

Rapid Face-Selective Adaptation of an Early Extrastriate Component in MEG

Alison Harris and Ken Nakayama

Harvard University, Cambridge, MA, USA

Adaptation paradigms are becoming increasingly popular for characterizing visual areas in neuroimaging, but the relation of these results to perception is unclear. Neurophysiological studies have generally reported effects of stimulus repetition starting at 250–300 ms after stimulus onset, well beyond the latencies of components associated with perception (100–200 ms). Here we demonstrate adaptation for earlier evoked components when 2 stimuli (S1 and S2) are presented in close succession. Using magnetoencephalography, we examined the M170, a “face-selective” response at 170 ms after stimulus onset that shows a larger response to faces than to other stimuli. Adaptation of the M170 occurred only when stimuli were presented with relatively short stimulus onset asynchronies (<800 ms) and was larger for faces preceded by faces than by houses. This face-selective adaptation is not merely low-level habituation to physical stimulus attributes, as photographic, line-drawing, and 2-tone face images produced similar levels of adaptation. Nor does it depend on the amplitude of the S1 response: adaptation remained greater for faces than houses even when the amplitude of the S1 face response was reduced by visual noise. These results indicate that rapid adaptation of early, short-latency responses not only exists but also can be category selective.

Keywords: face perception, magnetoencephalography, M170, object recognition, repetition effects

Introduction

Adaptation, reduced neural response following repeated presentation of a stimulus, is a well-known electrophysiological phenomenon (Desimone 1996; Brown and Xiang 1998). With the rising use of functional magnetic resonance imaging (fMRI), adaptation has become a valuable tool for probing the representations underlying neural activation. In such “fMR-adaptation” experiments, the reduction in the hemodynamic response to repeated presentation of the same stimulus is measured. This adaptation can then be compared with that for another stimulus that differs from the 1st in a single given dimension (e.g., viewpoint, position). If 2 stimuli that vary in a single dimension produce equivalent adaptation to that seen for repetition of a single stimulus, it is assumed that the neural representation is invariant for that dimension.

Using adaptation paradigms, researchers have characterized the properties of a number of areas in the ventral visual pathway (Grill-Spector and others 1999; Gauthier and others 2000; Kourtzi and Kanwisher 2000; Henson and others 2003; Andrews and Ewbank 2004; Winston and others 2004; Rotshtein and others 2005). Yet, because the hemodynamic response integrates over several seconds of neural activity, it is unclear whether the “adaptation” measured with fMRI is linked to perceptual mechanisms. To address this question, we must turn to neurophysi-

ological techniques such as event-related potentials (ERP) and magnetoencephalography (MEG), which have superior temporal resolution to fMRI.

In fact, a number of neurophysiological studies suggest that fMR adaptation in visual areas may be taking place after perceptual processing has occurred. Evidence for high-level visual processing is seen in the evoked neurophysiological response within 150–200 ms after stimulus onset: by 170 ms postonset, there is a larger peak for faces than for other stimuli. Yet, neurophysiological correlates of repetition effects have generally been reported substantially later, at 250–300 ms post onset (Puce and others 1999; Itier and Taylor 2002; Schweinberger and others 2002). This has led some researchers to propose that fMR adaptation of many visual areas reflects reentrant or “top-down” processing (Henson 2003).

Nonetheless, there is some evidence of repetition effects at the earlier latencies (100–200 ms) corresponding to perceptual processing. At longer exposure durations (>1 s) associated with behavioral shape aftereffects, Kovács and others (2006) recently reported attenuation of the N170 and vertex positive potential (VPP), 2 “face-selective” responses at 150–200 ms post-onset measured with ERP.

More akin to the paired-repetition paradigms commonly used in fMRI, Jeffreys (1996) found reduction in the amplitude of the VPP with “double-pulse” presentation at shorter exposures (200 ms). Remarkably, this adaptation appeared to be face selective, with a dramatic attenuation for faces preceded by faces but not for faces preceded by other objects. Unfortunately, Jeffreys’ (1996) result is largely qualitative, with data from a single sensor (Pz) in only 2 subjects.

Here we systematically investigated Jeffreys’ (1996) adaptation effect using MEG. We focused on the M170, an early (150–200 ms) component that shows a higher amplitude response to faces than to a variety of other stimuli, including houses, cars, animals, flowers, tools, and textures (Bentin and others 1996; Sams and others 1997; Liu and others 2000; Itier and Taylor 2004). We quantified adaptation at the M170 by examining how it varies with stimulus onset asynchrony (SOA) (Experiment 1), whether it depends on the low-level physical attributes of the stimulus (Experiment 2), and whether it varies with the amount of face signal in the adapting image (Experiment 3).

Materials and Methods

General Design

In 3 experiments, we systematically examined attenuation of the M170 response using Jeffreys’ (1996) double-pulse presentation paradigm (Fig. 1). In this method, 2 stimuli (S1 and S2) are presented in succession with an intervening interstimulus interval (ISI). Adaptation is the

reduction in the amplitude of the evoked response to the S2 stimulus due to the prior presentation of S1.

Experiment 1 investigated the dependence of “double-pulse adaptation” of the M170 on the SOA between the 1st and 2nd stimulus. In Experiment 2, we sought to determine whether the adaptation depended on low-level physical stimulus attributes. Finally, in Experiment 3, we tested whether attenuation of the M170 was dependent on the amplitude of the M170 response to the adapting stimulus.

Subjects

A total of 34 subjects between the ages of 18 and 40 were recruited from local universities for all 3 experiments. In Experiment 1, 9 subjects were tested; 2 were excluded because of the presence of alpha wave (due to wakeful relaxation) in their data. In Experiment 2, 13 subjects were tested, of whom 3 were excluded due to alpha wave. Twelve subjects were tested in Experiment 3, but 1 subject was excluded due to contamination of the M170 response by the earlier P100m component in the 12.5% and 25% face conditions (resulting in unusually large S1 amplitudes in these conditions). All subjects were right handed with normal or contact-corrected vision. 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 (MIT) Committee on the Use of Humans as Experimental Subjects.

Stimuli

All stimuli were 200 × 200 pixels, subtending an angle of 4.4° × 4.4°, and were presented on a gray background with a central black fixation point. In Experiment 1, stimuli consisted of grayscale photographs of faces and houses (50 exemplars each). Stimuli for Experiment 2 included the same grayscale photographs as in Experiment 1, along with line drawings and 2-tone versions of the face stimuli created in Adobe® Photoshop® (Fig. 3*a*). In Experiment 3, 5 levels of white noise were added to the same grayscale face photographs, resulting in images containing between 12.5% and 100% face signal. Examples of the faces in noise can be seen in Figure 4*a*.

Procedure

Experiment 1 consisted of 800 trials of 8 conditions (100 trials each), with 2 stimulus conditions (face-face and house-face) and 4 ISIs (100, 200, 300, and 600 ms). All conditions (stimulus × ISI) were randomly interleaved. Each trial consisted of 2 stimuli, S1 and S2, presented for 200 ms each followed by a 1.2-s fixation (Fig. 2*a*). S1 and S2 were always different faces. The subject was instructed to press a button every time a target female face (displayed at the beginning of the experiment) appeared; the other faces were all male. In all, 12.5% of the total trials consisted of the target face; these trials were randomly intermixed with the experimental trials. Target trials were excluded from the analysis.

Experiment 2 consisted of 700 trials of 7 adapting conditions (100 trials each): full face, eyes, nose, mouth, line-drawing faces (with features but no shading), 2-tone faces (with shading but no distinct features), and the control category of houses. Only the data from the line drawing and 2-tone face conditions are presented here. Trials of all conditions were randomly interleaved. The SOA was fixed at 400 ms. The subject again performed a target detection task with the same target female face; 10% of the total trials consisted of the target face. Target trials were again intermixed with experimental trials but excluded from the analysis.

In Experiment 3, the experimental S1 conditions consisted of faces with the 5 levels of noise (12.5%, 25%, 37.5%, 50%, and 100% face signal) plus an S1 condition of houses (without noise). An additional pure noise S1 condition was included for all but the 1st 3 subjects. S2 was always a noise-free (100%) face. The different conditions (100 trials each) were randomly interleaved. The SOA was again fixed at 400 ms. Subjects were asked to perform a face detection task on the S1 stimulus, pressing the right button if a face was present or the left button if they could not detect a face.

Data Acquisition

MEG recordings were made using a 157-channel whole-head system with superconducting quantum interference device (SQUID) based

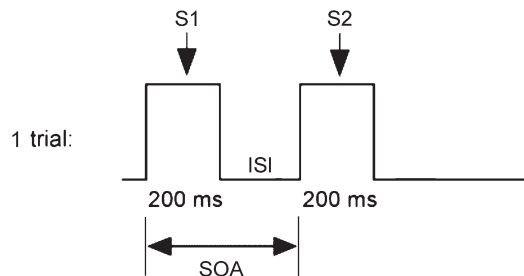


Figure 1. Schematic of the double-pulse adaptation paradigm designed by Jeffreys (1996). Each trial consists of the presentation of 2 stimuli (S1 and S2), with an ISI.

first-order gradiometer sensors (Kanazawa Institute of Technology MEG System at the KIT/MIT MEG Joint Research Laboratory at MIT). Magnetic brain activity was digitized continuously at a sampling rate of 500 Hz and was filtered with direct current 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 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. For further details, see Harris and others [2005].) The peak amplitude in the M170 range was determined for each sensor in each condition and then normalized to the M170 response to the S1 face condition at that sensor. In Experiments 2 and 3, separate average waveforms were also computed for each S1 stimulus condition and normalized to the M170 response in the S1 face condition (100% face, in Experiment 3). In all 3 experiments, statistical and graphical analysis used the normalized sensor values or their averages rather than the raw amplitude values as there is substantial variation between individuals in the raw amplitude of the M170 response.

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 purposes of averaging, amplitudes in right hemisphere sensors were multiplied by -1 to correct for this polarity difference.

Results

Experiment 1: Effect of SOA on Response Strength

The results of previous efforts to find adaptation using neurophysiology have been highly variable. Although a number of studies have found no effect of repetition in evoked potentials before a latency of 250 ms (Puce and others 1999; Itier and Taylor 2002; Schweinberger and others 2002), Jeffreys (1996) reported dramatic adaptation at latencies consistent with perceptual processing.

One seemingly minor methodological difference between these experiments may account for the discrepancy between their outcomes: the SOA used in stimulus presentation. (Note that the SOA is a feature of the stimulus presentation; it should not be confused with the aforementioned latency of 250–300 ms, which is a property of the evoked potential recorded from the brain.) Whereas the studies reporting no adaptation at 150–200 ms postonset have used SOAs greater than 1 s, the SOA of Jeffreys’

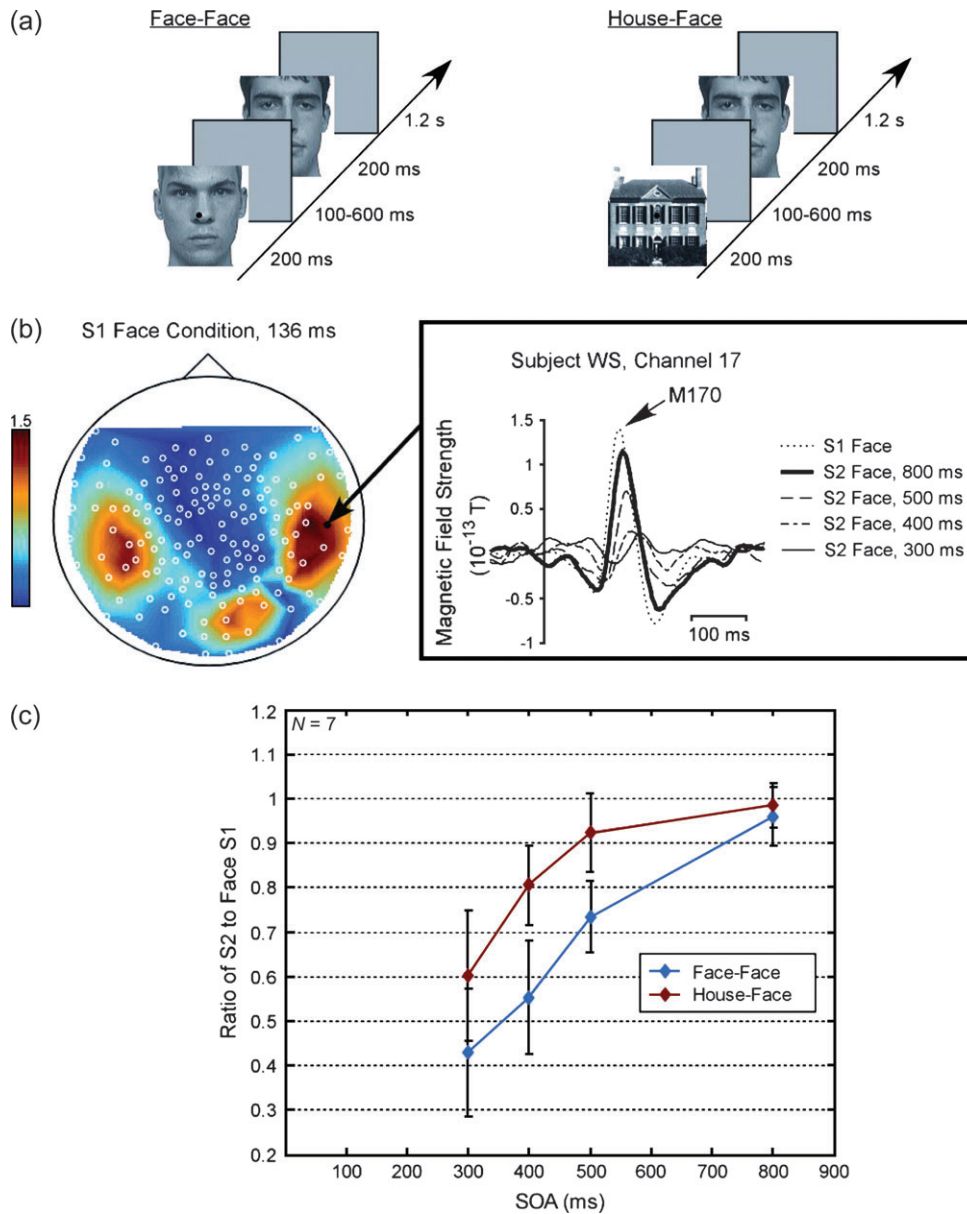


Figure 2. Double-pulse adaptation as a function of SOA. (a) Schematic of an individual trial for the face-face and house-face conditions. (b) An example of the M170 response in a single subject. Scalp distribution of the M170 response to the unadapted S1 face condition is shown to the left; the color bar indicates magnetic field strength in 10^{-13} T. The bilateral occipitotemporal dipoles that characterize the M170 are clearly visible. To the right, the response at a single sensor (indicated by arrow) is plotted for the S2 face conditions. Note that the polarity of the waveform has been reversed for ease of comprehension. (c) Adaptation of the M170 response as a function of SOA and stimulus category, averaged from 7 subjects. Adaptation increases significantly with decreasing SOA, but the amount of adaptation also appears to depend on the S1 category (face vs. house).

double-pulse paradigm is much shorter (400 ms). Supporting this idea, a study using both short and long SOAs (Trenner and others 2004) reported early repetition effects at an SOA of 67 ms but not at an SOA of 1000 ms (although this result may be explained by low-level habituation to image repetition [Debruille and others 1998]). Thus, SOA may be an important factor in adaptation of this early neurophysiological response. (Another major difference between Jeffreys (1996) and the other experiments cited above lies in the measurement of adaptation between rather than within categories [i.e., same vs. different exemplars]). Yet, although undoubtedly important, this distinction alone cannot explain prior failures to find early repetition effects, given the SOA-dependent early repetition

effects for identical exemplars reported by Trenner and others [2004].)

Therefore, our first experiment examined how double-pulse adaptation varies as a function of SOA. To systematically study the effect of SOA on adaptation, we parametrically varied the SOA between 300 and 800 ms (300, 400, 500, 800 ms). Also of interest was the category of the adapting stimulus (face vs. house); S2 was always a face. Importantly, the adapting and test stimuli were always different faces, so unlike Trenner and others (2004) attenuation of the response cannot be explained by low-level habituation to the specific image being presented. Figure 2a displays a schematic of a single trial for the face-face and house-face conditions.

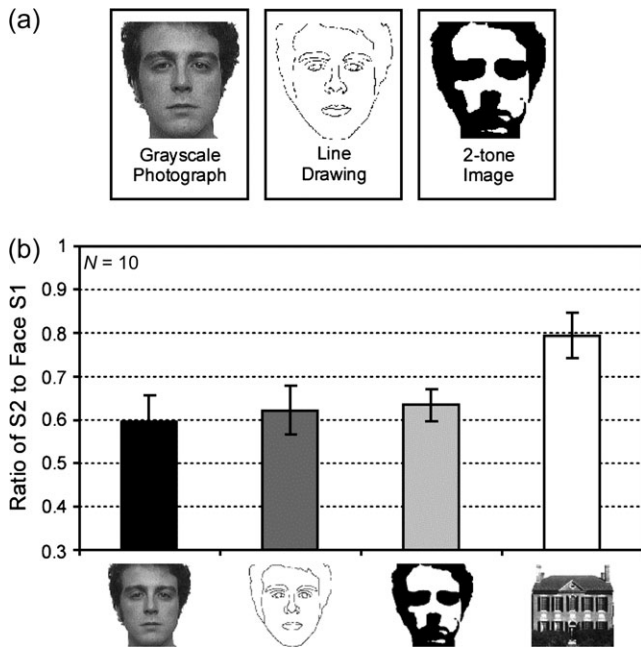


Figure 3. Double-pulse adaptation as a function of information in the S1 image. (a) Sample images depicting the 3 types of face representations used in the experiment. Although line drawings and 2-tone images are clearly recognizable as faces, they share few of the physical attributes present in the grayscale photograph stimuli. (b) Average data from 10 subjects. SOA was fixed at 400 ms. Despite the different physical stimulus properties of grayscale photographs, line drawings, and 2-tone images, all 3 types of face stimuli produce equal adaptation of the response to a 2nd grayscale face stimulus. Thus, adaptation cannot be explained by low-level habituation to the shared physical attributes of face stimuli.

Figure 2b displays the M170 response in a single subject. Overlaid on the sensor map is the scalp topography of the unadapted face condition at 136 ms, showing the bilateral occipitotemporal distribution of the M170 response. The response at a single sensor (indicated by arrow) to the different face-face conditions is plotted to the right of the scalp map. (Note that the polarity of the y axis has been inverted for ease of comprehension.) The dotted line indicates the M170 response to the S1 face presentation; each additional line represents the M170 to the S2 face at a different SOA. Adaptation of the M170 clearly increases with decreasing SOA.

This is even more apparent in Figure 2c, which displays the average normalized amplitude of the M170 as a function of SOA in 7 subjects. As can be seen, the M170 response to the 2nd face decreases in a linear fashion with decreasing SOA, indicating that the adaptation is dependent on ISI. A repeated-measures analysis of variance (ANOVA) confirmed this main effect of SOA as highly significant ($F_{3,18} = 11.04$, $P = 0.0002$). (Note that in Fig. 2 and all subsequent figures, error bars represent standard error between subjects, but statistical tests are computed between conditions within subjects. Thus, the degrees of freedom for the repeated-measures ANOVA are derived from $n - 1$ and $(n - 1)(N - 1)$, respectively, where n is the number of conditions being compared and N is the number of subjects.) However, this response attenuation is surprisingly brief: by an SOA of 800 ms, neither the face-face nor the house-face condition is significantly different from the unadapted S1 response to faces ($P > 0.5$, 1-sample t -tests).

In addition, Figure 2c indicates that the stimulus category of S1 also plays a role in the magnitude of adaptation. Faces

produce significantly more adaptation than houses ($F_{1,6} = 7.8$, $P = 0.03$). The interaction of SOA and stimulus category was marginally significant ($F_{3,18} = 3.13$, $P = 0.051$), reflecting the fact that the face-face and house-face conditions are significantly different at all but the longest (800 ms) SOA.

One concern regarding this adaptation effect is that of potential interference with, or contamination of, the test response from later components of the response to the 1st stimulus. For example, neurons in striate cortex are known to show an “offset potential” to the removal of the stimulus (Hubel and Wiesel 1959; Duysens and others 1996), and a late low-frequency component has also been reported at ventral face-selective sites in intracranial recordings (Allison and others 1999). However, later components are unlikely to account for the adaptation, as offset potentials have not been reported following the intracranial N200, which is analogous to the M170 (Allison and others 1999). Likewise, we failed to find any offset potential at sensors measuring the M170. Also, our data preprocessing included baseline correction and high-pass filtering, which should remove later low-frequency components from the data.

Thus, we have successfully observed adaptation of the M170. In keeping with Jeffreys (1996) and Trenner and others (2004), we found that stimulus repetition can modulate the amplitude of evoked responses well before the 250- to 300-ms latencies usually reported in the literature, suggesting that adaptation need not reflect reentrant or top-down processing. The strength of this response attenuation is critically dependent on the SOA between the 2 stimuli: by an SOA of 800 ms, the M170 shows nearly complete recovery. The small SOA range over which the double-pulse presentation is effective may serve to explain why it has been so rarely reported in past studies using much longer SOAs.

In addition to SOA, the reduction in M170 amplitude also appears to depend on the category of the adapting stimulus. Although there is a general effect of double-pulse presentation, at every SOA tested within the effective time range (<800 ms), S1 faces produce a greater attenuation of amplitude than S1 houses. Therefore, adaptation of the M170 appears to be face selective.

However, this face-selective adaptation could alternatively be explained as arising from low-level habituation to basic physical stimulus attributes, such as spatial frequency content. Because faces share more of these properties with each other than they do with houses, greater adaptation might be expected for the face-face condition—even when the images presented are of 2 different individuals. To address this concern, in our 2nd experiment, we examined whether face-selective adaptation of the M170 is dependent on the low-level physical properties of the S1 stimulus.

Experiment 2: Effect of S1 Format on Adaptation

In Experiment 2, we wished to exclude low-level habituation as a source of the face-selective adaptation of the M170. In order to do so, it was necessary to test the adapting power of stimuli that differ from grayscale photographic images of faces in their physical attributes yet were nonetheless recognizable as faces. Shown in Figure 3a are 2 stimulus classes that meet these criteria: line drawings and 2-tone images.

Line drawings and 2-tone images are relatively sparse representations, containing only a fraction of the information present in natural images. In line drawings, generally only lines corresponding to structural features (e.g., convexities/concavities,

edges) are used, excluding energy at low spatial frequencies. The 2-tone images depict image structure through black and white alone, with light regions in white and dark regions and shadows in black. Thus, in 2-tone images, information about shading, hue, and texture is lost. Yet, despite the loss of information in line drawing and 2-tone representations, familiar objects rendered in both formats are usually readily recognizable to naive observers.

Therefore, in Experiment 2, we tested whether face-selective adaptation of the M170 could be explained by low-level habituation to physical stimulus attributes through the use of line drawings and 2-tone images, which are severely restricted in their physical information, as adapting images. (Note that the test stimulus was always a grayscale photograph of a face, and the SOA was fixed at 400 ms.) If the “face selectivity” of the adaptation merely reflects the shared low-level physical similarity between face photographs, we would expect line drawings and 2-tone face images to produce less adaptation of the response to a following grayscale photograph than 2 grayscale photographs in succession. On the other hand, if face selectivity depends on the perceived face stimulus itself, then both line drawings and 2-tone images of faces should adapt to a similar extent as an S1 grayscale photograph.

The results for 10 subjects are displayed in Figure 3*b*. Contrary to what would be expected if face selectivity were dependent on physical stimulus attributes, the adaptation of the response to S2 grayscale photographs is equivalent regardless of whether they are preceded by other grayscale photographs, line drawings, or 2-tone images. This result was confirmed by a repeated-measures ANOVA, which found no significant difference between the levels of adaptation for the 3 S1 face conditions ($F_{2,18} = 0.26, P = 0.8$). Yet all 3 conditions produced significantly greater adaptation than houses (grayscale photographs: $P = 0.003$, line drawings: $P = 0.0005$, 2-tone images: $P = 0.011$, uncorrected paired t -tests).

Although we have ruled out the idea that face-selective adaptation of the M170 is due to low-level habituation to physical stimulus attributes, another possibility is simply that the adaptation depends on the strength of the response to the previous stimulus. Stimuli that elicit larger responses, such as faces, could cause greater refractoriness at the neural level and hence reduced response to the S2 stimulus. Such adaptation would therefore be nonselective, even though it arises as a consequence of a face-selective S1 response. Because the amplitudes of the M170 responses to line drawing and 2-tone face stimuli are not significantly different from that to grayscale face photographs (all P values > 0.5 , paired t -tests), this account cannot be ruled out by Experiment 2. Therefore, in a 3rd experiment, we directly manipulated the amplitude of the M170 response to the S1 face to test this alternative.

Experiment 3: Testing for Amplitude Dependence of Adaptation

In our third experiment, we sought to clarify whether the face-selective M170 adaptation we had found was truly due to stimulus category or merely reflected greater refractoriness subsequent to the larger amplitude to S1 faces. To test these hypotheses, we manipulated the amplitude of the S1 face response by adding visual white noise (Fig. 4*a*), which is known to reduce the amplitude of the M170 (Jemel and others 2003; Horowitz and others 2004). In this experiment, the SOA was again fixed at 400 ms.

Figure 4*b* displays the different predictions for stimulus and amplitude accounts of the adaptation effect. If adaptation depends on the amplitude elicited by the 1st stimulus, we should see increasing adaptation (decreasing S2 amplitude) as the percentage of face signal in the image is increased. On the other hand, if the adaptation depends on what stimulus category is presented at S1, there should be approximately equal adaptation across all noise levels, provided that the face is still perceived. (Pilot behavioral data collected in 4 subjects after MEG data acquisition indicated that even at the highest levels of noise used in the experiment, face detection performance was at ceiling in 3 out of 4 subjects.)

The results are presented in Figure 4*c*. As expected from previous reports, the amplitude of the M170 response increases with decreasing noise in a fairly linear fashion. A repeated-measures ANOVA on the S1 data found a highly significant main effect of noise level ($F_{4,40} = 21.58, P = 1.5 \times 10^{-9}$), with a significant linear contrast ($F_{1,10} = 92.68, P = 2.25 \times 10^{-6}$). Thus, we have successfully manipulated the amplitude of the M170 response to the S1 stimulus.

Yet, despite the decreasing amplitude of the S1 response with greater noise, the adaptation of the S2 response remains surprisingly constant. No significant difference among the S2 responses was found in a repeated-measures ANOVA ($F_{4,40} = 1.91, P = 0.128$). Remarkably, it seems that even very noisy face images—images that cannot elicit a full-amplitude M170 response—are still capable of producing the same adaptation effect as those without noise. Thus, the adaptation appears to depend on whether S1 and S2 are from the same (perceived) stimulus category, rather than simple S1 amplitude.

We can also directly compare the magnitude of adaptation when the amplitudes of the S1 face and house are equated (Fig. 5*a*). If adaptation is dependent on S1 amplitude, there should be equal adaptation by faces and houses of equivalent S1 amplitude (left panel). If adaptation is stimulus selective, however, we should still see a difference between house-face and face-face conditions even when S1 face and house amplitudes are the same (right panel).

Figure 5*b* shows the adaptation associated with houses and 50% faces. These 2 S1 conditions are not significantly different in amplitude (paired t -test, $P = 0.263$). Nonetheless, even these degraded face stimuli produce more powerful adaptation of the S2 face than the full-strength house stimuli (paired t -test, $P = 0.002$). Again, adaptation appears to be face selective rather than amplitude dependent.

Eight of the 11 subjects also saw faces preceded by pure noise. In these 8 subjects, the S1 response to the pure noise stimulus was slightly higher than that to 12.5% faces (0.58 vs. 0.51) on average. Yet, when the S2 face was preceded by noise, the amount of adaptation was no different than that for faces preceded by houses (0.82 vs. 0.82; $P = 0.99$, paired t -test), whereas 12.5% faces produce roughly equivalent adaptation to noise-free (100%) faces (0.60 vs. 0.55; $P = 0.46$, paired t -test). This provides further support for the view that the face stimulus, rather than the response amplitude, is responsible for the face-selective adaptation of the M170.

Discussion

Here we investigated adaptation of the early, short-latency M170 response using double-pulse presentations. In contrast with previous results, which reported repetition effects starting

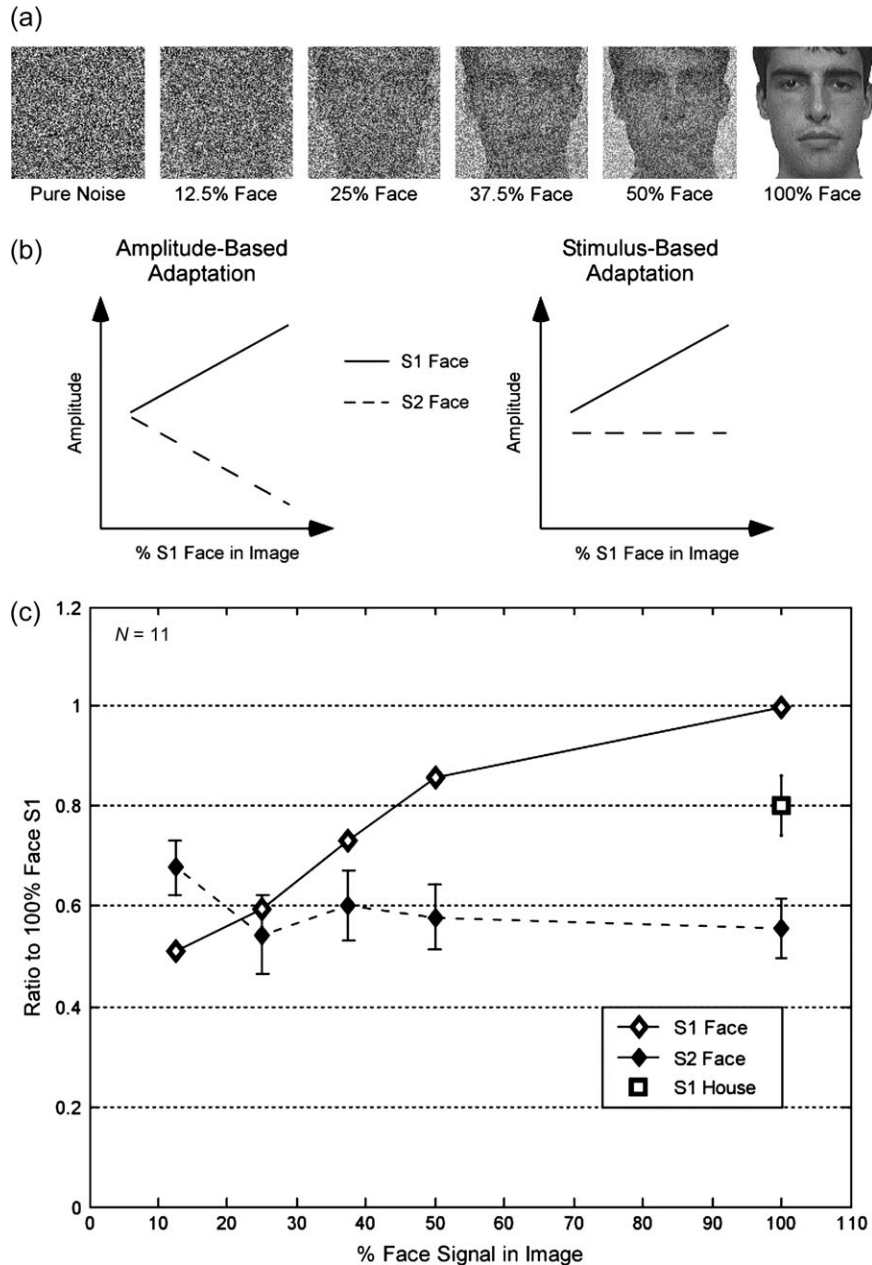


Figure 4. Double-pulse adaptation as a function of face signal in the S1 image. (a) Sample images, depicting the levels of white noise used to manipulate S1 amplitude. (b) Predictions: if adaptation is amplitude dependent (left), the amount of adaptation should increase with increasing S1 amplitude (hence, the amplitude of the S2 response should decrease). If adaptation is stimulus dependent (right), adaptation should remain constant across noise levels. (c) Actual results: with decreasing face signal in the image, the response to the S1 face condition (open diamond) decreases to below the level of the S1 house response (open square). Yet the S2 face response (filled diamond) remains roughly constant across all noise levels, indicating that adaptation depends on the stimulus category rather than amplitude of the S1 response. SOA was fixed at 400 ms.

only after 250–300 ms poststimulus onset, we found that adaptation can indeed occur at earlier stages of the evoked response. This adaptation, critically dependent on SOA, is short lived: by an SOA of 800 ms, the signal shows complete recovery. Given that most prior studies used SOAs over 1000 ms, it is thus unsurprising that few prior reports of such early adaptation effects exist.

Adapting stimulus category also plays a role in the magnitude of the adaptation: adaptation of the response to the test face is greater when it is preceded by another face than when it is preceded by a house. Thus, M170 adaptation appears to be face selective.

This selectivity cannot be explained as a function of low-level habituation (Experiment 2) or nonselective refractoriness (Experiment 3). In Experiment 2, we found that when grayscale photographs of faces were preceded by line drawings or 2-tone face images, which have substantially reduced physical information, adaptation was equivalent to that for photographs preceded by other face photographs. Thus, adaptation of the M170 does not reflect low-level habituation but rather the perceived stimulus category of the S1 image.

In Experiment 3, we tested whether the face selectivity of the adaptation is dependent on the amplitude of the S1 response by manipulating S1 amplitude through the addition of noise.

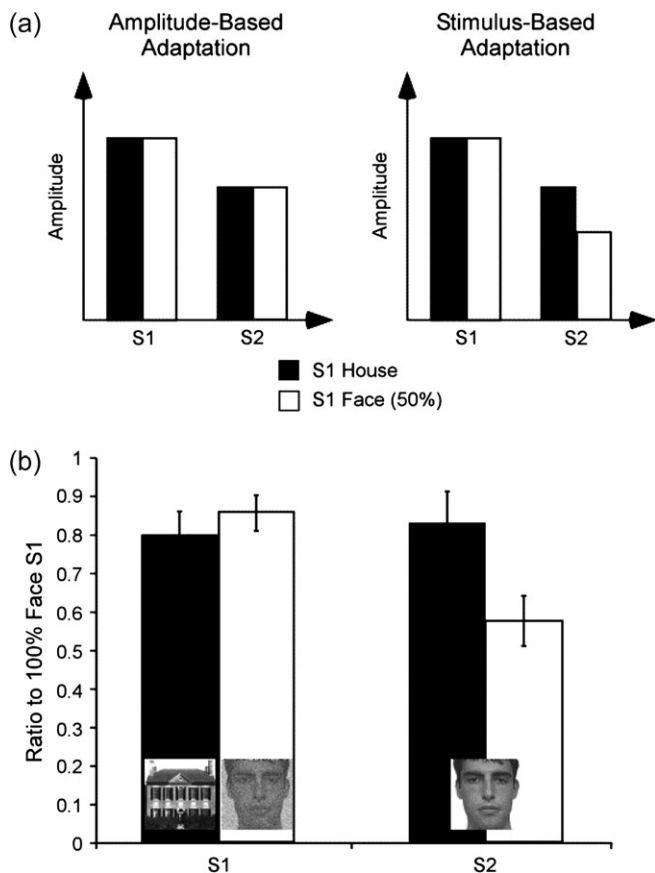


Figure 5. Direct comparison of the magnitude of adaptation to face and house stimuli of equal S1 amplitude. (a) Predictions: if adaptation is amplitude dependent (left), S1 stimuli that elicit M170 responses of equal amplitude should produce equivalent adaptation of the S2 response, regardless of the S1 stimulus category. If adaptation is stimulus selective, there should be greater adaptation of the S2 response by faces, even if the S1 amplitude to faces is no greater than that to houses. (b) Actual results: S1 faces produce significantly greater adaptation than houses, even though the S1 responses to face and house stimuli are equivalent in amplitude. This further supports a stimulus-selective account of double-pulse adaptation at the M170.

Despite the decreasing amplitude of the M170 with increasing noise, adaptation remains roughly constant across noise levels. Direct comparison of adaptation between house and face conditions of equivalent S1 amplitude likewise reveals a significantly greater adaptation effect in the face condition.

Together, these results demonstrate that adaptation of the M170 not only exists independently of low-level repetition effects but also is truly face selective in nature. In fact, Experiment 3 suggests that the adaptation may be a more face-selective measure than the M170 itself. A truly face-selective response should be unaffected by low-level changes like the addition of noise, as long as such changes do not affect perception of the face. The M170 itself fails this definition by decreasing in magnitude with increasing noise, even when the face image remains clearly visible as such. For example, an image with 50% face signal produces an M170 response with amplitude roughly 85% as large as the 100% face image (Fig. 4c). Yet the adaptation produced by an image that is 50% face is equivalent to that seen for a face image that is noise free.

Therefore, this technique may better assess the nature of face selectivity at the M170 than simple amplitude measurements. The use of different adapting stimuli (e.g., inverted faces, face

parts, schematic/cartoon faces) as probes can help determine which aspects of the face stimulus are important to early processing and what the nature of that early processing might be.

In addition to delineating the properties of the M170 response, face-selective double-pulse adaptation can inform our understanding of repetition effects in the brain. First, comparison of repetition effects at different neurophysiological components and latencies can give us a more complete picture of the time course of visual processing. Compared with the early-evoked C1 component measured at occipital sensors (Musselwhite and Jeffreys 1983), later components such as the M170 and N250r show both slower recovery and increasing selectivity of adaptation, culminating with semantic processing and recognition at latencies of 400–600 ms (Schweinberger and others 2002; Pickering and Schweinberger 2003). The short time course of adaptation at 170 ms after stimulus onset, along with its insensitivity to identity, suggests that this component represents a coarse detection or categorization mechanism. In contrast, adaptation to individual exemplars is not seen until latencies of 250–300 ms and has been localized to more anterior sources (Schweinberger and others 2002). Together, these data suggest that visual categorization and identification occur at different temporal stages (and possibly in distinct neural populations), constraining models of visual processing (e.g., Riesenhuber and Poggio 2000).

The rapid double-pulse adaptation reported here also complements recent ERP work by Kovács and others (2006), demonstrating category-selective response attenuation of the analogous N170 component with prolonged exposure (>1 s). It is generally accepted that the term adaptation has been used to refer to a number of processes occurring at different timescales and perhaps by different mechanisms. The results of Kovács and others (2006) and our own data may reflect such different long- and short-term adaptation effects, respectively. However, although their experiment used a longer S1 presentation duration (5000 ms), the ISI between adapting stimulus and test was within the range used in our experiments (200 ms). Therefore, it is unclear whether these 2 sets of results are tapping into fundamentally different adaptation processes or instead both reflect a single adaptation process dependent on ISI. Further research will be necessary to disentangle these 2 possibilities.

Finally, double-pulse attenuation can aid in our understanding of repetition effects through comparison with the adaptation effects measured with other techniques, particularly fMRI. Of course, there is no reason to necessarily expect correspondence between repetition effects measured with fMRI and MEG. The attenuation reported here with MEG occurs for relatively transient components, lasting less than 100 ms each, which could be averaged out over the longer time interval measured by fMRI.

Response attenuation in fMRI has been reported for several face-selective brain regions, including a portion of the lateral occipital complex (Grill-Spector and others 1999), the occipital face area (OFA; Gauthier and others 2000), the fusiform face area (FFA; Gauthier and others 2000; Andrews and Ewbank 2004; Eger and others 2004; Winston and others 2004; Rotshtein and others 2005), and the superior temporal sulcus (Andrews and Ewbank 2004; Winston and others 2004). However, methodological concerns prevent straightforward comparison of these results with the response attenuation of the M170 reported here. First of all, due to the coarse spatial resolution of MEG, it is unclear which of these areas is the primary source of the M170, if indeed a single primary source exists. Halgren and

others (2000) localized the magnetic dipole of the M170 to the fusiform gyrus, consistent with the location of the FFA. However, a number of ERP studies have suggested that the source of the analogous N170 signal is more likely to be a more lateral region such as the occipitotemporal sulcus (Bentin and others 1996) or lateral temporal cortex (Watanabe and others 2003).

Furthermore, the above studies differ from our experiment in stimuli and design. In contrast to our results, these experiments found an effect of face identity (with repetition of identity producing greater adaptation) at the OFA and FFA. However, in many of these studies, the “same identity” condition simply consists of the same physical stimulus of a face repeated at the same location. Thus, under these conditions, identical faces could produce greater adaptation either because areas such as the FFA encode face identity or by virtue of the additional low-level habituation produced by identical image repetition. Although a low-level explanation may not account entirely for the adaptation of the FFA (Eger and others 2004; Rotshtein and others 2005), it underscores the methodological differences between these studies and our experiments. These discrepancies must be addressed before we can meaningfully compare the adaptation effects measured here with those reported using fMRI.

In conclusion, we have shown that rapid adaptation effects can be measured even earlier than the 250-ms latency commonly reported. This adaptation at 170 ms after stimulus onset is dependent on the SOA, with shorter SOAs producing greater adaptation. By an SOA of 800 ms, however, the signal shows complete recovery. The magnitude of the adaptation also depends on the category of the S1 stimulus, not the amplitude of the S1 response, and cannot be explained by habituation of early visual areas to low-level stimulus attributes. Furthermore, unlike the amplitude of the M170 itself, this adaptation effect is not sensitive to the addition of noise. The double-pulse adaptation paradigm thus has the potential to probe with greater sensitivity the nature of early face-selective processing.

Notes

Address correspondence to Dr Alison Harris, Vision Sciences Laboratory, Department of Psychology, Harvard University, Cambridge, MA 02138, USA. Email: aharris@alum.mit.edu.

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