

Rapid Adaptation of the M170 Response: Importance of Face Parts

Alison Harris¹ and Ken Nakayama²

¹Department of Neurology, Hospital of the University of Pennsylvania, Philadelphia, PA 19104, USA and ²Department of Psychology, Harvard University, Cambridge, MA 02138, USA

Face perception is often characterized as depending on configural, rather than part-based, processing. Here we examined the relative contributions of configuration and parts to early “face-selective” processing at the M170, a magnetoencephalographic response approximately 170 ms after stimulus onset, using adaptation. Previously (Harris and Nakayama 2007), we showed that rapid successive presentation of 2 stimuli (stimulus-onset asynchrony < 800 ms) attenuates the M170 response. Such adaptation is face-selective, with greater attenuation when faces are preceded by other faces than by houses. This technique therefore provides an independent method to assess the nature of this early neurophysiological marker. In these experiments, we measured the adapting power of face configurations versus parts using upright and inverted faces (Experiment 1), face-like configurations of black ovals versus scrambled nonface configurations of face parts (Experiment 2), and isolated face parts (Experiment 3). Although face configurations alone do not produce face-selective adaptation, scrambled and even isolated face parts adapt the M170 response to a similar extent as full faces. Thus, at least for the relatively early face-selective M170 response, face parts produce face-selective adaptation but face configurations do not. These results suggest that face parts are important at relatively early stages of face perception.

Keywords: configural processing, face perception, magnetoencephalography, object recognition, repetition effects

Introduction

Faces comprise one of the most important, yet most difficult to discriminate, natural visual categories for human observers. Yet despite their relative homogeneity, normal observers can obtain diverse information from faces, including age, attractiveness, emotional state, and identity.

How, then, does the visual system accomplish this feat? One popular theory holds that faces are somehow “special,” differing from the majority of visual stimuli in their manner of processing. Empirical evidence in favor of this supposition comes from the “face inversion effect” (Yin 1969): inversion detrimentally affects perception and recognition performance for faces much more so than for other stimuli.

Inversion is therefore interpreted as disrupting the special processing that normally occurs for faces. As to the nature of this processing, influential work by Diamond and Carey (1986) and Farah et al. (1998) has led to a distinction between configural (or holistic) and part-based processing (see also McKone et al. 2001). According to this account, upright faces are processed in a qualitatively different way from other objects, in terms of the relationships between parts rather than the parts themselves. Experiments by Freire et al. (2000) and Le Grand

et al. (2001) have supported this idea, finding that inversion has a much greater impact on sensitivity to the “second-order” configural relations (spacing between face parts) than on sensitivity to parts.

Yet the exact relationship between inversion and configural processing remains a subject of debate. Recent experiments correcting for confounds in subject strategy and task difficulty have failed to replicate the above-mentioned results, instead finding equal impairment in sensitivity for configural and part changes with inversion (Riesenhuber et al. 2004; Yovel and Kanwisher 2004). Although these findings are still consistent with a dichotomy between parts and wholes, some researchers have argued that the inversion effect merely reflects reduced efficiency, not a qualitative processing difference (Sekuler et al. 2004).

Attempts to find neural correlates of configural processing have been similarly contentious. Neuroimaging of “face-selective” brain regions with functional magnetic resonance imaging (fMRI) has had mixed results, with some researchers reporting greater activation for upright faces (Yovel and Kanwisher 2004, 2005), and others finding little or no difference (Haxby et al. 1999; Aguirre et al. 1999).

In neurophysiology, extensive study has focused on a large and reliable difference in the response to faces versus other objects at approximately 170 ms poststimulus onset (Bentin et al. 1996; Sams et al. 1997; Liu et al. 2000; Itier and Taylor 2004). This N170 (in event-related potentials) or M170 (in magnetoencephalography [MEG]) shows a consistent 10-ms delay in latency for inverted relative to upright faces (Bentin et al. 1996; Eimer 2000; Rossion et al. 2000; Itier and Taylor 2002), sometimes accompanied by an increase in amplitude. Similar enhancements of N170 amplitude have been reported with configural manipulations such as scrambling (George et al. 1996) and “thatcherization” (Milivojevic et al. 2003; Carbon et al. 2005).

However, the interpretation of such increases in N170/M170 amplitude is complicated by the finding that eyes alone produce a response equal to or greater than that to whole faces or scrambled face configurations (Bentin et al. 1996). Based on this result, Bentin et al. originally asserted that “[the] N170 is not dependent on the spatial integrity of facial components as would be predicted for a holistic face-processing mechanism” (Bentin et al. 1996, p. 558). More recently, other researchers using different manipulations have reached a similar conclusion, arguing that the N170 response is driven primarily by the eye region (Schyns et al. 2003; Smith et al. 2004; Itier et al. 2006).

In this article, we applied a rapid adaptation paradigm to examine the M170 response to parts versus configurations. Adaptation, the phenomenon of reduced responsiveness or sensitivity following repeated presentation of a stimulus

(Desimone 1996; Brown and Xiang 1998), has been more recently utilized in fMRI to characterize the representations underlying neural activation (Henson 2003). In these “fMR-adaptation” studies, the response to repeated presentation of the same stimulus is compared with that for 2 stimuli varying only along a given dimension. If 2 stimuli varied along one dimension yield the same amount of adaptation as repetition of a single stimulus, we can conclude that the response of the neural population is invariant for that particular dimension.

This concept has recently been extended to human neurophysiology by Kovacs et al. (2006), who showed category-selective adaptation of the N170 response for longer adapting durations (>1 s), and ourselves (Harris and Nakayama 2007). Using the “double-pulse” paradigm (Fig. 1*a*) originally pioneered by Jeffreys (1996), in which 2 stimuli are presented with a brief interstimulus interval, we found that the M170 response to a stimulus was dramatically reduced (Fig. 1*b*) by the prior presentation of another stimulus within a relatively short range of stimulus-onset asynchronies (SOAs) (<800 ms). Furthermore, like the amplitude of the M170, this adaptation appears to be face-selective, with greater attenuation of the response for faces preceded by other faces than for faces preceded by houses or pure noise (Fig. 1*c*). The “face selectivity” of this M170 adaptation cannot be explained by low-level properties of the adapting stimulus (e.g., spatial frequency, contrast), as the response to a grayscale photograph of a face is similarly attenuated regardless of whether the adapting face image is a photograph or a line drawing (Harris and Nakayama 2007).

An even more extreme example was seen when we degraded the facial image with increasing amounts of visual noise. The addition of visual noise is known to affect the measured amplitude of the N170 response (Jemel et al. 2003; Horowitz et al. 2004), and, as expected, the amplitude of the response to the adapting stimulus was severely reduced. Yet its adapting power remained constant, as can be seen clearly in Figure 1*d*, in which the amplitude of the test response is plotted against the amplitude of the response to the adapting stimulus. Despite the decreasing amplitude of the response to the adapting face stimulus with increasing noise, as indicated by its position along the abscissa, its adapting power remains roughly the same and much greater than that of the house. Thus, a degraded “face” stimulus that evokes a very small amplitude M170 itself can have equivalent adapting power to a full, noise-free grayscale face.

Therefore, this double-pulse adaptation technique provides a potentially revealing method for characterizing face processing. Because it is unaffected by low-level visual properties, it may provide a more sensitive measure of which aspects of the face stimulus are important for eliciting the face-selective M170 component. In these experiments, we examined the relative contribution of face configurations and face parts in upright versus inverted faces (Experiment 1), face configurations of nonface parts versus face parts in nonface configurations (Experiment 2), and isolated face parts (Experiment 3).

Materials and Methods

General Design

In 3 experiments, we examined the relative importance of face parts and face configurations for the M170 response using a double-pulse presentation paradigm (Jeffreys 1996). Adapting and test stimuli were presented for 200 ms each, with a blank interstimulus interval of 200 ms,

for a SOA of 400 ms. Adaptation was measured as the effect of the presentation of the adapting stimulus on the evoked response to the test stimulus. The test stimulus was always an upright face.

Experiment 1 compared the adapting power of upright versus inverted faces, as well as the effect of identity (same vs. different person). In Experiment 2, we examined the amount of adaptation produced by face configurations of nonface parts (black ovals) versus scrambled nonface configurations of face parts. Finally, in Experiment 3, we tested the adapting power of isolated face parts (eyes, nose, mouth). All 3 experiments included a further control adapting condition of houses.

Subjects

A total of 36 data sets were collected from 32 individuals between 18 and 40 years of age recruited from local universities. All subjects were right handed with normal or contact-corrected vision. Twelve individuals participated in Experiment 1, of whom 1 was excluded due to unusual scalp topography (probably from incorrect head placement) and one due to strong alpha wave amplitude (due to wakeful relaxation) in the data. Eleven subjects were recruited for Experiment 2 (2 of whom had participated in Experiment 1), of whom 2 were excluded due to strong alpha wave amplitude. Thirteen individuals participated in Experiment 3, of whom 2 had been subjects in one of the previous 2 experiments; 3 were excluded due to strong alpha wave amplitude in their data. Informed consent was obtained from all subjects, and the study was approved by the Harvard Committee on the Use of Human Subjects in Research and the Massachusetts Institute of Technology Committee on the Use of Humans as Experimental Subjects.

Stimuli

All stimuli were created from 200 × 200 pixel grayscale photographs, subtending 4.4° × 4.4° of visual angle, and were presented on a gray background with a central black fixation point. All 3 experiments included grayscale photographs of faces and houses (50 exemplars each). In Experiment 1, to prevent low-level habituation to physical properties of the stimulus in the “same identity” conditions, all adapting face images were lit from the left, whereas all test images were lit from the right. Thus, although the identity of the individual was preserved within the trial, low-level image properties varied from the adapting to test image.

For Experiment 2, additional stimuli were modified in Adobe Photoshop software as follows (50 exemplars each): 1) external face contour only, 2) face configuration only, and 3) face parts only (Fig. 3*a*). In the configuration-only stimuli, the face parts in each face were replaced with black ovals of the same size in the corresponding locations. The parts-only stimuli contained face parts rearranged in nonface configurations (varied across stimuli). Because some results in the behavioral literature have indicated that the external contour can interact with the other components of the face in recognition tasks (Haig 1986; Sinha and Poggio 1996), configuration and parts stimuli were presented without the external contour. (Rectangular, rather than oval, borders were used to further prevent any perception of a face external contour.) Finally, there were 2 additional control categories of the external face contour (jaw line, ears, and hair) by itself and the full face (parts and configuration) cropped to exclude the external contour (Fig. 4).

Additional stimuli for Experiment 3 were 50 exemplars each of isolated eyes, noses, and mouths presented on a gray background.

Procedure

All experiments consisted of 100 trials of each adapting condition, randomly interleaved. In Experiment 1, there were 500 trials of 5 adapting conditions: 2 face conditions (identity, orientation) in a two-by-two factorial design (Fig. 2*a*) plus the control condition of houses. The adapting and test stimuli could be the same or different individuals, and the adaptor could be upright or inverted. (The test stimulus was always an upright face.) The subject was given 2 buttons and instructed to press the right-hand button if the 2 stimuli were the same individual and the left-hand button if they were different individuals. Accuracy (d-prime) was calculated for each subject and is displayed in Figure 2*d*.

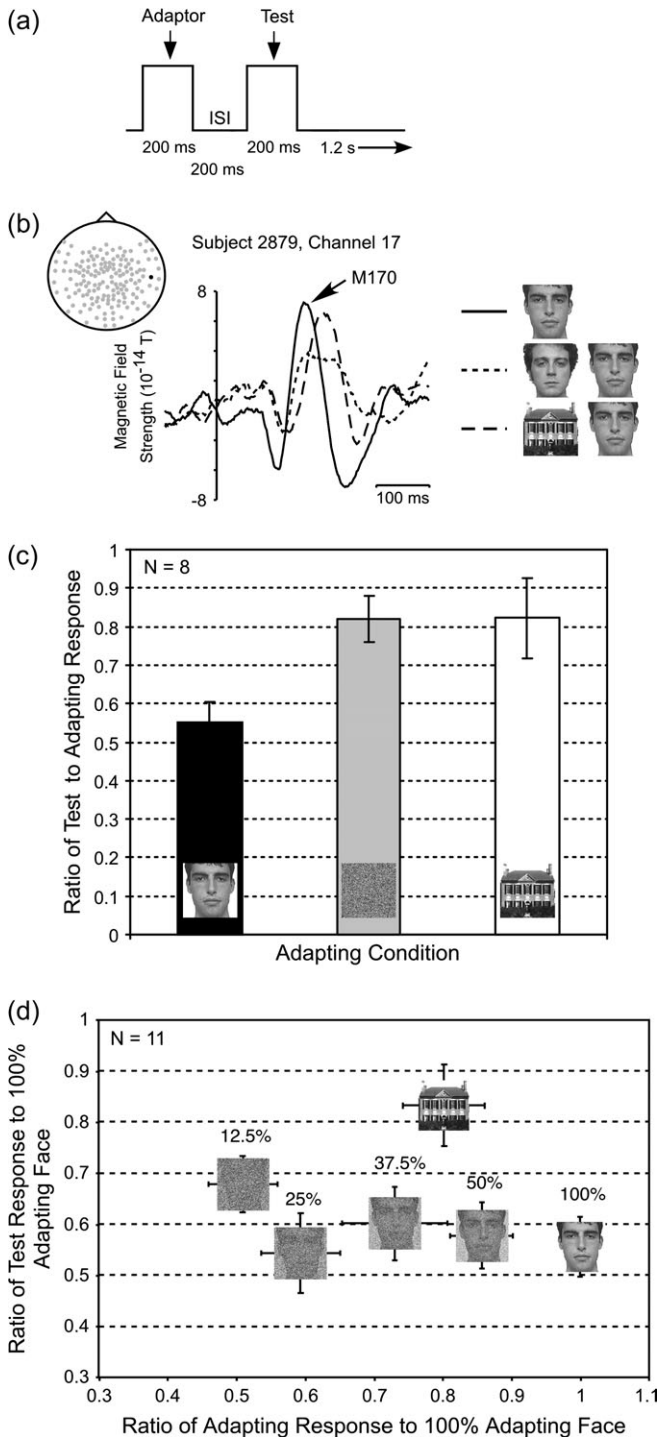


Figure 1. Face-selective double-pulse adaptation of the M170 response. (b)–(d) display new analyses of data previously presented in Harris and Nakayama (2007). (a) The double-pulse presentation paradigm of Jeffreys (1996). Adapting and test stimuli are presented for 200 ms each with an intervening blank interstimulus interval (ISI) of 200 ms. Adaptation is measured as the reduction in response to the test stimulus as a function of the prior presentation of the adapting stimulus. (b) Sample data from a single channel (black dot on scalp map at left) in an individual subject, showing the M170 response to the adapting face stimulus (unbroken line), a test face stimulus that has been preceded by another face (dotted line), and a test face stimulus preceded by a house (dashed line). The reduction in the M170 response is face selective, with greater attenuation of the response when the adapting stimulus is a face than when it is a house. In this experiment, the SOA was fixed at 400 ms. (c) Amplitude of the M170 response to the test (second) stimulus, normalized to the response to the adapting (first) face stimulus. Again, although there is a general reduction in the

Experiment 2 consisted of 600 trials of 6 adapting conditions: full face, face without external contour, external contour only, internal configuration only, internal parts only, and houses.

Experiment 3 consisted of 700 trials of 7 adapting conditions: full face, eyes, nose, mouth, line drawing faces (with features but no shading), and 2-tone faces (with shading but no distinct features). Data from the line drawing and 2-tone conditions were previously presented in Harris and Nakayama (2007) and will not be discussed here.

In Experiments 2 and 3, the subject was instructed to press a button every time a target female face (displayed at the beginning of the experiment) appeared. Ten percent of the total trials consisted of the target face; these trials were randomly intermixed with the experimental trials but excluded from analysis.

Data Acquisition

MEG recordings were made using a 157-channel whole-head system with superconducting quantum interference device (SQUID)-based first-order gradiometer sensors (Kanazawa Institute of Technology MEG System at the KIT/MIT MEG Joint Research Lab at MIT). Magnetic brain activity was digitized continuously at a sampling rate of 500 Hz and was filtered with DC high-pass and 200-Hz low-pass cutoff and a 60-Hz notch.

Analysis

Data analysis was performed in MEG160 (Yokogawa Electric Corporation and Eagle Technology Corporation, Tokyo, Japan), the proprietary software for the MEG system, and in MATLAB (Mathworks, Andover, MA). Average waveforms were computed in each subject using a window of 500 ms (100 ms before and 400 ms after stimulus onset). The averaged waveforms were then baseline corrected, smoothed with a moving average, and high-pass filtered (3 Hz, Hanning window).

The latency of the M170 response was obtained by examining the waveforms at all sensors in the adapting face condition; sensors were then selected for further study using an amplitude threshold of 30 fT. (This threshold was chosen for practical reasons, as it excludes most spurious activity in this time range while retaining the majority of actual M170 responses [Harris and Nakayama 2007]). The peak amplitude in the M170 range was determined for each sensor in each condition and then normalized to the M170 response to the adapting face condition at that sensor. Statistical and graphical analysis used the normalized sensor values or their averages rather than the raw amplitude values.

Due to the nature of the magnetic field generated by electric currents in the brain, the B field corresponding to the M170 in the right hemisphere constitutes a magnetic “sink,” which is commonly denoted by a negative sign; for averaged analyses, peak amplitudes in right hemisphere sensors were multiplied by -1 to correct for this polarity difference.

Results

Experiment 1: Upright Versus Inverted

In Experiment 1, we investigated the effect of inversion on the face-selective adaptation of the M170 response. The face inversion effect is often considered the hallmark of configural or holistic processing, though this view has recently been questioned (Sekuler et al. 2004). Given the importance of the face inversion effect in the behavioral literature, our first experiment

response to the test face with immediate prior presentation of another stimulus, such as white noise or a house, this attenuation is significantly larger when the adapting stimulus is another face. (d) Face-selective adaptation of the M170 response is independent of the amplitude of the response to the adapting stimulus. When the amplitude of the response to the adapting face stimulus is decreased through the addition of white noise, the magnitude of the face-selective adaptation effect remains constant. The number above each data point indicates the percentage of face signal in the image, relative to noise, for that adapting face condition (varied between 12.5% and 100% face signal).

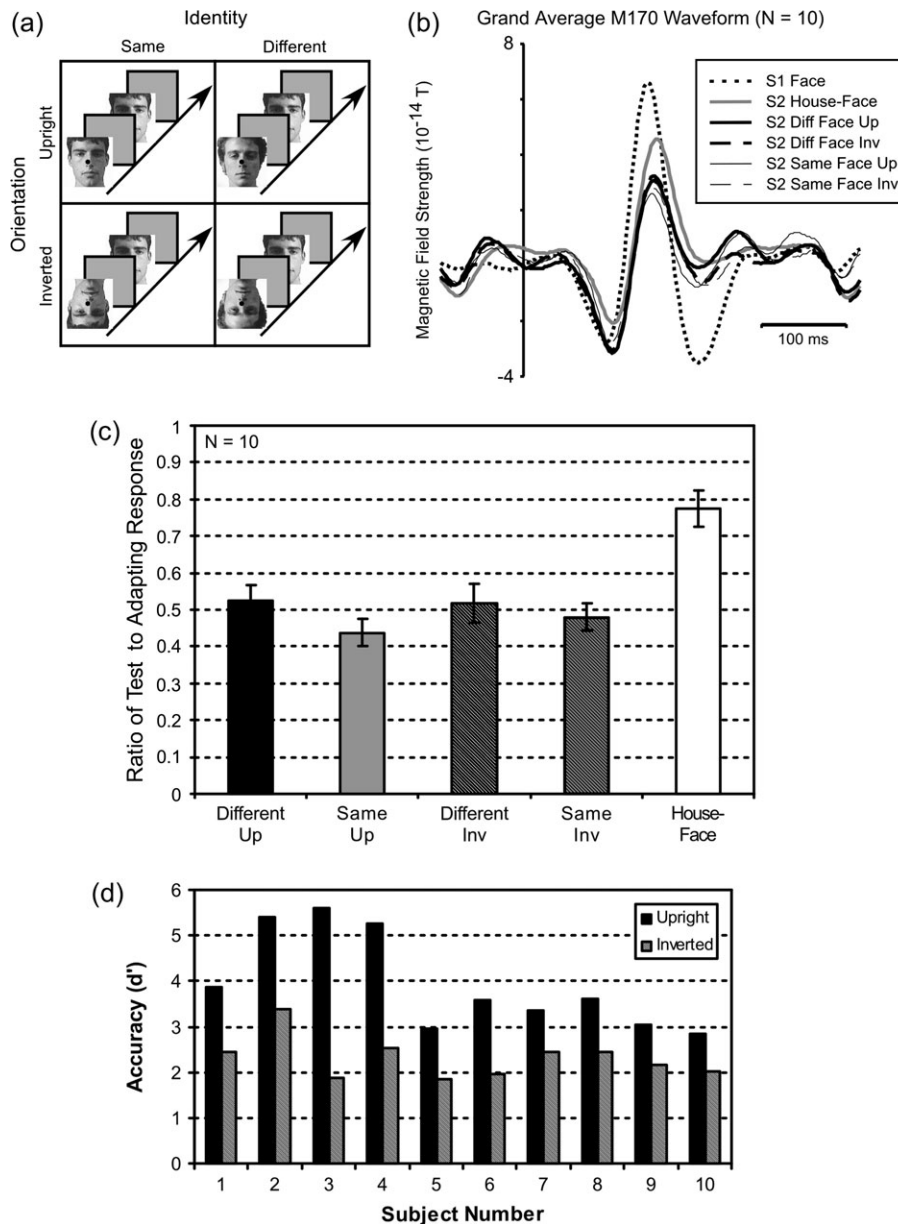


Figure 2. Adaptation to upright and inverted faces. (a) The 4 adapting face conditions in this experiment, manipulating identity (same vs. different) and orientation (upright vs. inverted). The test stimulus was always an upright face. Note that the adapting and test images were lit from opposite sides in order to prevent low-level habituation to image repetition in the same identity condition. (b) Grand average waveform showing adaptation as a function of adapting face identity and orientation, averaged across 10 subjects. Although there is a general effect of double-pulse presentation even for faces preceded by houses, the M170 response to faces preceded by faces shows significantly greater attenuation. (c) Average peak amplitudes for test conditions normalized by the M170 response to the unadapted (S1) face stimulus. Consistent with the grand average waveform, there is small but significantly greater adaptation to same identity versus different identity. However, upright and inverted faces produce equivalent adaptation. (d) Behavioral data. On each trial, subjects responded whether the 2 images were of the same individual or of different individuals. In contrast with their neurophysiological data, all subjects show a behavioral inversion effect, with much greater accuracy when the first face is upright than when it is inverted. Therefore, although identity is encoded at the M170 response, this representation appears unlikely to mediate behavioral recognition.

sought to determine how inversion affects face-selective adaptation of the M170.

Two identity conditions (same/different) and 2 orientation conditions (upright/inverted) were combined for a total of 4 experimental adapting face conditions (Fig. 2a) plus houses. In all these conditions, the second stimulus was always an upright face. Subjects were asked to press a right-hand button if the 2 images were the same individual or a left-hand button if they were 2 different individuals, allowing us to simultaneously measure the behavioral face inversion effect.

The grand average waveform, calculated by averaging across all 10 subjects, is displayed in Figure 2b. Raw amplitudes and latencies for all conditions in this and following experiments are given in Table 1. Consistent with previous results, we found a significant delay in the latency of the M170 response to inverted faces compared with upright faces ($P = 5.93 \times 10^{-5}$, paired t -test), as well as a trend toward greater M170 amplitude for the inverted relative to the upright face condition ($P = 0.07$, paired t -test). (An additional permutation test found this effect to be significant ($P = 0.036$.) In terms of adaptation, although

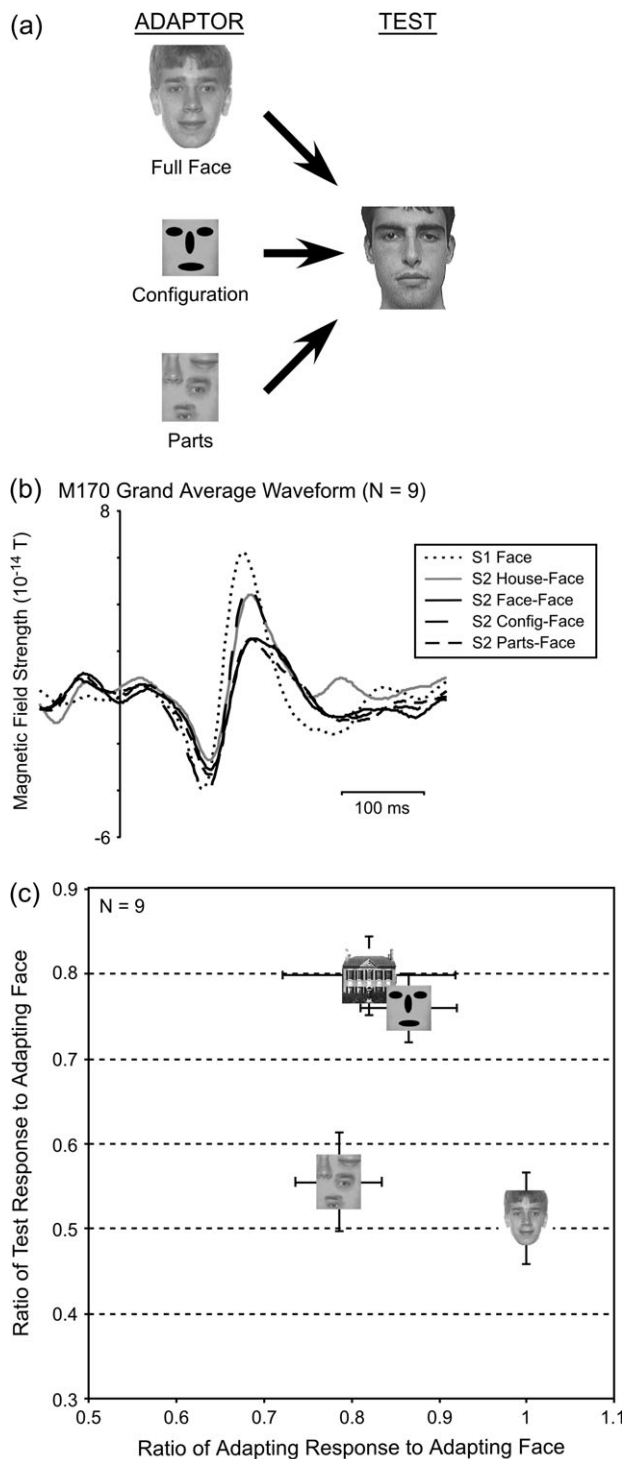


Figure 3. Adaptation to face configurations and parts. (a) The different adapting stimuli in this experiment, based on aspects of the face thought to contribute to behavioral recognition: full face (top), face configuration (middle), and face parts (bottom). (b) Grand average waveform showing adaptation to face configurations and face parts, averaged across 9 subjects. Although face parts produce the same face-selective adaptation as full faces, face configurations do not. (c) Adaptation to face configurations and parts as a function of adapting stimulus amplitude. Just as in the grand average waveform, face parts and face configurations differ in their adapting power, even though they elicit S1 M170 responses of similar amplitude. Therefore, it appears that the M170 response is sensitive to face parts rather than the configuration of these parts.

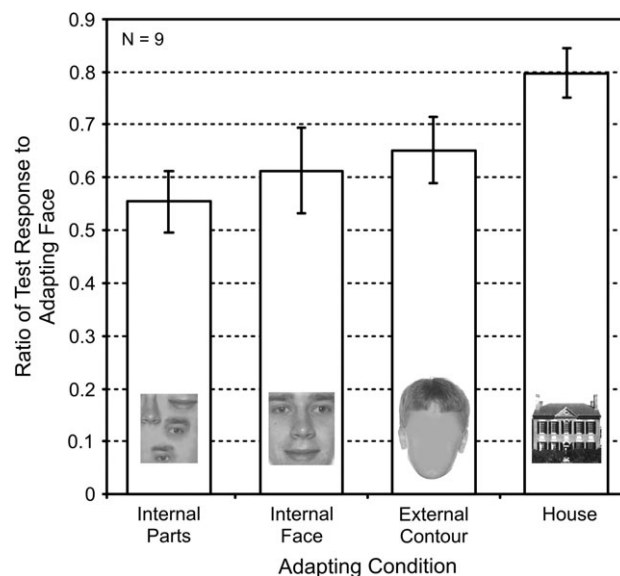


Figure 4. Adaptation to internal face parts compared with the external face contour (jaw line, ears, and hair), and the combination of internal parts and configuration. Neither the external contour nor the internal face information produced greater adaptation than that seen for scrambled internal parts alone, suggesting that rapid adaptation of the M170 is driven primarily by internal face parts.

there is a general effect of double-pulse presentation even in the house-face condition, the M170 response to faces preceded by faces (either of the same or different identity) shows even greater attenuation. Although slightly greater for repetitions of the same identity, this face-selective adaptation does not appear to depend on orientation, with equal adaptation of the response in upright and inverted conditions.

This pattern was confirmed in the analysis of M170 peak amplitudes, normalized to the unadapted S1 face response, displayed in Figure 2c. (Note that, because these averages are computed on sensor-wise ratios of test to adapting face stimuli, the values here are slightly different from what would be obtained using the raw amplitude values in Table 1.) Again, upright and inverted faces adapt the following upright face with equal power.

Given that N170/M170 latency is considered a more reliable indicator of inversion than amplitude, it is possible that differential effects of double-pulse adaptation on latency of the test category can be found for upright versus inverted adaptors. As can be seen in Table 1, however, there were no significant differences among the test conditions ($F_{4,36} = 1.69$, $P = 0.174$), though all showed significantly longer latencies than the adapting face condition (all P values < 0.01). Therefore, while double-pulse presentation results in increased M170 latency relative to single presentations, this latency increase is not diagnostic of face-selective adaptation. The similar latency of the M170 response following various adapting stimuli further suggests that a single neural mechanism underlies both face-selective and nonselective adaptation, whereas the amplitude of such adaptation reflects the selectivity of the neural response.

Additionally, the comparison of different versus same identity across orientations revealed a small but significant effect of identity. This was corroborated by a repeated-measures analysis of variance (ANOVA) ($F_{1,9} = 7.83$, $P = 0.02$) on the 4 face conditions. Main effects of hemisphere and orientation, and all

interactions, were not significant (all P values > 0.1). Thus, there is no differential effect of orientation in the M170 adaptation: instead, upright and inverted faces both produce the same face-selective adaptation. In contrast, there is a clear inversion effect in the behavioral data of all 10 subjects (Fig. 2*d*).

Because the behavioral inversion effect is often taken as evidence of configural processing, this result suggests that the configuration of the face is not represented at the M170 response. (In this context, the significant effect of identity could be explained as greater adaptation to the repeated presentation of the same face parts.) In fact, given the dissociation between neurophysiology and subject responses, it could be argued that the M170 reflects part-based processing prior to the configural processing associated with the behavioral face inversion effect.

Yet the relationship between inversion and configural processing remains somewhat ambiguous, as this conclusion is at least partly based on tasks that are confounded in terms of subject strategy or difficulty (Riesenhuber et al. 2004; Yovel and Kanwisher 2004). Therefore, in our second experiment, we tested the importance of face configuration versus face parts more directly through the use of stimuli orthogonally manipulated to contain either configuration or parts.

Experiment 2: Configuration Versus Parts

As discussed above, the equal neurophysiological adaptation obtained for upright and inverted faces in Experiment 1 suggests that configuration may not be represented at the M170 response. In order to test this possibility more directly, in our second experiment we compared the adapting power of stimuli orthogonally manipulated to contain only face configuration or only face parts (Fig. 3*a*).

Figure 3*b* shows the grand average M170 waveform for the 4 conditions of interest in Experiment 2. Even in this relatively crude average, there is a strikingly clear differentiation among the conditions in terms of their adapting power: although face parts produce a similar face-selective attenuation of the M170 response to that for full faces, face configurations alone are no better adaptors than houses.

Yet one possible concern with this experiment was that, in contrast to the stimuli used in Experiment 1, the M170 response to the adaptors had been quantified less extensively. Therefore, one potential issue in this experiment was the effect of the amplitude of the M170 response to the adapting stimulus. Adapting stimuli that elicit larger M170 responses could cause reduced response to the test stimulus due to nonspecific neural changes such as greater refractoriness. Although the response to the adapting stimulus is face selective, such adaptation would be nonselective, depending only on the amplitude of the response to the prior stimulus. As mentioned earlier, our previous work using faces in visual noise argues against this “amplitude-dependent” explanation of adaptation (Harris and Nakayama 2007; see also Fig. 1*d*). Previous work by Liu et al. (2002), using similar stimuli, also found no significant difference between M170 responses to parts-only and configuration-only stimuli (although with a significant 2-way interaction by MEG component). However, to ensure that amplitude of the response to the adapting stimulus cannot explain the results in Experiment 2, adaptation was examined relative to the M170 responses to the adapting stimulus conditions.

Figure 3*c* displays the adapting power of each stimulus condition as a function of its amplitude. Again replicating our finding of face-selective adaptation, we see significantly greater attenuation of the M170 when the test stimulus is preceded by a face than when it is preceded by a house ($P = 0.005$, paired t -test). Although face configurations and parts elicit M170 responses of similar amplitude ($P = 0.13$, paired t -test; for raw amplitudes, see Table 1), these stimuli differ strikingly in their adapting power. In keeping with the grand average data (Fig. 3*b*), face parts without configuration produce the same face-selective adaptation as whole faces ($P = 0.46$, paired t -test). In contrast, configurations alone produce only the smaller and more general adaptation also seen for houses ($P = 0.45$, paired t -test).

Thus, despite eliciting M170 responses of roughly equal amplitude, face parts and face configuration differ in the magnitude of adaptation that they produce. Therefore, it seems that the parts of the face, but not the configuration of those parts, are represented at the stage of processing indexed by face-selective adaptation of the M170 response. In fact, in terms

Table 1
Average M170 amplitude and latency, Experiments 1–3

	Adapt	Test	
		Amplitude (10^{-14} T)	Latency (ms)
Experiment 1	Face upright	7.79 (0.69)	148.1 (2.78)
	Face inverted	8.6 (0.87)	155.3 (2.8)
	House	6.74 (0.81)	152 (2.79)
Experiment 2	Face	8.68 (0.71)	154.2 (8.92)
	Configuration	7.69 (0.99)	160.4 (10.7)
	Parts	6.92 (0.82)	166.7 (10.2)
	Face internal	8.2 (0.85)	160.8 (10)
	External	6.67 (0.75)	161.5 (9.71)
	House	7.29 (1.02)	155.5 (8.57)
Experiment 3	Face	8.27 (0.63)	148.9 (2.86)
	Eyes	7.46 (0.77)	173.9 (3.41)
	Nose	3.86 (0.33)	196.1 (6.28)
	Mouth	4.39 (0.45)	197.9 (6.56)
	House	6.73 (0.64)	155.4 (4.85)

Parentheses indicate standard error of the mean.

of adaptation, face configuration is no better than the completely different stimulus category of houses.

One possible alternative explanation for these results is that they are based on low-level physical differences between the stimuli in the configuration and parts conditions. According to this argument, the “scrambled” parts stimuli preserve the low-level physical stimulus features present in full face stimuli (e.g., contrast, spatial frequency) but the face-configured black ovals do not, and thus, face-selective adaptation is observed only for parts. However, as mentioned in the Introduction, such an explanation is unlikely. In our previous work (Harris and Nakayama 2007), we have shown that adaptation of the M170 response to a photographic face image is similarly face selective regardless of whether the adapting face is a photographic, line-drawing, or 2-tone image. Because the latter 2 manipulations exclude a great deal of image information, including cues to shading, hue, and texture, yet nonetheless produce face-selective adaptation, differences in low-level image properties are unlikely to account for the results in this experiment.

Another question regarding these stimuli is the extent to which adaptation may be influenced by the external contour (jaw line, ears, and hair). Previous behavioral data suggest that the external contour may play an important role in face recognition (Haig 1986; Sinha and Poggio 1996), but because the external contour is missing from our parts and configuration stimuli, it is unclear how these aspects of the face may interact. To address this issue, we included 2 additional control conditions: the external contour by itself and the face (both parts and configuration) excluding the external contour. Table 1 and Figure 4 display the amplitude of adapting and test M170 responses, respectively, for these conditions. These stimuli are no better adaptors than face parts alone, falling roughly between internal parts and configurations in adapting power. In fact, these stimulus conditions do not differ statistically in adapting power from houses (external contour: $P = 0.063$; internal face: $P = 0.057$, paired t -test), in contrast to face parts ($P = 0.001$, paired t -test). (Note that with this number of pairwise comparisons among test conditions, the Bonferroni-corrected threshold would be $\alpha = 0.008$.) Yet, because full faces, which also contain external contour and configuration information, produce large attenuation of the M170 response, it appears that these different aspects of the face are integrated in a nonlinear manner at this stage of processing. Nonetheless, these data suggest that rapid adaptation of the M170 response is driven largely by internal part information, rather than configuration or the external contour.

Given that the face-selective adaptation of the M170 appears to depend on the presence of internal face parts, one obvious question is that of whether this adaptation is specific to any particular face part or rather depends critically on the presence of more than one face part. Thus, in Experiment 3, we examined the adapting power of individual face parts presented in isolation.

Experiment 3: Isolated Face Parts

In Experiment 2, we demonstrated that internal face parts in scrambled nonface configurations produce face-selective adaptation of the M170 response, whereas face configurations composed of nonface parts do not. Thus, the presence of face parts appears to be important for face-selective adaptation.

One important question that follows from this data is the specificity of adaptation to individual face parts. Is it driven by all the face parts together or a single face part? In the latter case, can each of the individual face parts produce equivalent adaptation or is all of the adaptation due to the presence of one face part alone? This issue is of particular interest given the previous characterization of the N170 as driven primarily by the eye region (Bentin et al. 1996; Schyns et al. 2003; Smith et al. 2004; Itier et al. 2006).

Figure 5 shows the resulting adaptation for eyes, noses, and mouths both in the grand average waveform (Fig. 5*a*) and as a function of the amplitude of the response to the adapting stimulus (Fig. 5*b*). Replicating the previous finding of Bentin et al. (1996), whole faces elicited a much larger M170 response than either noses or mouths ($P = 2 \times 10^{-5}$ and $P = 0.001$, respectively, uncorrected paired t -tests). However, we failed to find a higher response to eyes alone than to whole faces ($P = 0.5$, paired t -test). All 3 part conditions produced M170 latencies significantly longer than that to faces (face vs. eyes: $P = 5.15 \times 10^{-6}$; face vs. nose: $P = 1.85 \times 10^{-5}$; face vs. mouth: $P = 5.67 \times 10^{-6}$, paired t -tests), again in keeping with Bentin et al. (1996).

Although isolated face parts such as the nose and mouth produce noticeably smaller M170 responses than full faces, their adapting power nearly equals that of the full face. Contrary to what would be expected from an account of the M170 as an “eye detector,” this result is not restricted to the condition of eyes alone but is also seen for noses and mouths. A repeated-measures ANOVA likewise revealed no significant difference among these conditions ($F_{5,45} = 1.0$, $P = 0.4$), but they all produce significantly more adaptation than houses ($P = 0.004$, paired t -test). Strikingly, even face parts such as the nose and mouth that elicit extremely small M170 responses—even less than that to houses—produce significantly greater adaptation, again supporting our claim that this adaptation is face selective. Along with the findings from Experiments 1 and 2, these results suggest that any part of the face is sufficient to produce adaptation of the neural activity indexed by the M170.

Discussion

In these experiments, we used a rapid adaptation technique to examine whether the processing indexed by an early face-selective neurophysiological response is part-based or configural in nature. As discussed in the Introduction, face perception is often conceptualized in terms of a dichotomy between these 2 types of analysis, with upright faces normally undergoing configural processing.

Previous attempts to determine the relation of early face-selective neurophysiological components to configural processing have had conflicting results. Although several researchers have argued that the N170 response appears to be driven primarily by the eye region (Bentin et al. 1996; Schyns et al. 2003; Smith et al. 2004; Itier et al. 2006), other researchers have argued instead that the N170 indexes configural processing on the basis of changes in its amplitude and/or latency when configural information is manipulated through inversion (Bentin et al. 1996; Eimer 2000; Rossion et al. 2000; Itier and Taylor 2002), thatcherization (Milivojevic et al. 2003; Carbon et al. 2005), or scrambling (George et al. 1996; Liu et al. 2002).

The double-pulse presentation method provides an alternative means of addressing this question. Like amplitude, which is greater for faces than for nonface stimuli, double-pulse

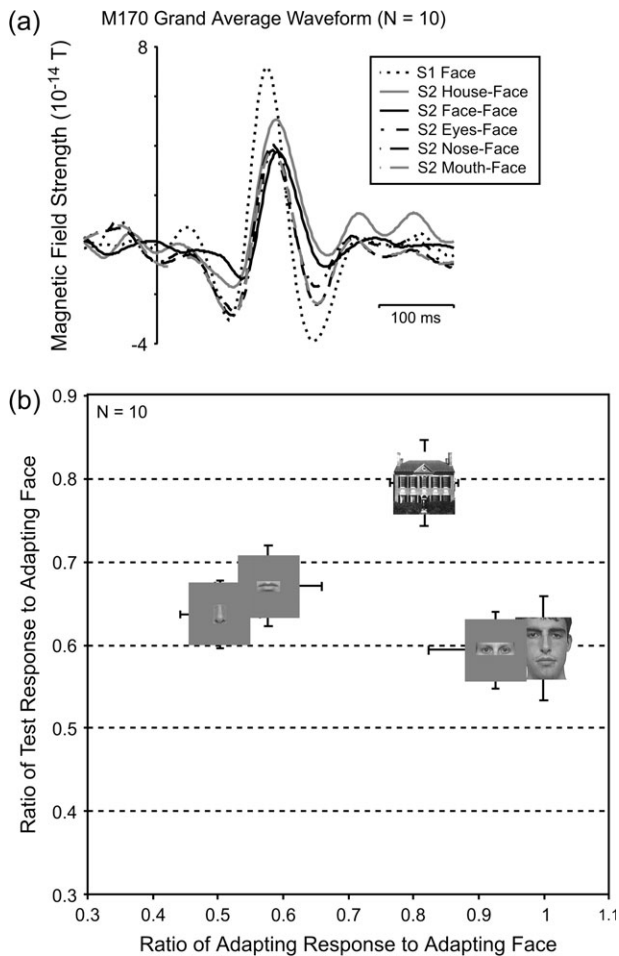


Figure 5. Adaptation to isolated face parts, shown (a) in grand average waveforms and (b) as a function of adapting stimulus amplitude. All individual face parts produce roughly the same face-selective adaptation as full faces, even though the amplitude of the response to the adapting stimuli of noses and mouths is smaller even than that to houses. Together with the previous results, this data argues that the M170 response is sensitive to all face parts and not to configuration.

adaptation of the M170 response is face selective, with greater attenuation for faces preceded by other faces than by nonface stimuli. However, although amplitude is affected by manipulations of low-level image properties, such as the addition of visual noise, adaptation is not, making it arguably a better measure of category selectivity.

Therefore, we utilized the double-pulse paradigm to examine the relative importance of face configurations versus face parts at the M170. In Experiment 1, we compared the adapting power of inverted versus upright faces. Despite recent data suggesting that inversion only reflects a quantitative difference in efficiency of processing (Sekuler et al. 2004), for much of the field it remains the hallmark of configural, as opposed to part-based, processing. Yet we found no neurophysiological effect of inversion: upright and inverted faces were equally powerful adaptors for the test face. In contrast, the behavioral data showed a clear inversion effect. This dissociation suggests that, insofar as the behavioral inversion effect reflects a dichotomy of configural versus part-based processing, configural information is not represented at the stage of processing indexed by the M170 response.

In Experiments 2 and 3, we tested the sensitivity of the adaptation to face parts and configuration more directly through the use of stimuli orthogonally manipulated to contain only face configuration or face parts (Experiment 2) or isolated face parts (Experiment 3). Surprisingly, although face configurations composed of nonface parts are no more effective adaptors than houses, face parts in nonface configurations produce face-selective adaptation equal to that from full faces. Furthermore, any individual part of the face appears to be nearly as effective an adaptor as the entire face, despite the fact that some face parts, such as noses and mouths, elicit very little M170 response.

Together, these results suggest that the M170 response reflects the action of a “structural encoder” (Bruce and Young 1986) that is sensitive to face parts rather than configuration. This conclusion is inconsistent with the idea of the M170 as an index of configural processing. However, the evidence for such an interpretation has been largely based on 2 related phenomena: increases in latency seen for inverted faces, and increases in amplitude reported for inverted, scrambled, and “thatcherized” faces. In fact, such increases in latency and/or amplitude are not specific to configural manipulations: eyes alone, for example, produce as much amplitude enhancement as scrambling of configuration and delay latency even more than inversion (Bentin et al. 1996). Similarly, Itier et al. (2006) have recently reported significant inversion effects at the N170 for a variety of stimuli besides faces, including cars, chairs, and nonhuman (ape) faces. Furthermore, studies that report increases in amplitude with manipulations of configuration often contain potential stimulus confounds. Although thatcherized faces, in which the configuration of the eyes and mouth are inverted, elicit increased N170 amplitude (Milivojevic et al. 2003; Carbon et al. 2005), this effect may also reflect changes in emotional arousal and/or attentional orienting (e.g., Carretie et al. 2001) due to the grotesque appearance of these stimuli.

Our data suggest that internal face parts, rather than face configurations, play an important role in rapid face-selective adaptation. Yet these findings also raise questions about the neural mechanisms of double-pulse adaptation itself. In particular, attenuation of the M170 response does not appear to be dependent on the amplitude of the adapting stimulus: isolated face parts, which in some cases elicit dramatically smaller M170 responses than full faces, nonetheless produce a similar extent of response attenuation. How can a nose or mouth, a suboptimal stimulus in terms of M170 amplitude, reduce the much larger response to the subsequent presentation of a face?

One potential explanation for this finding arises from the technical limitations of MEG recording. It is known that under a spherical model of brain conductance, as assumed in MEG, the lead field, or magnetometer sensitivity distribution, falls off toward the center of the sphere (Hämäläinen et al. 1993). Thus, more lateral neural sources likely contribute more to the externally measured MEG signal. The smaller M170 to isolated face parts, then, rather than reflecting a weak response from a lateral generator, could instead represent a larger signal from a more medial source, the attenuated form of which is measured at the scalp. (Eyes, which elicit an M170 response of similar amplitude to that for full faces, are commonly thought to be represented in relatively lateral regions such as occipitotemporal gyrus [Bentin et al. 1996] or superior temporal sulcus [e.g., Allison et al. 2000].) In fact, such medial “face-part-specific” sites have been reported in intracranial electrode

recordings from ventral inferotemporal cortex (McCarthy et al. 1999). Similarly, Jeffreys (1996), in recordings from midline scalp electrodes (*Cz*, *Pz*), reported a comparable vertex-positive potential for full faces and face parts such as noses and mouths.

Therefore, the existence of face-part-specific medial generators may play a key role in resolving the discrepancy between amplitude and adaptation results for face parts. These sources could mediate face-selective adaptation directly, for example through a “sharpening” of the response of a single neural population (Wiggs and Martin 1998). In this scenario, reduction of the overall signal reflects attenuation of spurious nonselective neural activity, whereas selective neural response remains constant; such an account is consistent with our previous results for face-selective M170 adaptation in visual noise (Harris and Nakayama 2007).

Alternatively, face-selective adaptation could arise from rapid interactions between adjacent and intermingled neural populations. One conception for the latter type of system comes from McCarthy et al. (1999), who noted that “it is possible that the outputs from cortical processors of individual face parts are integrated by a single cortical region that could conclude on the basis of the accumulation of partial information that a face is present. This conclusion could be reached in less time than the full time required to process any individual face part” (pp. 441–442). The nonlinear interaction of external contour, internal face parts, and face configuration observed in Experiment 2 is consistent with this latter account.

Together, these data suggest that the face-selective processing indexed by rapid adaptation of the M170 reflects encoding of individual face parts. To what end is such part-based processing employed? One possible answer, derived from computational modeling, is in face detection or categorization: in fact, image fragments (especially those of “intermediate complexity,” similar to the face parts in our experiment) can carry detailed information for object classification (Ullman et al. 2002). Yet part-based representations may be utilized in face recognition as well. Evidence consistent with this idea comes from the “featural prototype effect” (Cabeza and Kato 2000), the behavioral tendency to falsely recognize a new face composed of the features from previously seen faces, and neuropsychological data from CK, a patient with severe object agnosia but intact face perception, who also shows normal recognition of face parts (Moscovitch et al. 1997). Likewise, we found adaptation to be greatest when the identity of the adapting and test faces was the same. In keeping with recent findings by Jacques and Rossion (2006), our data further suggest that such effects of identity at the M170 are dependent on representations of individual face parts.

In conclusion, using adaptation, we have probed the representation of faces at the M170 component in MEG. Our findings suggest that, at least at early stages of processing indexed by the M170, face parts, but not face configuration, play a critical role in face-selective adaptation. Future work must determine more fully the relationship of these part-based representations to the temporal stages and functional organization of face processing in the brain.

Notes

Conflict of Interest: None declared.

Address correspondence to Alison Harris. Email: amharris@post.harvard.edu.

References

- Aguirre GK, Singh R, D’Esposito M. 1999. Stimulus inversion and the responses of face and object-sensitive cortical areas. *Neuroreport*. 10:189–194.
- Allison T, Puce A, McCarthy G. 2000. Social perception from visual cues: role of the STS region. *Trends Cogn Sci*. 4:267–278.
- Bentin S, Allison T, Puce A, Perez E, McCarthy G. 1996. Electrophysiological studies of face perception in humans. *J Cogn Neurosci*. 8: 551–565.
- Brown MW, Xiang J-Z. 1998. Recognition memory: neuronal substrates of the judgement of prior occurrence. *Prog Neurobiol*. 55:149–189.
- Bruce C, Desimone R, Gross CG. 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J Neurophysiol*. 46:369–384.
- Bruce V, Young A. 1986. Understanding face recognition. *Br J Psychol*. 77:305–327.
- Cabeza R, Kato T. 2000. Features are also important: contributions of featural and configural processing to face recognition. *Psychol Sci*. 11:429–433.
- Carbon CC, Schweinberger SR, Kaufmann JM, Leder H. 2005. The Thatcher illusion seen by the brain: an event-related brain potentials study. *Brain Res Cogn Brain Res*. 24:544–555.
- Carretie L, Mercado F, Tapia M, Hinojosa JA. 2001. Emotion, attention, and the ‘negativity bias’, studied through event-related potentials. *Int J Psychophysiol*. 41:75–85.
- Desimone R. 1996. Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci USA*. 93:13494–13499.
- Diamond R, Carey S. 1986. Why faces are and are not special: an effect of expertise. *J Exp Psychol Gen*. 115:107–117.
- Eimer M. 2000. The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*. 11:2319–2324.
- Farah MJ, Wilson KD, Drain M, Tanaka JN. 1998. What is “special” about face perception? *Psychol Rev*. 105:482–498.
- Freire A, Lee K, Symons LA. 2000. The face-inversion effect as a deficit in the encoding of configural information: direct evidence. *Perception*. 29:159–170.
- George N, Evans J, Flori N, Davidoff J, Renault B. 1996. Brain events related to normal and moderately scrambled faces. *Brain Res Cogn Brain Res*. 4:65–76.
- Haig ND. 1986. Exploring recognition with interchanged facial features. *Perception*. 15:235–247.
- Hämäläinen M, Hari R, Ilmoniemi RJ, Knuutila J, Lounasmaa O. 1993. Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Rev Mod Phys*. 65:413–497.
- Harris AM, Nakayama K. 2007. Rapid face-selective adaptation of an early extrastriate component in MEG. *Cereb Cortex*. 17:63–70.
- Haxby JV, Ungerleider LG, Clark VP, Schouten JL, Hoffman EA, Martin A. 1999. The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*. 22:189–199.
- Henson RNA. 2003. Neuroimaging studies of priming. *Prog Neurobiol*. 70:53–81.
- Horowitz SG, Rossion B, Skudlarski P, Gore JC. 2004. Parametric design and correlational analyses help integrating fMRI and electrophysiological data during face processing. *Neuroimage*. 22:1587–1595.
- Itier RJ, Latinus M, Taylor MJ. 2006. Face, eye and object early processing: what is the face specificity? *Neuroimage*. 29:667–676.
- Itier RJ, Taylor MJ. 2002. Inversion and contrast polarity affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. *Neuroimage*. 15:353–372.
- Itier RJ, Taylor MJ. 2004. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cereb Cortex*. 14:132–142.
- Jacques C, Rossion B. 2006. The speed of individual face categorization. *Psychol Sci*. 17:485–492.
- Jeffreys DA. 1996. Evoked potential studies of face and object processing. *Vis Cogn*. 3:1–38.
- Jemel B, Schuller AM, Cheref-Khan Y, Goffaux V, Crommelinck M, Bruyer R. 2003. Stepwise emergence of the face-sensitive N170 event-related potential component. *Neuroreport*. 14:2035–2039.

- Kovács G, Zimmer M, Bankó E, Harza I, Antal A, Vidnyánszky Z. 2006. Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cereb Cortex*. 16:742-753.
- Le Grand R, Mondloch CJ, Maurer D, Brent HP. 2001. Early visual experience and face processing. *Nature*. 410:890
- Liu J, Harris A, Kanwisher N. 2002. Stages of processing in face perception: an MEG study. *Nat Neurosci*. 5:910-916.
- Liu J, Higuchi M, Marantz A, Kanwisher N. 2000. The selectivity of the occipitotemporal M170 for faces. *Neuroreport*. 11:337-341.
- McCarthy G, Puce A, Belger A, Allison T. 1999. Electrophysiological studies of human face perception. II: response properties of face-specific potentials generated in occipitotemporal cortex. *Cereb Cortex*. 9:431-444.
- McKone E, Martini P, Nakayama K. 2001. Categorical perception of face identity in noise isolates configural processing. *J Exp Psychol Hum Percept Perform*. 27:573-599.
- Milivojevic B, Clapp WC, Johnson BW, Corballis MC. 2003. Turn that frown upside down: ERP effects of thatcherization of misoriented faces. *Psychophysiology*. 40:967-978.
- Moscovitch M, Winocur G, Behrmann M. 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *J Cogn Neurosci*. 9:555-604.
- Riesenhuber M, Jarudi I, Gilad S, Sinha P. 2004. Face processing in humans is compatible with a simple shape-based model of vision. *Proc Biol Sci*. 217:S448-S450.
- Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, Crommelinck M. 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport*. 11:69-74.
- Sams M, Hietanen JK, Hari R, Ilmoniemi RJ, Lounasmaa OV. 1997. Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience*. 77:49-55.
- Schyns PG, Jentzsch I, Johnson M, Schweinberger SR, Gosselin F. 2003. A principled method for determining the functionality of brain respects. *Neuroreport*. 14:1665-1669.
- Sekuler AB, Gaspar CM, Gold JM, Bennett PJ. 2004. Inversion leads to quantitative, not qualitative, changes in face processing. *Curr Biol*. 14:391-396.
- Sinha P, Poggio T. 1996. I think I know that face. . . . *Nature*. 384:404.
- Smith ML, Gosselin F, Schyns PG. 2004. Receptive fields for flexible face categorizations. *Psychol Sci*. 15:753-761.
- Ullman S, Vidal-Naquet M, Sali E. 2002. Visual features of intermediate complexity and their use in classification. *Nat Neurosci*. 5: 682-687.
- Wiggs CL, Martin A. 1998. Properties and mechanisms of perceptual priming. *Curr Opin Neurobiol*. 8:227-233.
- Yin RK. 1969. Looking at upside-down faces. *J Exp Psychol*. 81:141-145.
- Yovel G, Kanwisher N. 2004. Face perception: domain specific, not process specific. *Neuron*. 44:889-898.
- Yovel G, Kanwisher N. 2005. The neural basis of the behavioral face-inversion effect. *Curr Biol*. 15:2256-2262.