

Beauty in the Brain of the Beholder

Minireview

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Facial beauty is an honest signal of the genotypic and phenotypic quality of the bearer. Beautiful people are thus regarded as high-value mates who maximize reproductive success by producing viable offspring. Here, the functional neuroanatomy of facial beauty is reviewed and placed into the context of the distributed model for human face perception. A proposed extension of the distributed model is provided, which takes into account the neuroanatomy of beautiful face perception.

Background

Evolutionary theory suggests that facial beauty signals the optimum reproductive status of the bearer; it thus dictates that we are drawn to those who are attractive in order to maximize our success in reproducing offspring with a strong chance of survival (references in Symons, 1979). Take, for example, the effect of estrogen on female faces; estrogen markers, such as fat deposits in the upper cheek and lip area, signal fertility and readiness for reproductive effort (Perrett et al., 1998). While these markers are considered attractive by male observers, the estrogen to testosterone ratio fluctuates with age such that female faces “masculinize” as the bearer gets older. Estrogen thus provides female faces with a marker of youth—a marker that signals the optimal fertility period for human females. Additionally, in readying the body for reproductive effort, estrogen diverts resources away from systemic functions such as cellular repair mechanisms and immunocompetency. Facial estrogen markers could thus be considered an honest signal of the genotypic quality of the bearer, i.e., only those individuals strong enough to promote such a display can afford to handicap vital functions. The same principle can be applied to male faces, where testosterone, which diverts resources away from immune function and toward the development of sexually dimorphic facial traits, e.g., larger eyebrow ridges, contributes to the advertisement of genotypic quality (Grossman, 1985). Such overt displays of systemic handicap allow observers to formulate judgments of the relative good health of the bearer. A further facial marker considered attractive and indicative of the genetic superiority of individuals from either sex is “fluctuating asymmetry”—the extent to which the left half of the face is the same as the right. The optimum development of facial symmetry is impeded by environmental stressors in utero, thus the more symmetrical a face is the less that person has been exposed to developmental stress (Thornhill and Moller, 1997).

However, the evolution of highly complex social

groups that are unique to human culture has ensured that culturally specific characteristics are also transmitted with facial beauty. Secondary sexual indicators on male faces do not suggest that the bearer will place considerable investment in parental input. Indeed, men with symmetrical faces are less likely to accept fidelity and will invest less time with offspring. When considering paternity, men with facial characteristics that signal a limited opportunity to attract multiple mates would be considered to contribute more to reproductive success than those advertising an ability to attract more than one partner (Penton-Voak et al., 1999). Interestingly, men with neonatal facial characteristics, which advertise a limited opportunity to attract potential partners, tend to have positive personality traits attributed to them by female observers that may correlate with subsequent behavior. However, these personality traits are not indicative of actual behavior and may be fallible. To this end, female observers may consider male faces to be attractive if their same-sex peers consider them to be attractive as well. Thus, by copying the mate choice of same-sex peers, female observers act to increase the reliability of any assessments of facial attractiveness (references in Thornhill and Gangestad, 1999).

Clearly, the ethology of beautiful face perception is complex, and considering the importance of selecting high-value mates, the distinction needs to be made between beautiful faces that are rewarding in the sense that they have an adaptive value (i.e., attractive different-sex faces) and those that are merely aesthetic (i.e., attractive same-sex faces). An attractive female face may be aesthetic but may also signal good genes that will positively correlate with the genetic strength in any offspring. However, to male observers, attractive male faces cannot constitute such a sociobiological advertisement and can only be considered aesthetic. Considering the adaptive benefit behind perception of different-sex facial beauty and the subsequent motivated behavior that occurs in observers assessing it, the brain areas implicated in reward function that underpin appetitive behavior are likely to be active with their perception. However, considering the sole aesthetic value in attractive faces of members of the same sex, natural selection would have shaped any “beauty detectors” in the brain to become specialized for same- or different-sex faces, but not both. While neuroimaging studies of facial beauty are scant, recent investigations do suggest sex-differentiated responses for perception of beautiful faces, these studies are discussed later (Aharon et al., 2001; O’Doherty et al., 2003). However, our current understanding of the cognitive neuroanatomy of face perception does not account for these findings. To better understand facial beauty and the brain, a brief discussion of the neuroanatomy of face perception is needed.

Neuroanatomy of Face Perception

The distributed human neural system for face perception (distributed face model) is the most contemporary neuroanatomical model encompassing what is known of face processing to date (Haxby et al., 2000). This model is primarily based on functional neuroimaging data and

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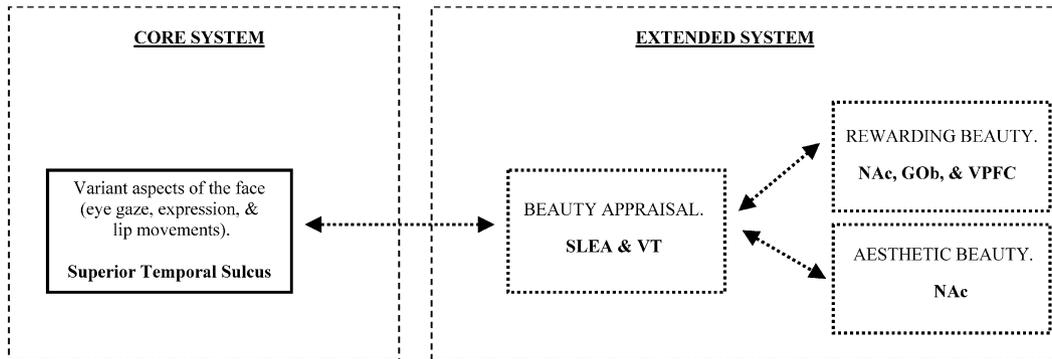


Figure 1. Proposed Extension of the Distributed Human Neural System for Face Perception

The solid lines represent parts of the existing model, while the broken lines represent the proposed extension. Initial appraisal of facial beauty takes place in the SLEA and the ventral tegmentum (VT), where activity is reflected with a positive signal response in the orbitofrontal gyrus (GOB), nucleus accumbens (NAc), and ventromedial prefrontal cortex (VPFC) for rewarding beauty only. However, deactivation in the SLEA results in concomitant deactivation in the NAc during perception of aesthetic beauty.

parses out the various processes involved in face perception into two main systems. The first of these is the core system that is involved in visual analysis of the face. The second is the extended system, which projects out from the core system and computes the various types of information gleaned from the face. Inside both the core and extended systems there is further functional modularity. Within the core system, the visual analysis of the variant aspects of the face (e.g., eye gaze, expression, and lip movement) are computed in parallel to the invariant aspects of the face, such as the perception of identity. The functional subdivision of the extended system is based on the computation of spatial attention, prelexical speech perception, emotion, and unique biographical information. Each of the subdivisions within the extended and core systems compute their respective functions in parallel; however, there is reciprocal feedback between most of the units in the model (see Figure 1).

Unlike previous cognitive models of face processing, the distributed face model has neurological specificity, with each unit in the model mapped to a distinct substrate. The core system consists of the inferior occipital gyri, which mediate perception of early visual features of the face. The inferior occipital gyri project into the superior temporal sulcus (STS) and lateral fusiform gyrus, which computes variant (expression) and invariant (identity) facial aspects, respectively. The lateral fusiform then projects forward along the anterior temporal cortex, where personal semantic information regarding the face is represented, thus instigating familiarity. In parallel to this, the superior temporal sulcus has reciprocal projections to the intraparietal sulcus, where spatial attention from the face is processed. The ability to shift spatial attention from facial cues, such as interpretation of gaze direction, is a fundamental skill allowing successful interaction in complex social groups. The superior temporal sulcus also works in concert with regions within the superior temporal gyrus that are responsive to movements unique to speech. Finally, there is reciprocal connectivity between the superior temporal sulcus and regions of the brain involved in emotion processing, such as the amygdala, orbitofrontal gyrus, and the ante-

rior insula. One area described in the distributed face model, the amygdala, has rich connections to many other areas implicated in reward and is thus pertinent to our discussion of the cognitive neuroanatomy of facial beauty.

Classically, the amygdala is thought to process threat-related facial expressions (e.g., fear and anger); however, it also plays a part in mediation of other expressions and social cognition in general (Adolphs, 2001). Recent studies of the amygdala suggest that it may also process meaning from the face that is unrelated to the facial expression being used as stimuli. This epiphenomenal activity may be indicative of how the observer feels. Take, for example, the now robust finding that direct eye gaze engenders activity in the observer's amygdala. While the ability to correctly infer the direction of gaze is a fundamental human trait, it does, quite paradoxically, have ambiguous meaning. Direct gaze can signal potential threat but it can also indicate interpersonal attraction (Haxby et al., 2002). The fact that presentation of facial expressions of happiness (which are considered to be more attractive than other expressions) and looking at people who you love evokes activity in the amygdala suggests that this area of the brain may play a crucial role in beautiful face perception (Bartels and Zeki, 2000). ***The Extended Amygdala and Reward System***

The amygdala is an umbrella term for a functionally and anatomically heterogeneous collection of nuclei that reside in the superomedial aspect of the anterior temporal lobes. The dense reciprocal interconnections that convey information to and from a wide variety of neural areas ensure that the amygdala (or amygdaloid complex) is well situated to play an important role in the computations that underpin the perception of beautiful faces. The various nuclei that constitute the amygdala are defined according to the particular functional criteria adopted, but it is generally agreed that there are two main clusters, these being the older and smaller corticomедial group and the basolateral group (references in Aggleton, 2000).

The sublenticular (below the lentiform body) extended amygdala of the basal forebrain (SLEA) projects from the corticomедial group into the stria terminalis to form an extension of the "core amygdala." The stria terminalis

project into the caudate body and to the nucleus accumbens. Due to the relay nature of the amygdala, the nucleus accumbens thus enjoys reciprocal connectivity between the insular cortex, the hippocampal formation, the medial prefrontal cortex, as well as the orbitofrontal gyrus (Heimer et al., 1997). Further evidence showing projections from the corticomedial group to the dopaminergic brain reward areas does suggest that it may play an initial role in perception of beautiful faces, with the brain reward system being “activated” at subsequent stages (Fudge and Haber, 2000).

The areas of the brain that mediate reward are diverse but are linked together through the medial forebrain bundle—a complex structure consisting of approximately 60 fiber bundles that project through the lateral hypothalamus toward the rostral basal forebrain. The ventral tegmentum is a dopaminergic site that is connected by a descending component of the medial forebrain bundle. The ventral tegmentum also projects to other areas of the brain, such as the nucleus accumbens and the orbitofrontal gyrus, which are now seen to play a role in the brain reward process (Rolls, 2000). These systems would have evolved to ensure the appetitive drive toward stimuli that were beneficial to our survival as a species. In light of the adaptive benefits behind beautiful faces, one would hypothesize involvement of these substrates. Recently, functional magnetic resonance imaging (fMRI) was applied in an effort to understand more about the processes mediating perception of beauty (Aharon et al., 2001; O’Doherty et al., 2003). The results of these investigations place facial beauty alongside emotion and speech as a fundamental condition that can be read from the face and also suggest that aesthetic and rewarding properties of beautiful faces are processed separately.

Neuroimaging Studies of Facial Beauty

In the Aharon et al. (2001) study, a behavioral task was first given to a group of heterosexual male observers who were asked to rate the attractiveness of average and beautiful male and female faces. This task revealed a clear difference between the beautiful and average sets, regardless of the sex of the face. However, this difference was modulated by the amount of time that the observer saw faces belonging to a particular group. The beautiful female faces were rated as more attractive with each presentation, while the average female faces were rated as less attractive. On the other hand, the beautiful and average male faces did not reveal such a separation of ratings with subsequent presentations. A second cohort of male observers underwent another behavioral task where they could manipulate the length of time that a picture of a face remained on the screen. The duration of presentation could be extended or shortened when the subject pressed a specific key on a keyboard. It was hypothesized that male observers would make multiple keypresses to gaze longer at those faces that were rewarding (i.e., the attractive female faces). Perhaps unsurprisingly, the results confirmed this hypothesis, with male observers choosing to gaze longer at the beautiful female faces. There was no difference between the length of time the observers chose to look at the average female and male faces and the attractive male faces. These results converge on a behavioral dissociation of the qualities that constitute facial beauty.

While male observers judged both beautiful male and female faces to be attractive, they only found the beautiful female faces to be rewarding to look at and rated them as more attractive with multiple presentations. Moreover, even though beautiful male and female faces were rated to be equally attractive, the male observers only expended effort (via multiple key presses) to gaze longer at the beautiful female faces, showing that only these faces were rewarding.

To investigate the neural mechanisms involved in perception of rewarding and aesthetic facial beauty, a third cohort of male observers were presented with pictures of male and female faces (both average and attractive) in a block design imaging experiment. To ensure that the fMRI results were not contaminated by the attentional modulation of gaze, all material was presented to the subjects tachistoscopically (200 ms), and each picture was separated with an interstimulus period of 3800 ms.

Several regions of interest were first defined by comparing engendered activity in all experimental conditions with any activity revealed within the control period (which only consisted of a fixation cross). This analysis served to localize the regions of interest that were subsequently studied for the specific experimental effects. Presenting male subjects with beautiful female faces (which would involve both reward and aesthetics) engendered significant activity in both the right orbitofrontal gyrus and bilateral nucleus accumbens. This analysis also revealed activity, albeit at a lower threshold, in the ventral tegmentum and SLEA. The brain areas revealed with the analysis of the rewarding beautiful faces represent a subcortical distributed system, with each component contributing a specific role to perception of facial beauty.

Lesions to the subthalamic nucleus reduce the rewarding effect of stimulation in the medial forebrain bundle (Arvanitogiannis et al., 1996). The SLEA and the ventral tegmentum share a common pathway through the medial forebrain bundle, and activity has been revealed in the dopaminergic neurons of the ventral tegmentum to salient sensory events which have no relationship to reward (Horvitz, 2000). It may be the case that the SLEA and the ventral tegmentum operate together to form an “appraisal unit” that is the first, and common stage, in perception of beautiful faces. On the other hand, the orbitofrontal gyrus is specifically active when the subject is anticipating a reward outcome that could contain either a positive or negative valence (Schultz and Dikenson, 2000). The dopaminergic meso-accumbens pathway plays a central role in the initiation of motivated behavior, with the nucleus accumbens involved in the assessment of reward expectancy (Breiter and Rosen, 1999). Thus, these areas of the heterosexual male brain encompass the appraisal, anticipation, and assessment of the reward value inherent in beautiful female faces.

Aharon et al. (2001) then investigated the effects of the aesthetics of facial beauty only (i.e., beautiful male faces versus average male faces). As before, the ventral tegmentum was active; however, the SLEA revealed a negative signal response (deactivation), suggesting that these areas may respond together in an additive manner for aesthetics in rewarding faces only. In addition to this, a bilateral deactivation was revealed in the nucleus accumbens. The pattern of activity revealed in the nu-

nucleus accumbens for aesthetic beauty is supported by studies of reward expectancy. For example, a decrease in the fMRI signal from baseline is revealed when an expected reward is not delivered (Knutson et al., 2001). It would seem likely that the bilateral deactivation in the nucleus accumbens for the Aharon et al. (2001) study signaled an absence of reward expectancy toward the beautiful male faces.

In a later fMRI (event related) experiment, the cortical response to male and female beautiful faces for observers of both sexes was studied (O'Doherty et al., 2003). In this study, no activity in the nucleus accumbens was revealed when male and female subjects were shown attractive and average faces of both sexes. However, as Aharon et al. (2001) showed a positive and negative signal change for attractive female or male faces, the presence of activity in the nucleus accumbens cannot be considered an artifact brought about with the use of a block experimental design. It remains to be tested whether or not deactivation in the nucleus accumbens when observers are shown attractive same-sex faces is unique to the heterosexual male population. Interestingly, this study also revealed activity within the ventromedial prefrontal cortex for heterosexual male observers viewing attractive female faces. Given the role that the ventromedial prefrontal cortex may play in social reasoning, it seems likely that it works in concert with the orbitofrontal gyrus to compute reward expectancy in a possible social context (references in Adolphs, 2001). Even so, the pattern of activity revealed for the analysis of aesthetic and rewarding beautiful faces is not accounted for in the distributed face model; modifications of the extended system of this model are proposed to account for these findings.

Beauty in the Brain

The data to hand suggest that the SLEA and the ventral tegmentum serve a pivotal role in the initial appraisal of beautiful faces. As described above, the amygdala receives input from the superior temporal sulcus. However, as the computations carried out by the SLEA and ventral tegmentum, and the subsequent projections to the nucleus accumbens, are distinct from emotion processing per se, they are represented alongside the "emotion module" in the distributed face model and not projected out from within. The projection from the STS to the SLEA and ventral tegmentum is supported by work showing modulation of the brain reward system by eye gaze, a manipulation previously found to engender activity in the anterior bank of the STS (Haxby et al., 2002).

When subjects are presented with beautiful faces that are rewarding, engendered activity in the sublentiform nucleus is mirrored with activity in the ventral tegmentum, orbitofrontal gyrus, and nucleus accumbens. However, beautiful faces that are merely aesthetic engender a negative signal change (deactivation) in the SLEA and the nucleus accumbens. Due to the opposite directions of signal response in the nucleus accumbens for perception of aesthetic and rewarding beautiful faces, these computations are represented separately. Therefore, projections from the module representing the SLEA/ventral tegmentum diverge into two separate pathways—the first represents the processing of rewarding beautiful faces, and the second represents the aesthetic. The

proposed module for the rewarding beautiful faces also represents activity in the orbitofrontal gyrus and ventromedial prefrontal cortex, as activity here was specific to this set of faces only (see Figure 1).

One caveat has to be stressed: as noted above, few neuroimaging studies on facial beauty exist, and as such, the proposed extensions of the distributed face model will have to remain provisional until the necessary empirical investigations confirming their robust validity are carried out.

Selected Reading

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