

# Sex-related similarities and differences in the neural correlates of beauty

Camilo J. Cela-Conde<sup>a,1</sup>, Francisco J. Ayala<sup>b,1</sup>, Enric Munar<sup>a</sup>, Fernando Maestú<sup>c</sup>, Marcos Nadal<sup>a</sup>, Miguel A. Capó<sup>a</sup>, David del Río<sup>c</sup>, Juan J. López-Ibor<sup>d</sup>, Tomás Ortiz<sup>c</sup>, Claudio Mirasso<sup>e</sup>, and Gisèle Marty<sup>a</sup>

<sup>a</sup>Laboratory of Human Systematics, Universidad de las Islas Baleares, 07122 Palma de Mallorca, Spain; <sup>b</sup>Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697; <sup>c</sup>Centro de Magnetoencefalografía Dr. Pérez Modrego, Universidad Complutense, 28040 Madrid, Spain; <sup>d</sup>Institute of Psychiatry and Mental Health, San Carlos Clinical Hospital, Universidad Complutense, 28040 Madrid, Spain; and <sup>e</sup>Instituto de Física Interdisciplinar y Sistemas Complejos, Consejo Superior de Investigaciones Científicas (CSIC), 07122 Palma de Mallorca, Spain

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**The capacity to appreciate beauty is one of our species' most remarkable traits. Although knowledge about its neural correlates is growing, little is known about any gender-related differences. We have explored possible differences between men and women's neural correlates of aesthetic preference. We have used magnetoencephalography to record the brain activity of 10 male and 10 female participants while they decided whether or not they considered examples of artistic and natural visual stimuli to be beautiful. Our results reveal significantly different activity between the sexes in parietal regions when participants judged the stimuli as beautiful. Activity in this region was bilateral in women, whereas it was lateralized to the right hemisphere in men. It is known that the dorsal visual processing stream, which encompasses the superior parietal areas, has been significantly modified throughout human evolution. We posit that the observed gender-related differences are the result of evolutionary processes that occurred after the splitting of the human and chimpanzee lineages. In view of previous results on gender differences with respect to the neural correlates of coordinate and categorical spatial strategies, we infer that the different strategies used by men and women in assessing aesthetic preference may reflect differences in the strategies associated with the division of labor between our male and female hunter-gatherer hominin ancestors.**

aesthetic preference | brain lateralization | gender differences | human evolution | magnetoencefalography

Neuroimaging studies have elucidated a basic picture of the neural correlates of the appreciation of beauty. Activity has been reported during aesthetic preference tasks in a network of brain regions, including the frontal pole, orbitofrontal cortex, left dorsolateral prefrontal cortex, caudate nucleus, temporal poles, anterior cingulate cortex, and occipital cortex (1–4). Behavioral experiments have shown that men and women rate the beauty of visual artistic and decorative stimuli in different ways (5, 6), but the extent to which the neural correlates of decisions about aesthetic beauty are influenced by the gender of the participants, is currently unknown.

Gender differences in brain activity related with cognitive (7–9) and affective (10, 11) processes have been reported in many instances, showing in many cases differences in lateralization pattern. Such tasks as word generation, spatial attention, and working memory, are lateralized differently in women and men, although not all studies are consistent (12).

The present study seeks to identify differences and similarities in brain activity between male and female participants while rating the beauty of artistic and non-artistic visual stimuli, by means of magnetoencephalography (MEG)—a technique that detects changes in the magnetic fields generated by the postsynaptic activity of neurons, with a temporal resolution of milliseconds. We also seek to ascertain whether any possible differences between the sexes are due to evolutionary processes that occurred along the evolution of the human lineage or in an earlier primate ancestor. If gender-

related differences are identified in relatively conserved brain regions, it is possible that they were inherited from our primate ancestors. If, conversely, differences between men and women appear in brain regions known to have undergone considerable modifications after the human and chimpanzee lineages split, it is likely that they are due to evolutionary processes that were especially relevant to the hominin way of life.

Most gender differences identified in our study correspond to parietal regions. In the genus *Homo*, parietal development leading to brain globularity has been described by palaeoneurologists as a “modern pattern,” characteristic of *Homo sapiens*. In contrast, allometric vertical development, frontal enlargement, and parietal relative shortening would be characteristic of an archaic structural trajectory shared by non-modern taxa, specially *Homo erectus* and *Homo neanderthalensis* (13, 14).

## Results

**Summary.** MEG data were recorded while participants viewed images of unfamiliar paintings by artists from different artistic schools, and “natural” photographs depicting diverse objects and landscapes, urban and rural (Fig. 1). Participants were asked to indicate whether they found each image beautiful or not, emphasizing the importance of expressing their own impressions.

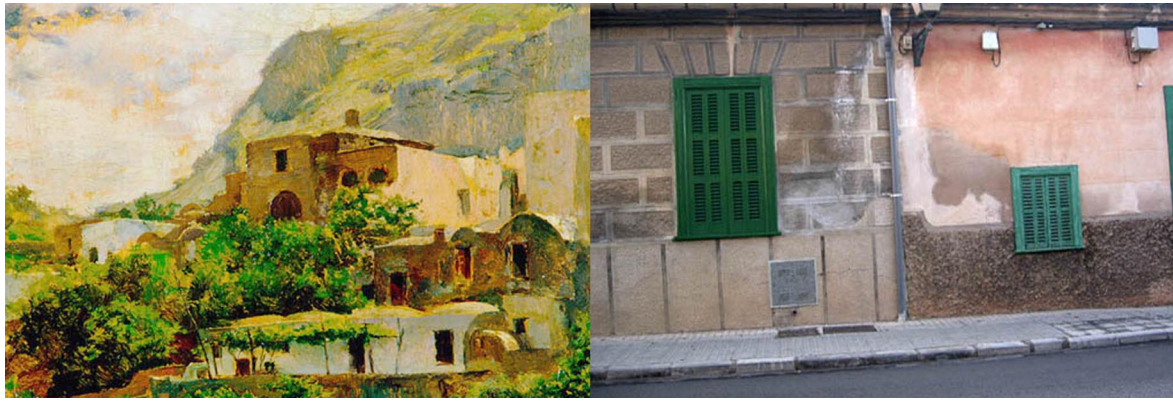
The results (Table 1 and Fig. 2) show that within particular time frames certain brain regions exhibited different activity for stimuli rated as beautiful than for stimuli rated as not beautiful. During the initial 300 ms there were no differences in brain activity associated with stimuli rated beautiful rather than not beautiful, in either women or men. Brain activations in the different time windows are depicted in Fig. 2 and detailed in Table 1. During the 300- to 700-ms interval, activity was greater in parietal regions for stimuli rated as beautiful than for those rated as not beautiful. Moreover, whereas in women this activity was found in both hemispheres, in men it was mainly located in the right hemisphere. Our analysis also revealed small foci of activity in left hemispheric areas that have been shown to be involved in somatosensory (BA 3, 43) (16) and, slightly, in motor (BA 4, 6; see Table 1) (17) tasks.

With regards to the main effects of aesthetic preference, our results show that there is no differential brain activity associated with stimuli rated as beautiful and not beautiful before 300 milliseconds after stimulus onset. Between 300 and 400 ms clear differences in activity appear in a large region of the left superior parietal cortex, and a small region of the left inferior parietal cortex, in the supramarginal gyrus. These regions show activity differences (beautiful more activity than not beautiful) until  $\approx$ 500 ms. After 400 ms the differences extend to superior and inferior right parietal

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<sup>1</sup>To whom correspondence may be addressed. E-mail: cjcela@atlas.com.es or fjayala@uci.edu.



**Fig. 1.** Two examples of the stimuli used in the experiment. (Left) “Paisaje de Capri” (1878), painting by Francisco Pradilla y Ortiz, printed with permission from the Museo Nacional del Prado (Madrid, Spain) Archivo fotográfico. (Right) Photograph of an urban landscape.

regions. Fig. 3 shows the areas that were more activated in beautiful than in not-beautiful perception, regardless of the participant’s gender (that is, the main effects of aesthetic preference).

**Activity in Motor and Somatosensory Areas.** The differences detected in motor and somatosensory areas might be attributed to brain processes related with the physical activity of the response, because participants were asked to lift a finger to signal their response. However, the experiment counterbalanced the response mode, such that half of the participants lifted their finger to indicate they thought the stimulus they were seeing was beautiful, whereas the other half did so to show they thought it was not beautiful. Activity in premotor and motor cortex has been shown in other contexts to be related with tasks involving spatial cognition (18) and mental rotation (19).

In our experiment, the sensation of beauty associated with visual stimuli might involve heightened spatial cognitive processes, increased somatosensory perception, and the planning and execution of movements. Viewers would “navigate,” so to speak, through the space offered by the beautiful image, in agreement with a view recently argued by Freedberg and Gallese (20).

Kawabata and Zeki (1) found greater activity in the motor cortex when participants viewed images they considered to be ugly. Calvo-Merino *et al.* (21) found that beauty ratings of filmed dance movements were related with the right premotor cortex (activity was greater for beautiful stimuli). These authors proposed that the motor system is involved in aesthetic preference at 2 different levels: (i) basic processing and withdrawal behaviors, and (ii) a “form of motor resonance,” as part of activity in a broader network of regions integrating the “mirror system.” However, 4 earlier studies found activity in the prefrontal cortex while participants performed aesthetic preference tasks (see ref. 22 for a review). Differences between the results found in ref. 3 and this article can be attributed

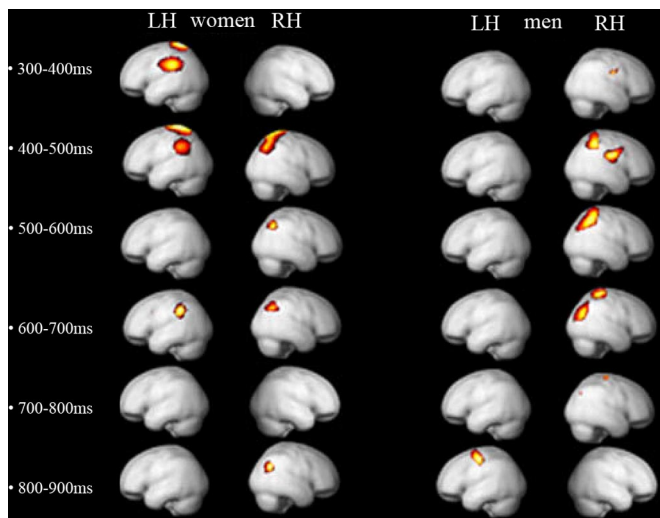
to the source reconstruction model used. The single dipole approach (used by 3) models 1 dipole for every point in time. However, the Minimum Norm Estimation (MNE) procedure used in the present article assesses the possible contribution of 3004 dipoles at each point in time, taking into account the possibility of distributed sources. Another important difference is the threshold for selecting the dipoles. Cela-Conde *et al.* (3) used a GOF (Goodness of fit) and correlation  $>0.9$ . This threshold tends to overestimate part of the activity, such that it is possible that other activity, taken into account with the MNE, is overlooked by the single dipole method. In the present article we chose MNE instead of the single dipole, because we assume that the aesthetic decision process can be distributed in different brain regions rather than being localized in a particular one. The MNE takes this possibility into account, but the single dipole does not.

**Angular Gyrus.** The most relevant results involve activity in the angular gyrus (AG), which is greater for stimuli rated as beautiful in both sexes, and is sustained for a relatively long time interval (500–600 ms for both men and women, and again 700–800 ms for men and 850–900 ms for women). AG activity has been associated with the processing of categorical and coordinate spatial relations (23) and during saccadic eye movements (24), and thus AG activity is not surprising while viewing objects. However, this does not explain why there are statistically significant differences between beautiful and not-beautiful stimuli. The observation of AG activity during non-canonical as opposed to canonical viewing of objects (25) is helpful in the interpretation of our results. Unusual orientations can be described as non-canonical—a cone standing on its point and not on its base, for instance. Thus, it seems that unusual presentation of objects is related to key aspects of the appreciation of beauty, a view that has been asserted by a number of investigators (26–29). Seashore and Metfessel (30) pointed out many years ago

**Table 1. Brain areas in which activity is significantly greater for stimuli rated as beautiful rather than not beautiful**

Subject gender	Time interval					
	300–400	400–500	500–600	600–700	700–800	800–900
Female	Left superior parietal (BA 7)	medial postcentral and left superior parietal (BA 5–3)	Right angular gyrus (BA 39)	Left inferior parietal (BA 40)	No differences	Right angular gyrus (BA 39)
Male	Right postcentral (BA 43)	Right postcentral (BA 43) and right inferior parietal (BA 40)	Right angular gyrus (BA 39)	Right superior parietal (BA 7) with an extension towards the angular gyrus (BA 39)	Right angular gyrus (BA 39) and right precentral-postcentral (BA 4–3)	Left precentral-postcentral (BA 6–4)

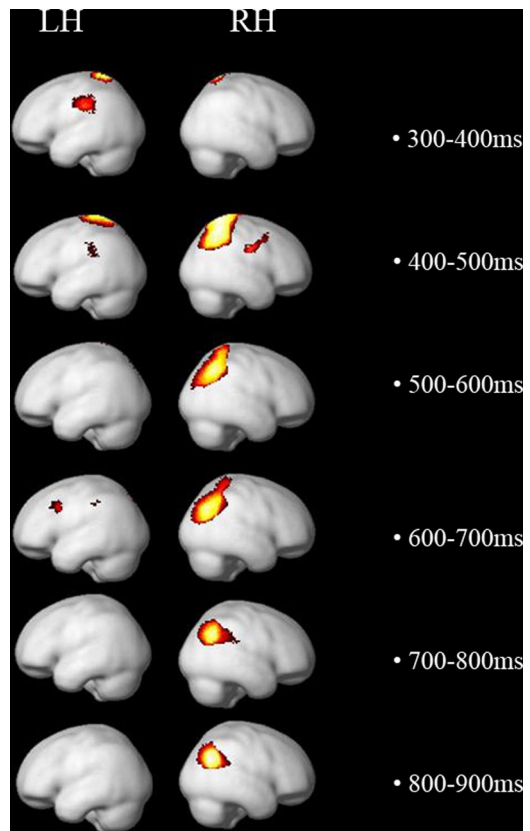
All reported differences are statistically significant ( $P < 0.001$ ). Areas correspond to those used by Tzourio-Mazoyer *et al.* (15). In parentheses: BA, Brodmann area, following Brodmann’s nomenclature.



**Fig. 2.** Brain areas in which activity is significantly greater ( $P < 0.001$ ) for stimuli rated as beautiful rather than not beautiful by women and men during different time intervals. The time window between 300 and 400 ms showed left superior parietal lobe (SPL) and inferior parietal lobe (IPL) in women and right inferior motor area (IMA) in men. The time window 400–500 ms showed bilaterally SPL and IPL in women and right SPL and IMA in men. A 500–600-ms time window showed right IPL in women and right SPL and IPL in men. The time window 600– to 700 ms showed left and right IPL in women and right SPL and IPL in men. In the time window between 800 and 900 ms, differences were concentrated on the right IPL in women and right motor area in men.

that, in music, deviation from the regular constitutes an art principle. Similarly, fauvism, which depicts unusually colored objects, has been associated with distinctive neural correlates of visual perception (31). Accordingly, our results may imply that unexpected depictions of familiar objects and, in general, ambiguity (32), which require spatial abilities of rotation and transformation, are a primary component of aesthetic preference in both sexes.

**Differences Between the Sexes: Categorical vs. Coordinate Spatial Strategies.** Our results showing an early activity of parietal areas for stimuli rated as beautiful in both sexes seem to indicate that the processing of spatial relations is crucial in the human appreciation of beauty. However, as our results clearly show, activity in the parietal regions is bilateral in the case of women but lateralized to the right hemisphere in the case of men. This is not atypical for many kinds of activity; many studies have found that male visual structures and processes tend to be hemispherically asymmetrical, but they tend to be more symmetrical for women (33). The lateralization differences between men and women identified in the present experiment can be explained by Kosslyn's (34) notion of 2 separate processes that code and represent 2 different kinds of spatial relations among objects. Categorical spatial relations refer to positions of objects or their parts in broad categories of location regarding other elements, such as “above or below,” “left or right,” “in front or behind,” “inside or outside.” These categorical spatial relations play a role in tasks that do not require a precise location. Conversely, coordinate spatial relations involve more precise metrical information about distances among objects. Hugdahl *et al.* (35) have noted that in a mental rotation task men tend to use coordinate spatial relations, whereas women tend to process spatial relations in a categorical fashion. These strategies are associated with activity in different hemispheres. The left hemisphere seems to be more involved in the exploration of categorical spatial relations, whereas processes in the right hemisphere seem to underlie coordinate spatial relations (23, 36, 37). Hence, it appears that women and men engage different strategies of spatial analysis during aesthetic preference activity. Strongly lateralized activity in



**Fig. 3.** Brain areas in which activity is significantly greater ( $P < 0.001$ ) for stimuli rated as beautiful rather than not beautiful by all participants during different time intervals. The time window 300–400 ms showed superior parietal lobe (SPL) bilaterally and left inferior parietal lobe (IPL). The time window 400–500 ms again showed SPL and IPL bilaterally and in addition right inferior motor area (IMA). The time window 500–600 ms showed right SPL and right IPL. The time window 600–700 ms showed right SPL, IPL bilaterally and left mid frontal gyrus. The time window 700–800 ms showed right IPL and 800–900-ms right IPL.

the right hemisphere suggests that men use coordinate-based strategies. Conversely, activity in both hemispheres, although mainly and longer in the left hemisphere, suggests women rely on categorical strategies more than men do.

## Discussion

Numerous cladistic episodes have given rise to different lineages throughout human evolution. At least 3 cladistic events are generally recognized: (i) separation between the human and chimpanzee lineages; (ii) appearance of the genus *Homo* and its divergence from the paranthropines (robust hominins); and (iii) emergence of the species *Homo sapiens*, whose likely sister group was *Homo neanderthalensis* (38). It is possible to identify anatomical apomorphies—i.e., distinctive derived traits—that distinguish each of those lineages and that are used to identify each taxon. However, the significance of derived traits is more than taxonomical. The adaptive success of the taxon after a phylogenetic event is usually grounded precisely on its apomorphies. Examining the sets of primitive and derived traits of a new lineage may suggest hypotheses concerning the selective processes that shaped the lineage.

Behavioral traits may also be considered apomorphies, at least in the broad sense. Indeed, distinctive behaviors often are greatly significant to account for a lineage's adaptive strategies. Thus, it is common to refer to bipedalism as a distinctive feature of the tribe Hominini, the manufacture of increasingly sophisticated tools as distinctive of the genus *Homo*, and symbolism as distinctive of *H. sapiens*. Symbolism, in this context, includes such phenomena as



language, and the production of objects that are considered beautiful but may not have obvious practical use.

Particular lineages are associated with distinctive apomorphies, but large taxons may consist of several lineages, which are in turn differentiated by distinctive traits. Thus, within the genus *Homo* and even within a single “species” such as *Homo erectus s.l.*, there is considerable variation in anatomical features, which, in the opinion of at least some authors, justify the identification of several species among the Middle Pleistocene hominins (39). One feature that varies among taxa is the degree of gender dimorphism, which has inspired models of human evolution that assume different adaptive strategies in males and females (40). Here, we raise the question whether differences may also have evolved in the human lineage concerning appreciation of the beauty of objects, symbols, and art. If such sex-related differences have evolved, the issue arises, how could they be detected?

The use of symbols and the capacity to appreciate the beauty of objects and to create them is generally accepted as a significant event in the evolution of *H. sapiens*. Indeed, the capacity to produce and to appreciate aesthetic objects is frequently regarded as an important step in the evolution of the human mind, although when this capacity first appeared is a matter of contention (38). Social behavior, language, a variety of mental capacities and neurological functions, and even diseases, such as schizophrenia, have been related with the appearance of the capacities to appreciate beauty and to produce beautiful objects. Making beautiful objects may indeed be an indication of a capacity to appreciate beauty (41, 42). Together with social organization, the cognitive capacity expressed by the use of symbolism may have decisively contributed to the demographic expansion and geographic dispersion of *H. sapiens* (43).

The importance of aesthetic appreciation in human evolution is evident. The value of object decoration—including the decoration of the body itself—for expressing social behaviors in all cultures has been noticed by anthropologists, ethologists, and psychologists (44). The most obvious explanation for the perception of beautiful features in objects, and for the tendency to decorate the human body, is sexual selection. Selective processes related with gender have granted different primate species the visual perception of color, particularly in the body of opposite-sex conspecifics (45). It is reasonable to hypothesize that the human species, capable of altering its own appearance through decorative colors and drawings, must have evolved the capacity to appreciate beauty. The production and appreciation of colors and symbolic representation may, thus, have first evolved in association with sexual selection. Once these traits appeared they could be used for a variety of purposes in social life.

When did the capacity to appreciate beauty evolve? The evolutionary changes associated with the necessary cognitive development for appreciating the beauty of objects is often linked to the appearance of symbolism (46). However, there is no universal agreement as to what counts as evidence for symbolism and symbolic behavior. Alternative proposals include the manufacture of any symmetric object without any apparent practical use (47–49), or of explicitly decorative ornaments, or of the pigments used to paint them (50, 51). For some authors, the construction of objects resembling a human body would be sufficient evidence of symbolism (52), whereas others assert that only realistic paintings or sculptures, i.e., works of art, can be considered as true manifestations of a symbolic capacity. The arguments in favor of the various and often contradictory points of view have been reviewed by Appenzeller (53). In any case, the production of decorative and artistic objects is widely considered as a fundamental stage in the emergence of modern human behavior. But, the study of the human brain processes related with the cognitive activity of appreciating beauty or art is still in its infancy.

A valuable clue to trace the evolutionary roots of the gender-related differences that we have identified underlying aesthetic preference is to assess whether the differences involve a brain

region exhibiting primitive or derived traits. When compared with monkeys and apes, the human parietal cortex exhibits a number of derived aspects. Hence, the parietal differences between men and women would have occurred after the first cladistic event mentioned above—i.e., the separation of chimpanzee and human lineages—and probably impacted spatial cognition. Humans differ from other primates in certain features related with the cortical representation of the magnocellular visual pathway, linked to the analysis of motion, perspective, relative size of objects, and depth (54). The human brain area V3A (a secondary visual area) is sensitive to motion cues and uses them to extract 3-dimensional information, whereas the monkey area V3A does not share this function (55). Orban *et al.* (55), using comparative fMRI (a technique for measuring brain activity that detects the changes in blood oxygenation linked to neural activity) data and computerized brain warping, have suggested that the ventral and dorsal visual streams have not evolved equally along the human lineage. Rather, the areas included in the ventral stream, related with object representation and categorization, have undergone a smaller expansion than those of the dorsal stream, which are involved in the representation of space and the analysis of visual information to organize action. The parietal areas of the dorsal stream receive only information from the magnocellular system, which support the aforementioned idea of an enhancement of the magnocellular cortical representations during human evolution (56).

If it is accepted, as we suggest, that the parietal regions in humans, when compared with other primates, are derived (apomorphic), the question arises whether it is possible to identify the cladistic event within the hominin lineage that accounts for this evolutionary modification. Obviously, we cannot use the same comparative methods that are used when comparing humans with living primates. Nevertheless, investigations of the endocranial morphology of different taxa of the genus *Homo* have provided some insight (13). According to Bruner *et al.* (13), the brain of modern humans evolved after a parietal development that “may have represented a key to surpass the encephalization constraints imposed by the archaic structural model.” The differences between the decorative objects found in Neandertal and modern human sites support that idea of a “modern brain” capable of appreciating beauty and its uses in different ways (53). Our results suggest that parietal regions of the brain of modern humans, which exhibit clearly derived traits, have a crucial role in the visual appreciation of beauty.

If the dorsal visual pathway has been subjected to evolutionary pressures that have led to the aforementioned modifications during human evolution, we can confidently assume that sex-related differences in this pathway appeared after the human and chimpanzee lineages split. It can also be assumed that some gender-related differences are related to events of significant importance throughout human evolution. We have identified differences between men and women in brain processes involved in aesthetic preference. How could the evolution of these differences be interpreted in phylogenetic terms? Silverman’s and Eals’s (57) “hunter-gatherer hypothesis” (HG-H) of gender differences in spatial abilities provides the most convincing scenario. They argue that the differences in spatial ability between men and women were associated with the division of labor between the sexes in hunting and gathering. Tracking animals and foraging for plant food involve different spatial scenarios and, hence, require different kinds of spatial skills. Silverman and Eals (57) suggest that abilities involved in hunting include the orientation in relation to objects and locations that may be in or out of view, and thus require cognitive transformations that allow keeping an accurate orientation while moving. Conversely, foraging requires recognizing and remembering the contents of varied object assemblies and the spatial relations between objects.

The hunter-gatherer hypothesis does not regard gender differences in the performance of spatial tasks as the product of different



source model are evenly placed at each node of the mesh representing the white/gray matter interface (68). The SPM5 template used contained 3,004 dipole locations. This dipole mesh was used to calculate the forward solution using a spherical head model. A spherical head model is known to be sufficient to estimate a good approximation of the physical head properties and to compute the magnetic field propagation of the forward model (69). The inverse solution (the estimation of the current source density based on the MEG topography) was calculated using the l2 Minimum Norm solution implemented in "in-house MaTLab-code." To estimate the underlying current source density (the source strength at each node of the MNI phantom brain) of the evoked field, the MNE was computed for each time point, subject, and condition. Finally, for each subject and condition, the MNE solutions were divided in 100-ms steps and averaged across the time windows. The resulting MNE averages were submitted to statistical parametric mapping analysis.

**Data Analysis.** The images were analyzed by means of the SPM5 (Statistical Parametric Mapping) software, implemented on MatLab 6.5, using the mod-

ule M/EEG. The experimental design included an intersubject variable (gender) and an intrasubject variable (aesthetic preference, with the levels beautiful and not beautiful). Differences between the levels were contrasted by means of t tests (implemented on SPM5) with a  $P < 0.001$  ( $t = 3.33624$ ) with no adjustment to control. The extent threshold was set to  $k = 10$  voxels. The statistically significant differences found correspond to: (i) brain activity in females when comparing beautiful and not-beautiful stimuli; (ii) brain activity in males when comparing beautiful and not-beautiful stimuli.

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- Kawabata H, Zeki S (2004) Neural correlates of beauty. *J Neurophysiol* 91:1699–1705.
- Vartanian O, Goel V (2004) Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport* 15:893–897.
- Cela-Conde CJ, et al. (2004) Activation of the prefrontal cortex in the human visual aesthetic perception. *Proc Natl Acad Sci USA* 101:6321–6325.
- Jacobsen T, Schubotz RI, Höfel L, von Cramon DY (2006) Brain correlates of aesthetic judgment of beauty. *NeuroImage* 29:276–285.
- Polzella DJ (2000) Differences in reactions to paintings by male and female college students. *Perceptual Motor Skills* 91:251–258.
- Furnham A, Walker J (2001) The influence of personality traits, previous experience of art, and demographic variables on artistic preference. *Personality Individual Differences* 31:997–1017.
- Haier RJ, Jung RE, Yeo RA, Head K, Alkire MT (2005) The neuroanatomy of general intelligence: Sex matters. *NeuroImage* 25:320–327.
- Bell EC, Willson MC, Wilman AH, Dave S, Silverstone PH (2006) Males and females differ in brain activation during cognitive tasks. *NeuroImage* 30:529–538.
- Boghi A, et al. (2006) The effect of gender on planning: An fMRI study using the Tower of London task. *NeuroImage* 33:999–1010.
- Azim E, Mobbs D, Jo B, Menon V, Reiss AL (2005) Sex differences in brain activation elicited by humor. *Proc Natl Acad Sci USA* 102:16496–16501.
- Piefke M, Weiss PH, Markowitsch HJ, Fink GR (2005) Gender differences in the functional neuroanatomy of emotional episodic autobiographical memory. *Hum Brain Mapp* 24:313–324.
- Sommer IEC, Aleman A, Bouma A, Kahn RS (2004) Do women really have more bilateral language representation than men? A meta-analysis of functional imaging studies. *Brain* 127:1845–1852.
- Bruner E, Manzi G, Arsuaga JL (2003) Encephalization and allometric trajectories in the genus *Homo*: Evidence from the Neandertal and modern lineages. *Proc Natl Acad Sci USA* 100:15335–15340.
- Bruner E (2004) Geometric morphometrics and paleoneurology: Brain shape evolution in the genus *Homo*. *J Hum Evol* 47:279–303.
- Tzourio-Mazoyer N, et al. (2002) Automated anatomical labelling of activations in spm using a macroscopic anatomical parcellation of the MNI MRI single subject brain. *NeuroImage* 15:273–289.
- McGlone F, et al. (2002) Functional neuroimaging studies of human somatosensory cortex. *Behav Brain Res* 135:147–158.
- Matsumoto R, et al. (2007) Functional connectivity in human cortical motor system: A cortico-cortical evoked potential study. *Brain* 130:181–197.
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. *Annu Rev Neurosci* 27:169–192.
- Eisenegger C, Herwig U, Jancke L (2007) The involvement of primary motor cortex in mental rotation revealed by transcranial magnetic stimulation. *European J Neurosci* 25:1240–1244.
- Freedberg D, Gallese V (2007) Motion, emotion and empathy in esthetic experience. *Trends Cognit Sci* 11:197–203.
- Calvo-Merino B, Jola C, Glaser DE, Haggard P (2008) Towards a sensorimotor aesthetics of performing art. *Consciousness Cognit* 17:911–922.
- Nadal M, Munar E, Capó MA, Rosselló J, Cela-Conde CJ (2008) Towards a framework for the study of the neural correlates of aesthetic preference. *Spatial Vis* 21:379–396.
- Baciu M, et al. (1999) Categorical and coordinate spatial relations: fMRI evidence for hemispheric specialization. *Neuroreport* 10:1373–1378.
- Mort DJ, et al. (2003) Differential cortical activation during voluntary and reflexive saccades in man. *NeuroImage* 18:231–246.
- Terhune KP, et al. (2005) Recognition of objects in non-canonical views: A functional MRI study. *J Neuroophthalmol* 25:273–279.
- Berlyne DE (1970) Novelty, complexity, and hedonic value. *Percept Psychophys* 8:279–286.
- Berlyne DE (1971) *Aesthetics and Psychobiology* (Appleton-Century-Crofts, New York).
- Humphrey NK (1973) The illusion of beauty. *Perception* 2:429–439.
- Martindale C, Moore K (1988) Priming, prototypicality, and preference. *J Exp Psychol Hum Percept Perform* 14:661–670.
- Seashore CE, Metfessel M (1925) Deviation from the regular as an art principle. *Proc Natl Acad Sci USA* 11:538–542.
- Zeki S, Marini L (1998) Three cortical stages of colour processing in the human brain. *Brain* 121:1669–1885.
- Zeki S (2001) Artistic creativity and the brain. *Science* 293:51–52.
- Amunts K, et al. (2007) Gender-specific left-right asymmetries in human visual cortex. *J Neurosci* 27:1356–1364.
- Kosslyn SM (1987) Seeing and imagining in the cerebral hemisphere: A computational approach. *Psychol Rev* 94:148–175.
- Hugdahl K, Thomsen T, Erslund L (2006) Sex differences in visuo-spatial processing: An fMRI study of mental rotation. *Neuropsychologia* 44:1575–1583.
- Chabris CF, Kosslyn SM (1998) How do the cerebral hemispheres contribute to encoding spatial relations? *Curr Directions Psychol Sci* 7:8–14.
- Okubo M, Michimata C (2004) The role of high spatial frequencies in hemispheric processing of categorical and coordinate spatial relations. *J Cognit Neurosci* 16:1576–1582.
- Cela-Conde C, Ayala FJ (2007) *Human Evolution. Trails from the Past*. (Oxford Univ Press, New York).
- Cela-Conde CJ, Ayala FJ (2003) Genera of the human lineage. *Proc Natl Acad Sci USA* 100:7684–7689.
- Lovejoy CO (1981) The origin of man. *Science* 211:341–350.
- Ambrose SH (2001) Paleolithic technology and human evolution. *Science* 291:1748–1753.
- Balmer M (2002) What made humans modern? *Science* 295:1219–1225.
- Mellars P (2006) Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proc Natl Acad Sci USA* 103:9381–9386.
- Boyd B (2005) In *The Literary Animal: Evolution and the Nature of Narrative*, eds Gottschall, Wilson DS (Northwestern Univ Press, Evanston, IL) pp 147–176.
- Dixon A, Dixon B, Anderson M (2005) Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes, and human beings. *Ann Rev Sex Res* 16:1–19.
- Gabor L (2007) in *Handbook of Theories and Methods in Archaeology*, eds Bentley A, Maschner H (Altamira Press, Walnut Creek, CA), pp 283–296.
- Marshack A (1995) A Middle Paleolithic symbolic composition from the Golan Heights: The earliest known depictive image. *Curr Anthropol* 37:357–365.
- Bednarik RG (1995) Concept-mediated Marking in the Lower Paleolithic. *Curr Anthropol* 36:605–634.
- Bednarik RG (1997) The global evidence of early human symboling behaviour. *Hum Evol* 12:147–168.
- Kuhn SL, Stiner MC, Reese DS, Gulec E (2001) Ornaments of the earliest Upper Paleolithic: New insights from the Levant. *Proc Natl Acad Sci USA* 98:7641–7646.
- Bouzouggar A, et al. (2007) From the cover: 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proc Natl Acad Sci USA* 104:9964–9969.
- Marshack A (1997) The Berekhat Ram figurine: a late Acheulian carving from the Middle East. *Antiquity* 71:327–337.
- Appenzeller T (1998) Art: Evolution or Revolution? *Science* 282:1451–1454.
- Preuss TM, Coleman GQ (2002) Human-specific organization of primary visual cortex: Alternating compartments of dense Cat-301 and Calbindin immunoreactivity in layer 4A. *Cerebral Cortex* 12:671–691.
- Orban GA, Van Essen D, Wim Vanduffel W (2004) Comparative mapping of higher visual areas in monkeys and humans. *Trends Cognit Sci* 8:315–324.
- Barton RA (2006) Primate brain evolution: Integrating comparative, neurophysiological, and ethological data. *Evol Anthropol* 15:224–236.
- Silverman I, Eals M (1992) in *The Adapted Mind*, eds Barkow J, Cosmides L, Tooby J (Oxford Univ Press, New York) pp 487–503.
- Silverman I, et al. (2000) Evolved mechanisms underlying wayfinding: Further studies on the hunter-gatherer theory of spatial sex differences. *Evol Hum Behav* 21:201–213.
- Silverman I, Choi J, Peters M (2007) The Hunter-Gatherer Theory of Sex Differences in Spatial Abilities: Data from 40 Countries. *Arch Sex Behav* 36:261–268.
- Hyde JS, Linn MC (1988) Gender differences in verbal ability: A meta-analysis. *Psychol Bull* 104:53–69.
- Looff WR, Baranowski M (1971) An analysis of five measures of sensation seeking and preference for complexity. *J General Psychol* 85:307–313.
- Frith CD, Nias DKB (1974) What determines aesthetic preferences? *J General Psychol* 91:163–173.
- Chevrier J, Delorme A (1980) Aesthetic preferences: influence of perceptual ability, age and complexity of stimulus. *Percept Motor Skills* 50:839–849.
- Maestu F, et al. (2002) Spanish language mapping using meg: a validation study. *NeuroImage* 17:1579–1586.
- Hauk O, Keil A, Elbert T, Müller MM (2002) Comparison of data transformation procedures to enhance topographical accuracy in time series analysis of human EEG. *J Neurosci Methods* 113:111–122.
- Dale AM, et al. (2000) Dynamic statistical parametric mapping: combining fMRI and MEG for high-resolution imaging of cortical activity. *Neuron* 26:55–67.
- Collins DL, et al. (1998) Design and construction of a realistic digital brain phantom. *IEEE Trans Med Imaging* 17:463–468.
- Mangin JF (1995) From 3D magnetic resonance images to structural representations of the cortex topography using topology preserving deformations. *J Math Imaging Vis* 5:297–318.
- Sarvas J (1987) Basic mathematical and electromagnetic concepts of the biomagnetic inverse problem. *J Phys Med Biol* 32:11–22.