Laterality effect (face perception)

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Face recognition is an essential skill that in many species is associated with apparently specialized neurological and cognitive mechanisms. This chapter summarizes some of the behavioral and neuroscientific research on laterality effects in face perception, with a focus on face identity processing in humans and animals.

Laterality Effects: Humans

Certain regions of the human ventral visual pathway, which plays a crucial role in visual recognition, tend to respond vigorously to particular types of visually presented objects, such as buildings, words (in literates), and faces. The most famous face-selective region is no doubt the fusiform face area (FFA) that tends to selectively respond to faces relative to other visual objects. The FFA might however act as a hub in a whole network of face-responsive areas. Two other well-known face-selective regions are the occipital face area (OFA) and the superior temporal sulcus (STS). As can be seen in figure 1, all three show a laterality effect with more pronounced face selectivity in the right hemisphere.

Right-Hemisphere Dominance of Human Face Processing

Neuroimaging, electrophysiology, and behavioral studies all support the general advantage of the right hemisphere in face processing. The face-sensitive N170 event-related potential component is right-lateralized. People also tend to be faster at processing faces presented to the left visual field – which projects to the right hemisphere – compared to the right visual field. Similarly, when shown chimeric human faces (figure 2) composed of either the left or right side of a picture of an original whole face, people are likely to perceive the left chimera rather than the right chimera as resembling the original. Interestingly, this might not extend to the perception of monkey faces, at least not for observers with limited exposure to monkeys, indicating that the laterality effect could be experience-dependent or, perhaps less likely, species-dependent (for the role of experience in visual object recognition, see e.g. Sigurdardottir & Gauthier, 2015). Tachistoscopic presentation of faces in split-brain patients has also confirmed the dominance of the right hemisphere for face recognition. Electrical stimulation of the right fusiform gyrus has been found to induce the conscious perception of faces, while stimulation of face-related regions in the left fusiform gyrus caused a non-face visual change, although this could be dependent on hemispheric dominance for language processing and/or handedness. Research has also shown that unilateral right damage can lead to prosopagnosia (facial recognition disorder), at least in right-handed individuals. There are a few reports of left-handed people with prosopagnosia with unilateral left damage, suggesting the possible role of handedness in face lateralization. However, face-selective regions in left-handed individuals still appear to be right-lateralized, with the exception of FFA that seems to be less lateralized or even left-lateralized in most left-handers.

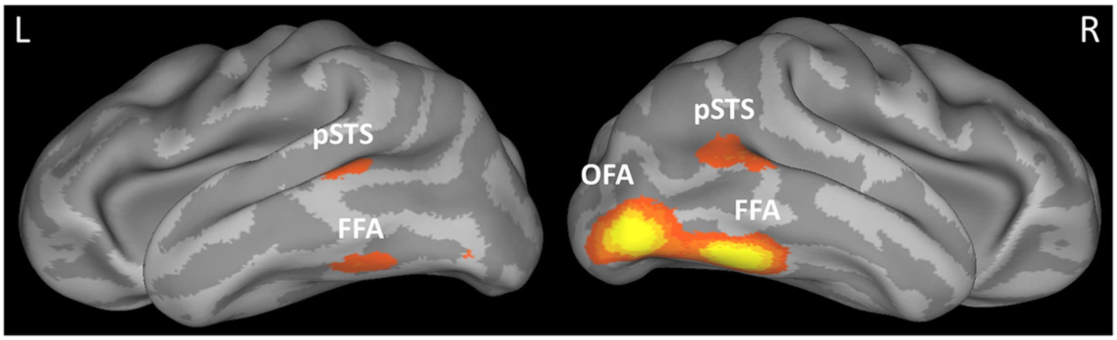

Figure 1. Laterality of neural face processing in the human brain. The fusiform face area (FFA), occipital face area (OFA), and the posterior part of the superior temporal sulcus (pSTS) of the left (L) and right (R) hemispheres are shown. The yellow/orange shows face selectivity, here defined as the contrast of faces vs. non-face objects. The image is originally from Huang, L., Song, Y., Li, J., Zhen, Z., Yang, Z., & Liu, J. (2014). Individual differences in cortical face selectivity predict behavioral performance in face recognition. *Frontiers in Human Neuroscience*, *8*, 483. The image is used according to a Creative Commons (CC BY) license. Copyright © 2014 Huang, Song, Li, Zhen, Yang and Liu.

Origins of Hemispheric Differences

There is a debate on whether the general right hemisphere dominance for face processing is due to prespecified properties of the neural network (nature) or if it is experience-related and the network becomes specialized after repeated exposure or training (nurture). Unlike selectivity for some other object classes, face selectivity has a delayed developmental trajectory, where lateralized face-selective areas such as FFA, OFA, and STS are not consistently found in young children. It is possible that such a trajectory is predefined, but it could also be due to increased visual expertise with faces, in particular increased reliance on so-called configural processing (perceiving relations among features, such as where the eyes are relative to the nose, although the term might refer to a few distinct processes, see e.g. Maurer, Le Grand, & Mondloch, 2002) in which the right hemisphere might excel. The right lateralization of neural face processing has also been suggested to be influenced by competition during reading acquisition between neural representations of visually presented faces and words in the left hemisphere (language processing is generally left-lateralized).

Consistent with this hypothesis, some research has indicated that the degree of face lateralization varies with literacy (see e.g. Dundas, Plaut, & Behrmann, 2013). The lateralization shift of the FFA in left-handers has also been suggested to be a result of reduced left hemisphere neural competition between faces and words. On the other hand, seemingly consistent with prespecified face perception mechanisms, right-lateralized face-selective neural responses have been reported in young infants well before reading acquisition. Nonetheless, depriving the right – but not the left – hemisphere of visual input during infancy selectively impairs later ability for configural processing of faces (specifically, sensitivity to spacing of facial features). Thus, laterality effects in face processing might be driven by a mixture of predefined hemispheric biases and visual experience.

Hemispheric Specialization

Although various studies have shown the dominance of the right hemisphere in face processing, the right and left hemispheres are likely both involved in face recognition but in different ways. The right hemisphere is superior at processing low spatial frequency information from faces while the left hemisphere appears to be more specialized for processing high spatial frequencies. Related, while the right hemisphere is more involved in configural processing of faces, the left hemisphere might show superiority for featural or analytic processing of faces. When faces are inverted, judging their configuration becomes difficult, and this eliminates or reduces the right hemisphere advantage. These findings are in line with neuropsychological evidence, indicating that prospopagnosic patients, who tend to have right hemisphere lesions, might perform equally well when matching upright and inverted faces (no face inversion effect). Divided visual field methodology studies have also shown the superiority of the left hemisphere when feature-by-feature processing of faces was induced by task manipulation. For more information on laterality effects in human face perception, see e.g. Gainotti (2013) and Júnior, de Sousa, & Fukusima (2014).

Laterality Effects: Animals

The visual system of non-human primates shows many similarities with that of humans. The Rhesus macaque system is best documented, but visual face processing in other primates, other mammals such as sheep, and even other non-mammalian species, has been studied. For reviews on face processing in animals, see e.g. Kendrick (2006), Leopold & Rhodes (2010), Parr (2011), and Tate, Fischer, Leigh, & Kendrick (2006).

Primates

Chimpanzees, like humans, can quickly identify individual conspecifics by their faces. Chimpanzee face recognition is impaired by distortion of the configuration of faces. Like humans, chimpanzees find it more difficult to recognize inverted compared to upright conspecific and human faces (face inversion effect), often thought to be due to disruption of configural processing which in humans is right-lateralized. Accordingly, some evidence supports that face processing in chimpanzees is right-lateralized. For example, when chimeric chimpanzee or human faces were made by vertically flipping a half-face around the midline (see example in figure 2), chimpanzees showed a tendency to choose a left rather than right face-half chimera as being more similar to an original centrally presented whole face. This probable right hemisphere advantage might increase with age and/or experience with faces. Accordingly, configural face processing in chimps might be experience-dependent, as no reliable face inversion effect in chimps was found for the faces of an unfamiliar species (brown capuchins), and their configural processing also appears to be greater for chimpanzee faces than human faces. It should be noted that chimpanzees tend to be right-handed, and handedness could possibly be related to brain asymmetries in face processing. There are however some apparently conflicting results, where chimps were equally likely to match a left and right chimera to an original whole face.

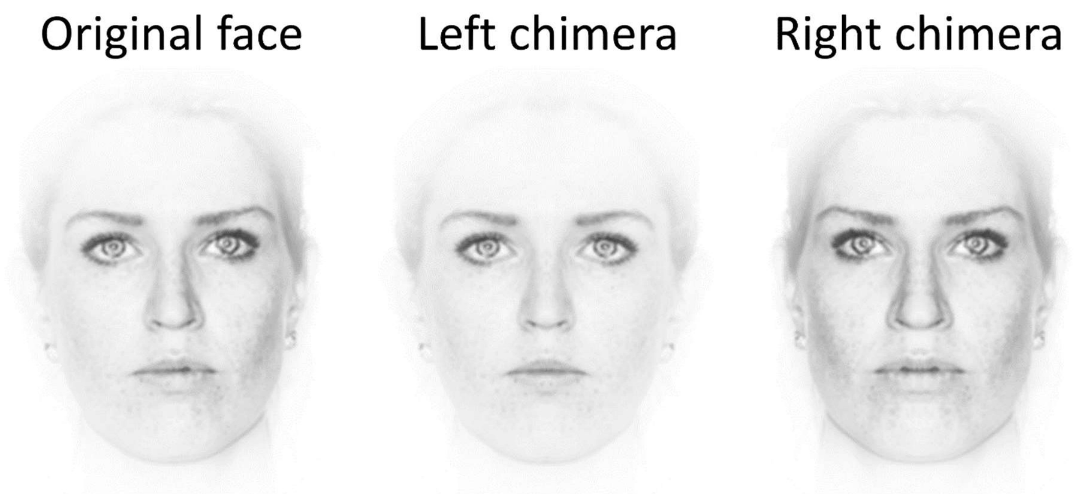

Figure 2. Laterality effects in face perception have been measured by face chimeras. Here, the left and right parts of an original face (author HMS) were used to make two chimeric faces, one from the left half-face image and one from the right. Humans and some animals tend to choose a left rather than a right chimera as being similar to an original full face.

Rhesus macaques can also distinguish between conspecifics based on their faces, and a whole network of interconnected face-responsive regions has been mapped in the macaque brain. Some behavioral studies have reported a lack of lateralization of face processing in macaques. For example, a study using chimeric faces (figure 2) revealed that macaques failed to show asymmetry for face matching with either monkey or human faces. Possibly related, a face inversion effect in macaques has not consistently been found (although some studies do report such an effect), which has been interpreted in favor of less reliance on configural – and presumably right-lateralized – processing as opposed to featural processing. Consistent with this, even infant macaques with no previous exposure to faces can discriminate between faces based on both facial features and their spacing or configuration. Early work on split-brain Rhesus macaques also found no lateralization for learning to discriminate photographs of monkeys. fMRI studies have also reported bilateral face-selective activity in the monkey temporal cortex, although some do report more extensive right-hemispheric activation for faces. There are also some split-brain studies that support right-hemisphere superiority in macaques, particularly for upright as opposed to inverted faces. To complicate matters even further, early single-cell recordings in macaques reported a more abundant population of face-selective neurons in the left compared to right temporal cortex, hinting that monkeys and humans might use a qualitatively similar mechanism for face processing with a different direction of cerebral asymmetry. Left hemisphere lateralization for learning to discriminate monkey faces has also been reported specifically for female macaques. The lateralization of face processing in other monkey species has not been extensively studied, although stronger activation in the right temporal cortex in vervets has been reported for the passive viewing of faces in comparison to non-face objects.

Non-Primates

Some non-primate species are reported to have right-lateralized visual face processing. Domestic dogs can identify the face of their owner, and many dogs discriminate between the face or head of their owner and that of another familiar person. Dogs show greater activation in a putative dog face area of the right temporal cortex when observing faces of dogs or humans as compared to non-face objects. Sheep also show greater activity in the right compared to left inferior temporal cortex when viewing upright faces but not inverted faces. Sheep also recognize conspecific faces more by the left visual field (right hemisphere advantage), and this effect is stronger for familiar faces. Interestingly, while sheep can discriminate between human faces, they show a smaller inversion effect for human faces than seen with sheep faces, and in general show little indication of configurally processing human faces. Sheep also have no left visual field advantage or even a slight right field advantage for human faces. This might suggest a role of expertise for developing a right brain hemisphere advantage for the configural processing of faces but could also be consistent with an innate species-specific mechanism. Laterality effects in face processing have rarely been studied in non-mammals, but there are some studies that provide support. For example, the right hemisphere of chicks appears to be better equipped for visually processing information relevant to the recognition of other chicks, and several species of teleost fish are reported to mainly use right-side brain structures when viewing conspecifics.

Summary

To summarize, while the lateralization of face processing in non-human primates is somewhat controversial, humans appear to share right hemisphere lateralization for face processing with animals as diverse as dogs and sheep and possibly even some birds and fish. Although by no means conclusive, these results could indicate that some face processing capabilities might be shared among mammals, and some researchers have even suggested that lateralization of the visual analysis of stimuli provided by conspecifics is shared by all vertebrates (Sovrano, Rainoldi, Bisazza, & Vallortigara, 1999).

Acknowledgements

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Figure Comments

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Figure 2: Figure 2 was made by author HMS.

Cross-References

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- Canine cognition
- Canine sensory systems
- Composite effect
- Configural perception
- Domain Specificity
- Face-Selective Neurons: Comparative Perspectives
- Face processing in different brain areas and face recognition
- Feature learning theory of categorization
- Filial Imprinting
- Hemispheric specialization
- Hormones and face preferences
- Imprinting
- Inversion effect
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