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

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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 (Richter & Gauthier, 2013; Rossion, 2013; Young, Hellaowell, & 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, 1979; Carneau, 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, Buh, & 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 (Hilger & 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 & Ebwank, 2004; Grill-Spector et al., 1999; Rotstein, 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 different. In the eyes condition, a horizontal band containing the eyes differed between the two faces, which were alike in all other
aspects. In the mouth condition, only a band containing the mouth differed, while in the nose condition, only a band containing the nose differed.

Eight photographs of faces of young Caucasian males, frontal view with neutral expressions were taken from the HVEM-FIVE database. Images were converted to grayscale and distinguishing features (moles, facial hair) were removed using Adobe Photoshop CS (www.adobe.com), and then entered into Matlab (www.mathworks.com) for luminance matching. To remove external features (hair, ears, chin) a gray mask with an oval aperture was placed over each face, resulting in an oval facial image of 547 pixels in height and 400 pixels in width.

To create pairs of face stimuli in which the top and bottom halves were similar in the degree of difference between the first and the second face, vertical half-face stimuli were created by cropping the oval images exactly at midpoint. The physical discriminability between any two upper faces or any two lower faces was then assessed using an ideal observer technique (see below). Top face-half pairs were linked with bottom face-half pairs that matched in terms of similar discriminability.

To generate composite faces with eyes, mouth, or nose changes for the face-part conditions, ‘feature bands’ were created by dividing the face into three bands containing an equal number of pixels. Pairs of faces differing only in one feature band were created by inserting one feature band from another face and keeping the other two feature bands constant (Fig. 1). To reduce lines of sharp contrast arising from aligning faces, first we used the “Patch” tool in Photoshop to evenly blend a small (10 pixel width) area around the line, and then added a 7.5% Gaussian noise mask to the entire image.

2.3. Ideal observer analysis

To determine the physical differences between a pair of stimuli, face images were entered into an ideal observer analysis. The ideal observer is a simulation of a two-alternative forced-choice task in which contrast threshold for face discrimination at 82% accuracy was measured. At each trial one face randomly chosen out of two alternatives was presented as the test stimulus at a contrast that was determined by a psychophysical staircase, and embedded in Gaussian white noise with fixed variance. The ideal observer has knowledge of the complete face stimulus set, the contrast on each trial and the statistics of the noise, and responds based on minimum distance between the noisy test stimulus and the two equally likely face alternatives. This decision rule, under the current conditions, is equivalent to Bayesian a posteriori maximization and thus is statistically optimal (Tjan, Braje, Legge, & Kersten, 1995). Thus, the ideal observer’s response at each trial was based on

$$
\sum (S - C)^2
$$

where S is the noisy stimulus, c is the contrast at a given trial, and $F_1$ and $F_2$ are the two possible face templates in a given session.

2.4. Human behavioral experiment

To examine how humans perceive the changes to the face images created above using the observer criteria, each subject who performed the fMRI experiment also completed a same/different task using these same face stimuli. Subjects were tested one or more weeks after their fMRI session. A trial consisted of two faces presented sequentially for 900 ms each, separated by an inter-stimulus interval of 100 ms, the same timing parameters of the fMRI experiment, followed by a response period of 2 s. To reduce contributions from low-level retinotopic processes, the second face within a pair was offset left by 2.4° horizontally and upwards by 2.4° vertically from the central position of the first face. The task was to respond whether the faces were the same or different. There were 102 total trials, 90 ‘same’ and 90 ‘different’, presented in a pseudo-random order. Each of the six ‘different’ conditions was tested in a separate block and given in random order across subjects, with 16 trials for each ‘different’ condition per subject. Reaction times and percentage correct were collected and combined into a single efficiency score (Morein-Zamir, Chua, Franko, Nagelkerke, & Kingston, 2007; Townsend & Ashby, 1983), calculated for each subject and for each condition. Dividing the accuracy by the latency, we obtained an index that is higher for more efficient performance. For scaling purposes, we used the log (latency, ms) resulting in the formula: Efficiency = Accuracy/log (Latency).

After the experiment, each subject was asked what strategy they used to perform the task. All but one subject reported scanning the entire face, with this exception reporting that he looked exclusively at the mouth. His efficiency scores reflected this, with better efficiency for the mouth and lower faces, and his ratio for upper versus lower face-half efficiency more than three standard deviations different from the other subjects. Hence his data were excluded from the behavioral analysis and the correlation arm of the fMRI analyses. Two subjects who were excluded from fMRI analysis based on excessive movement were also excluded from behavioral and correlation analyses.

2.5. fMRI experiment

2.5.1. Imaging parameters

Subjects were scanned in a Philips 3.0 T scanner at the UBC MRI Research Centre. T2*-weighted scans using an echo planar imaging were used to collect data from 36 interleaved axial slices (TR 2000 ms, TE 30 ms, FOV = 240 x 216 mm, 3 mm thickness with 1 mm gap, voxel size 3 x 3 mm, 128 mm reconstruction matrix, reconstructed voxel size 1.88 x 1.6 mm). These were co-registered onto a T1-weighted anatomical image (EPI) sequence, 170 axial slices, FOV = 256 x 200 mm, voxel size = 1 x 1 mm, slice thickness 1 mm, from each participant.

2.5.2. Localizer scan

The HVEM dynamic multiple localizer scan was run twice on each subject to identify face-selective regions of the visual cortex (Fox, Iaria, & Barton, 2009). The localizer consisted of grayscale video clips of faces, bodies, objects, Fourier-phase scrambled faces, and Fourier-phase scrambled objects. Each stimulus block included six video clips lasting 1.5 s separated by a 500 ms blank screen. Stimulus blocks were separated by a 12 s fixation cross. Each condition was repeated five times per run. Attention was monitored by asking participants to press a button on an MRI-compatible button-box when the same video clip was presented twice in a row.

2.5.3. Adaptation experiment

The adaptation paradigm included seven face-pair conditions: (1) same face, (2) different whole, (3) different top half, (4) different bottom half, (5) different eyes, (6) different nose, and (7) different mouth. Based on the recent findings that

\[
E_l(f_j) = \frac{1}{2} \frac{1}{C_0} \left( \frac{C_1}{C_2} \right)^2
\]

$$
Ef = \frac{\sum (S - C)^2}{C_0}
$$

Fig. 1. Examples of stimuli used in the different conditions, showing one of the eight face-pairs used. The same stimuli were used for the ideal observer, behavioral, and fMRI experiments. For illustrative purposes only, the red rectangles indicate the image component that was changed in the alternating face. In the whole-same condition, the same face is presented repeatedly (same). In the whole-different condition, the face of one person is alternated with that of another. In the top face-half condition, the bottom face-half is repeated, but the top face-half alternates between two different people. Similarly in the bottom face-half condition, only the bottom face-half alternates. On the right are the three different features conditions, in which either the eyes, nose or mouth alternates between images, with the rest of the face remaining constant. In the behavioral experiment, each face-pair was presented once sequentially, and subjects were asked whether the two facial images were the same or different. In the fMRI-adaptation experiment, each face-pair was presented four times (eight images) per block. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)
two alternating images are sufficient to obtain adaptation, i.e. reduced BOLD signal for repeated stimuli and the release from adaptation, i.e. recovery of the BOLD signal (Davies-Thompson et al., 2012), an alternating blocked (AB) design was used to present the stimuli (Fig. 1). Face A was presented for 900 ms, followed by a 100 ms blank interstimulus interval, then face B of the pair for 900 ms, and then another 100 ms blank interval. This alternation was repeated four times (ABABABAB), giving eight images per block. Blocks were separated by a gray fixation screen containing a central crosshair that lasted 8 s. Each block for each condition was repeated eight times. To avoid stimulus habituation, a different face pair was used for each repetition. Blocks from different conditions were mixed together in a counterbalanced order, resulting in a total of 56 blocks. Stimuli were back-projected onto a screen located inside the scanner bore, approximately 68 cm from subjects’ eyes, using Presentation 14.0 (www.neurobs.com). The stimuli spanned approximately 11° of visual angle. To control for effects of attention across conditions, while ensuring that subjects watched the face stimuli, subjects were given the task of indicating pressing a button on the button-box when they saw a face that was 8% smaller than the other faces within the block. Each block had one target face and its position in the sequence of faces was pseudorandom and counterbalanced across the eight possible positions.

Before scanning, subjects took part in a practice run consisting of six blocks of face stimuli that were not used in the experiment. 2.5.4. fMRI analysis

Brainvoyager XQ (www.brainvoyager.com) was used for all fMRI analysis. Preprocessing steps included time correction (cubic spline interpolation), 3D motion correction (trilinear/sinc interpolation), and high-pass temporal filtering (GLM-Fourier, 2 sines/cosines) were performed on all functional data. Two out of the 25 subjects were removed from further analysis due to excessive movement. After combining the two multiple-localizer scans, face-selective regions-of-interest (ROIs) were defined for each subject individually using the contrast “faces - objects” at p < 0.05 with Bonferroni correction for multiple comparisons. To define the core face-network areas in both hemispheres, contiguous clusters of at least 10 voxels located on the lateral surface of the inferior occipital gyrus were designated as the OFA, on the lateral mid-portion of the fusiform gyrus as the FFA, and on the posterior segment of the superior temporal sulcus as the pSTS.

We also isolated two control regions. First, to determine whether the responses in face-selective regions were reflecting lower level processing, the peak response in an early visual region for each condition was measured. An occipital pole box mask was drawn centered around the calcarine fissure of each subject (coordinates x = 14, y = –52, z = 16; –16, 6, 16), in which a subject had more than one irregularly shaped face-selective cluster within the expected location of a ROI, the time series of both clusters were averaged. Each stimulus block was normalized by subtracting the zero point for each ROI, the time series of the BOLD response was then converted from image intensity units to percentage signal change by subtracting and then normalizing the mean response during the experiment scan ([x̄—mean]/[mean*100]) (Andrews et al., 2010; Davies-Thompson, Goons, & Andrews, 2005; Calvan et al., 2006). If a subject had more than one irregularly shaped face-selective cluster within the expected location of a ROI, the time series of both clusters were averaged. Each stimulus block was normalized by subtracting the zero point for that stimulus block from the subsequent time points. These normalized data were then averaged across subjects to obtain the mean time course for each condition. The peak response was defined as the average of the response at 8, 10, and 12 s after block onset (Kourtzi & Kanwisher, 2001).

2.6. Statistical analysis

Discrimination thresholds in the ideal observer analysis were entered as the outcome variables in a repeated-measures ANOVA with Condition as a factor (whole-different, top face-half, bottom face-half, eyes, mouth, and nose). The efficiency scores from the human behavioral experiment were entered as the outcome variables in a repeated measures ANOVA with Condition as a factor (whole-same, whole-different, top face-half, bottom face-half, eyes, mouth, and nose), and Subject as a random factor. In all three analyses, to explore the basis of interactions, we used paired-samples t-tests, two-tailed, for planned comparisons. In the fMRI experiment, these p<posteriori comparisons were done particularly between each of the six ‘different’ conditions with the whole-same condition, to determine which conditions showed a significant release from adaptation. To avoid an inflated Type I error rate, we adjusted the alpha level with Bonferroni correction for multiple comparisons, which are reflected in the p-values. fMRI peak responses were also entered into repeated measures ANOVAs for each of the control regions.

To determine whether the neural responses in the face-selective ROIs were parametrically related to the perceptual differences or physical differences in the stimuli, we combined the subjects’ neural responses from the fMRI experiment with their efficiency scores from the behavioral task, and the discrimination thresholds from the ideal observer analysis (see Supplementary material). More specifically, though, because physical and psychophysical measures might themselves be correlated, to estimate the individual contribution of these two measures we also performed a partial correlation analysis. Partial correlations were run for each subject: the discrimination thresholds from the ideal observer were included as a constant when correlating the neural response with the efficiency scores, and efficiency scores included as a constant when correlating the neural response with the ideal observer analysis. Correlations were then Fisher’s r-transformed, (2r)/(1+r) and entered into two-tailed, one-sample t-tests (compared to 0 with Bonferroni correction) to detect significant correlations.

3. Results

3.1. Ideal observer analysis

This experiment assessed the physical differences between the face pairs used in the ‘different’ conditions. The repeated-measures ANOVA for the six ‘different’ conditions (whole-different, top face-half, bottom face-half, eyes, mouth, and nose) found a significant main effect of Condition (F(5,35) = 168.87, P < 0.001, Fig. 2A). Changes to the whole face required the least contrast to detect (M = 165, SD = 13). Pairwise and counterbalanced t-tests for planned comparisons (with Bonferroni correction) showed that the contrast threshold for distinguishing changes to the top face-half (M = 120, SD = 8.1) did not significantly differ from that for distinguishing changes to the bottom face-half (M = 116, SD = 9.6; t(7) = 1.41, P = 0.20), confirming that our selection of the eight face images had successfully matched the top and bottom halves for visual similarity. For changes to the individual features, which were not selected by such criteria, eye changes (M = 115, SD = 8.8) required significantly less contrast to detect than changes to the mouth (M = 98, SD = 9.8; t(7) = 5.52, P < 0.002) or changes to the nose (M = 70, SD = 13.1; t(7) = 9.44, P < 0.001). Mouth changes were also more easily detected than nose changes (t(7) = 4.82, P = 0.004).

3.2. Behavioral experiment

To assess how subjects perceive changes to the face, all subjects participated in a same/different behavioral experiment. This analysis includes 22 subjects, after excluding two subjects with excessive motion during fMRI, and the one subject who reported using an anomalous strategy focusing on the mouth alone. Average accuracy and reaction times for the different conditions are shown in Table 2. A repeated-measures ANOVA revealed a significant main effect of Condition (F(6,126) = 67.43, P < 0.001, Fig. 2B). Pairwise and counterbalanced t-tests for planned comparisons (with Bonferroni correction) showed that subjects were better at detecting changes to the whole face (M = 0.34, SD = 0.02) than when no changes occurred (M = 0.31, SD = 0.03; t(21) = 3.28, P = 0.004). Changes to the top face-half (M = 0.32, SD = 0.03) were easier to detect than changes to the bottom face-half (M = 0.21, SD = 0.08; t(21) = 6.02, P < 0.001). For changes to the individual features, subjects were better at detecting eye changes (M = 0.33, SD = 0.02) than mouth changes (M = 0.20, SD = 0.08; t(21) = 7.36, P < 0.001) or nose changes (M = 0.10, SD = 0.08; t(21) = 12.43, P < 0.001). Mouth changes were also more easily detected than nose changes (t(21) = 6.49, P < 0.001).

3.3. fMRI experiment

The six core areas, the OFA, FFA, and pSTS bilaterally, were identified with the dynamic localizer in most of the 23 subjects who met criteria based on head motion during scanning (Table 1 and Fig. 3): the mean Talairach coordinates are reported in Table 1.
The right FFA was identified in 14 subjects, and of these, eight subjects had voxels that did not overlap with the right FFA that were defined as FBA*. The occipital pole box mask was drawn for all subjects. During the adaptation scan, subjects had performed a target detection task. A one-way ANOVA showed no difference in response times ($F(6,126)=0.33$, $P=0.92$) between conditions, suggesting the difference in the neural responses between conditions noted below were not due to differences in attention levels during scanning. The peak response was measured for each of the six conditions in each ROI (Fig. 4). A repeated-measures ANOVA with main factors of hemisphere (right, left), ROI (ODA, FFA, pSTS) and Condition (whole-same, whole-different, top face-half, bottom face-half, eyes, mouth, nose) showed a significant main effect of ROI ($F(2,28)=57.27$, $P < 0.001$) and Condition ($F(6,84)=3.43$, $P=0.004$), but not for Hemisphere ($F(1,14)=3.91$, $P=0.07$). There was no interaction between Hemisphere and Condition ($F(6,84)=0.94$, $P=0.47$), or between ROI and Condition ($F(12,168)=1.43$, $P=0.16$). There was an interaction between Hemisphere and ROI ($F(2,28)=6.98$, $P=0.003$), indicating differences in the response across hemispheres. Finally, there was no significant 3-way interaction among ROI, Hemisphere and Condition ($F(12,168)=0.87$, $P=0.58$).

Planned comparisons showed that in the FFA, there was a significant effect of Condition for both the right ($F(6,132)=5.35$, $P < 0.001$) and left FFA ($F(6,108)=6.24$, $P < 0.001$). In the right FFA, compared to the whole-same condition ($M=1.04$, $SD=0.48$), there was release of adaptation to changes in the top face-half ($M=1.32$, $SD=0.40$; $t(22)=3.94$, $P=0.006$), the eyes ($M=1.36$, $SD=0.53$; $t(22)=6.09$, $P < 0.001$), and the whole-different condition ($M=1.23$, $SD=0.43$; $t(22)=3.00$, $P=0.042$), but no release of adaptation to changes to the bottom face-half ($M=1.18$, $SD=0.53$; $t(22)=1.88$, $P=0.044$), mouth ($M=1.09$, $SD=0.40$; $t(22)=0.76$, $P=0.99$) or nose ($M=1.11$, $SD=0.44$; $t(22)=0.93$, $P=0.39$). Similarly, compared to the whole-same condition ($M=0.88$, $SD=0.54$), the left FFA showed a release of adaptation for the whole-different condition ($M=1.23$, $SD=0.66$; $t(18)=3.57$, $P=0.012$), the top face-half ($M=1.22$, $SD=0.73$; $t(18)=4.18$, $P=0.006$), and the eyes ($M=1.33$, $SD=0.83$; $t(18)=4.12$, $P=0.006$), as well as the bottom face-half ($M=1.16$, $SD=0.65$; $t(18)=3.16$, $P=0.03$), but not for changes in the mouth ($M=0.97$, $SD=0.55$; $t(18)=1.25$, $P=0.09$) or nose ($M=1.07$, $SD=0.59$; $t(18)=2.48$, $P=0.09$).

In the right OFA, there was a significant effect of Condition ($F(6,126)=2.22$, $P=0.045$). Although the overall trend across conditions in the right OFA appeared similar to the right FFA, planned comparisons showed no significant release of adaptation after correcting for multiple comparisons. There was no effect of Condition in the left OFA ($F(6,114)=1.25$, $P=0.29$).

We also explored the lack of differential adaptation effects in right OFA in a post hoc analysis. Two possible explanations that could account for the lack of adaptation or correlation effects include insufficient sample size, or inclusion of overlapping voxels from another region that are not as strongly face-selective. To test this latter hypothesis, we localized voxels using a faces → Bodies contrast at $P < 0.05$ (Bonferroni corrected) within the previously defined right OFA ROIs (Faces → Objects). We designated these new clusters as right OFA*, and repeated the adaptation and correlation analyses. The repeated-measures ANOVA again showed a
significant main effect of Condition \( F(6, 96) = 2.73, P = 0.017 \) based on the responses of 17 localized right OFA \(^\ast\) clusters. The planned comparisons in right OFA \(^\ast\) showed a significant release of adaptation to changes in the top face-half \( M = 1.51, SD = 0.82, t(16) = 3.49, P = 0.003 \), and eyes conditions \( M = 1.52, SD = 0.83; t(16) = 3.50, P = 0.003 \), and a trend towards release of adaptation in the whole-different condition \( M = 1.43, SD = 0.71; t(16) = 1.88, P = 0.078 \) (Fig. 5). There was no significant release of adaptation to changes in the bottom face-half \( M = 1.31, SD = 0.70; t(16) = 1.08, P = 0.30 \), nose \( M = 1.34, SD = 0.73; t(16) = 1.01, P = 0.33 \), or mouth \( M = 1.24, SD = 0.68; t(16) = 0.18, P = 0.86 \) conditions.

The pSTS showed no difference in the response to conditions in either the right \( F(6,126) = 1.38, P = 0.23 \) or left hemisphere \( F(6,108) = 0.87, P = 0.52 \). Also, our control analyses showed, first, that neither the right FBA nor FBA \(^\ast\) showed any differences in the response to conditions \( F(6, 108) = 1.14, P = 0.34; F(6,42) = 0.19, P = 0.98 \) (Fig. 5). Second, for the occipital pole, an ANOVA showed no effect of Condition \( F(6,132) = 1.38, P = 0.23 \), suggesting that the significant effects found in the face-selective regions did not reflect processing at earlier stages of the visual system (Fig. 4).

### 3.4. Partial correlation analysis

Data from 22 subjects was entered into the partial correlation analysis (Fig. 6). One-sample t-tests showed that for the right FFA, peak responses on fMRI were correlated with human efficiency
scores (Zr=0.34, t(21)=4.67, P<0.001) but not with the ideal observer's discrimination thresholds (Zr= -0.07, t(21)= -0.84, P=0.41). A paired-samples t-test showed that the peak fMRI response in this region was significantly more correlated with human efficiency scores than with the ideal observer's discrimination thresholds (t(21)= 3.13, P<0.01). The left FFA showed a similar pattern, with significant correlations of the peak fMRI responses with human efficiency scores (Zr=0.27, t(17)=2.48, P<0.05) but not with the ideal observer analysis (Zr= -0.02, t (17)= -0.15, P=0.88). Unlike the right FFA, however, there was only a trend towards a significant difference between how well human efficiency and ideal observer measures correlated with the left FFA response (t(17)=1.79, P=0.09).

Peak responses in the right OFA were not correlated with either the human efficiency scores (Zr=0.13, t(20)=1.40, P=0.18), or the ideal observer thresholds (Zr=0.05, t(20)=0.36, P=0.73). Peak responses in the left OFA were also not correlated with either efficiency scores (Zr=0.17, t(18)=1.49, P=0.16) or discrimination thresholds (Zr=0.06, t(18)=0.58, P=0.57). There was no significant difference between how well human efficiency scores and ideal observer discrimination measures correlated with the OFA response (right OFA: t(20)=0.64, P=0.53; left OFA: t(18)=0.86, P=0.40). In our post hoc analysis of rOFA*, there were no significant correlations between peak responses and either human efficiency scores (Zr=0.21, t(16)=1.51, P=0.15) or ideal observer thresholds (Zr=0.02, t(16)=0.12, P=0.91). There was no significant difference in correlations between efficiency score and ideal observer (t(16)=0.63, P=0.54) (Fig. 7).

Peak responses in the right pSTS correlated with human efficiency scores (Zr=0.24, t(20)=2.19, P<0.05), but not with ideal observer thresholds (Zr= -0.12, t(20)= -0.97, P=0.34). Responses in the left pSTS correlated with neither human efficiency scores (Zr=0.06, t(17)=0.83, P=0.42) nor with ideal observer thresholds (Zr=0.06, t(17)=0.40, P=0.70). There was again no difference between how well human efficiency scores and ideal observer thresholds correlated with the STS response (right pSTS: t(20)=1.75, P=0.10; left pSTS: t(17)=0.35, P=0.73).

In our two control analyses, first, peak responses in right FBA and FBA* were not correlated with either human efficiency scores (Zr=0.095, t(13)=0.68, P=0.51; Zr= -0.077, t(7)=0.99, P=0.36) or ideal observer thresholds (Zr=0.173, t(13)= -0.54, P=0.60; Zr= -0.19, t(7)= -0.73, P=0.49), and there were no significant differences between correlations to efficiency score and ideal

![Graph](image-url)
observer in these regions (t(13) = 0.65, P = 0.53; t(7) = 0.87, P = 0.42) (Fig. 7). Finally, there were no significant correlations between peak fMRI responses in the occipital pole with either human efficiency scores (Zr = 0.13, t(21) = 1.31, P = 0.21) or ideal observer thresholds (Zr = -0.03, t(21) = -0.33, P = 0.75), and no difference between these measures in how well they correlated with the occipital pole response (t(21) = 1.02, P = 0.32).

Finally, we examined differences across regions. $2 \times 2$ ANOVAs examined differences between pairs of regions and analysis (ideal observer, behavioral measure). In the right hemisphere, there was a significant difference between the FFA and pSTS ($F(1,20) = 7.69$, $P = 0.01$) and analysis ($F(1,20) = 5.48, P = 0.03$), but no significant interaction ($F(1,20) = 0.18, P = 0.68$). This was driven by the behavioral measure being more correlated with the neural activity in the right FFA than in right pSTS ($t(20) = 2.70, P = 0.01$); however, there was no difference between these two regions to the ideal observer ($t(20) = 1.68, P = 0.11$). There were no differences in correlation to either measure between any other regions in the right hemisphere ($P > 0.05$), suggesting similar response profiles for the OFA and FFA. Finally, there were no significant effects or interactions in the left hemisphere.

In summary, these results suggest that bilateral FFA is sensitive to the subjective perception of feature differences, but not the physical differences in a facial image, that activity in the right FFA correlates more with a feature-salience hierarchy in subjective perception than with physical image differences, and that the right STS but not the left STS shows activity that correlates with this feature-salience hierarchy in subjective perception.$^2$

4. Discussion

We used an fMRI-adaptation technique to ask whether the core face-processing network shows a feature-salience hierarchy for facial features similar to that reported in the perceptual literature, and if so, whether this correlated with either the physical properties of the facial image, as determined by an ideal observer analysis, or the human psychophysical data for discriminating those features. We found that the right and left FFA showed differential sensitivity to features from different regions of the face, generally due to greater release from adaptation if the eyes or the upper face differed between images. However, this was not found for the OFA or the pSTS. A parametric analysis found that the pattern of release of fMRI-adaptation across different conditions correlated with the human perceptual data in the FFA bilaterally, with stronger correlations in the right FFA, where the neural signal was significantly more correlated with the human perceptual data than with the physical properties of the images. There was also a significant correlation of neural signal with human perceptual data in the right pSTS. These findings suggest that the feature-salience hierarchy characteristic of human face perception is best reflected by activity in the right and left FFA, and to an extent in the right pSTS.

Many behavioral studies have demonstrated the importance of the eye region in identity recognition (Garneau, 1973). More recent studies have shown that low-level contrast properties around the eyes contribute to recognition of faces (Glad et al., 2009), and that responses in the FFA reflect these low-level visual properties (Yue et al., 2011). To determine whether the human behavioral pattern of greater emphasis on the eye region may have been due simply to greater physical differences in the upper versus the lower half of facial images, one study used the Bubbles technique to measure face identification by human subjects versus an ideal observer when only small regions of the face were visible (Gosselin & Schyns, 2001). Although the eye region had the most diagnostic information for judging face identity for both humans and the ideal observer, the two were only partially correlated, suggesting that the emphasis on eyes in the human behavioral data does not simply reflect the physical properties of the image. Similarly, we found that even when the top and bottom halves of the face were equated for physical differences by the ideal observer, human subjects still showed better discriminative performance for the top face-half. Hence humans show a greater perceptual sensitivity to structural aspects of the upper face that is not simply reducible to image properties. Our fMRI-adaptation study was directed at revealing the possible neuroanatomical basis for this perceptual feature-salience hierarchy. While there are other studies that show fMRI-adaptation by face parts or partial faces (Andrews et al., 2010; Harris & Aguirre, 2008, 2010; Liu et al., 2010), the relative contributions of different face parts to the neural signal, and how this relates to the physical and perceptual properties of the stimuli, have not previously been compared.

Many studies have established that regions of the core face network such as the FFA show adaptation to repeated images of the same face (Andrews et al., 2010; Fox, Moon, Iaria, & Barton, 2009; Grill-Spector & Malach, 2001; Harris & Aguirre, 2008; Schiltz & Rossion, 2006). Other studies found release from adaptation in the right FFA when either the top or bottom half of the face changed (Schiltz et al., 2010; Schiltz & Rossion, 2006). We found release of adaptation in the right FFA when the top half of the face changed and in the left FFA when either the top or the bottom half changed. The reason for this discrepancy is not clear, but methodological differences may have contributed: subjects in the previous studies were asked to fixate on the top half in a composite face task, whereas subjects in our study were free to fixate where they liked. Across individual feature bands, our study found a release of adaptation in the right and left FFA when the eyes changed, but not when the nose or mouth changed. These results are supported by a previous study showing a greater MR signal change when the eyes changed than when the mouth changed (Harris & Aguirre, 2010). However, this study did not directly compare these two conditions to an adapting “same” condition. Our initial analysis of the OFA did not show any adaptation effect for either the whole face or face parts, but a post hoc examination of more face-specific voxels in the right OFA showed release of adaptation to the top face-half and eye conditions, suggesting that effects similar to those observed in right FFA might be present in the right OFA. This indicates that despite more robust adaptation effects in the FFA, processing of face parts in identity coding is likely a property of a network of regions or neuronal subpopulations within these regions. The pSTS also did not show any adaptation effects. Given that our faces differed in identity rather than expression, this is consistent with other studies showing that the activity in pSTS is not sensitive to changes in facial identity (Andrews et al., 2010) or only so when subjects are judging facial expressions (Fox, Moon, et al., 2009). Finally, we did not find adaptation effects in either fusiform control region (FBA or FBA$^*$), suggesting that effects of face parts are not a general property of fusiform processing. This was important because a previous study has shown release of adaptation in regions corresponding to FBA to whole face changes, using high-resolution fMRI (Weiner, Sayres, Vinberg, & Grill-Spector, 2010).

One important property of the core face processing network that has not been explored in previous studies is the degree to which the neural signal correlates either to the physical properties of faces, or to the human perceptual experience of faces. In this

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$^2$ In this study, we decided a priori to use the peak fMRI signal change as a measure of adaptation. An alternate method is to use an adaptation ratio (Avetisov, 2010). To determine whether this affects the results, we computed an adaptation ratio of “Condition/Whole different” as the fMRI response, and repeated the partial correlation to behavioral and ideal observer measures. An identical pattern was observed in the FFA and the OFA. For the right pSTS, the correlation to behavior was no longer significant. The reason for the discrepancy is unclear. One possibility is that pSTS effects are not as robust. Another possibility is that smaller, more variable signals in pSTS accentuated noise with an adaptation ratio. See Supplementary Fig. 2.
study, combining fMRI data with the subjects’ perceptual data, as well as with an ideal observer analysis of physical properties of faces, allowed us to perform a parametric correlation analysis. This correlation analysis again suggests that the feature-salience hierarchy is generated by activity in a network of regions, rather than by activity in any single region. We found that peak responses in both right and left FFA correlated with the perceptual efficiency of the subjects performing the study, but not with the contrast discrimination thresholds of the ideal observer analysis. Activity in the right pSTS also correlated only with human perceptual efficiency, while activity in the left pSTS did not show any relationship. This suggests that effects consistent with human perceptual experience are evident in the face processing network. This is reminiscent of findings from previous studies that used morphed faces to study categorical effects in the perception of face identity. These found release of adaptation in the right FFA only when the changes between one facial image and another caused subjects to perceive the images as being from different identities (i.e. crossing a category boundary lying between the two identities) (Fox, Moon, et al., 2009; Rotstein et al., 2005).

The fact that a stronger correlation to human perceptual efficiency than to physical image differences was found only in the right FFA is consistent with a converging body of evidence for dominance of the right hemisphere in face perception. First, tachistoscopic studies and studies of split-brain patients show a left visual field advantage for recognizing faces (Gazzaniga & Smylie, 1983; Sergent & Bindra, 1981). Second, face-selective activity on fMRI is larger in area, more statistically significant, and more consistently identified across subjects in the right than in the left hemisphere (Fox, Iaria, et al., 2009; Kanwisher et al., 1997). Third, transcranial magnetic stimulation of the right but not the left OFA impairs face discrimination (Pitcher, Walsh, Vowel, & Duchaine, 2007). Fourth, early deprivation of visual input to the right but not to the left hemisphere impedes the development of normal face recognition (Le Grand, Mondloch, Maurer, & Brent, 2003). Finally, acquired prosopagnosia occurs mainly with damage to bilateral or right occipitotemporal cortex (Barton, 2008; de Renzi, 1986). However, the left FFA was also significantly correlated to behavioral measures and showed adaptation effects identical to those in right FFA. Therefore, it is unclear whether the feature salience-hierarchy is a product of this right-dominant face processing network, or a product of purported feature-based strategies that may lateralize to the fusiform regions in the left hemisphere (Hillger & Koenig, 1991; Rossion et al., 2000).

An interesting question for future study might explore the minimum amount of face that has to change in order to produce a perceptual release of adaptation, and whether this differs across face parts or combinations of parts. A recent study compared whole face changes to subpart changes (one eye, both eyes, eyes–mouth, and eyes–nose–mouth) in the face inversion paradigm (James, Arcurio, & Gold, 2013). In behavioral data, they found a face inversion effect for whole face, eyes–mouth–nose, and eyes–mouth inversion, but not for one or both eyes alone. Also, the right FFA showed inversion effects for whole face but not for face parts. Of course, inversion studies address issues related to expertise processing and possible holistic mechanisms, which differ significantly from the question we sought to address, about the saliency of different parts in identity encoding.

The mechanisms that generate the feature-salience hierarchy in the FFA and in behavioral performance remain unclear. Our results and those of other studies (Gosselin & Schyns, 2001) show that the hierarchy cannot be entirely attributed to differences in physical properties between the top and bottom halves and between the features of human faces. Attention or other top–down processes may play a role, particularly since there is considerable evidence that the relative importance of different face regions varies according to the task (Malcolm et al., 2008). For judgments of emotional state from facial expressions, the pattern of diagnostic information shifts in the face from one expression to another (Smith et al., 2005), just as it does between judgments of identity, gender or expression (Schyns et al., 2002).

Finally, we note that subjects in our study were free to fixate on any part of the face during both the behavioral and fMRI experiments. It is possible that the emphasis on the eyes could be simply explained by a greater number of fixations in the eye-region of the presented stimuli. However, fixation preference is itself an important part of our perceptual experience of faces, and allowing subjects to freely move their eyes is ecologically the most valid approach. The alternative with forced, fixed, or randomly placed fixation onto a facial frame might interfere with natural perception of faces. Nevertheless, if fixation patterns were responsible for the hierarchical patterns that emerged from our neuroimaging data, one might also have expected to see this reproduced in the data for the occipital pole. Since this region represents foveal vision, fixation on the eyes alone would have meant that the eyes would have been the dominant percept in this retinotopic region, and hence we should have seen significantly more release from adaptation for the eyes than for the mouth at the occipital pole.

This is the first study to systematically compare the fMRI adaptation response across face parts changes while correlating this signal to both the perceptual and physical properties of the face stimuli. Our behavioral results confirmed a feature-salience hierarchy for human face perception, in which the top half of the face is more salient than the bottom half, and the eyes are more salient than the nose and mouth. Our fMRI-adaptation experiment found that activity in the FFA reflected the human perceptual data, but not the physical properties of facial images. Although the pattern of adaptation was most robust in the FFA, there was a similar pattern in other regions as well, particularly the OFA. These results suggest that the feature-salience hierarchy reflects activity within a network of face-selective regions, with an important contribution from FFA.

**Author contribution**

J.L., R.P., I.O., J.B., and J.D.T. designed the experiments and wrote the paper. J.L. and R.P. collected the data. J.L., R.P., and J.D.T. analyzed the data.

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**Appendix A. Supporting materials**

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.10.016.

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