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

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Contributed by Francisco J. Ayala, January 12, 2009 (sent for review January 9, 2008)

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.

Results

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 hemisphere 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 ∼500 ms. After 400 ms the differences extend to superior and inferior right parietal


The authors declare no conflict of interest.

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www.pnas.org/cgi/doi/10.1073/pnas.0900304106

PNAS | March 10, 2009 | vol. 106 | no. 10 | 3847–3852
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 that brain activity might be related to the presentation of objects as well.

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

<table>
<thead>
<tr>
<th>Subject gender</th>
<th>Time interval</th>
<th>Left superior parietal (BA 7)</th>
<th>Left inferior parietal (BA 40)</th>
<th>Right angular gyrus (BA 39)</th>
<th>No differences</th>
<th>Right angular gyrus (BA 39)</th>
<th>Right superior parietal (BA 7) with an extension towards the angular gyrus (BA 39)</th>
<th>Right angular gyrus (BA 39) and right precentral-postcentral (BA 4–3)</th>
<th>Left precentral-postcentral (BA 6–4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>300–400</td>
<td>medial postcentral and left superior parietal (BA 5–3)</td>
<td>Right angular gyrus (BA 39)</td>
<td>Left inferior parietal (BA 40)</td>
<td>No differences</td>
<td>Right angular gyrus (BA 39)</td>
<td>Right superior parietal (BA 7) with an extension towards the angular gyrus (BA 39)</td>
<td>Right angular gyrus (BA 39) and right precentral-postcentral (BA 4–3)</td>
<td>Left precentral-postcentral (BA 6–4)</td>
</tr>
<tr>
<td>Male</td>
<td>400–500</td>
<td>Right postcentral (BA 43) and right inferior parietal (BA 40)</td>
<td>Right angular gyrus (BA 39)</td>
<td>Right superior parietal (BA 7) with an extension towards the angular gyrus (BA 39)</td>
<td>Right angular gyrus (BA 39) and right precentral-postcentral (BA 4–3)</td>
<td>Left precentral-postcentral (BA 6–4)</td>
<td></td>
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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.
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 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 taxa may consist of several lineages, which 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
levels of a single ability, but as the result of the use of different spatial strategies that involve different abilities. Women tend to be more aware than men of objects around them, including those that seem irrelevant to the current task (57), whereas men out-perform women in navigation tasks (58). Men tend to solve navigation tasks by using orientation-based strategies involving distance concepts and cardinal directions, whereas women tend to base their activities on remembering the location of landmarks and relative directions, such as “left from,” or “to the right of” (58).

It could be argued, against this scenario, that differences between women and men regarding spatial strategies are the result of the particular conditions and gender roles that have become established in developed societies. However, an experimental study involving 7 extant ethnic groups, has provided support to the hunter-gatherer hypothesis of human spatial gender differences (59). In all 7 hunter-gatherer groups, men scored significantly higher than women did in a test of 3-dimensional mental rotations.

Conclusions

Our experiment reveals that visual aesthetic appreciation involves high-level cognitive activity, both in women and men. Given that differences appear from 300 ms onwards, it seems that the brain activity identified in the present study cannot be reduced to simple perceptual processes.

The main focus of activity in both sexes is in the parietal lobe. The parietal activity is bilateral in the case of women but lateralized to the right hemisphere in the case of men. The gender-related differences in the neural correlates of the aforementioned cognitive activity indicate that there might be different processing strategies for beauty in women and men. Specifying these differential strategies remains to be ascertained. As we have argued, a possible explanation for the greater lateralization in men than in women could be grounded on differences between exploration strategies. Women would carry out an exploration of categorical spatial relations. The processes occurring in the right hemisphere of male participants suggest an exploration strategy based on coordinate spatial relations.

However, there are other alternatives to the interpretation based on spatial exploration strategies. It is generally accepted that the right parietal cortex is associated with global visual attention and the left with local attention. Perhaps women make use of both global and local features in making their judgments, whereas men only rely on global features.

Another hypothesis could link our observations to language. Women obtain higher scores on a diversity of verbal and language tasks (60). Perhaps women are more likely to associate the images with verbal labels than men, producing the lateralizing differences in neural activity. This hypothesis deserves further experimental work before seriously being taken into consideration.

Even though the specific cognitive processes related with the appreciation of beauty are still to be determined, we propose an explanation for the evolutionary features of such capacity related with sexual selection. Silverman’s and Eals’s (57) hunter-gatherer hypothesis of gender differences in spatial abilities provides the most convincing scenario. Differences in spatial ability between men and women would be associated with the division of labor between the sexes in hunting and gathering.

In any case, given that parietal spatial-processing streams show certain derived traits present only in our species, it seems quite probable that gender-related differences in this pathway appeared after the human and chimpanzee lineages split.

Methods

Subjects. Ten female and 10 male neurobiology students (average age 23.6 years for women, 25.1 years for men) at the Universidad Complutense (Madrid), with no previous training or special interest in art, volunteered to participate in this study. They all had normal or corrected vision and normal color vision. All were right-handed. All participants gave informed consent.

Stimuli. All participants were presented with the same set of photographs of either artistic paintings or natural objects, divided into 5 groups: (i) 50 pictures of abstract art; (ii) 50 pictures of classic art; (iii) 50 pictures of Impressionist art; (iv) 200 photographs of landscapes, artifacts, urban scenes, and the like (true-life pictures from the Master Clips Premium Image Collection, IMSI, San Rafael, CA; the book Boring Postcards, London, Phaidon Press; and photographs taken by us). The artistic styles were decided following the collection Movements in Modern Art from the Tate Gallery, London, but we added European paintings of the XVII and XVIII centuries and Popular Art pictures, like Halloween and Christmas cards. The objective was to present to the subjects a variety of artistic styles to increase their range of aesthetic judgment. To avoid the activation of facial-recognition brain mechanisms, pictures containing close views of humans were not included. Four different sets of stimuli (2 artistic and 2 natural) were used for the participants’ preliminary training.

Observations. All stimuli were adjusted to the same resolution (150 pixels per inch) and dimensions (12 × 9 cm). They were homogenized by 3 operations (see 3 for additional details). First, a behavioral test of semantic judgment was performed to assess the effect of pictorial complexity in aesthetic perception (61–63). 711 stimuli were shown to 14 voluntary subjects (undergraduate university students) on the screen of a Macintosh PowerPC, asking the subjects to score a picture’s complexity from 1 to 10. All pictures receiving a mean around 4.51 points were discarded. Second, the color spectrum of the visual stimuli was adjusted. We analyzed 503 stimuli selected in the previous step, measuring their color spectrum by means of photoshot 6 (Adobe Systems) run on a Macintosh Power Mac G4. Third, the light reflected by stimuli was measured, in a dark room, by means of a Minolta Auto Meter IV F digital photometer placed 40 cm from the screen with an angle of 40° reflected light. Stimul: –356 lux and –365 lux were discarded. A total of 400 stimuli reasonably homogenized in regards to pictorial complexity, color spectrum, luminosity, and light reflection were thus obtained.

Technique. The technique used to register brain activity was magnetoencephalography (MEG). Participants received a short briefing about the technique and the aesthetic preference task they were required to carry out before entering the MEG isolated room. Half of the male and half of the female participants were asked to indicate, by raising a finger, that they found the image to be beautiful. The other half of the participants were asked to raise a finger if they although the image was not beautiful.

We found no differences in the frequencies of beautiful and not-beautiful judgments between the 2 sexes. \( \chi^2(1) = 0.0023, P = 0.96 \). After the MEG session, each participant performed a behavioral test. They were asked to rate the beauty of each of the same stimuli that they saw previously on a 1 to 9 Likert scale. We assured the differences between men and women’s ratings of the 400 stimuli by means of Student’s t tests. There were no significant differences between men and women’s beauty ratings for any of the 400 stimuli. The details of the observations are posted at http://evocog.es/index.php?option=com_content&view=category&layout=blog&id=36&Itemid=59.

Image Acquisition. The methods underlying MEG data collection and analysis are described in Maest et al (64) and are outlined only briefly here. MEG recordings were made with a whole-head neuromagnetometer (Magnes 2500 WH, 4-D Neuroimaging) consisting of 148 magnetometer coils. The instrument is housed in a magnetically shielded room designed to reduce environmental magnetic noise that might interfere with biological signals. The variables taken into account in the MEG protocol and the procedure were the following:

1. Signal analysis. The MEG signal was filtered “online” with a bandpass filter set between 1 and 50 Hz, and digitalized with a sampling rate of 254 Hz, during a time window of 1,050 ms including a 150 ms prestimulus period. The epoch data obtained for each participant were baseline-corrected and noise-reduced. Each single trial event-related field was visually assessed to reject those exhibiting eye movements, blinks, or movement artifacts. Artifact-free epochs of each channel and subject were averaged across each condition. The minimum number of trials obtained after artifact rejection was 90.

2. Source analyses. The MNE procedure, commonly used in MEG source reconstruction and described in detail elsewhere (65), was used for estimating the cortical origin of the brain response. Because MEG sources are believed to be restricted to the pyramidal neurons of the cortex (66), the dipoles of the source space model were restricted to a cortical surface extracted from a structural MRI dataset of a tessellated cortical mesh template surface derived from the Montreal Neurological Institute (MNI) phantom brain (67) and implemented in SPMS (www.fil.ion.ucl.ac.uk/spmsoftware/spms) served as a brain model to estimate the current source distribution. Typically the dipoles of the distributed
Data Analysis. The images were analyzed by means of the SPM5 (Statistical Parametric Mapping) software, implemented on MatLab 6.5, using the mod-

Acknowledgments. We thank Drs. Antonio Damasio and Oshin Vartanian for comments on the manuscript and Museo del Prado (Madrid, Spain) for kind permission to use the pictures of stimuli in this study. This work was supported by R-D Projects of the Spanish Ministerio de Educación y Ciencia UM2007-64086/ FIS0, SEJ2007-64374/PSIC, and FIS-2004-00953 R+D, as well as by European Commission Project GAIA (FP6-NEST Contract 043309).

25. Terhune KP, et al. (2005) Recognition of objects in non-canonical views: An fMRI study of the left Minimising 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.

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