The Representation of Parts and Wholes in Face-selective Cortex

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Abstract

Although face perception is often characterized as depending on holistic, rather than part-based, processing, there is behavioral evidence for independent representations of face parts. Recent work has linked "face-selective" regions defined with functional magnetic resonance imaging (fMRI) to holistic processing, but the response of these areas to face parts remains unclear. Here we examine part-based versus holistic processing in "face-selective" visual areas using face stimuli manipulated in binocular disparity to appear either behind or in front of a set of stripes [Nakayama, K., Shimojo, S., & Silverman, G. H. Stereoscopic depth: Its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, 18, 55–68, 1989]. While the first case will be "filled in" by the visual system and perceived holistically, we demonstrate behaviorally that the latter cannot be completed amodally, and thus is perceived as parts. Using these stimuli in fMRI, we found significant responses to both depth manipulations in inferior occipital gyrus and middle fusiform gyrus (MFG) "faceselective" regions, suggesting that neural populations in these areas encode both parts and wholes. In comparison, applying these depth manipulations to control stimuli (alphanumeric characters) elicited much smaller signal changes within faceselective regions, indicating that the part-based representation for faces is separate from that for objects. The combined adaptation data also showed an interaction of depth and familiarity within the right MFG, with greater adaptation in the back (holistic) condition relative to parts for familiar but not unfamiliar faces. Together, these data indicate that face-selective regions of occipito-temporal cortex engage in both part-based and holistic processing. The relative recruitment of such representations may be additionally influenced by external factors such as familiarity.

Disciplines

Medicine and Health Sciences

Comments

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INTRODUCTION

Faces are arguably one of the most important classes of visual stimuli encountered by human observers. Whether by innate mechanisms or prolonged experience, we are a species of "face experts," highly sensitive to the array of social signifiers embedded in faces, including age, race, emotional state, and identity.

In fact, it is commonly accepted that faces receive "special" processing in the human brain. Converging evidence from a number of fields, including electrophysiology (Perrett, Rolls, & Caan, 1982; Bruce, Desimone, & Gross, 1981), neuropsychology (Moscovitch, Winocur, & Behrmann, 1997), and, most recently, functional neuroimaging (Gauthier et al., 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), has localized "face-selective" processing to the ventral inferotemporal cortex, particularly the occipito-temporal and fusiform regions.

Behavioral studies, meanwhile, have suggested that processing of faces differs from that of other stimuli not only in anatomical loci but also in the mental operations involved. Key evidence for this idea comes from the "face inversion effect" (Yin, 1969), the observation that inversion differentially impairs perception of faces relative to other stimuli. This phenomenon has been taken to demonstrate that upright faces, unlike other object classes, undergo very little part-decomposition and are instead represented in a "holistic" manner (Farah, Wilson, Drain, & Tanaka, 1998). When the face is inverted, holistic processing is thought to be disrupted, resulting in impaired performance. This holistic model of face perception has received support from a number of experimental paradigms, including recognition of aligned versus misaligned "composite" faces (Young, Hellawell, & Hay, 1987) and matching of face parts presented in isolation or within the face context (Tanaka & Farah, 1993).

In its strongest form, the holistic hypothesis posits that the face is encoded as a template or gestalt, with no explicit representation of its component features (Tanaka & Farah, 1993; Farah, 1990). By this view, recognition of inverted faces relies on a separate part-based system that may also be involved in object recognition (Searcy & Bartlett, 1996; Bartlett & Searcy, 1993; Farah, 1990). Supporting this view, Haxby et al. (1999) reported that ventral extrastriate regions responding preferentially to another class of objects (houses) showed increased activation to inverted, relative to upright, faces.

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Nonetheless, there is some evidence for separate representation of individual face parts in the human visual system (Cabeza & Kato, 2000; Leder & Bruce, 1998; Macho & Leder, 1998). For example, Cabeza and Kato (2000) reported an increased likelihood to falsely recognize a face composed of features from previously viewed faces, or "prototype effect," comparable to that for prototypes based on configuration. Such effects do not necessarily rely upon a part-based object recognition system: C.K., a patient with severe object agnosia, is nonetheless capable of identifying isolated face features (Moscovitch et al., 1997).

It is therefore likely that both face parts and their grouping into a whole are represented within the face-processing stream. However, although functional magnetic resonance imaging (fMRI) has revealed a number of "face-selective" brain regions, with larger responses to faces versus other visual stimuli, researchers have only recently examined the relation of such activations to holistic and part-based processing. Using inversion and composite face manipulations, respectively, Yovel and Kanwisher (2005) and Schiltz and Rossion (2006) have reported responses matching the behavioral hallmarks of holistic processing in "face-selective" areas on the middle fusiform gyrus (MFG), particularly in the right MFG (Schiltz & Rossion, 2006), and, to a lesser extent, the inferior occipital gyrus (IOG).

Although these two studies strongly implicate "face-selective" occipito-temporal regions in holistic processing of faces, neither fully addresses the question of how such areas respond to face parts. Inversion is a technically elegant manipulation, as differences in response cannot be explained by variation between the upright and inverted stimuli in low-level physical stimulus properties. However, the assumption that the face inversion effect indexes only a change from holistic to part-based processing has recently been challenged by Sekuler, Gaspar, Gold, and Bennett (2004), who argue instead that the face inversion effect arises from quantitative decreases in processing efficiency for inverted faces. Consequently, it is unclear whether inverted faces truly elicit part-based as opposed to holistic processing.

Given the uncertainty regarding inversion, other methods of measuring holistic versus part-based processing would be preferable. One such alternative was devised by Schiltz and Rossion (2006), who measured responses to aligned versus misaligned composite faces. In contrast to inversion, the link between composite face alignment and holistic processing is undisputed; however, these stimuli also have the disadvantage of varying in their low-level stimulus properties.

In this study, we investigated how "face-selective" occipito-temporal regions observed with fMRI respond to face parts versus wholes using a stereoscopic manipulation of face perception (Figure 1). Derived from the work of Nakayama, Shimojo, and Silverman (1989), these stimuli use binocular disparity to create either a percept of a face behind a set of bars (Figure 1A, left), or strips of a face floating in front of a background (Figure 1A, right). Critically, these two conditions are identical *aside from the change in binocular disparity* (Figure 1B). Yet the first case will be "filled in" by the visual system and perceived as a normal face occluded by bars, whereas the latter cannot be completed amodally, and so is perceived in terms of its constituent parts.

These stimuli thus provide a powerful means of testing holistic versus part-based processing without inversion or changes in the physical properties of the face stimulus. Here we demonstrate behaviorally that the manipulation of stereoscopic depth in these stimuli differentially engages holistic and part-based processing. We then present results of three fMRI experiments using these stimuli to more fully probe the representation of wholes and parts in "face-selective" ventral visual areas. Finally, because previous behavioral evidence suggests that familiarity may modulate holistic representations by making them more reliable or robust (Young, Hay, McWeeny, Flude, & Ellis, 1985; Ellis, Shepherd, & Davies, 1979), we examine the interaction of this depth manipulation and familiarity within face-selective regions.

METHODS

Experiment 1: Behavior

Subjects

Twenty-eight individuals between the ages of 18 and 35 years were recruited from local universities. All subjects had normal or contact-corrected vision and normal stereoscopic vision. Data from an additional subject were excluded due to average performance at chance. In this and all following experiments, informed consent was obtained from all subjects, and procedures followed institutional guidelines and the Declaration of Helsinki.

Stimuli

Stimuli consisted of six 250×250 pixel images of female faces created in the GenHead software program (www.genemation.com/), cropped using an elliptical bounding box to remove external contour information. These were placed in a 288×288 pixel stimulus with disparity cues, subtending $5.8° \times 5.8°$ of visual angle.

Procedure

The experimental procedure (Figure 2A) was adapted from Tanaka and Farah (1993). Subjects were told that they would be tested on their ability to learn face–name associations. The experiment began with a study phase, in which the six target stimuli (without disparity cues) and associated names were presented five times in a random order for 5 sec each. Immediately following

Figure 1. Stimuli derived from Nakayama et al. (1989). (A) Schematic of binocular disparity manipulation. When the stripes are in front (left), the face is ''filled in'' by the visual system and perceived in a holistic manner. When the face is in the frontal depth plane (right), amodal completion cannot occur, so the face is perceived in terms of its parts. (B) Examples of actual stimuli used in the fMRI experiments. The stripes are positioned to appear at 9 or 5 min of binocular disparity either in front of or behind the face stimulus when viewed with red/green anaglyphic glasses.
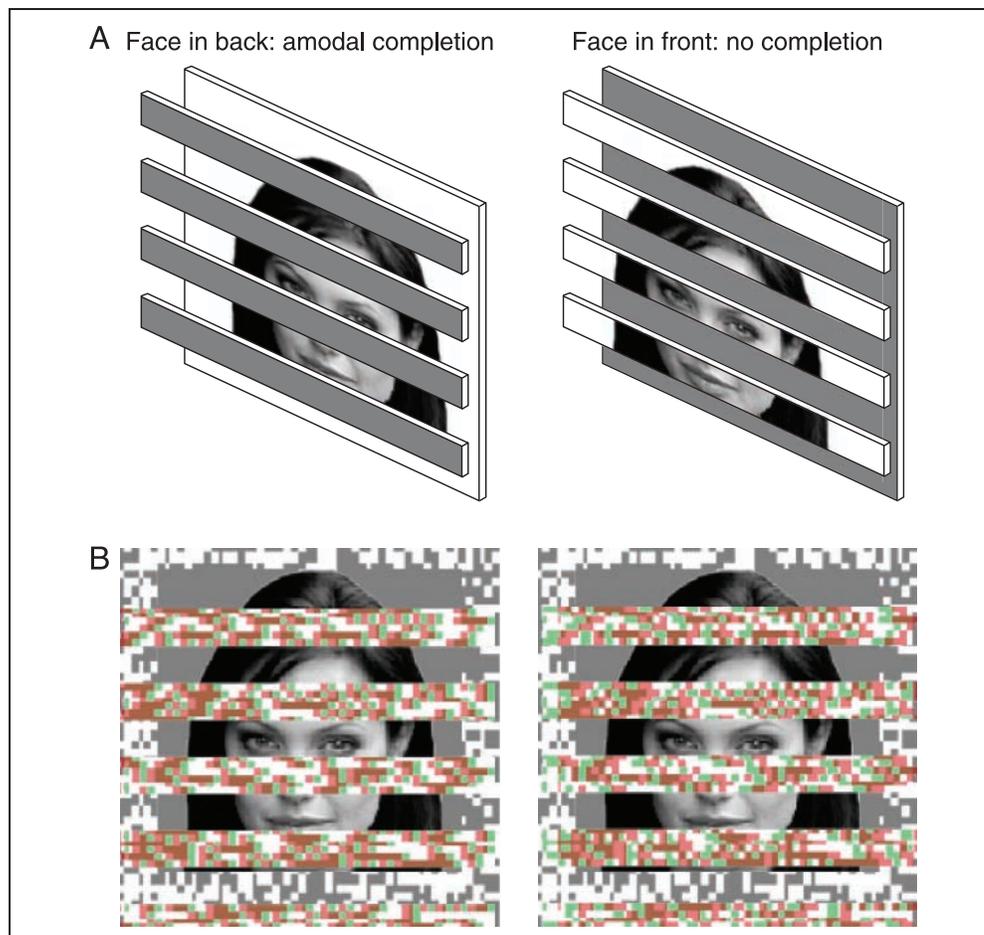
learning, a two-choice recognition task was administered in which subjects had to identify which face, or which face part, matched a given name. Foils were taken from one of the other learned faces, and the target and foil faces differed only with respect to the individual feature being tested (eyes, or nose and mouth). Each face served as a foil for only one other face in the set.

Experiment 2: fMRI Block Design

Subjects

Ten subjects between the ages of 18 and 35 years with normal or contact-corrected vision and normal stereo-scopic vision were recruited from local universities. Two additional subjects were excluded due to excessive head movement during scanning.

Stimuli

Stimuli were created from 200 × 200 pixel gray-scale photographs of famous celebrities and unfamiliar indi-viduals (20 exemplars each). The unfamiliar faces were drawn from portfolio photographs of aspiring actors, and were selected to match the famous faces in sex, hair color and style, and attractiveness. These stimuli were placed into an image consisting of a gray background noise pattern overlaid with noise-patterned red and green stripes positioned to appear at 5 min or 9 min of disparity either in front of or behind the face stimulus when viewed with anaglyphic (red/green) glasses (Fig-ure 1B). The finished stimuli were 250 × 250 pixels, subtending 5.3° × 5.3° of visual angle, and were pre-sented on a black background. An additional category of phase-scrambled noise was also included as a control.

Procedure

The experiment consisted of a block design with two depths (front, back) crossed with three stimulus types (famous, unfamiliar, and noise) for a total of six con-ditions (Figure 4A). Each run contained 12 blocks, lasting 30 sec each, constrained to consist of four ''sub-blocks,'' with each sub-block containing all three stimulus types at a single depth (all front or all back). Within sub-blocks, noise blocks were always shown first and the order of the subsequent familiar and unfamiliar face blocks was randomized. This design ensured that the perception of depth would be stable during the blocks containing face stimuli. Each stimulus was displayed for

Figure 2. Behavioral experiment procedures and results. (A) Procedure, derived from Tanaka and Farah (1993). After familiarization with a set of six female faces and associated names, subjects were presented with a two-choice recognition task in which they had to identify which face, or which face part, matched a given name. (B) Results. Performance for whole faces presented in the front disparity condition was significantly worse than that for whole faces in the back condition, and similar to that for isolated parts. This result confirms that the disparity manipulation does indeed affect whether the face is processed holistically (back condition) or in terms of its parts (front condition). Error bars in this and all subsequent graphs reflect standard error.
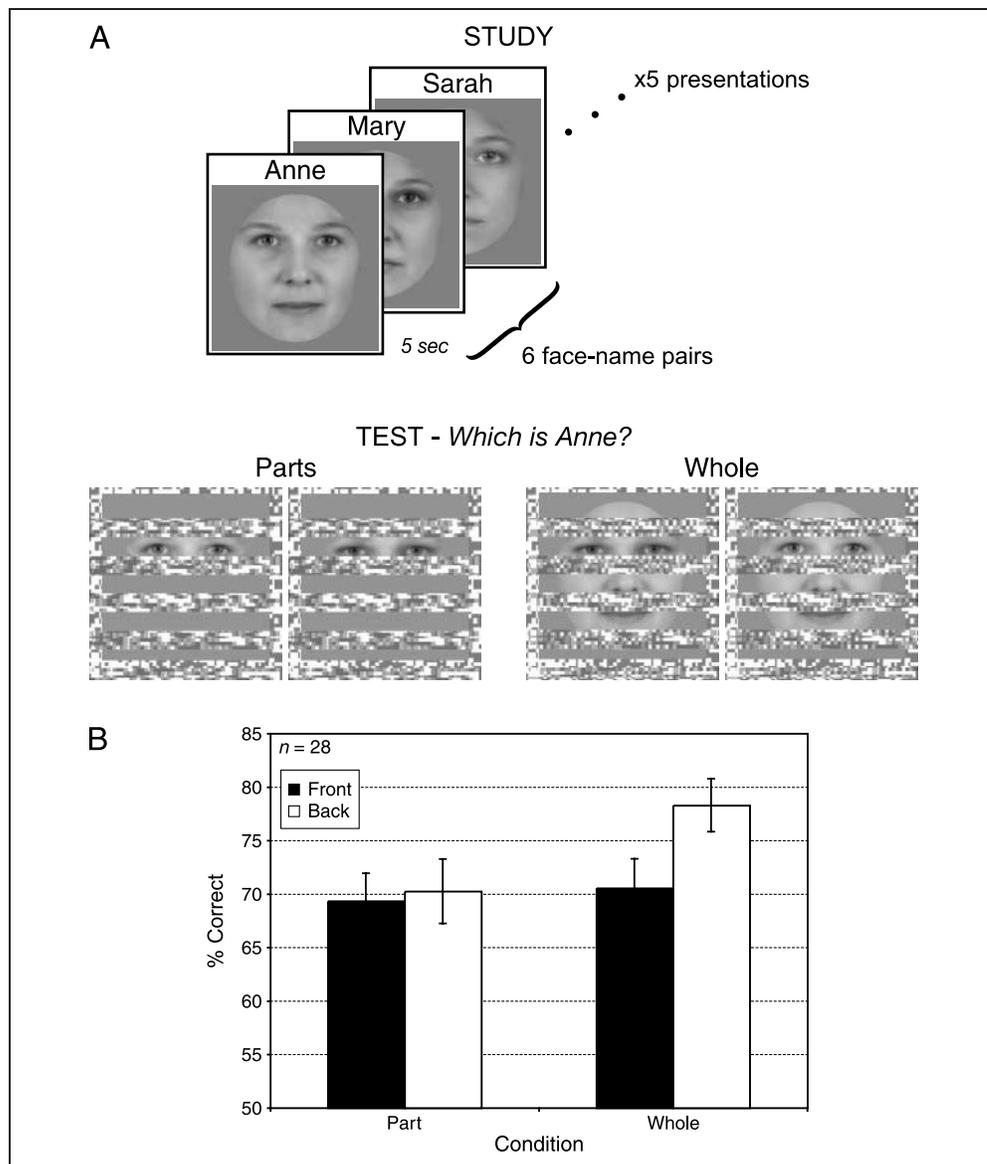
1.5 sec. During each block, subjects performed a "two-back" working memory task for all conditions. Six runs of approximately 6 min each were acquired for each subject. Prior to scanning, all subjects performed a familiar/unfamiliar judgment task with a subset of the face stimuli to confirm that they were familiar with the celebrities depicted in the famous condition (mean accuracy: 84.6%).

MRI Scanning

Scanning was performed on a 3-Tesla Siemens Trio using an eight-channel surface array coil. Echo-planar blood oxygenation level-dependent fMRI data were collected at a TR of 3 sec, with 3 × 3 × 3 mm isotropic voxels covering the entire brain. Head motion was minimized with foam padding. A high-resolution anatomical image (3-D MPRAGE) with 1 × 1 × 1 mm voxels was also acquired for each subject. Visual stimuli were presented using an Epson 8100 3-LCD projector with Buhl long-throw lenses for rear-projection onto a Mylar screen, which subjects viewed through a mirror mounted on the head coil. Subject responses were recorded using FORP (www.curdes.com/newforp.htm) fiber-optic button boxes.

MRI Preprocessing and Analysis

Blood oxygenation level-dependent fMRI data were processed using the VoxBo (www.voxbo.org/) software package. After image reconstruction, the data were sinc interpolated in time to correct for the fMRI acquisition sequence, motion corrected, transformed to a standard spatial frame (MNI, using SPM2; www.fil.ion.ucl.ac.uk/spm), and spatially smoothed with a 3 (Experiment 2) or 2 (Experiments 3 and 4) voxel full-width, half-maximum 3-D Gaussian kernel. Within-subject statistical models were created using the modified general linear model (Worsley

& Friston, 1995). Experimental conditions were modeled as step-functions, and then convolved with an average hemodynamic response function (Aguirre, Zarahn, & D'Esposito, 1998). Nuisance covariates were included for effects of scan, global signals, and spikes in the data due to sudden head movement.

Anatomical regions of interest (ROIs) were defined individually for each subject using the main effect of both types of faces (famous, unfamiliar) versus baseline, defined either as phase-scrambled noise (block design) or fixation trial (event-related adaptation). Left and right regions anatomically corresponding to the IOG and MFG were manually selected using the anatomical guidelines and the contrast of all faces versus noise (Experiment 2) or fixation (Experiments 3 and 4), with a threshold of $t \geq 3.5$. For each of these functionally defined ROIs, beta values were extracted; in Experiments 3 and 4, these values were then normalized by the response to the main effect to equate for signal strength across ROIs. All graphs and statistical analyses use these normalized values. Talairach coordinates for locations of activity were derived from the initial MNI coordinate space after applying the mni2tal transformation (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach).

Experiment 3: fMRI Adaptation Paradigm

Subjects

Thirteen subjects between the ages of 18 and 35 years with normal or contact-corrected vision and normal stereoscopic vision were recruited from local universities. It was necessary to exclude an unusually high number of additional subjects, possibly due to the relative monotony of the target detection task used here and in Experiment 4. Twelve subjects were excluded due to excessive head movement or scanner noise (3 subjects), self-reported drowsiness (3 subjects), improper visual correction (2 subjects), or failure to find main effects of face presentation and/or adaptation (4 subjects). It is important to note that decisions to exclude subjects were made prior to analysis of any aspects of the data relevant to the hypotheses of the study.

Stimuli

Stimuli were the same as in Experiment 2, with the addition of 20 new exemplars for a total of 40 exemplars per condition.

Procedure

The experiment consisted of eight experimental conditions (Figure 5A): two depths (front, back) crossed with two levels of familiarity (famous, unfamiliar) and two trial types (same, different). An additional condition consisting of the gray noise background with a fixation dot

was included as a baseline. On each trial, two stimuli were displayed for 1.1 sec each, with an interstimulus interval of 100 msec, during which the stripes in the corresponding disparity were displayed on the gray noise background. Following the second stimulus, there was an intertrial interval of 700 msec, in which the fixation image (gray noise pattern, no stripes) was shown. Subjects were instructed to monitor for the occurrence of a target fearful face, which they saw at the beginning of each run. Target trials constituted 5% of total trials, were randomly interleaved with the other conditions, and were excluded from the analysis. Six runs of approximately 6 min each were acquired for each subject. There were 80 trials per condition (2 trials per stimulus), for a total of 720 trials in the experiment. The order of trials was pseudorandom (determined by use of the OptSeq routine; http://surfer.nmr.mgh.harvard.edu/optseq/). Prior to scanning, all subjects performed a familiar/unfamiliar judgment task with a subset of the face stimuli to confirm that they were familiar with the celebrities depicted in the famous condition (mean accuracy: 87%). Scanning and analysis parameters were identical to Experiment 2, except that experimental conditions were modeled as delta functions.

Experiment 4: fMRI Adaptation for Faces vs. Alphanumeric Characters

Subjects

Seven subjects between the ages of 18 and 35 years with normal or contact-corrected vision and normal stereoscopic vision were recruited from local universities. Data from an additional four subjects were excluded due to excessive head movement (2 subjects) or failure to find main effects of face presentation and/or adaptation (2 subjects).

Stimuli

Stimuli were the same as in Experiment 3, with the addition of two new categories of familiar (Latin) and unfamiliar (Cherokee) typographical characters, both from the Plantagenet Cherokee font (Figure 6A). There were a total of 35 exemplars per condition.

Procedure

The experimental procedure was the same as that in Experiment 3, but with a total of 16 conditions: two stimulus conditions (faces, characters) crossed with two depths, two levels of familiarity, and two levels of repetition. Subjects were instructed to monitor for infrequent images from a separate target category (flowers), indicating whether the target appeared in the front or back depth plane. Trial order was pseudorandom (computed using the optseq2 program). Seven runs of

approximately 9 min each were acquired for each subject, with 70 trials per condition (2 trials per stimulus), for a total of 1260 trials in the experiment. Prior to the functional scans, all subjects performed a familiar/unfamiliar judgment task with the face and character stimuli to confirm that they were familiar with the images (mean accuracy: 85.7% faces, 93.9% characters). Scanning and analysis parameters were as described for Experiments 2 and 3 above.

Response of "Face-selective" ROIs to Other Object Categories

To confirm the "face-selectivity" of ROIs examined in Experiments 3 and 4, six subjects from Experiments 3 and 4 participated in a block-design experiment in which they viewed other natural object categories. Subjects viewed 2 runs consisting of 4 blocks each of fixation, faces, scenes (cityscapes), common everyday objects, and phase-scrambled noise patterns, for a total of 240 trials. Stimuli consisted of 400×400 pixel color images (36 exemplars per condition), subtending $8.44° \times 8.44°$ of visual angle. Blocks were always presented in the same order (fixation, face, scene, object, scrambled), with each stimulus displayed for 900 msec and no intervening ISI. Subjects performed a two-back task throughout the experiment. For the analysis of functional "face-selectivity," the evoked responses to the blocks of face, object, scene, and scrambled stimuli were measured versus the fixation baseline within the ROIs previously defined for each subject in Experiment 3 or 4.

Mapwise Random Effects Analysis of the Effect of Depth

To examine the effect of depth, data from Experiments 3 and 4 were combined ($n = 20$). The estimated beta map for the difference between front and back presentations of faces were obtained for each subject. These maps were entered into a second-level analysis, with region-wise significance determined by permutation testing (Nichols & Holmes, 2002). The main effect of stimulus presentation (all face conditions minus fixation trials) was used to define an ROI comprising all areas with a visual response. The effect of depth was then examined within this ROI.

RESULTS

Here we use stimuli derived from the work of Nakayama et al. (1989) to test responses to whole faces versus parts, by creating either a percept of a face behind a set of stripes (Figure 1A, left) or strips of a face floating in front of a background (Figure 1A, right). Critically, these two conditions differ only in the *change in binocular disparity* (Figure 1B). Yet, the first case will be "filled in" by the visual system and perceived as a normal face oc-

cluded by bars, whereas the latter cannot be completed amodally, and so is perceived in terms of its constituent parts. In Experiment 1, we demonstrated this behaviorally using a modified version of the paradigm of Tanaka and Farah (1993). We then ran a series of neuroimaging experiments examining the responses to these stimuli in face-selective ventral visual areas using a block design (Experiment 2), an event-related adaptation paradigm (Experiment 3), and a control visual category of alphanumeric characters (Experiment 4).

Behavioral Results

The manipulation of stereoscopic depth in the stimuli of Nakayama et al. (1989) appears to differentially engage holistic and part-based processing. We tested this idea using a modified version of the "whole-versus-part superiority effect" (Tanaka & Farah, 1993). In their original experiment, Tanaka and Farah found improved recognition of individual face parts when the parts were presented within the context of a whole face, supporting the idea that faces are processed holistically rather than in terms of their parts. Notably, the whole face stimuli are identical in every respect except for the part to be recognized, demonstrating an improvement in performance for parts within the context of a face despite the absence of any additional visual information to support the discrimination. In our version of this experiment, the presentation of face parts in isolation or in context of the face was crossed with the two binocular disparity conditions (Figure 2A). Given our claim that the faces in front are perceived in terms of their parts, we would expect this manipulation to reduce the superiority effect for whole-face stimuli.

The results from 28 subjects are displayed in Figure 2B. Although results for the back depth condition successfully replicate the original superiority effect for whole faces, performance for parts and wholes in the front condition was roughly similar. This was reflected statistically in a two-way repeated-measures analysis of variance (ANOVA), which found significant main effects of test condition [part vs. whole, $F(1, 27) = 5.7$, $p = .012$, one-tailed], depth [front vs. back, $F(1, 27) = 4.98$, $p = .017$], and a significant two-way interaction of test condition and depth [$F(1, 27) = 3.5$, $p = .037$]. Paired t tests confirmed that the interaction was driven largely by the difference in performance between WholeFront and WholeBack conditions ($p = .001$, one-tailed), whereas accuracy in PartFront and PartBack conditions was roughly equivalent ($p = .38$, one-tailed). Thus, the binocular disparity manipulation does indeed affect whether faces are perceived in a holistic or part-based fashion.

fMRI Results: Overview

As demonstrated by our behavioral results, the manipulation of binocular disparity provides a compelling

means of recruiting holistic versus part processing without relying on the face inversion effect or changing basic image properties. In three fMRI experiments, we used these stimuli to examine the response of face-selective cortical regions to face wholes and parts. Additionally, presentation depth (back or front) was crossed with the familiarity of the presented faces, as previous behavioral studies indicate that recognition of familiar faces may benefit from more effective processing of the internal face gestalt (Young et al., 1985; Ellis et al., 1979). We tested whether face parts are represented within face-selective brain areas, and if the familiarity of a face modulates the degree of holistic neural processing. In the third fMRI experiment, we further compared the responses in face-selective areas for the preferred category of faces and a control visual class of alphanumeric characters.

Using fMRI, we measured the responses in "face-selective" regions of the ventral inferotemporal cortex to stimuli varying in depth (front, back) and familiarity (famous, unfamiliar). Analyses focused on two ROIs: the MFG (Figure 3, top) and the IOG (Figure 3, bottom), known to have higher responses to faces than to a variety of other stimuli (Gauthier et al., 2000; Kanwisher et al., 1997; McCarthy et al., 1997). These regions were defined individually in each subject; Figure 3 reflects the overlap of ROIs across all subjects in the three fMRI

experiments ($n = 30$). For each ROI, Talairach coordinates of the voxel with greatest overlap across subjects correspond well to those previously reported (Kanwisher et al., 1997) for these regions (right MFG: 39, −53, −17; left MFG: −36, −53, −14; right IOG: 39, −82, −9; left IOG: −39, −81, −8).

fMRI Results: Block Design

In our first fMRI experiment, we used a block design to examine whether part-based, as opposed to holistic, processing is reflected in the bulk neural signal from face-selective areas. Binocular disparity (front or back) was crossed with three stimulus types: famous faces, unfamiliar faces, and phase-scrambled noise images (Figure 4A). For each face condition, the corresponding noise condition was subtracted to remove any low-level effects of depth on the signal and isolate the face-specific effect of disparity.

Figure 4B displays the results of the blocked experiment. As can be seen, front depth conditions, associated with part-based processing, elicit similar responses to the holistic back depth conditions across all ROIs. Likewise, a repeated-measures ANOVA for each ROI found no significant effects ($ps > .1$) except for a three-way interaction in the IOG driven by a lower response to famous faces in the front depth condition in the left IOG
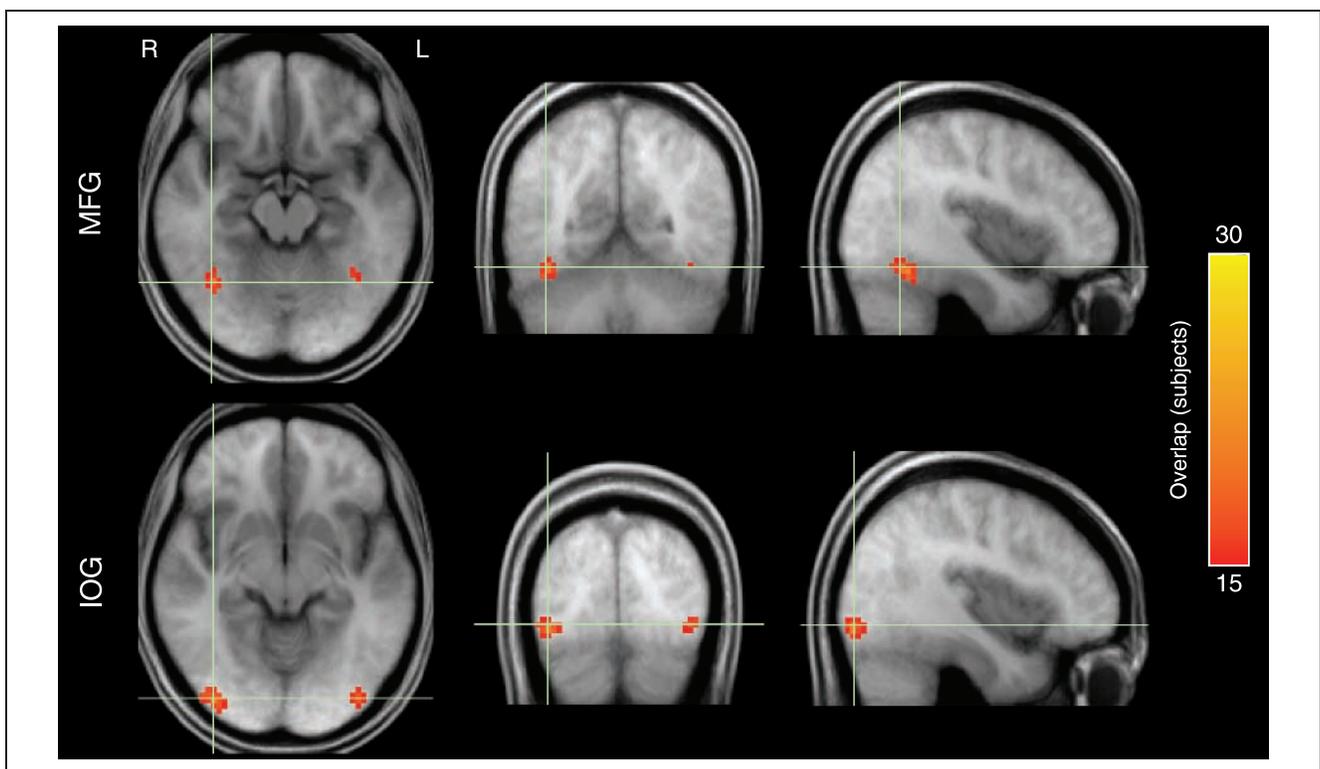

Figure 3. Regions of interest (ROIs) in fMRI. ROIs were defined individually in each subject using the contrast Faces > Fixation. These maps reflect the overlap of ROIs across subjects in three experiments ($n = 30$), and correspond to the MFG and the IOG. The ROIs are displayed atop the average of the registered anatomical images across subjects.
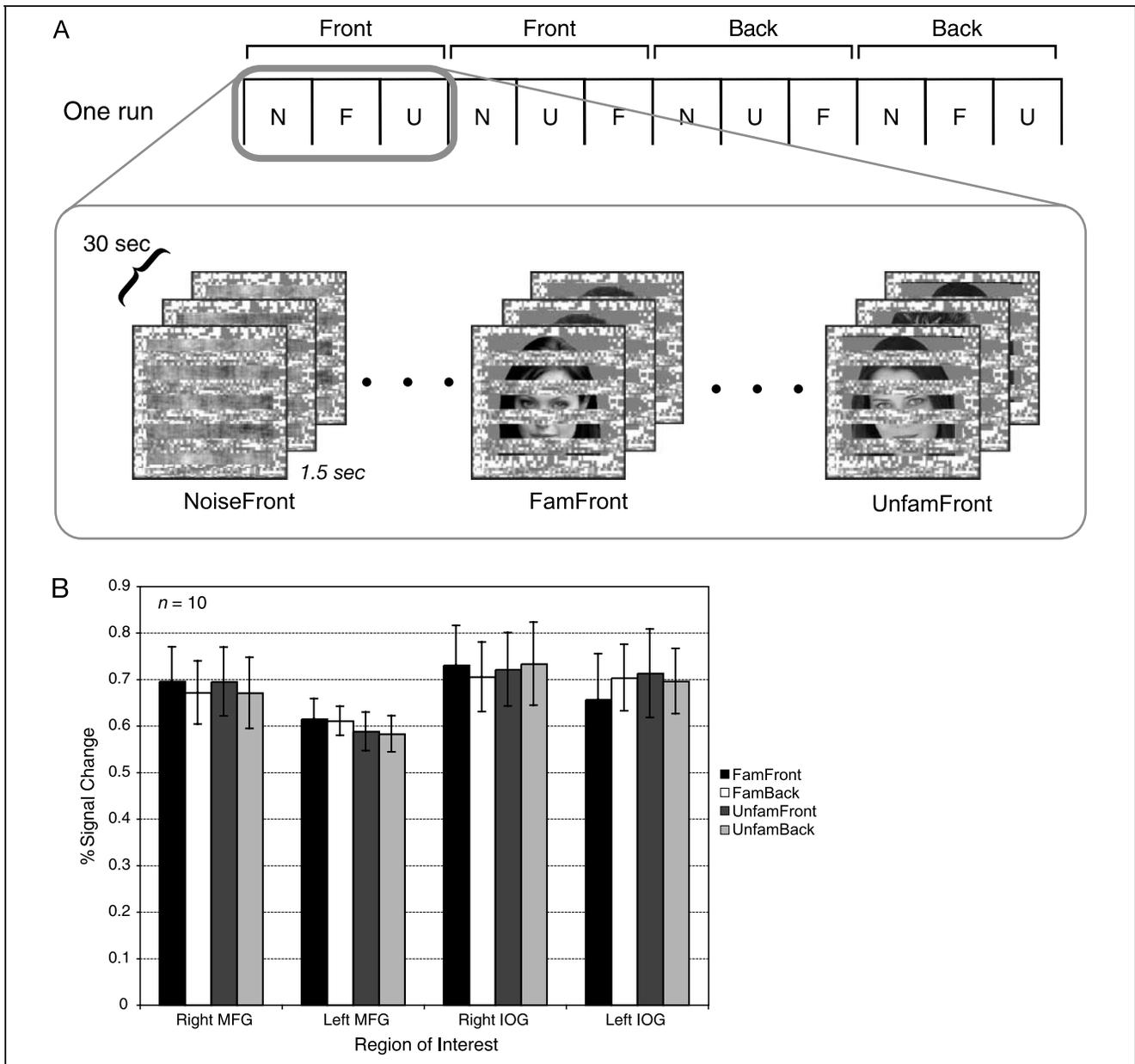
Figure 4. Blocked fMRI experiment procedure and results. (A) Procedure. Two depths (front, back) were crossed with three stimulus types (famous, unfamiliar, and noise) for a total of six conditions. Each run contained 12 blocks, lasting 30 sec each, divided into four ''sub-blocks'' of all three stimulus types at a single depth (all front or all back). Within sub-blocks, noise blocks were always shown first to ensure stable perception of depth for the subsequent face blocks, and the order of the familiar and unfamiliar face blocks was randomized. Subjects performed a ''two-back'' working memory task. (B) Results. Despite the difference in behavioral performance for faces in the front versus back condition (Figure 2B), there were no significant effects of depth or familiarity in the block design.

$[F(1, 9) = 13.355, p = .005]$. These data suggest that both face parts and wholes are represented within face-selective regions of the visual cortex.

This finding appears to stand in contrast to prior results supporting a role for face-selective regions in holistic processing (Schiltz & Rossion, 2006; Yovel & Kanwisher, 2005). However, this inconsistency may be explained by a basic difference in experimental design between these studies and our first fMRI experiment. These previous studies employed adaptation, the phenomenon of reduced neural activity following repeated presentation of

the same stimulus (Henson, 2003; Grill-Spector et al., 1999). By comparing the reduction in activity for stimuli which differ in a single given dimension (e.g., viewpoint), one can infer the representations underlying neural responses. If two stimuli varying in a single dimension produce equivalent adaptation as is seen for repetition of a single stimulus, it is assumed that the neural representation is invariant for that dimension. Conversely, differences in adaptation between conditions suggest that these dimensions have separate representations at the neural level.

In fact, previous studies that have examined the neural correlates of inversion without an adaptation paradigm have often found little or no difference in the response to upright and inverted faces within "face-selective" regions (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999; Kanwisher, Tong, & Nakayama, 1998). Thus, experimental design may play an important role in whether patterns of neural activity differentially associated with holistic processing are observed in "face-selective" regions. Accordingly, in our second fMRI experiment, we examined the effects of depth and familiarity using an event-related adaptation paradigm.

fMR Adaptation to Faces

In our second fMRI experiment, we used an adaptation paradigm to probe for differential effects of part-based versus holistic processing, as measured by the depth manipulation. Because our first experiment demonstrated equal responses in "face-selective" regions to stimuli at front and back disparities, adaptation is an ideal means of assessing the neural representations associated with these conditions. Subjects were instructed to monitor for the appearance of an infrequent target fearful face among pairs of faces which could be same or different, familiar or unfamiliar, and appearing in front of or behind noise stripes (Figure 5A). Adaptation was calculated as the difference in percent signal change between different and same trials for each condition after normalization for average signal strength in each ROI.

If activation in face-selective areas reflected holistic processing alone, we would expect to see significant adaptation effects only for faces in the back (holistic) depth condition. Instead, all ROIs showed greater responses to pairs of different faces versus repetition of the same face, regardless of depth (Figure 5B). A five-way repeated-measures ANOVA (ROI × Hemisphere × Depth × Familiarity × Repetition) confirmed this pattern, showing a highly significant main effect of repetition [$F(1, 12) = 51.2, p = 1.6 \times 10^{-5}$], but no significant interaction of depth and repetition ($F < 1$). Additionally, there was a significant interaction of ROI and repetition [$F(1, 12) = 27.3, p = .0003$], due to a greater relative magnitude of adaptation in the MFG relative to the IOG.

Figure 5. Adaptation fMRI experiment procedure and results. (A) Procedure. The experiment consisted of eight experimental conditions: two depths (front, back) crossed with two stimulus types (famous, unfamiliar) and two trial types (same, different). The gray noise background image with a fixation dot was included as a baseline condition. On each trial, two stimuli were displayed for 1.1 sec each with an interstimulus interval of 100 msec. The intertrial interval was 700 msec, in which the baseline fixation image was shown. Subjects were instructed to monitor for the occurrence of a target fearful face, which they saw at the beginning of each run. (B) Results. Adaptation, measured as decreased neural response to repetition of the same face (Same) relative to presentation of two different faces (Different), is roughly equivalent regardless of depth condition (Front or Back) in both the MFG and the IOG. Consistent with the block-design data (Figure 4), these results support the existence of representations for both whole faces and their individual parts within the face-selective cortex.
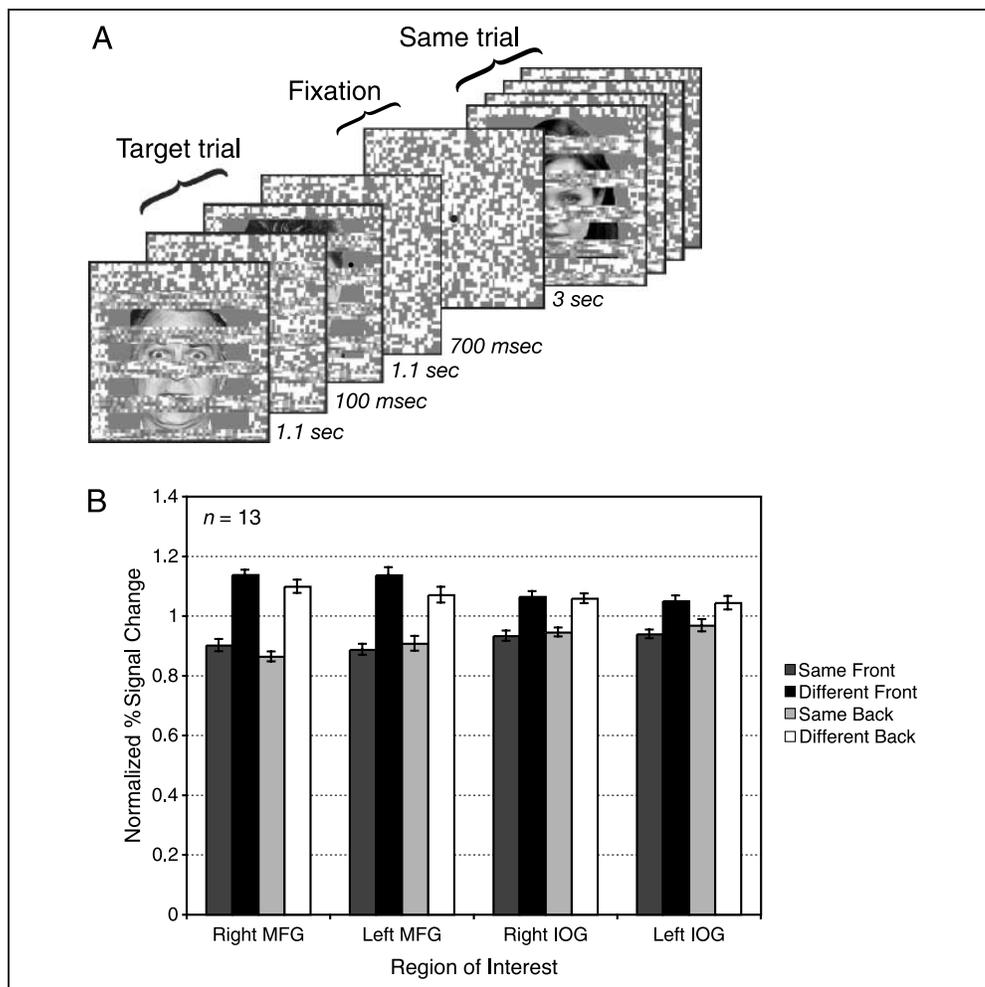
Thus, the results of our block-design experiment cannot be explained as arising from experimental insensitivity to differential holistic processing. Rather, both the block design and adaptation paradigms support a single conclusion: that face parts, as well as face wholes, are represented within face-selective visual areas in the occipito-temporal cortex. These data therefore provide an important constraint on models of how faces are encoded within the human visual system.

Our finding that face-selective areas of the human brain represent both whole faces and their individual parts challenges the strong form of the holistic hypothesis, which would hold that part-based analysis only occurs within object-processing cortex. However, face-selective regions are also known to respond to nonface objects, albeit to a lesser extent, and it has been demonstrated that even these reduced responses carry enough information to discriminate among nonpreferred categories (Haxby et al., 2001). Thus, it is possible that the representation of face parts within the face-selective cortex is, nonetheless, mediated by an object recognition system. Although the equal magnitudes of response and adaptation for the front and back conditions make this interpretation unlikely, the previous experiments also cannot rule it out, as both used a control condition of unstructured visual noise. Therefore, in a fourth experiment, we examined the neural responses in face-selective areas to depth manipulations of faces versus another class of objects, alphanumeric characters.

fMR Adaptation to Faces vs. Alphanumeric Characters

In our final experiment, we compared adaptation across depth conditions for faces and nonface objects to determine whether part-based processing of faces is subserved by a more general object recognition system. Note that here we use the term "part-based processing" broadly to indicate stimulus recognition by component decomposition, as opposed to the narrower sense of specific face features (eyes, nose, mouth).

To examine the role of part-based processing of nonface objects, we included another experimental category: alphanumeric characters. Like faces, the representation of alphanumeric characters appears to be biased toward the center of the visual field (cf. tools; Hasson, Levy, Behrmann, Hendler, & Malach, 2002), and these stimuli lend themselves readily to amodal completion. In addition, in contrast to other object classes, the familiarity of alphanumeric characters can be readily manipulated, as all subjects presumably have been exposed to the exemplars of the Latin alphabet but not to a wide variety of other writing systems in existence. This allows for the construction of a fully factorial design crossing stimulus type (face/character) with familiarity, depth, and repetition.

In this experiment, faces and alphanumeric characters were crossed with familiarity (famous vs. unfamiliar faces, Latin vs. Cherokee characters) and repetition for a total of 16 conditions (Figure 6A). Subjects were instructed to monitor for the appearance of images from an infrequent target category (flowers, 35 exemplars). Face-selective ROIs were defined by the main effect of all face conditions versus baseline fixation trials. Adaptation was again measured as the proportional difference in percent signal change between same and different trials in each condition.

Of critical importance is the response of "face-selective" regions to alphanumeric characters. If all part-based processing within the MFG and the IOG reflects the operation of an object-processing system, we would expect adaptation to be roughly equivalent for faces in the front condition and characters. If, on the other hand, part-based processing for faces is mediated by face perception mechanisms, the response to faces in the front condition should be higher than that to alphanumeric characters.

Figure 6B displays the results for the MFG and the IOG in seven subjects. As can be clearly seen, alphanumeric characters elicited smaller responses in both the MFG and the IOG relative to faces in the front depth condition, although the difference is greatest within the MFG. Likewise, the magnitude of adaptation is much greater for faces in both depth conditions than for characters. A five-way repeated-measures ANOVA crossing ROI, hemisphere, stimulus type, depth, and repetition confirmed this pattern, showing a significant main effect of stimulus type [$F(1, 6) = 51.4, p = .0004$], as well as a significant interaction of stimulus type and repetition [$F(1, 6) = 13.1, p = .011$]. Paired t tests confirmed that this interaction reflected a significant adaptation effect for faces ($p = 8.3 \times 10^{-5}$) but not for characters ($p = .04$; Bonferroni corrected $\alpha = .025$).

We also examined the response within the "character-selective" cortex defined by the subtraction of faces from alphanumeric characters (Figure 6C, left). Although the two-way interaction of stimulus type and repetition was not significant [$F(1, 6) = 1.36, p = .29$], the four-way interaction of hemisphere, stimulus type, depth, and repetition did achieve significance [$F(1, 6) = 14.8, p = .009$], reflecting greater adaptation within the left hemisphere "character" area for faces in the front depth condition and characters in the back condition, versus the opposite pattern in the right hemisphere (Figure 6C, right), although direct comparisons of these conditions were not significant. Although we have no theoretical expectations regarding the object-processing cortex, these results provide an intriguing counterpoint to those in face-selective areas, especially given the proposed functional division between the right and left hemispheres in terms of global versus local processing (Parkin & Williamson, 1987), as well as the known importance of the left hemisphere for language.

Figure 6. Comparison of adaptation for faces and alphanumeric characters. (A) Stimuli. The procedure was identical to that in Experiment 3 (Figure 5), with the addition of familiar (Latin) and unfamiliar (Cherokee) alphanumeric characters. Subjects were instructed to monitor for the occurrence of a target stimulus class of flowers (35 exemplars). (B) Adaptation in "face-selective" cortex, defined by greater response to faces versus fixation baseline. Both the MFG and the IOG showed a much smaller response and reduced adaptation for characters relative to faces, suggesting that part-based processing of faces is not mediated by a more general object recognition system. (C) Adaptation in "character-selective" cortex. Left: Subtraction of face from character conditions revealed bilateral activations in the inferotemporal cortex posterior and superior to the "face-selective" MFG (Talairach coordinates of maximum overlap across subjects, right: 45, −67, −6; left: −45, −67, −8). Right: These "character-selective" areas showed a significant interaction of hemisphere, stimulus type, depth, and repetition, with greatest adaptation in the left hemisphere to characters in the back and faces in the front depth conditions. This pattern is consistent with presumed functional specialization of the left and right hemispheres for language and local versus global visuospatial processing.
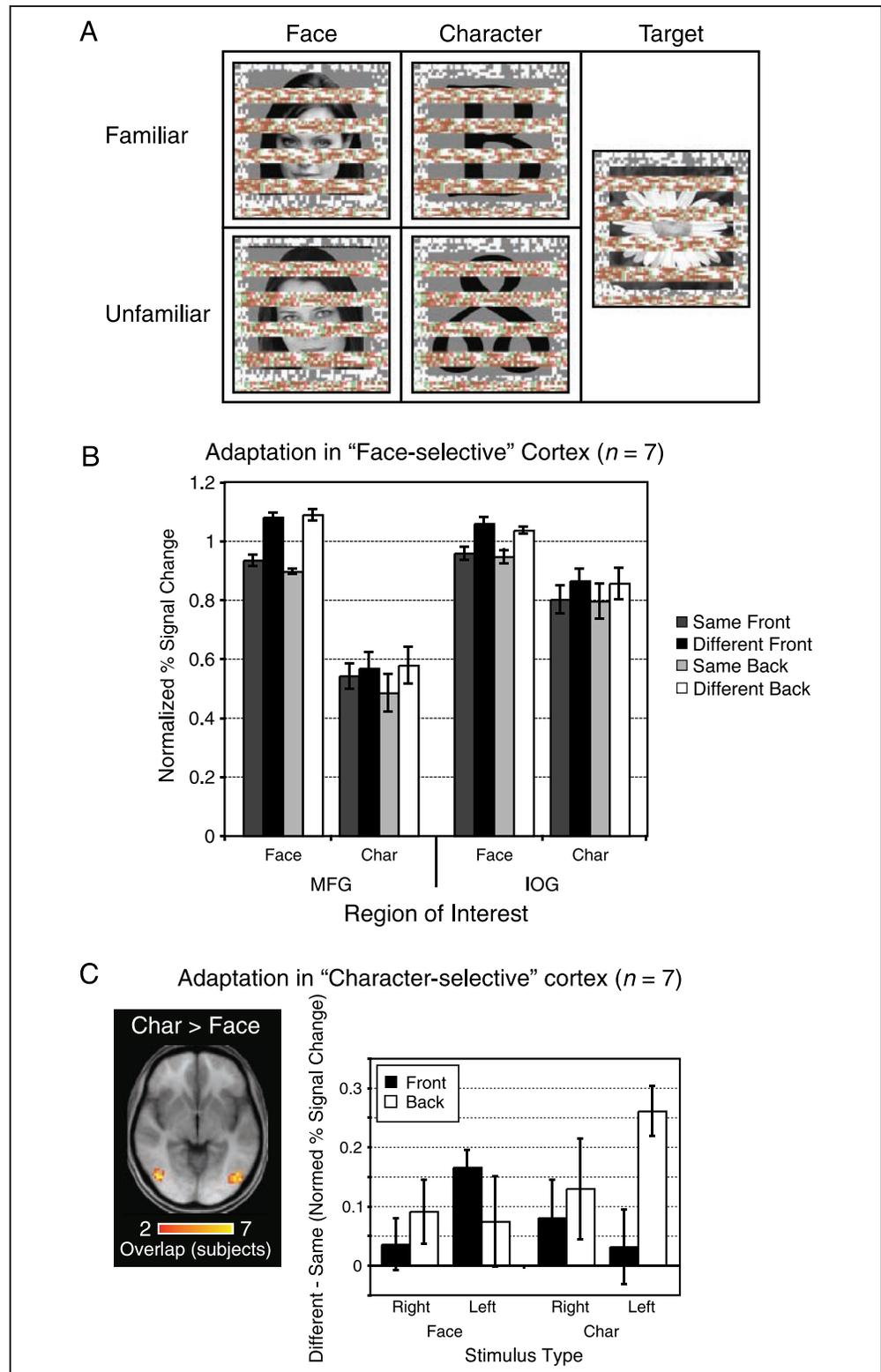
Thus, the results from Experiment 4 do not support the idea that part-based representations of faces within face-selective areas are mediated by an object recognition system. Rather, independent part-based representations of faces appear to be encoded within the same neural substrates associated with holistic processing (Schiltz & Rossion, 2006; Yovel & Kanwisher, 2005), particularly in the MFG. Meanwhile, our data from "character-selective" areas suggest that insofar as face parts and wholes are differentially represented within the object recognition

stream, such differences appear to reflect broad hemispheric variation in processing.

Response of ''Face-selective'' ROIs to Other Object Categories

In Experiment 4, we examined the responses in ''face-selective'' regions defined by the comparison of faces versus fixation for both faces and a nonface object category, alphanumeric characters. Although these ROIs were defined without reference to alphanumeric characters, they nonetheless showed a significantly higher response to faces than to characters, further supporting the idea that face parts are represented within the ''face-selective'' processing stream rather than by a separate object recognition system.

However, because alphanumeric characters differ in their low-level properties from faces, and may in fact be processed in separate parts of the occipito-temporal cortex (McCandliss, Cohen, & Dehaene, 2003), it is unclear whether our findings for these stimuli would generalize to other object categories. Therefore, in a separate analysis, we further examined the responses of the ROIs defined in Experiments 3 and 4 to stimulus categories commonly used in functional localization of ''face-selective'' areas: faces, scenes, everyday objects, and phase-scrambled noise patterns. Within the ''face-selective'' ROIs of six subjects (defined by Face > Fixation), the response to faces was dramatically larger than that to other stimulus categories [mean % signal change (SEM) across all ROIs: face = 2.56 (0.03), scene = 1.57 (0.03), object = 1.55 (0.02), scrambled = 0.08 (0.02)]. A repeated-measures ANOVA confirmed this result, showing a highly significant main effect of condition [$F(3, 15) = 49.7, p = 5 \times 10^{-8}$], with a simple contrast analysis showing significantly greater activations to faces than to scenes [$F(1, 5) = 57.1, p = .001$], objects [$F(1, 5) = 176.8, p = 4.3 \times 10^{-5}$], and phase-scrambled patterns [$F(1, 5) = 66.9, p = .0004$]. The difference between faces and objects was significant not only at the population level but in individual subjects (all subjects, all regions, p values between .04 and 7×10^{-16}). Thus, ''face-selective'' regions defined by the comparison of faces and fixation in Experiments 3 and 4 also show greater activation to faces versus a variety of real-world stimuli with shared visual properties, further supporting the point that the response to face parts in such areas reflects face-specific rather than general object processing. Combined with the Talairach coordinates listed previously in this article, these data further suggest that the regions defined here as the MFG and the IOG are consistent with the ''face-selective'' fusiform face area (FFA) and occipital face area (OFA) defined by separate functional localization in prior experiments (e.g., Yovel & Kanwisher, 2005).

fMRI Results: Familiarity Analysis

As described above, behavioral evidence suggests that face processing may be modulated by familiarity (Young

et al., 1985; Ellis et al., 1979). Accordingly, we also examined the interaction of processing type (as assessed by depth) and face familiarity in our adaptation paradigm. Data from Experiments 3 and 4 were combined for this analysis, yielding results from a total of 20 subjects.

Because increased familiarity is thought to produce more robust or reliable holistic encoding (Young et al., 1985; Ellis et al., 1979), our initial analysis centered on the familiar conditions. If familiar faces are processed in a largely holistic fashion, we would expect greater adaptation in the back depth condition, associated with holistic processing, relative to the front depth condition. Alternatively, if part-based and holistic representations were engaged equally by familiar faces, there should be no difference between the two depth manipulations.

Figure 7A displays the amount of adaptation for familiar faces by depth condition within left and right ROIs. In keeping with the predictions of a holistic model of familiar face processing, the right MFG shows greater adaptation for famous faces when they are presented in the back depth associated with holistic processing. In left hemisphere ROIs, on the other hand, the direction of the effect is reversed, with greater adaptation in the front (part-based) depth condition relative to the back. A four-way repeated-measures ANOVA with ROI, hemisphere, depth, and repetition as factors confirmed this interaction of hemisphere, depth, and repetition [$F(1, 19) = 5.57, p = .029$].

Thus, despite neural adaptation for the back depth condition in face-selective regions of both hemispheres, only in the right hemisphere is there differential adaptation for familiar faces consistent with a holistic hypothesis. Indeed, even within the right hemisphere, this effect appears to be localized to the right MFG (Figure 7A). Supporting this idea, post hoc analysis comparing the mean responses to familiar faces in the front and back conditions approaches significance within the right MFG ($p = .06$, paired t test).

Unlike the familiar face data, results for unfamiliar faces in front and back depth conditions show no such interaction effects (Figure 7B). Across both ROIs and hemispheres, adaptation to unfamiliar faces appears to be slightly higher in the front condition associated with part-based processing. However, a four-way repeated-measures ANOVA failed to find any significant effects of depth ($p > .1$). Therefore, it seems likely that unfamiliar faces engage holistic and part-based face-selective processing to a similar extent.

Taking the familiar and unfamiliar data together, we see the same pattern of slightly greater adaptation in the front depth condition across the majority of face-selective regions examined here. The notable exception is the right MFG, which displays greater adaptation for familiar faces in the back depth condition relative to front, and the opposite pattern for unfamiliar faces (Figure 7C). Although the individual paired comparisons are not significantly
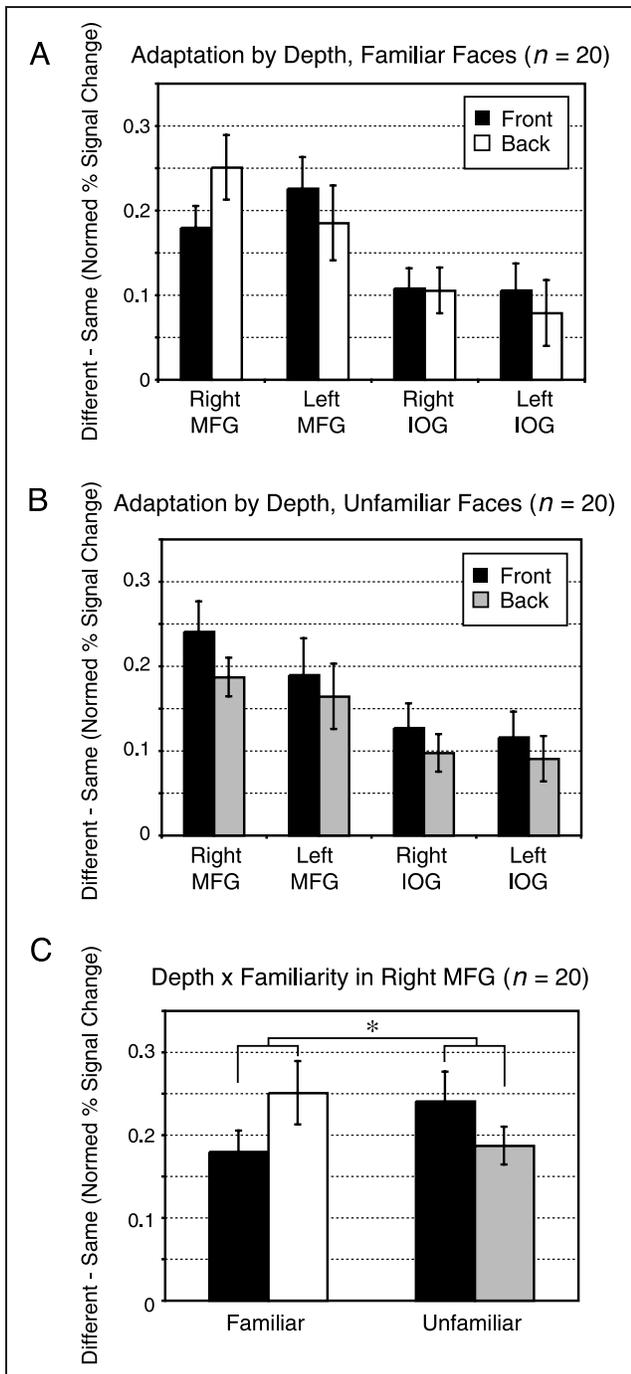
Figure 7. Familiarity analysis of combined adaptation data. (A) Interaction of familiarity and depth for familiar faces, across hemispheres and ROIs. A significant three-way interaction of hemisphere, depth, and repetition reflects the greater adaptation in the back (holistic) depth condition relative to the front (part-based) in the right hemisphere, versus the opposite pattern in the left hemisphere. (B) Interaction of familiarity and depth for unfamiliar faces, across hemispheres and ROIs. In contrast to the data for famous faces in part (A), no significant differences among conditions were seen. (C) Interaction of familiarity and depth within the right MFG. The crossover interaction of familiarity and depth was significant, suggesting that the relative recruitment of holistic or part-based representations within this ROI may be modulated by familiarity.

different, this crossover interaction is statistically significant ($p = .027$, paired t test), suggesting that holistic encoding within the right MFG is influenced by the familiarity of the stimulus. These results therefore expand upon previous work linking the right MFG to holistic processing (Schiltz & Rossion, 2006) by demonstrating that such encoding may be modulated by factors external to the stimulus itself, such as familiarity.

fMRI Results: Depth Analysis

In the preceding experiments, we have demonstrated that ventral face-selective areas respond equally to faces manipulated in binocular disparity to appear in front of or behind a set of stripes, despite behavioral evidence that the latter are perceived holistically, whereas the former are not. However, because the behavioral and neuroimaging data were collected in different individuals over separate sessions, one potential concern is whether subjects in the neuroimaging experiment perceive the binocular depth.

To address this issue, we analyzed the effect of depth in the combined data from the adaptation paradigm (20 subjects). The combination of all areas responding to visual stimulation (all face conditions > fixation baseline) was defined as the ROI. The effect of depth was then analyzed as the subtraction of all front from all back face conditions.

Greater activation to back versus front depth was visible in three areas (Figure 8): a left hemisphere area close to the occipital pole corresponding to area V1 (Talairach coordinates: -14, -91, -0.5) and more dorsal regions bilaterally. Talairach coordinates for these latter areas (right: 29, -93, 14; left: -18, -93, 9) place them in the vicinity of V3A, a visual area which has been implicated in perception of stereoscopic depth (Tsao et al., 2003; Mendola, Dale, Fischl, Liu, & Tootell, 1999).

Thus, the lack of differential activation to back versus front depth conditions within face-selective regions cannot be attributed to an inability to distinguish these stimuli across the entire brain. Instead, the similar responses to the two depth conditions in these areas reflect a rough equivalence of processing, with both part-based representations of faces and their integration into a whole.

DISCUSSION

Although face perception is often characterized in terms of holistic, as opposed to part-based, processing, there is some evidence for independent representations of face parts. Yet despite a growing neuroimaging literature on holistic processing, there has been little study of how face parts are represented in face-selective areas of the brain. In this article, we have presented a novel approach to this question through the application of a
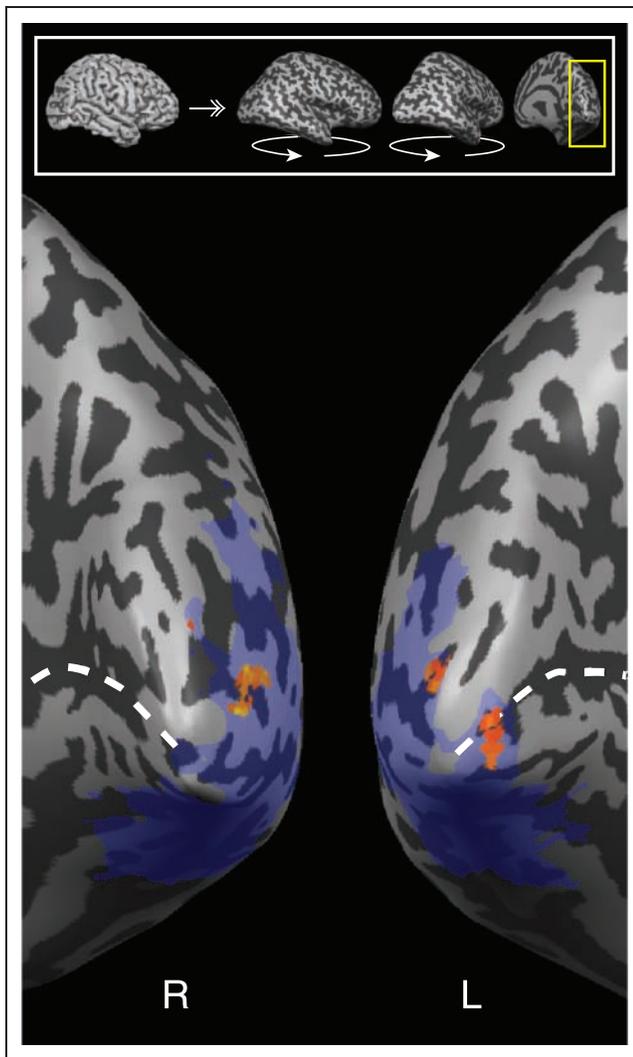
Figure 8. Mapwise random effects analysis of the effect of depth. Activations for the subtraction of front from back face conditions meeting a threshold of $t(df = 19) = 3.04$ with a cluster size of 15 voxels (corresponding to a region-wise $\alpha = .05$ by permutation analysis) are displayed on the most posterior sections of an "inflated" brain. The inset at the top of the figure illustrates the perspective for the right hemisphere, presented at left below. White dotted lines indicate the approximate position of the calcarine sulcus in each hemisphere and the blue shading indicates the region within which a main effect of stimulus presentation versus fixation was observed.

binocular disparity manipulation derived from Nakayama et al. (1989).

In these stimuli, a set of bars are manipulated in depth to appear either in front of or behind a face image. Although the first case will be "filled in" by the visual system and will undergo normal holistic processing, the latter cannot be completed amodally and is perceived in terms of its parts. We confirmed this behaviorally using a modification of the "part-versus-whole superiority effect" of Tanaka and Farah (1993).

Using these stimuli, we then ran a series of experiments using fMRI to test whether parts and wholes are differentially represented by face-selective areas of the

ventral visual stream. In three experiments using a block design (Experiment 2), an event-related adaptation paradigm (Experiment 3), and comparison to a nonpreferred object category (Experiment 4), we found that, to the contrary, both face wholes and parts elicit similar activation within face-selective areas.

Given that face-selective regions in the visual occipitotemporal cortex appear to represent both face parts and wholes, how are such representations instantiated at the neural level? One possibility is suggested by the work of Sugase, Yamane, Ueno, and Kawano (1999), who found that single neurons in macaque temporal lobe convey information about both global (face versus geometric shape) and fine-grained (facial expression, identity) categories, and that these different scales of representation occur at different latencies. Similarly, single neurons within the face-selective regions examined here could represent both global structure and detailed component information.

Alternatively, the pattern of results seen here could stem from rapid interactions between spatially adjacent but functionally discrete neural populations, which respond selectively to face parts or whole faces. Just such an architecture has been described in intracranial recordings of the inferotemporal cortex (McCarthy, Puce, Belger, & Allison, 1999), which found "face-part-specific" responses at recording sites medial to those with a greater response to whole faces. Likewise, in electrophysiological recordings from monkey superior temporal sulcus, some "face cells" have been observed which also respond well to component facial features (Perrett et al., 1982), whereas others show reduced response when the feature composition of the face is disrupted (e.g., by removing eyes) (Bruce et al., 1981).

In either case, the existence of independent representations for face wholes and parts within face-selective regions argues against the idea that the latter are processed by a more general object recognition system, as might be predicted by a strong form of the holistic hypothesis. Instead, the system responsible for processing faces in a holistic manner also contains independent representations of individual face parts. This finding is consistent with neuropsychological data from Patient C.K., who, despite his severe object agnosia, is nonetheless able to recognize both whole faces and face parts (Moscovitch et al., 1997).

In contrast, previous neuroimaging data collected by Haxby et al. (1999) suggest that brain regions associated with object recognition are recruited to process face parts. Critical to this interpretation, however, is the assumption of an explicit link between inversion, the stimulus manipulation used in this experiment, and part-based processing. As discussed previously, this idea has recently come into question, as other researchers have argued that inversion reflects a quantitative change in processing efficiency rather than a qualitative dichotomy (Sekuler et al., 2004). In any case, the notion of inversion as merely

a disruption of part integration probably represents an oversimplification of the mental processes involved in perceiving stimuli manipulated in this manner. [Notably, recognition performance for object stimuli such as houses and airplanes, which are presumably processed in a part-based manner even when upright, is also impaired by inversion, although not to the same extent as for faces (Yin, 1969).]

The technique presented here therefore provides a more direct means of studying holistic versus part-based processing than the inversion effect. As shown in Experiment 4, this method is potentially applicable to a range of stimuli besides faces, and can be used to probe holistic and part-based representations more generally within the visual system. For example, in the current work, we are agnostic as to whether "part-based" face processing should be conceptualized as the specific representation of individual features (eyes, nose, mouth) or a more general strategy of component decomposition. Further research using the binocular disparity manipulation could prove informative regarding this and other questions about holistic and part-based processing.

Although faces in the front and back depth conditions generally elicited similar responses in face-selective areas, changes in depth were not without neural correlates. A whole-brain analysis of the main effect of depth revealed activation corresponding to area V3A, which has been implicated in stereoscopic depth perception (Tsao et al., 2003; Mendola et al., 1999).

Furthermore, even within the face-selective cortex, the roughly equivalent responses to the two depth conditions were modulated by the additional factor of familiarity, particularly in the right MFG. Previous work by Schiltz and Rossion (2006) has demonstrated the importance of this area for holistic processing of faces. Our finding of increased adaptation in the back (holistic) depth condition to famous faces is therefore reasonable, as familiar faces arguably have more robust holistic representations. Importantly, these results should not be taken as evidence that holistic processing is reserved for familiar faces alone: in fact, equal and nonzero adaptation effects were seen for unfamiliar faces in both back (holistic) and front (parts) depth conditions. Rather, these data suggest that although faces undergo both holistic and part-based processing, external factors such as familiarity can influence the extent to which these different representations are engaged.

In conclusion, we have used a novel application of a binocular disparity manipulation to examine the representation of face parts and wholes within face-selective regions of the ventral visual cortex. Our finding that there appears to be roughly equivalent holistic and part-based encoding within the face processing stream challenges the strong form of the holistic hypothesis and provides an important constraint for models of how face processing occurs within the brain. Additionally, the interaction of familiarity and depth within the right MFG illustrates the potential modulatory influence of factors

external to the stimulus itself. Together with previous findings using magnetoencephalography (Harris & Nakayama, 2006), these results argue that, despite the focus on holistic processing in the face perception literature, part-based representations form an important aspect of face-selective responses within the brain.

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