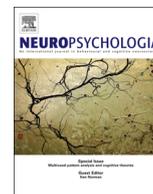




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Neuroanatomic correlates of the feature-saliency hierarchy in face processing: An fMRI -adaptation study



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ABSTRACT

Previous fMRI studies suggest that faces are represented holistically in human face processing regions. On the other hand, behavioral studies have also shown that some facial features are more salient than others for face recognition: the neural basis of this feature-saliency hierarchy is not known. We used fMRI-adaptation together with a behavioral discrimination task and an ideal observer analysis to ask (1) whether different face parts contribute different amounts to the neural signal in face responsive regions, and (2) whether this response correlates more with the behavioral performance of human subjects or with the physical properties of the face stimuli. Twenty-three subjects performed a same/different discrimination experiment to characterize their ability to detect changes to different face parts. The same subjects underwent an fMRI-adaptation study, in which limited portions of the faces were repeated or changed between alternating stimuli. The behavioral study showed high efficiency in identity discrimination when the whole face, top half, or eyes changed, and low efficiency when the bottom half, nose, or mouth changed. During fMRI, there was a release of adaptation in the right and left fusiform face area (FFA) with changes to the whole face, top face-half, or the eyes. Changes to the bottom half, nose or mouth did not result in a significant release of adaptation in the right FFA, although bottom-half changes resulted in a release of adaptation in the left FFA. Adaptation in the right and left FFA and the right pSTS was correlated with human perceptual efficiency but not with ideal observer measures of the physical image differences between face parts. The feature-saliency hierarchy of human face perception is therefore reflected in the activity in the right and left FFA and right pSTS, further supporting the key role of these structures in our perceptual experience of faces.

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1. Introduction

Recent neuroimaging studies show that face perception involves an extensive network of cerebral regions. Particularly important may be three regions in an occipitotemporal “core”, which respond more to faces than to any other category of complex objects. These include an area in the inferior occipital gyrus, known as the occipital face area (OFA) (Gauthier et al. 2000), an area in the lateral fusiform gyrus, known as the ‘fusiform face area’ (FFA) (Kanwisher, McDermott, & Chun, 1997), and an area in the posterior superior temporal sulcus (pSTS) (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Although these areas show an increase in BOLD signal on fMRI when the subject is viewing faces, that observation alone does not establish whether these regions

make critical contributions to face processing, and if so, in which aspects of face perception they participate. Such limitations have motivated the development of complementary approaches, such as using neuroimaging in patients with cerebral lesions to correlate behavioral deficits with the effect of lesions on the face processing network (Barton, Hanif, & Ashraf, 2009; Fox, Hanif, Iaria, Duchaine, & Barton, 2011).

Another method for determining the contribution of an area to specific perceptual processes is to correlate its neural activity with the subject’s behavioral performance on a task. Face processing has certain signature behavioral patterns that appear more distinct for faces than for other objects. One is the face inversion effect, in which turning a face upside down impairs the ability of subjects to recognize it, far more so than for other objects (Yin, 1969). Using the fMRI-adaptation technique, in which the neural response is reduced for repeated presentations of a preferred stimulus, allowing one to deduce the preferred stimulus property being processed in that area (Grill-Spector & Malach, 2001), one study found that adaptation was only reduced or ‘released’ in the FFA when upright faces changed in identity. This suggested that the FFA was

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encoding the identity of upright but not inverted faces (Yovel & Kanwisher, 2005).

A second example is the ‘composite face effect’, in which the ability to recognize the top or bottom half of a face is altered if it is fused with the other half of a different face, but not if the two halves are misaligned (Richler & Gauthier, 2013; Rossion, 2013; Young, Hellawell, & Hay, 1987). Two fMRI-adaptation studies have found a neuroimaging parallel to this observation (Schiltz, Dricot, Goebel, & Rossion, 2010; Schiltz & Rossion, 2006): in the right FFA, the response to faces adapted as expected if the face was repeatedly viewed, but if either the top or bottom was changed, this adaptation was released, just as much as when the entire face was changed. A similar effect occurs when the external features (hair, chin, face outline) of a face are replaced by the external features of a different face, causing the internal features to appear different, even though they have not changed (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Young, Hay, McWeeny, Flude, & Ellis, 1985). Here too an fMRI-adaptation study found a complete release of adaptation in the FFA when either the internal or the external features of the face changed (Andrews et al., 2010).

Both the face-inversion effect and the composite face effect are cited as evidence that human subjects perceive faces holistically, rather than as a collection of individual face parts. The fact that the FFA also shows neuroimaging correlates of the face inversion and composite face effects suggests that the type of perceptual processing occurring in the FFA may underlie the holistic nature of face perception in human subjects. In addition to holistic processing, face perception shows other behavioral signatures. One well-established property is that face perception is characterized by a ‘feature salience hierarchy’: that is, some facial features are more important and more emphasized than others in face recognition (Shepherd, Davies, & Ellis, 1981). The feature salience hierarchy differs from the composite face effect in that the latter examines how altering one face part influences the perception of another part, to show that processing is integrated across the whole face, whereas studies of feature saliency examine the relative importance of different facial components to a particular task. Thus, the upper face half is superior to the lower face half for identifying faces (Fisher, 1975; Garneau, 1973), and changes to the hair and eyes are more easily detected than changes to the mouth, nose, or chin (Baker, 1967; Matthews, 1978). Using the ‘Bubbles’ technique, in which only small parts of the face are shown randomly to an observer trying to identify the face, it has been shown that the eyes contain more diagnostic information for face identity recognition, while other features become more important in other tasks, such as recognizing certain emotional expressions (Schyns, Bonnar, & Gosselin, 2002; Smith, Cottrell, Gosselin, & Schyns, 2005; Vinette, Gosselin & Schyns, 2004). Eye-movement studies have consistently reported that subjects look more at the eyes when recognizing faces (Henderson, Williams, & Falk, 2005; Vinette et al., 2004), though again this balance changes when the task switches to identifying certain expressions (Malcolm, Lanyon, Fugard, & Barton, 2008). Many individuals with prosopagnosia, who are impaired in recognizing facial identity, do not show this normal preference for fixating on the eyes, and have more problems perceiving changes in the eyes than in the mouth region (Barton, 2008; Bukach, Le Grand, Kaiser, Bub, & Tanaka, 2008; Caldara et al., 2005).

Although behavioral studies showed dissimilarities in the way different facial features are perceived, few studies have attempted to investigate the neuroanatomic correlates of this feature-salience hierarchy. Human intracranial electrophysiological recordings have demonstrated regions in ventral occipitotemporal cortex that show N200 responses to face parts, with a gradient of decreasing amplitude and increasing latency over the feature order of eyes, mouth and nose (McCarthy, Puce, Belger, & Allison, 1999). Recent fMRI studies have also shown that the OFA, pSTS and FFA can be activated by face parts

(Harris & Aguirre, 2008; Liu, Harris, & Kanwisher, 2010). One interesting study found the release of adaptation with changes in the eyes but not with changes in the mouth (Harris & Aguirre, 2010). However, although this study equated the stimuli for physical similarity, it did not examine the relative contributions of physical versus subjectively perceived differences. In the current study, we include an ideal observer analysis to measure the physical properties of the stimuli, and also a behavioral experiment to measure the perceptual experience of the stimuli, which we correlated with findings from fMRI-adaptation. If components of the core face-processing network show a feature-salience hierarchy similar to that seen in the behavioral data, this would strengthen the view that neural activity in these regions plays a critical role in our perceptual experience of faces.

A second related question is whether this feature-salience hierarchy shows the right hemispheric dominance typical of most neuroimaging studies of face perception (Kanwisher et al., 1997), or possibly even a reverse left dominance. One PET study found that matching whole faces produced greater activity in the right fusiform gyrus than matching the eyes or the mouth, while the reverse was true for the left fusiform gyrus (Rossion et al., 2000). They argued that this suggested the left fusiform gyrus is more involved in feature-based processing of faces, noting evidence from tachistoscopic studies of a left hemisphere (right visual field) superiority when subjects were either detecting differences between faces differing by only one face part, or identifying a single feature that was shared by target and probe faces (Hillger & Koenig, 1991).

In this study, we employ a sensitive fMRI adaptation paradigm (Davies-Thompson, Newling, & Andrews, 2012) to measure the sensitivity of ROIs to changes in different facial parts. Similar to previous fMRI adaptation paradigms (Yovel & Kanwisher, 2005; Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Rotshtein, Henson, Treves, Driver, & Dolan, 2005), this technique measures the reduction of the BOLD signal in the face processing regions of the brain in response to repeated stimuli. We changed the upper versus the lower face, as well as smaller horizontal bands containing the eyes, the nose or the mouth separately. Release from adaptation was assessed in six previously localized face-selective areas, namely the OFA, FFA, and pSTS bilaterally. We then compared the activity patterns on fMRI with (a) behavioral data for the efficiency of these subjects in a same/different task using the identical face stimuli, which would reflect the psychophysical discriminability of these different features in human subjects, and (b) measures of physical similarity of images of the parts used, as assessed with an ideal observer technique.

2. Methods

2.1. Subjects

Twenty-five healthy participants with no history of neurological dysfunction, vascular disease or cognitive complaints took part in both the fMRI and behavioral components of the study (14 females, mean age=22.9, range 20–29). All participants were right-handed with corrected visual acuity of 20/20. The protocol was approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital, and written informed consent was obtained for all subjects in accordance with The Code of Ethics of the World Medical Association, Declaration of Helsinki (Rickham, 1964).

2.2. Stimuli

To determine the contribution of different face parts to the neural signal in face-responsive regions of the brain, an adaptation paradigm with seven face-pair conditions was created. In the *whole-same* condition, the first and second faces were identical. In the *whole-different* condition, the first and second faces differed in all aspects. In the *top face-half* condition, the bottoms of the two faces were identical, but the tops differed. In the *bottom face-half* condition, the tops were identical but the bottoms differed. In the *eyes* condition, a horizontal band containing the eyes differed between the two faces, which were alike in all other

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