety of fruits, vegetables and cereals. They are further provided with different kinds of enrichment devices once every day, with at least one item per individual (for more information, see http://wkprc.eva.mpg.de/english/files/enrichment.htm). Apes were not forced to participate and could choose to stop participating at any time during the study; they were never deprived of food or water. They were rewarded with highly valued food items, such as bananas, apples and grapes. Research was conducted in the observation rooms.

No medical, toxicological or neurobiological research of any kind is conducted at the WKPRC. Research was non-invasive and strictly adhered to Germany's legal requirements. The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology, which serves the same function as an Institutional Animal Care and Use Committee. Animal husbandry and research complied with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria", the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior (ASAB).

We used the same stimuli as in Experiment 1. Thus, humans and apes were presented with exactly the same choices. Like humans, the apes were required to perform a two-alternative forced choice task in which they had to choose between the same pairs of images previously described. But, in order to adjust to the particularities of working with non-human primates, several modifications were introduced, most notably the inclusion of an infrared touchscreen via which the apes made their selection. This screen was calibrated so its coordinates matched that of a 19-inch computer monitor placed right behind it, in which the black and white stimuli were presented at a resolution of 1280 x 1024 (86.27 PPI), achieving a real size of 10.01 x 10.01 cm per image. All participants were familiar with this setup as they had used it in other studies.

The apes could move freely in the observation room, so the fixation cross was replaced by an initialization cross between trials. This cross had to be touched each time in order for the stimuli to be displayed, thus helping direct the participant's attention to the screen where the stimuli where shown. To further engage them in the task, the apes were rewarded in a quasi-random manner on 50% of the trials, such that they were not rewarded in consecutive trials and they did not go without a reward in more than two consecutive trials. To be consistent with previous training procedures, rewards were accompanied by a beeping sound associated with a correct response. Furthermore, to avoid any possible bias derived from an association between rewards and chosen images, the screen remained blank for 500 ms. after the enlarged selected image was shown. Following this, the beeping sound indicated whether the reward would or would not be delivered. Rewards were usually pieces of apple, although some pieces of grape and banana were also given. Finally, due to differences in the refresh rate of the computer screens used to present the stimuli to humans and apes, the latter viewed the images for 84 ms, compared to 80 ms for the humans in Experiment 1. Both presentation durations are consistent with previous literature [11,14].

Trials began with the initiation cross displayed on the computer screen. Once the ape touched it, a pair of images was shown for 84 ms and then replaced by two gray squares. Upon touching of one of these squares, the selected image reappeared, enlarged. After 1 sec of enlarged presentation, the computer screen remained blank for 500 ms, after which a beeping sound was presented depending on whether or not a reward was given.

In order to ensure that the apes could perform the task, they had to pass two training sessions on different days before proceeding to the experimental condition. These sessions differed only in that the stimuli presented were a subset of those used previously as control stimuli [11], comprising objects with "a roughly equal mixture of curved and sharp-angled features" [11]. The criterion for a successful training session was selection of a stimulus on every trial. Nine participants met criterion after two sessions; a tenth failed. Each ape received 5 identical experimental sessions on different days. Data analysis was the same as in Experiment 1.

Experiment 4

This experiment was identical to Experiment 3, except that stimuli were presented until participants made a choice. As in Experiment 3, apes chose by touching one of the squares corresponding to the presented objects. As the same 9 apes that participated in Experiment 3 were tested, no additional training was necessary. Each ape again received 5 identical sessions across different days, and data analysis was the same as in previous experiments.

Results

Experiment 1

Preference. As hypothesized, participants chose the curved alternatives in the pairs significantly above chance level [$t(19) = 2.69$, $p = .007$, $d = .60$] (Fig 4). We also performed an item-by-item analysis based on the number of participants that chose the curved item in every pair. Thus, this analysis was carried out on the 40 (20 participants x 2 blocks) trials for each pair. As expected, objects with curved contours were chosen above chance level [$M = 58.25$; $SD = 8.2$; 95% CI: 54.75–61.75; $t(35) = 4.84$, $p < .001$; $d = .81$]. Thus, the preference for objects with curved contours was observed across participants and across image pairs (with large effect sizes).

Consistency. Choice consistency, defined as the percentage of pairs in which a participant chose the same image in the first and the second blocks, was above chance level [$t(19) = 4.54$, $p < .001$, $d = 1.016$] (Fig 5), with no difference between contour pairs [$M = 61.7$, $SD = 13.17$] and content pairs [$M = 60.7$, $SD = 12.50$], [$t(19) = .33$, $p = .746$, $d = .08$]. This indicates that participants preferentially chose the same item in the object pairs on both occasions.

Latency. We found no significant difference in average reaction time (RT) between the chosen curved alternatives [$M = 625$ ms, $SD = 148$ ms] and sharp-angled alternatives [$M = 629$ ms, $SD = 173$ ms], [$t(19) = .21$, $p = .839$, $d = .025$]. Similarly, there were no significant differences in RT between right [$M = 627$ ms, $SD = 156$ ms] and left responses [$M = 625$ ms, $SD = 157$ ms], [$t(19) = .22$, $p = .828$, $d = .016$] or between contour pairs [$M = 628$ ms, $SD = 152$ ms] and content pairs [$M = 622$ ms, $SD = 160$ ms], [$t(19) = .46$, $p = .653$, $d = .038$].

Experiment 2

Preference. Data from two outlier participants were excluded from the analyses, given that their values exceeded the 1.5 × IQR (interquartile range) mark. Results for the remainder of participants show that they did not choose the curved alternatives above chance level under free viewing time conditions [$t(26) = .173$, $p = .864$, $d = .03$] (Fig 4). This was still the case when including the 2 outliers in the analysis.

Consistency. Preferences were highly consistent across blocks [$t(26) = 6.5$, $p < .001$, $d = 1.25$] (Fig 5), with choices of the content pairs being significantly more consistent than those of the contour pairs [$t(26) = 3.29$, $p = .003$, $d = .39$; content pairs: $M = 76.5$, $SD = 17.6$; contour pairs: $M = 68.9$, $SD = 20.5$]. Thus, participants chose the same item in image pairs on

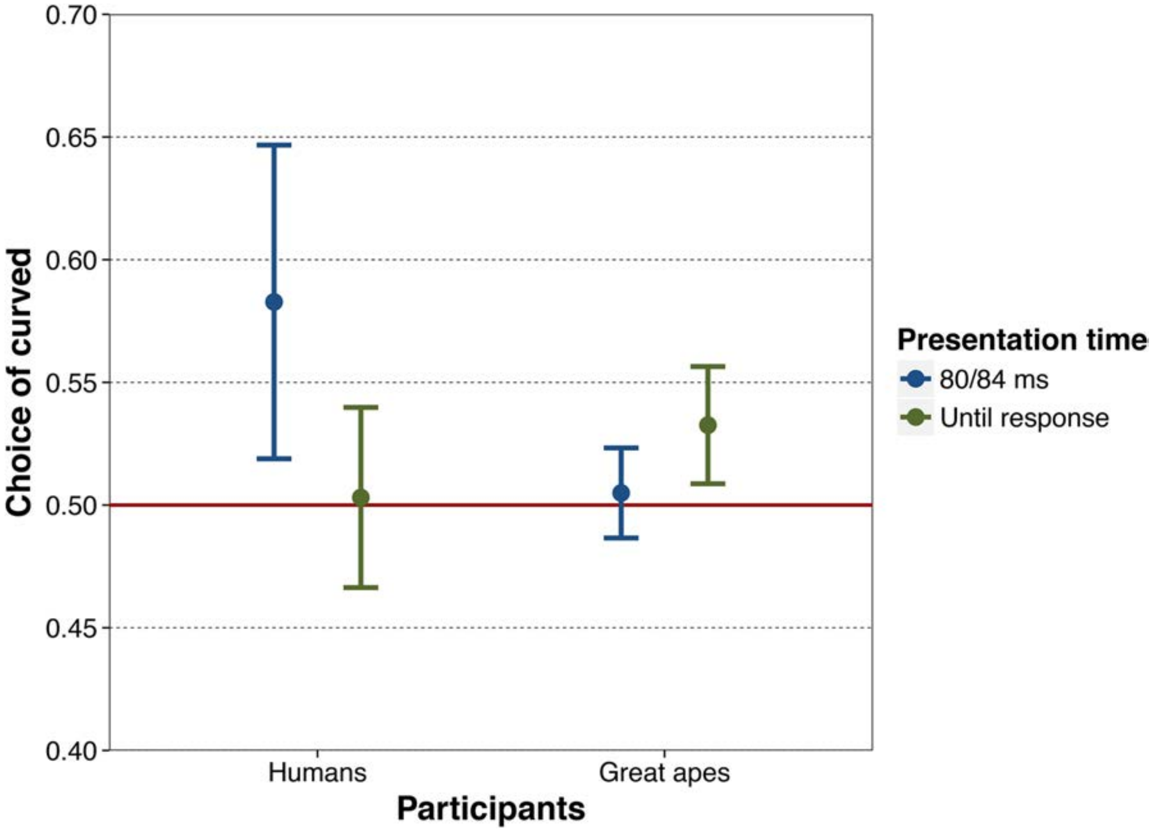

Fig 4. Proportion of curved stimulus choices by humans and great apes. From left to right, 95% confidence interval of the proportion of curved choices by humans when stimuli pairs were presented for 80 ms (Experiment 1) and until response (Experiment 2), and by great apes when stimuli pairs were presented for 84 ms (Experiment 3) and until response (Experiment 4). The red line at value .50 indicates chance-level choice.

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both presentations more often than not. Thus, the number of image pairs for which participants' choice was the same in both blocks was greater when the pairs differed in content than when they differed in contour.

Latency. There were no significant differences in the average reaction time (RT) when choosing curved alternatives [*M* = 946 ms, *SD* = 388 ms] or sharp-angled alternatives [*M* = 926 ms, *SD* = 390 ms], [$t(26) = 1.19$, $p = .244$, $d = .05$], or between right [*M* = 904 ms, *SD* = 359 ms] and left [*M* = 918 ms, *SD* = 370 ms] responses [$t(26) = .93$, $p = .36$, $d = .054$]. In contrast, the average RT for contour pairs [*M* = 935 ms, *SD* = 385 ms] was significantly longer than for content pairs [*M* = 884 ms, *SD* = 345 ms], [$t(26) = 2.73$, $p = .011$, $d = .14$].

Experiment 3

Preference. The percentage of items with curved contours chosen by each of the individual great apes after an 80 ms exposure is shown in the S2 File. Overall, apes did not preferentially select objects with curved contours above chance level [$t(8) = .62$, $p = .276$; $d = .207$] (Fig 4).

Consistency. Choice consistency was below chance level [$t(8) = 3.45$, $p = .009$, $d = 1.15$] (Fig 5) with no significant difference between contour and content pairs [$t(8) = .39$, $p = .703$, $d = .081$, contour pairs: *M* = 40.6, *SD* = 8.4, content pairs: *M* = 39.9, *SD* = 9.4]. Thus, for any object pair, the item selected in the first block did not necessarily correspond to the item

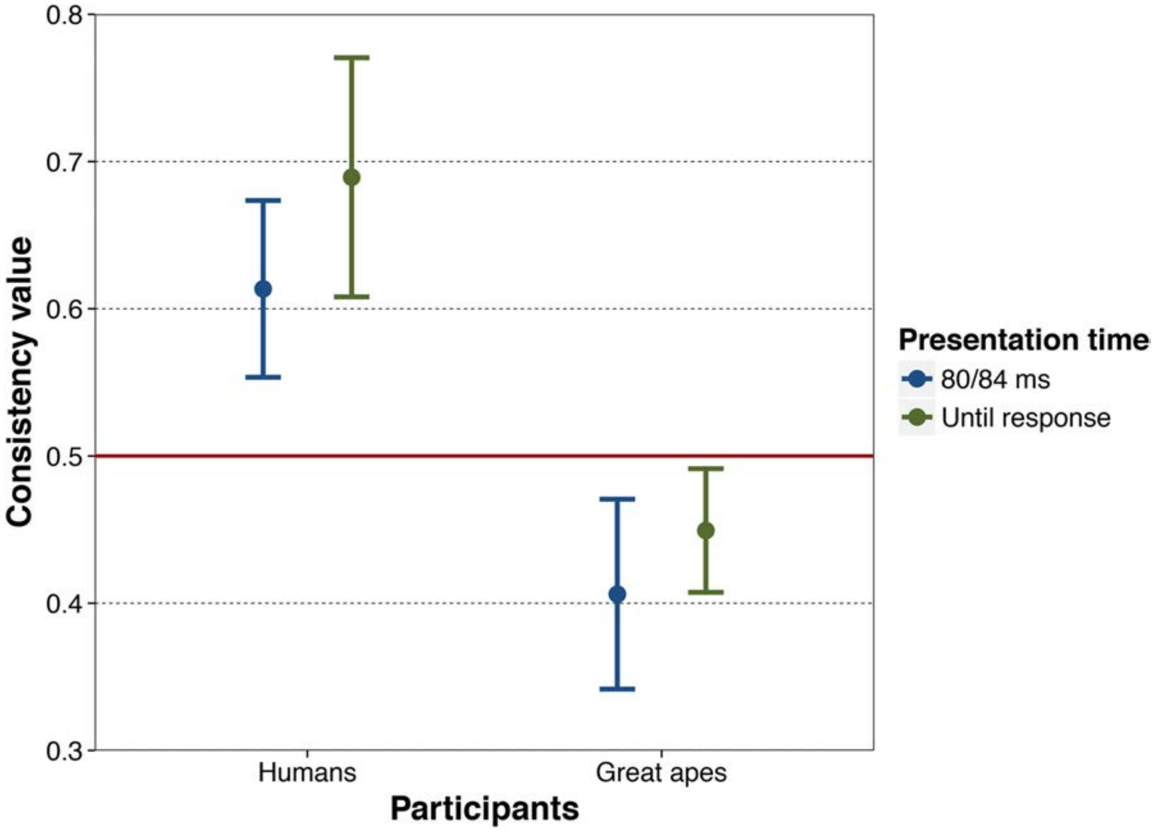

Fig 5. Consistency in the choice in humans and great apes. From left to right, 95% confidence interval of humans' choice consistency when stimuli pairs were presented for 80 ms (Experiment 1) and until response (Experiment 2), and by great apes when stimuli pairs were presented for 84 ms (Experiment 3) and until response (Experiment 4). The red line at value .50 indicates chance-level consistency.

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selected in the second block, revealing that apes' choices were largely unrelated to the identity of the objects in the pairs.

Latency. There were no significant difference in average RT between the curved alternatives [M = 673 ms, SD = 183 ms] and sharp-angled alternatives [M = 670 ms, SD = 167 ms], [$t(8) = .09$, $p = .927$, $d = .018$]. Similarly, there were no significant differences in RT between right [M = 764 ms, SD = 253 ms] and left choices [M = 694 ms, SD = 233 ms], [$t(8) = .74$, $p = .482$, $d = .287$] or between contour pairs [M = 672 ms, SD = 168 ms] and content pairs [M = 711 ms, SD = 185 ms], [$t(8) = 1.85$, $p = .101$, $d = .224$].

Experiment 4

Preference. The apes chose the objects with curved contours significantly above chance level [$t(8) = 3.15$, $p = .007$; $d = 1.05$] (Fig 4). An item-by-item analysis based on 90 trials (9 participants x 2 blocks x 5 sessions) revealed that participants chose objects with curved contours above chance [$M = 53.2$; $SD = 8.2$; 95% CI: 50.4–56.0; $t(35) = 2.36$, $p = .012$, $d = .393$]. Therefore, preference for curved objects was observed both across participants (with a large effect size) and across image pairs (with a moderate effect size). An analysis of the course of apes' choices over the 5 test sessions indicated that apes chose curved versions of the target pairs significantly above chance level even in the first session (they chose these alternatives on 57.1% of

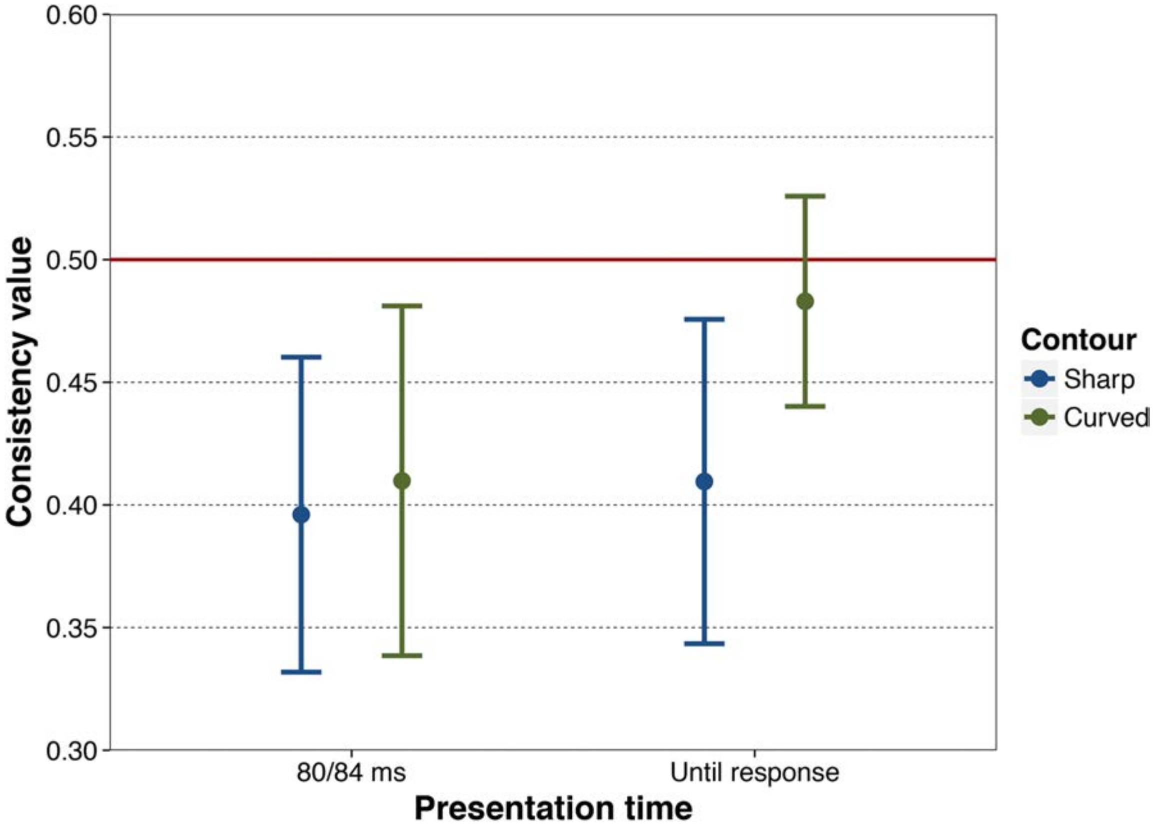

Fig 6. Consistency in the choice of curved and sharp-angled contours only in great apes. Consistency results from Experiments 3 and 4. From left to right, 95% confidence interval of great apes' choice consistency when stimuli pairs were presented for 84 ms for sharp-angled and curved contours (Experiment 3), and when stimuli pairs were presented until response for sharp-angled and curved contours (Experiment 4). The red line at value .50 indicates chance-level consistency.

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the trials; $t = 2.208$, $p = .027$, 95% CI: 50.8–63.1%), and that this pattern did not vary significantly across sessions (S2 File). Finally, a study of the effects of the random rewards showed that apes' choices in the second block were unrelated to whether their choices in block 1 had been followed by a reward or not (S2 File).

Consistency. Consistency was significantly below chance [$t(8) = 2.84$, $p = .022$, $d = 0.95$] (Fig 5) with no difference between contour pairs [$M = 44.9$, $SD = 5.46$] and content pairs [$M = 44.7$, $SD = 6.95$], [$t(9) = .12$, $p = .906$, $d = .04$]. However, apes were significantly more consistent when in the first block they chose the curved compared to the sharp-angled alternative [$t(8) = 2.51$, $p = .036$, $d = 1.04$] (Fig 6). Thus, the apes were more likely to choose the same alternative if in the first block they had chosen the curved rather than the sharp-angled one.

Latency. There was no significant difference in RT between the curved alternatives [$M = 849$ ms, $SD = 123$ ms] and sharp-angled alternatives [$M = 793$ ms, $SD = 203$ ms], [$t(8) = 1.16$, $p = .28$, $d = .34$]. Similarly, there were no significant differences in RT between right [$M = 830$ ms, $SD = 227$ ms] and left responses [$M = 848$ ms, $SD = 150$ ms], [$t(8) = .31$, $p = .767$, $d = .097$] or between contour pairs [$M = 827$ ms, $SD = 151$ ms] and content pairs [$M = 799$ ms, $SD = 192$ ms], [$t(8) = 2.08$, $p = .095$, $d = .369$].

Discussion and Conclusions

We found a double dissociation in choice preference and choice consistency between the human and ape groups tested in this study when confronted with pairs of objects that differed in the aspect of their contour. Regarding the choice patterns, both the human group and the ape group showed a preference for objects with curved (as opposed to sharp-angled) contours, albeit under different presentation conditions. In particular, the human group preferred objects with curved contours under brief presentation conditions (with a large effect size), but not under free viewing conditions. In contrast, the ape group showed the reverse pattern: they preferred objects with curved contours under free viewing conditions (with a moderate effect size), but not under brief presentation conditions. With regard to consistency, in each of their two experiments the human group showed choice consistency above chance levels, whereas the ape group showed choice consistency below chance levels. Participants in the human group tended to select in the same way when presented with the same stimuli pairs a second time, whereas those in the ape group did not. Next we discuss the implications of each finding in turn.

Human participants exposed to pairs of objects for 80 ms showed a preference for objects with curved contours over objects with sharp-angled contours. Our results are comparable to the values reported in previous studies [10–16]. This finding reinforces the notion that preference for curved contours is a robust finding, stable across different experimental paradigms. In contrast, when presented with the same stimuli under free viewing conditions, the human group showed no preference for curved contours. Interestingly, the only previous study failing to find a marked behavioral effect of curved contours [16] involved long presentations and used a behavioral approach-avoidance procedure similar to our own (Experiment 2). Although some other studies using long presentations reported an effect of curvature [10,13,15], participants were required to respond to questions about value judgments (attractiveness, pleasantness, liking, or beauty), rather than to produce an overt motor response.

The preference for curved contours with short but not long presentation times in the human group was reversed in the great ape group (Experiments 3 and 4). Unlike the human group, the great ape group showed no preference for objects with curved contours when presented for 80 ms (Experiment 3) but showed a preference under free viewing time conditions. It is unlikely that this disparity occurred because participants in the ape group were unable to perceive stimuli when presented for short durations. Research using visual masking paradigms —which measure visibility of a brief visual target followed by a mask—has shown that both humans and chimpanzees are able to perceive and respond to stimuli with 60 ms temporal asynchrony between target and mask [41]. Given that the presentation time in our experiments was slightly longer, the lack of preference for curved contours in the group of apes when stimuli were presented for short durations requires another explanation. One possibility is that ape participants were not looking at the screen continuously, therefore missing the briefly presented stimuli in some trials. Another possibility has to do with differences between humans and apes in processing visual objects. Humans show an advantage over chimpanzees in processing global features of objects [40, 42]. In our brief presentation task, thus, the global qualities of the presented objects—including contour, whether curved or sharp-angled—might have played a greater role in the decisions of participants in the human group than in the decisions of participants in the ape group. Further research is required to better understand how these factors might affect individuals' responses.

The human and ape groups differed in their choice consistency. Even when contour did not influence human participants' choice (under long stimuli presentations), their consistency scores were very high, even higher than when stimuli were presented for 80 ms. Their choices, thus, were not arbitrary, but tended to be systematic. Moreover, content pairs (depicting different objects with the same sort of contour) showed higher consistency than contour pairs (depicting the same object with different contours). This suggests that participants' choices were driven mainly by content, meaning, or preferences for other visual features. Thus, under longer presentation times, the human group's initial behavioral preference for curved contours, related to low-level features, may be superseded by more elaborate choices related to the content, semantic processing [14], or to other sources of visual preference.

In the ape group, choice consistency for both brief and free-viewing presentation modes was below 50%. It is conceivable that this result simply reflects the way the task was implemented. Apes were rewarded regardless of their response. Given that responses to either side of the touchscreen were followed by reinforcement that was response independent, they might have responded on the same side of the touchscreen for convenience. In other words, if one participant chose to respond mostly on one side and kept doing in the second block, were the alternatives in each pair were presented on opposite sides of the screen, the consistency necessarily dropped below 50%. This explanation is supported by the strong lateral bias, especially with short presentations, and the large variability among individuals.

One important goal of our study was to develop an experimental paradigm that could be administered to both humans and apes. This is important because the field of comparative cognition often relies on indirect comparisons across species, and requires more studies that test species on the same tasks [43]. Nevertheless, "there is no single method that can be applied without bias across taxa" [43], and although we have sought to standardize the essential features of our paradigm, some differences remain between the experiments carried out with the group of humans and the group of apes, something that is a common practice in comparative psychology [44, 45]. In our study, humans responded by using a keyboard and apes by using a touchscreen, humans performed the experiment in one session whereas apes received 5 sessions, and apes received random food rewards to maintain their motivation but humans did not. Note that we found that apes' preferences were not affected by the reward regime (S2 File).

In sum, our results showed that the human and ape groups shared a preference for curved over sharp-angled contours. Future studies are required to replicate and extend these results to individuals belonging to different cultures and with different upbringing histories. Although our data cannot refute the possibility that such preferences evolved independently in humans and apes, it is possible that the human preference for curved objects and avoidance of sharp-angled ones evolved from visual preferences in the common ancestor of humans, chimpanzees, and gorillas. Throughout the evolution of the human lineage this visual preference for curved contours seems to have become stronger, perhaps due to the increasing relevance of global configuration processing, and susceptible to the influence of semantic information and preferences for other perceptual qualities.

Supporting Information

S1 File. The ARRIVE Checklist. Animal Research Guidelines: Reporting In Vivo Experiments.
(PDF)

S2 File. Tables and other results. Individual results in apes, analysis whether apes choices were influenced by multiple test sessions and analysis of the influence of the rewards administered in block 1 on choices in block 2.
(PDF)

S3 File. Data Supporting Information. Raw data from experiments 1, 2, 3, and 4.
(XLSX)

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Author Contributions

Conceived and designed the experiments: EM GGP JC MN. Performed the experiments: GGP. Analyzed the data: EM GGP MN. Contributed reagents/materials/analysis tools: EM GGP JC MN. Wrote the paper: EM GGP JC MN. Facilities for experimental with great apes: JC. Designed the software for the experiments: GGP.

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5. DISCUSSION

Our research has not only yielded empirical findings of interest, but it provides a good example of a new approach to aesthetic cognition rooted in its biological functionality.

While the former can be of use to all those interested in curvature and visual perception, it is limited in scope, and –pending further research and replication– open to interpretation. On the other hand, approaching aesthetics from an embodied, naturalistic point of view requires to pragmatically adopt a certain mind-set that some will not find agreeable. Still, I find both dimensions to have their very own strengths, weaknesses and affordances; which I will consider and expand on in what follows.

Redefining Aesthetics

When, in a previous chapter, I stated my object of study by defining aesthetics, some readers might have gotten the idea that, by doing so, I was attempting to reach for its real, factual nature. Now, I would like to take a moment to dispel that notion.

The less abstract a field of study is, the easier it becomes to confound concepts and reality. We are quite certain we know what art –or aesthetics– is. We experience it every day, and are able to identify behaviours and objects as artistic or aesthetic with ease. Therefore –we reason– there must be an underlying quality linking each of these happenstances under such distinct concepts.

This line of thinking is sensible and sound. No other but Heidegger, in a piece that went later to become a classic of aesthetic philosophy, wrote:

> "It is said that what art is may be gathered from a comparative study of available artworks. But how can we be certain that such a study is really based on artworks unless we know beforehand what art is? [...] So we must move in a circle. This is neither *ad hoc* nor deficient. To enter upon this path is the strength, and to remain on it the feast of thought –assuming that thinking is a craft." (Heidegger, 2002, p.2)

In fact, engaging in such an empirical loop would be a laudable activity for any art critic or *aficionado*. It would provide a good understanding of his aesthetic *zeitgeist* and give a fair vantage point from which to value and curate contemporary artistic activity. But it would not bring much insight about the universal nature of art or aesthetics, if there was such a thing.

This realization could prompt us to open up new horizons by enlarging the empirical pool of data including different cultures and periods. This is, indeed, an increasingly popular approach. After an encyclopaedic and strenuous effort, researchers are happy to quit once they have produced a definition of aesthetics or art that fits both Western and Eastern tradition, classical and postmodern, ritual and individual experiences, disinterested and utilitarian intentionalities.

Not only are these new boundaries set around what amounts to a drop in the ocean of human experience, they usually result in unpractical and broad definitions that barely reflect the kind of phenomena the researcher set out to study in the first place.

We could, then, decide to go one step further. To abstract aesthetic experience in such a way that it becomes a broad faculty, which might even extend to other animals. It is obvious I find this approach to be more promising; but it would be a poor –and not uncommon– mistake to believe that, by following it, we have reached a final destination, and thus revealed the true nature of aesthetics.

Our human cognition is built so that we constantly seek answers. And while we happen to be a especially resilient mammal, there comes a time when we have no choice but to lay down mumbling "that must be it". We are also fairly sedentary and loyal to our own ideas. So, once such a point is reached, we settle down and start building an impressive and beautiful fortress.

This is the realm of just-so stories, and it might explain the limited impact of evolutionary approaches to human behaviour. Through the years, questioning just-so stories has become a second nature to me, as I find them to be the most dangerous threats to evolutionary and naturalistic thinking. "Those who love you the most, hurt you the most", they say. And –in this particular case– certainly so.

Surely, the evolutionary study of human behaviour has always been subjected to a series of constrains and prejudices that have hindered its development. Once an again, a new current would attempt to look at humans in light of biological knowledge, to soon be shunned down as a result of a series of unfounded fears. Accusations of reducing the complexity of human nature to that of a soulless ape, justifying the *status quo*, xenophobic ethnocentrism or biological determinism have been constant. Darwinists, cultural evolutionists, sociobiologists, and evolutionary psychologists, all have had to face a hostile environment which did not care much for understanding their premises and findings.

But instead of placing the blame in external forces, it is wiser and more constructive to look at the shortcomings of our own position. And the fact remains that just-so stories lie at the very core of evolutionary theory. Without knowledge of genetics, endocrinology or neuroscience –among others– and arising from a reasonably limited amount of empirical data, there are various reflections in Charles Darwin's own work that are but that –stories, hypothesis. Still, while evolutionary biology has grown out to be a sound, complex and formal body of knowledge, many contemporary claims regarding the evolutionary roots of human behaviour have little to offer that was not already present in *On the Origin of the Species* and *The Descent of Man*.

In fact, the field of evolutionary aesthetics has been witness to a good example of this kind of naïve narrative endeavours. In a misguided –if well intended– attempt, Ramachandran and Hirstein set themselves out to found the *Science of Art* (Ramachandran & Hirstein, 1999). They selected a set of eight heuristics underlying aesthetic experience in response to art. A plausible explanation was devised so that most visual artistic production could be explained in terms of a peak shift effect. This super stimulation of modular '*form primitives*' hard wired in our brain –usually by sexual selection– was decided to be the basis of human artistic behaviour and, by extension, aesthetics. It was quick and clean. *Veni, vidi, vici*.

That such prominent and qualified researchers could consider that there is no need to know and understand the conceptual specificities and distinctions regarding aesthetic experience and its relation to art is somewhat puzzling. That they could entertain the notion of explaining a complex set of cognitive processes with a simple, untested, assumption is –alas!– too common.

In other cases, what should have been the starting point of a promising research venture, becomes an end in itself. Researchers focus on piling up empirical evidence to prove an initial hypothesis; as if, by simply showing the plausibility of a given cognitive adaptation, something was accomplished.

Let us consider, for instance, the case of the Snake Detection Hypothesis (SDH). This theory states that different primates, including humans, have developed the ability to quickly detect the presence of snakes in their surrounding environment (Isbell, 2006). Being able to avoid a common predator would result in an increase in overall fitness, which would have prompted a cognitive adaptation through means of natural selection.

In 2006, Lynne Isbell produced an impressively thought out and documented paper in which snakes were posited to be a driving agent of primate visual specialization and brain expansion. Not only were her claims backed by empirical data, but neatly characterized as 9 testable core predictions followed by no less than 27 corollary hypothesis and predictions.

I firmly believe that Isbell's work should serve as a template for anyone willing to claim a certain cognitive trait to be the result of adaptive evolution. At the same time, I have some reserves when considering the usefulness of such an attempt.

If we take the SDH as a soft claim, there is no denying its productive value. *Snakes as agents of evolutionary change in primate brains* has been cited more than 220 times in ten years; while more than 70% of the papers that explicitly mention the term "snake detection hypothesis" were written after its publication. But, whereas Isbell's insights will continue to prompt many interesting pieces of research, establishing the factual reality of a snake detection mechanism in primates, or proving said predators to be a driven force behind our visual specialization and brain expansion, seems a pointless –if not impossible– endeavour.

"Correlation does not imply causation" might sound like a tired *cliché* by now, but it remains a basic axiom of scientific practice. If we were to provide sound evidence supporting all 9 core predictions proposed by Isbell, we would still be unable to prove the SDH. Furthermore, if there was a way to demonstrate such a hypothesis, the relevance that finding would have, in isolation, would be minimal.

In other words: providing sufficient evidence of the factual occurrence of a given phenomenon is a feasible and well defined task. Finding the true interpretation of that very isolated phenomenon is not only impossible –is useless. Most practical implications will be derived from proving the occurrence itself; while a better understanding of it will only be possible in the frame of a broader, well modelled theory of cognition.

A true evolutionary approach to the study of cognition should give it is place in nature, giving no mind to untestable historical narratives. In his insightful *Are We Smart Enough to Know How Smart Animals Are?*, Frans de Waal (2016) settles down on naming such an approach *evolutionary cognition*, after pointing out how *animal cognition* is erroneously reserved to the study of non-human animals. For once, I will dare to argue against the great ethologist. We should not make any effort to accommodate outdated notions downplaying the biologically informed study of behaviour as if it was a mere trend or methodological approach. Animal cognition[10] is the correct, contemporary term suited to describe this field; while *evolutionary cognition* should be reserved –in an analogous manner to *evolutionary biology*– to the attempts at understanding the natural history of cognitive processes.

Simply put: studying cognitive phenomena without taking in account the implications of evolutionary theory is akin to studying the sky and stars disregarding physics. You can do it and call it whatever you please; but it will not be science.

In this way, experimental psychology, ethology and physical anthropology, by simply placing behaviour in its natural context, have been more successful advancing the naturalistic understanding of cognition than those approaches that call themselves *evolutionary* without going beyond providing ready-made narrative explanations to observed phenomena.

This does not mean we should ignore natural history –not at all! When behaviourist first decided to focus their attention in measurable behavioural responses, following a black box model that was to be extended to every animal –including humans–, they made a sensible choice. They lacked many of the conceptual and technical tools underlying current cognitive science; so, by basing their studies in evident observable phenomena, they were set for a more reliable and productive research. But, as soon as this methodological choice turned into an ontological belief, it became poor science –to the point that its influence in contemporary research is minimal and often suspected.

In fact, while Cartesian dualism is often singled out as a negative influence in the contemporary philosophy of the mind, I find Platonic idealism to be a more ubiquitous and malignant baggage of Western thought. It is too often that what should have remained a methodological choice or a tentative hypothesis becomes a fossilized dogma; an end in itself of little practical use.

Therefore, we should focus in documenting and understanding cognitive phenomena in their natural role as part of a living organism subjected to evolutionary forces. Trying to guess the particular history of a given cognitive trait from fragmented and limited data is

[10] Or, simply, cognitive science –for the notion of cognition could arguably be extended beyond the animal realm.

not only prone to error, but might end up diverting our attention from more fruitful studies.

Until very recently, most research on SDH employed snake photographies as target stimuli. But in 2014, Vanessa LoBue got the idea to break down the snake body in its low level perceptual features, finding that curved lines were as salient as the images of snakes themselves (LoBue, 2014). As I will discuss later, this could mean that snake detection is not a specialized adaptation, but a concrete example of a general aesthetic primitive.

As we see, the problem is not that approaches such as that of SDH might be ill-suited to describe reality. It is that their lack of abstraction and unfounded certitude difficult communication outside of specialized fields and reduces the possible object and methods of study when addressing a particular phenomenon.

This ties back to the earlier-discussed need to differentiate the study of aesthetics from that of art. There is, undoubtedly, much to be learned from an empirical study of the arts. And such knowledge can be invaluable to better understand aesthetics. But both fields of study are of a very different nature, and should never be confused.

The study of the arts is the study of a certain cultural production derived from a variety of human cognitive traits, including aesthetics. Moreover, as long as arts are considered to involve the transmission of information through sensory means, their study and practice will help us better understand the nature of aesthetics.

In chapter 3 I wrote I regretted not making a stronger case for the distinction of both areas in our contribution to *The Cambridge Handbook of the Psychology of Aesthetics and the Arts*. And yet, for most of this chapter, my arguments have been referring to both fields of study as a whole. There is no denying that, historically, most research about aesthetics has been concerned with art. That is why often, even being aware of such distinction, authors find it difficult to talk about one without mentioning the other.

But the distinction exists and should be made explicit. Especially so if we are striving for an evolutionary informed approach. Being a cultural product, arts are not only dependant on human cognitive capacities, but on a historical context that determines expectations, traditions, uses and rules. In that way, trying to encompass such an activity within a broad category, spanning countless cultures and centuries, is not only myopic but doomed to failure.

On the other hand, aesthetics is an abstraction that models a certain ability common to most living beings –automatically transforming the continuous flow of sensory data into useful information. Therefore, it makes sense to look at it in the context of biology and natural history, and as building block of animal cognition.

Our experiments exemplify the way in which such an approach can be successfully implemented. We turned our attention towards human sensibility to contour, a phenomenon that visual art and design have often exploited. By modelling it as a case of a broad cognitive capacity, we were able to reduce it to its basics. This, then, allowed us to use more general and diverse kinds of stimuli in a task that has little resemblance to human artistic experience. By doing so, this task could be reliably extended to different cultures and species, prompting a similar response that could be fairly compared.

I believe this to be the most important contribution of our work; and it is my hope it will inspire others to look at aesthetics as a feature of animal cognition: a low-level set of sensory systems with a defined biological basis and function.

Comparative and cross-cultural research as a standard methodology Aesthetic cognition is posed to be feature present in most animals and common to all human cultures.
An ecological understanding of animal cognition Animals are autonomous living organisms shaped by evolutionary pressure as determined by a given environment. Cognition only makes sense in the context of such environment.
An embodied understanding of animal cognition If cognition is the act of processing sensory data, aesthetics is the low level, early stage of such process. Animal cognition, including human, should not be modelled as a disembodied, rational, discursive function
A research informed by typical animal behaviour and needs Focusing on the interaction of animals with their environment means understanding their niche and special capacities. Research in aesthetics should exploit those sensory situations and stimuli of most interest to each species.
A multimodal understanding of aesthetics If aesthetics informs an animal of its environment, the same kind of stimuli will often have similar effects when presented in different sensory modalities. Still, there might be conflicts and, as per the previous point, some modalities might be stronger than others.
A low level understanding of aesthetics The object of study of aesthetics should be the smaller functional element of a given phenomenon, which could be called an aesthetic primitive. If a stimulus can be broken into more basic features, but these features produce a different response to that of the original component, they should be considered distinct primitives on their own.

Table 2. Theoretical and methodological implications of the approach to aesthetics discussed

Preference for Curvature: How Little We Know

Our research has demonstrated that, when presented with two stimuli varying in contour, groups of humans belonging to different cultures –but also groups of non-human primates– tend to choose the one containing most curved features. In order to simplify, we have chosen to refer to this occurrence as *visual preference for curvature*.

As discussed in *Preference for curvature: A historical and conceptual framework*, this is a somewhat problematic simplification. There is a lack of a clear definition of *curvature* or *curved* in the literature. But, while we wait for a more than needed psychophysic study of the matter, employing a common term that is easily understandable seems a fair choice. Still, we often use the –slightly– more specific phrase *visual preference for curved contours*. By doing so, we are underlining that our results regard complex stimuli and might be unrelated to other studies that address curved lines and zig zags in isolation.

Whilst the interest for curvature was sparked by early 20th century empirical research on the emotional values of lines, most contemporary research employs geometrical forms, and images of real and abstract objects. It has not been proven that these two phenomena are in fact the same, but –literature being scarce– past findings are usually employed as arguments when discussing contemporary research on contour.

I believe that, until a proper definition of curvature is established, clearly denoting the kind of stimuli employed is a practical solution. It drives attention to an unresolved matter while, at the same time, making easier to identify different subjects of study; which would result especially useful if, at some point, curved contour and wavy lines were found to constitute different aesthetic primitives.

The use of *preference* might also be brought into question. Sceptics could consider a fault of anthropomorphism to talk of *preference* when referring to chimpanzees and gorillas. Here I would like to take a cue from de Waal (2016) and point out that –as far as I know– *preference* is the best way to describe what happens when, of two different possibilities, you systematically tend to choose that which belongs to the same type. It does not matter whether you are a human, a chimpanzee or –hypothetically– a crow. If you tend to choose the curved stimuli when presented with both sharp and curved possibilities, you *are preferring* curvature.

It has also been pointed out that our procedures with non-humans and humans are not fully comparable. For instance, while human participants were tested during a single session, chimpanzees and gorillas underwent five sessions spread among five days, that were later averaged. Also, due to budget and practical constraints, humans input was recorded by means of a keyboard, while chimpanzees and gorillas used a touch screen. Moreover, humans were given verbal instructions, which were absent when working with their primate cousins –though I certainly thanked my hairy volunteers for their cooperation, I did not go as far as to sit there and tell them what they were supposed to do!

Of these criticisms, I would only –hesitantly– accept that of differences in the ways in which participants were expected to interact with the stimuli. Knowing beforehand that using a touch screen would be the more practical solution when working with non-human primates, we should have employed a similar set up for humans. On the other hand, that would have limited our research in the field, not to mention that it would have supposed an extra layer of technological complexity –increasing the possibility of artefacts when working with communities not used to such devices.

In fact, this possibility highlights the fact that comparative psychology should not be identical, but comparable. As closer as we are to chimpanzees, we have different expectations and needs. I have –half-jokingly– pointed out that the apes did not receive verbal instructions when presented with the task. Disregarding that, actually, one reviewer did see this as problematic, the fact remains that we cannot –should not!– keep humans in a room, training them without verbal instructions until they learn the mechanics underlying the experiment. Humans expect direct communication from someone of their species. They also have a highly self-reflective cognition that might drive them to second guess the researcher when presented once and again with the same task. Chimpanzees do not care that much for our theories and get distracted by environmental noises, fallen pieces of fruit or lost strands of straw. That is the reason they must be tested during several sessions, so that data noise is filtered out.

In general, we should make an effort to design our experimental tasks so that they adapt to the peculiarities of the different species studied. With this in mind, it would be desired for future research to employ more familiar stimuli, and different tasks better suited for each species' everyday behaviour.

The aesthetics of curvature

The limited scope of our empirical data discourages me from making any claim about the universality, nature or origin of preference for curvature in primates. Still, when confronted with extant research, the data reinforces certain hypothesis and plausible interpretations that I will consider in what follows.

There is enough evidence to consider preference for curvature to be a strong tendency among humans. While publication bias might have obscured negative results, it is doubtful for the different findings collected in *Preference for curvature* to be mere coincidence. Of special relevance is Fantz and Miranda's (1975) report in infants; which, together with our own findings, make a strong case against cultural learning interpretations. If humans from different cultures, epochs and ages, together with chimpanzees and gorillas, show this tendency, it is unlikely that it results from a historical accident.

It can be argued that non-human primate preference for curvature is far from proved. Certainly, our research is unique enough to demand a cautious exegesis. It is perfectly possible I happened to come upon a particular group of chimpanzees and gorillas enamoured of curves. But, while the extension of this preference to other primates might require further research, our finding reinforces the idea that this phenomenon is universal to our species.

In the opposite direction, the evidence surrounding human preference for curvature makes unlikely –whilst possible– that the results obtained from chimpanzees and gorillas could be a simple matter of chance. Furthermore, I have carried out preliminary eye-tracking studies that seem to show that not only chimpanzees and gorillas, but also bonobos and orang-utans share this preference.

Unfortunately, practical limitations to the exploratory methodology employed in the eye-tracking studies I carried beg for a refinement of the experimental design, so that it is possible to obtain more reliable, noiseless data. The reader should decide whether to trust me when I say that, after testing groups belonging to all hominid genera, I have found them to show preference for curvature that is reflected not only in choice, but eye movement.

Actually, this claim should not be that surprising. As discussed earlier, different primate species have been shown to quickly detect images depicting snakes in a visual search when presented among distractor stimuli. In 2014, LoBue showed that human performance in detection tasks is not affected when the snake representation is reduced to a wavy, curved line.

That the whole Snake Detection Hypothesis could be explained in terms of preference for curvature is yet to be determined. It is certainly an intriguing possibility. For one, both phenomena have a fair amount of evidence supporting its occurrence. Furthermore, LoBue's deconstruction of the body of the snake shows that the low-level features that constitute it are enough to facilitate its detection. And my own preliminary investigation points at an overall faster fixation of curved contoured stimuli when compared to sharp contoured ones.

What about Moshe Bar and Maital Neta hypothesis of sharp angles conveying a sense of threat? (Bar & Neta, 2006) Would it not contradict the idea that snake detection and preference for curvature are related? Yes, it would. And that is the reason I doubt it to be true.

The very fact that researchers have been studying snakes as a constant environmental threat to primates –to the point of suggesting that they could be a driving force behind our expanded brain capacity and visual acuity– goes to show that it was not until we invented the knife that we had a need to worry about sharpness. In fact, upon closer examination, classical examples of sharp, threatening stimuli –such as claws or teeth– happen to be simply pointy, but curved. This is a perfect example of the need to properly conceptualize the phenomenon under study before throwing out wild guesses.

Still, how could preferring curved stimuli be related to detecting predators? Would it not be counterintuitive being cued to approach the kind of shape that best depict a common primate threat? If we consider this, there are three options when looking at the intersection between SDH, preference for curvature and LoBue's findings:

S1. Snake detection has nothing to do with threat detection. Primates happen to be good at detecting curved stimuli; be it because of preference, be it because of perceptual fluency, be it for any other reason. Snake detection is just a particular case of a generalized aesthetic capacity mistaken by researchers as an adaptive specialization.

S2. Snake detection is indeed a specialization, and has nothing to do with preference for curvature; in which case, LoBue's findings are likely an example of quick detection of curved lines, and not a deconstructed case of snake detection. It would be quite strange for primates to have developed the capacity to detect a particular threat based in its distinct contour features, whilst simultaneously being attracted to that very same kind of features.

S3. Wavy lines are, in fact, the elemental features that drive snake detection, a specialized adaptation evolved to avoid an environmental threat. Thus, wavy lines would constitute an aesthetic primitive, but of a completely different nature to that which drives preference for curvature.

If S1 is true, then humans and other primates should be more proficient when performing visual searches of curved stimuli than of sharp ones. Results similar to that obtained when researching snake detection should be found employing curve contoured images with very different semantic meaning. Also, participants should show a tendency to prefer snakes when presented in a 2AFC task together with other common, less curved predator.

Were S2 to be true, then there should be a tendency to avoid snakes, choosing other predators over them when presented in a 2AFC task. Curved contoured stimuli could or could not be rapidly detected; but, if they were, it would be interesting to study the interaction in tasks featuring both snakes and different kinds of curved contoured stimuli.

It would be difficult to demonstrate S3. It would contradict most findings of the first half of the 20th century regarding the emotional valence of lines, in which curved lines were usually associated with positiveness and calmness, and sharp ones with stress. Still, if something would count as evidence, would be replicating LoBue's findings while, at the same time, failing to find a similar visual search performance when employing different kinds of curved contoured stimuli.

Beyond visual perception

Most research on preference for curvature is focused on visual perception. This is somewhat shocking, as the haptic domain seems to be perfectly fitted –if not better– to produce aesthetic responses based on contour features. While it is true that diurnal haplorhines as a group are endowed with higher visual acuity than most mammals (Kirk & Kay, 2004), one cannot help but wonder whether this is an unwanted result of disembodied dualism.

There are, of course, exceptions; such as Jakesch and Carbon report on human preference for curvature on basis of haptic evaluation (Jakesch & Carbon, 2011).But, of particular interest for my work is a clever double experiment devised by Hess, Gryc and Hareli (2013).

Seeking to explore how shapes might influence our social interactions and judgements, they gave participants puzzles depicting human faces. Half the participants' puzzles were built of round pieces, where the other half received sharp ones. Upon completing the puzzle, participants were asked to make a series of personality judgements regarding the person whose face was formed by the puzzle. Those participants who were given round pieces found the individuals portrayed by their puzzles to be warmer and less aggressive.

Still, the authors considered the possibility that "the influence stems from the haptic experience [...] rather than from the shape *per se*". While I have trouble understanding how the haptic perception of a shape is less *shapey* than its visual perception, I have to applaud them for the approach they took to the follow-up experiment.

Instead of simply priming participants showing them curved and sharp cues, they covered a whole room with abstract forms of one contour or the other. While inside that room, participants took part in an economic trust game. As it happens, participants who played when the room was covered in curved shapes had a significant tendency to choose less aggressive strategies than those who were tested in the sharp covered one.

This finding goes beyond showing the aesthetic relevance of curved contour for human cognition. It proves the worth of studying aesthetics by means of controlling environmental cues instead of simply using direct stimuli; of engaging participants in meaningful interactions instead of subjecting them to passive observation. Testing aesthetics in a more natural –if controlled– context is a novel approach that begs to be explored.

A psychophysical definition of curvature
Properly modelling curvature in a testable and unequivocal way is a must that should not be delayed. It is important to establish the threshold of which degree of non-angularity actually constitutes curvature. There is also a need to understand the relation –if any– between isolated wavy lines and closed shapes.

Performance of primates when presented with curved targets in visual search tasks
There is ample evidence of the capacity of primates for detecting snakes in visual search tasks. LoBue's (2014) intriguing findings imply that this might be but an example of a generalized aesthetic sensitivity towards curvature or wavy lines. Were this to be true, the phenomenon described as preference for curvature could be more properly described. Then, the combined body of evidence would allow for claims of such aesthetic capacity being a feature of the primate family.

Probing the aesthetics of curvature down the phylogenetic tree
Aesthetic sensibility to curvature might be more common in the animal world that we acknowledge. It would not be unsurprising if the whole haplorhine branch were to share it. Furthermore, a 2AFC task could be easily adapted to test very different animals with high cognitive capacities and visual acuity, such as corvids.

Environmental and multimodal influence of curved contours in cognitive tasks
Hess and colleagues (2013) have shown how the effects aesthetic modification of environment has in human cognition can be tested and measured. Further exploring this method of study, by testing the influence curvature has in different cognitive processes and contexts, is a worthy pursuit.

Replication of previous findings
Even if there is a reasonable amount of evidence of curvature as an aesthetic primitive, the fact remains that the object of study is ill-defined and research has been fragmented and scarce. It is still needed to replicate or recreate previous studies, especially those from the first half of the 20st century, in order to strengthen the field.

Table 2. Research prospects

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6. CONCLUSSION

Aesthetics can be understood as a broad, low-level cognitive capacity used to ecologically inform behaviour in a bottom-up manner. This results in a naturalistic, gradual approach that focus on the mechanisms underlying aesthetic experience instead of some of its more notoriously influenced cultural phenomena, such as human arts.

Aesthetic experience can be further broken down into units of *aesthetic primitives*, a minimal set of sensory cues carrying meaningful information of use to a given species. This approach favours empirical, directed, controlled research that can be extended to populations of different species and/or cultures, so that findings can be reliably compared and illuminate each other.

An example of such a research program is our exploration of primate visual preference for curvature. By devising a modified two alternative force choice task which simulates an approach-avoidance scenario, we were able to prove the occurrence of said preference among a variety of human groups, as well as among captive gorillas and chimpanzees. Furthermore, preliminary research hints at the possibility that this phenomenon is also found in bonobos and orang-utans.

A revision of extant literature has shown a consistent trend of humans preferring curved contours and lines, even from infant age; which goes to support the hypothesis that curvature is an aesthetic primitive common, at least, to the *Hominidae* primate family. Still, the lack of unified concepts, methods and a proper psychophysic characterization of *curvature* call for a cautious interpretation and much needed research.

Further investigations concerning curvature –or any other aesthetic primitive– would benefit not only from clearly defining the object of study, but from devising replicable experiments adapted to the habits and habitat of the studied species, taking in account the different cognitive processes that could affect or be affected by the hypothesized nature of the aesthetic primitive, and controlling and exploring the interactions between different sensory domains.