



Visual mental imagery and perception produce opposite adaptation effects on early brain potentials

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ABSTRACT

Event-related potentials (ERPs) were recorded during a rapid adaptation paradigm to determine whether visual perception and visual mental imagery of faces recruit the same early perceptual processes. The early effect of face and object adaptors, either perceived or visualized, on test stimuli, was assessed by measuring the amplitude of the N170/VPP complex, typically much larger for faces than for other object categories. Faces elicited a robust N170/VPP complex, localized to posterior ventrolateral occipitotemporal cortex. Both visualized and perceived adaptors affected the N170/VPP complex to test faces from 120 ms post-stimulus, reflecting effects on neural populations supporting early perceptual face categorization. Critically, while perceived adaptors suppressed the amplitude of the N170/VPP, visualized adaptors enhanced it. We suggest that perceived adaptors affect neural populations in the neocortex supporting early perceptual processing of faces via bottom-up mechanisms, whereas visualized adaptors affect them via top-down mechanisms. Similar enhancement effects were found on the N170/VPP complex to non-face objects, suggesting such effects are a general consequence of visual imagery on processing of faces and other object categories. These findings support image-percept equivalence theories and may explain, in part, why visual percepts and visual mental images are not routinely confused, even though both engage similar neural populations in the visual system.

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Introduction

During visual mental imagery, neural representations of a visual entity are reactivated endogenously from long-term memory and maintained in working memory to be inspected and transformed, processes at the core of many common mental activities, such as spatial reasoning (e.g., Ganis et al., 2004; Kosslyn et al., 2006). A prominent class of theories (*image-percept equivalence* theories) postulates that visual mental images are supported by the same neural processes and representations underlying visual perception (e.g., Finke, 1985; Kosslyn, 1994; Kosslyn et al., 2006). The question of whether visual mental imagery and visual perception engage the same neural processes is important because it presents a dilemma: If the processes are the same in the two cases, then how can the brain distinguish visual percepts from visual mental images? Note that, although there is evidence that visual mental imagery of a stimulus can lead to false memories of having perceived the stimulus (e.g., Gonsalves et al., 2004), this situation is the exception, rather than the rule, and may relate more to issues of how prior experience is encoded

and subsequently retrieved from long-term memory, than how the brain distinguishes between ongoing internal activation of mental representations and ongoing perception of the world.

Although image-percept equivalence theories do not postulate that visual mental images and percepts are identical in every detail, they predict that many psychophysical effects (and the underlying neural processes) found with actual visual stimuli should also be present when these stimuli are only visualized (Kosslyn et al., 2006). Consistent with this prediction, a number of behavioral studies have shown that aftereffect illusions typically brought about by visual perception can also be produced by visual mental imagery. For instance, early work (Finke and Schmidt, 1978) showed that imaging bars against a colored background produces orientation-specific effects on subsequently presented gratings (McCollough effect) similar to those produced by actually perceiving the bars (see for extensive review, Kosslyn et al., 2006). However, other researchers have used behavioral data to argue that these types of results are artifacts due to experimenter expectancy or demand artifacts (Broerse and Crassini, 1980, 1984; Intons-Peterson, 1983; Intons-Peterson and White, 1981; Pylyshyn, 1981). Findings from behavioral data in sophisticated cognitive paradigms can be used to make strong inferences, but behavioral measures alone cannot determine conclusively the exact processes underlying an effect because the pattern of

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behavioral effects (e.g., response times, error rates) is the cumulative result of processing at multiple levels in the brain. Differences potentially can arise at any one or more of these levels and potentially influence the next, and so on down the line.

Recently, cognitive neuroscience has used neuroimaging to try to provide more direct evidence on the issue by showing that visual mental imagery elicits brain activation in regions engaged during visual perception of the same stimuli (e.g., Ganis et al., 2004; Ishai et al., 2000; 2002; Kosslyn et al., 1996; Mechelli et al., 2004; O'Craven and Kanwisher, 2000). For example, visualizing faces activates regions in inferotemporal cortex that are also activated while perceiving faces, whereas visualizing houses activates portions of the parahippocampal cortex that are also activated while perceiving houses (e.g., Ishai et al., 2002; O'Craven and Kanwisher, 2000). Functional magnetic resonance imaging (fMRI) results of this kind, however, are ambiguous, for two reasons. First, the limited temporal resolution of fMRI, relative to the rapid timing of neural processing, cannot distinguish between alternative time course scenarios. There is evidence that relatively early visual areas in the ventral stream participate not only in lower-level visual processing, but also in higher-level cognitive processing with a later time course (e.g., Lamme and Roelfsema, 2000). This late engagement may be supported by higher-level brain regions such as the anterior temporal and prefrontal cortices, which may exert top-down reactivation onto low-level visual areas over an extended processing time. Second, even ignoring the complex relationship between neural activity and hemodynamic responses (e.g., Logothetis and Wandell, 2004), neural populations may exhibit the same average activation but be in different functional states, due to their participation in different processes (Gilbert and Sigman, 2007; Schendan and Kutas, 2007). Such different functional states would not be evident in activation maps, but could be revealed by assessing how these neural populations react to subsequent probe stimuli.

The above considerations led us to address this question using scalp event-related potentials (ERPs) to monitor non-invasively neural adaptation effects on face processing induced by visual mental imagery and visual perception. Note that, although we focused on faces, the following ideas can be used to address the same question about other object categories as well. Neural adaptation, the phenomenon by which neural responses to a stimulus are modified (usually suppressed) by immediate repetition with a very short time delay between the first stimulus and the repeated stimulus (less than 500 ms) has been used to probe the properties of neural representations (e.g., Grill-Spector et al., 1999). The basic adaptation logic involves assessing neural activation to a *test stimulus* that is either preceded by an *adaptor stimulus* or not. The difference between the response elicited by non-adapted and adapted stimuli, respectively, is referred to as an *adaptation effect*. To study neural selectivity, the adaptor and test stimuli usually are identical, defining the maximal adaptation effect, and this is compared to a condition where the adaptor and test stimuli differ along one dimension of interest. If both adaptor stimuli produce similar effects on the test stimulus, it is concluded that the underlying neural representation is invariant for the manipulated dimension. For example, if the response of a neural population in the inferotemporal cortex to a test face is suppressed equally by presenting as adaptors either the same face or a larger face, then one can infer that this neural population implements a representation that is invariant to face size. By measuring neural processes with sufficient temporal resolution, the time course of this representational invariance can be monitored as stimulus processing unfolds. In humans, early adaptation effects with visual faces and objects have been reported in several studies using scalp ERPs (e.g., Itier and Taylor, 2002; Jeffreys, 1996; Kovacs et al., 2006), intracranial ERPs (e.g., Seeck et al., 1997), and event-related fields (ERFs) (e.g., Harris and Nakayama, 2007a, b; Noguchi et al., 2004), employing a broad range of adaptation durations and interstimulus intervals (ISI). Most

studies focused on reduced amplitude, as a result of the pre-exposure to adaptor stimuli, of two related brain potentials elicited by faces peaking between 140 and 200 ms post-stimulus, the N170 and the vertex positive potential, VPP (also known as P150, e.g., Schendan et al., 1998). This *N170/VPP complex* is largest for faces than other objects, and thought to index early perceptual processing of faces (e.g., perceptual categorization of faces) implemented in ventrolateral temporal regions (e.g., Bentin et al., 1996; Jeffreys, 1989, 1996; Joyce and Rossion, 2005; Schendan et al., 1998). Consequently, effects on the N170/VPP complex to faces are generally thought to show that the manipulation of interest affects early bottom-up perceptual processing of faces, as opposed to later stages (e.g., Henson et al., 2003; Trenner et al., 2004). Note, the literature has been somewhat confused about the consistency of early neural adaptation effects, due to collapsing results across a variety of repetition paradigms. Repetition paradigms may involve different neural mechanisms depending on (a) the duration of the stimuli, especially the adaptor, (b) the ISI between the first and repeated stimuli, and (c) whether intervening stimuli occur between first and repeated stimuli, and so studies investigating these different phenomena must be separated. For example, results showing no early effects of face repetition (e.g., Puce et al., 1999; Schweinberger et al., 2002b) using relatively long ISIs (~2 s) are actually entirely compatible with findings showing early effects of repetition (e.g., Harris and Nakayama, 2007b; Jeffreys, 1996; Kovacs et al., 2006) with short ISIs (200 ms or less) because different mechanisms likely mediate each case (see Huber, 2008 for a recent discussion about the relationship between adaptation and repetition priming).

We used this adaptation logic, while monitoring neural activity with ERPs, to investigate: i) whether visual mental imagery of faces engages similar neural populations involved in the perceptual categorization of faces, and whether the time course is consistent with early perceptual processes, and ii) whether the effect of engaging these neural populations is the same in both cases, as assessed by responses to subsequent test stimuli. If visualized face adaptors affect the N170/VPP complex evoked by a test face stimulus, then we can conclude that visual mental imagery of faces recruits neural processes supporting early face perception. Conversely, lack of effects on the N170/VPP complex may suggest that visualized adaptors do not affect neural populations and processes engaged by early face perception. Furthermore, if the pattern of effects on the N170/VPP complex (e.g., direction, latency, or magnitude) is the same for perceived and visualized adaptors, then, even at this early stage, the neural processes engaged by visual mental imagery and visual perception overlap. In contrast, different patterns of N170/VPP effects would indicate that visual mental imagery and visual perception may both affect neural populations involved in early face perception, but use distinct neural pathways. Such differences would reveal potential mechanisms that enable the brain not to confuse visual percepts and visual mental images. We emphasize that, although this study focuses on test faces because they elicit the largest N170 and VPP components, we do not mean that our findings are specific for faces: The same logic and inferences apply also to other object categories. Finally, this study was focused on the N170/VPP, but, for completeness, we also analyzed later ERPs implicated in initial cognitive processing of faces and objects that have a polarity-inverting scalp distribution similar to the N170/VPP: An occipito-temporal N250/Ncl from 200 to 300 ms implicated in subordinate categorization, category learning, short-term repetition priming, and stored face representations (e.g., Doniger et al., 2000, 2001; Henson and Rugg, 2003; Schweinberger et al., 2002b; Scott et al., 2006; Sehatpour et al., 2006), and N400-like components to faces and objects peaking from 300 to 500 ms implicated in categorization tasks, perceptual and conceptual knowledge, semantic priming, and long-term repetition priming (e.g., Barrett et al., 1988; Cooper et al., 2007; McPherson and Holcomb, 1999; Paller et al., 2007; Schendan and Kutas, 2002, 2007; Schweinberger et al., 2002a).

Materials and methods

Subjects

A total of 23 naive healthy volunteers, recruited from Tufts University and the greater Boston area, took part in the study for course credit or cash (9 females and 14 males, average age: 21 years; standard deviation of age: 1.03 years). All subjects had normal or corrected vision, and no history of neurological or psychiatric disease. The data from 4 subjects were not included in the analyses because they had too few usable trials, due to excessive eye movement artifacts. The demographics of these 4 subjects did not differ from that of the remaining 19 subjects. All procedures were approved by the Tufts University Institutional Review Board.

Stimuli

Perceptual adaptation

For the perceptual adaptation task, the stimuli were a total of 132 grayscale pictures of celebrities (e.g., Brad Pitt) and common objects (e.g., alarm clock). All pictures were square, subtending 6×6 degrees of visual angle, and they were framed by a white outline. The faces were frontal views, and the objects were good views (i.e., frontal, non-accidental views), like objects we have used to define object-sensitive cortex in fMRI studies (Schendan and Stern, 2007). There were 66 face–face and 66 object–face critical trials. The same number of filler object–object and face–object trials were also employed, randomly intermixed with the critical trials, to ensure subjects could not predict the category of the test stimulus. Thus, each picture was used four times to create 264 stimulus pairs, equally divided into face–face, object–object, face–object, and object–face pairs. As in Harris and Nakayama (2007b), we did not use identical adaptor and test stimuli for the face–face and object–object trials in order to minimize low-level adaptation effects due to repetition of simple stimulus features, such as local contour position and orientation, which may be found as early as V1 (e.g., Murray et al., 2006). Instead, the focus was on higher-order face processing in perceptual face-sensitive cortex.

Imagery adaptation

For the imagery adaptation task, the stimuli were 22 grayscale pictures of celebrities and common objects not used in the perceptual adaptation task. There were 55 face–face (f–f) and 55 object–face (o–f) critical trials. The same number of object–object (o–o) and face–object (f–o) trials were also used, randomly intermixed with the critical trials, to match the perceptual adaptation design. Each picture was seen 10 times as test stimulus (with more than 4 intervening trials between repeated presentations), half in match and half in non-match trials. Since this was the first study of the effects of visualized adaptors, identical adaptor and test stimuli were used for the imagery condition to maximize potential adaptation effects.

Procedure

Imagery study session

Before the study proper, while the electroencephalography (EEG) cap and other EEG electrodes were being applied, there was an extended imagery study session. Subjects were given both written and oral instructions to memorize the stimuli presented on the screen because later they would be asked to image them from memory. During this study session, on each trial, subjects were shown the name of an actor or an object, followed by the corresponding picture of that actor or object. Subjects were encouraged to study each stimulus for as long as they needed, before moving on to the next stimulus. Each stimulus was presented and studied in this manner 13 times to ensure subjects had perceptually detailed memories of each stimulus.

Imagery practice (and extended imagery study)

After the study session, there was a practice session to familiarize subjects with the timing of the task and to help them fine-tune their visual images. During this phase, subjects saw the name of one of the studied faces or objects for 300 ms, followed by a gray screen (average luminance of all stimuli) with a white frame matching the one surrounding all the pictures. Subjects were instructed to image the studied stimulus within the outline on the gray screen. They were told to press a key when they had a vivid image in mind, so that they could compare their visual image with the actual stimulus (triggered by the key press). After seeing the actual stimulus, subjects were encouraged to notice differences between their visual mental image and the actual stimulus, and they were free to adjust their internal images for as long as they liked before proceeding to the next trial. This process was repeated for each studied stimulus 3 times. After the practice session, subjects took part in the experiment proper. The imagery condition was always tested first, to ensure subjects still had detailed memories of the recently studied visual stimuli.

Imagery conditions

The structure of a trial in the imagery conditions (Fig. 1, right) was identical to that of the practice session. The name of a stimulus was presented for 300 ms, followed by a gray screen with a square outline matching the frame shown for every picture. Subjects were asked to generate a vivid visual image of the studied stimulus within this frame and to press a key as soon as they had done so. Subjects were asked not to move their eyes or to blink just before they pressed the key and afterwards during the rest of the trial. Next, there was a gray screen with only the white outline for 200 ms, followed by the test stimulus for 300 ms. The test stimulus was either the picture that was visualized or a picture in the other category (face or object) and trial types were intermixed randomly. The test stimulus was followed by a gray screen with a fixation dot and subjects pressed a key when they were ready to move on to the next trial. To minimize potential effects of expectancy on the test stimuli, the adaptor category did not predict the category of the following test stimulus (face, object). Furthermore, there was no active task on the test stimulus, other than fixating the center of the screen, in order to minimize cognitive and response factors of no interest in the ERPs, and to focus only on the effect of adaptors on test stimuli.

In addition to the theoretical reasons discussed earlier, a methodological reason for choosing this specific paradigm was that studying visual imagery with ERPs is complicated by the fact that there is considerable between-subject and intertrial variability in the time course of image generation. Thus, simply time-locking the ERPs to a probe telling subjects when to begin generating an image would result in ERPs that are substantially smeared in time, and probably not sufficiently time-locked for robust effects to be observed. The current paradigm avoided this problem by determining the effect of a visual mental image on a subsequently presented stimulus. With this self-paced paradigm, subjects had a variable time to generate a vivid image, but the effects on the test stimulus were precisely time-locked.

Perceptual conditions

The structure and timing of trials in the perceptual conditions were identical to those of the imagery conditions, except that, for the perceptual adaptation test session, subjects were physically shown the adaptation stimulus instead of visualizing it (Fig. 1, left). Subjects were instructed to look carefully at the adaptation stimulus and to press a key as soon as they knew the identity of the person or could categorize the object in order to continue with the trial.

Electrophysiological data acquisition

The electroencephalogram (EEG) was sampled at 250 Hz from Ag/AgCl electrodes (gain=20,000, bandpass filtering=.01 to 100 Hz). EEG

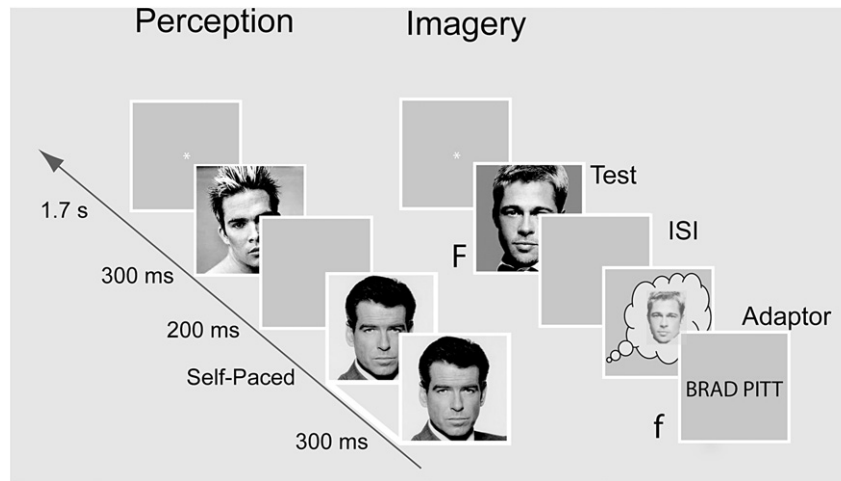


Fig. 1. Diagram of an experimental trial for the visual mental imagery and perception conditions (only f–F trials are described). Perception and imagery trials had a parallel structure. In the perception trials, left side of the figure, an adaptor face was perceived and subjects pressed a key as soon as they recognized it. The test face appeared 200 ms after the key press. In the imagery trials, right side of the figure, an appropriate face (the adaptor) was visualized upon seeing the corresponding word (which was on the screen for 300 ms). Subjects pressed a key as soon as they had generated a vivid mental image and the test face appeared 200 ms after this key press, as in the perception trials. There was no task on the test faces.

data were collected from 32 electrodes arranged in a geodesic array (Fig. 2), and loose lead electrodes below the right eye to monitor eye blinks, on the tip of the nose, and the right mastoid, all of which were referenced to the left mastoid. Horizontal eye movements were monitored using 2 electrodes placed on the outer canthi of the right and left eyes, referenced to each other. For most analyses, data were re-referenced off-line to an average reference (Dien, 1998). Electrode impedance was below 2 k Ω for the scalp and nose channels, and below 10 (usually 5 k Ω) for the eye channels.

ERP analyses

ERPs were averaged off-line for an epoch of 600 ms. Trials contaminated by blinks, eye movements, muscle activity or amplifier blocking were rejected off-line. A minimum of 20 artifact-free trials per subject per condition were averaged (median=45 trials). All measurements going into the analyses were relative to the 100 ms baseline period preceding stimulus onset.

Repeated measures ANOVAs were conducted on the mean amplitude of the average ERPs to assess the effects of the manipulations in the imagery and perception conditions on the N170/VPP complex. For the analyses, a 30 ms time window was used, which was centered around the mean peak latency of the N170/VPP complex (140–170 ms and 150–180 ms, for faces and objects, respectively, due to the slightly later peak latency of objects relative to faces, as detailed in the results). To assess the overall pattern of results, for each condition the first “lateral” ANOVA was carried out on the 13 pairs of lateral electrodes (see electrode montage in Fig. 2) and used 3 factors: Adaptor Category (face vs. object), Site (13 site pairs), and Hemisphere (left vs. right). The second “midline” ANOVA was carried out on the 6 midline electrodes and used 2 factors: Adaptor Category (faces vs. objects) and Site (6 midline sites). To parcellate the interactions between adaptor category and site found in the main analyses, we carried out focal ANOVAs on 3 pairs of occipitotemporal sites (17–18, 19–20, and 23–24, Fig. 2) where the N170 to faces is maximal (Bentin et al., 1996; Joyce and Rossion, 2005; Rossion and Jacques, 2007), using 3 factors: Adaptor Category, Site (3 site pairs), and Hemisphere. An ANOVA was also carried out on centrofrontal site 28, Cz, (Fig. 2), where the VPP to faces is usually maximal (e.g., Joyce and Rossion, 2005; Schendan et al., 1998), using Adaptor Category as factor. Although the data were low-pass filtered slightly (40 Hz) for the illustrations, all statistics were conducted on unfiltered data. We also conducted the same repeated measures ANOVAs on the mean amplitude of the P1

component, (100–120 ms time window, N170 sites), and on later ERPs, an N250/Nc1, and N400-like ERPs (200–300 ms, 300–500 ms time windows, respectively, over all sites).

Results

We begin with the results for face and object adaptors to define the basic category effect and show non-adapted baseline activity. Next, we present the ERPs to the perceptual adaptation conditions, followed by those to the imagery adaptation conditions. For brevity, we report only nontrivial effects of site and hemisphere (i.e., those interacting with the adaptor category factor).

Adaptor stimuli

Response times (RTs) to adaptors

The time subjects spent on the adaptors (in this self-paced paradigm) did not vary by adaptor category, as neither the main effect of adaptor category nor the interaction with condition (perception vs. imagery) were significant, $F(1,18) < .3$, in both cases ($p > .5$). However, subjects spent more time on the visualized than perceived adaptors, 3438 ms and 877 ms, respectively, as indicated by the main effect of condition, $F(1,18) = 317.0$, $p < .001$. This RT difference indicates that subjects took a few seconds to generate a vivid visual image, as expected.

ERPs to adaptors

The ERPs elicited by face and object adaptors during the first 500 ms for all the recording sites are shown in Fig. 2a. At posterior sites, an initial P1 (peaking at 100 ms post-stimulus) was followed by an N170 (peaking around 150 ms). At central and anterior sites, an N1 (peaking at 100 ms) and a VPP (peaking around 150 ms) were evident.

Faces showed a larger N170/VPP than objects (Fig. 2b), replicating this well-established finding (Itier and Taylor, 2002; Jeffreys, 1989, 1996; Jeffreys and Tukumachi, 1992; Jeffreys et al., 1992; Joyce and Rossion, 2005; Kovacs et al., 2006; Schendan et al., 1998). The lateral ANOVA showed a main effect of stimulus category, $F(1,18) = 11.24$, $\epsilon = 1$, $p < .005$, which varied by site, $F(12,216) = 39.91$, $\epsilon = .143$, $p < .001$, and site by hemisphere, $F(12,216) = 10.06$, $\epsilon = .41$, $p < .001$. The midline ANOVA showed an interaction between adaptor category and site, $F(5,90) = 38.31$, $\epsilon = .32$, $p < .001$.

The follow-up analysis on the N170 sites revealed that the N170 to faces was more negative than that to objects (N170 category effect), $F(1,18) = 50.29$, $\epsilon = 1$, $p < .001$. This effect was largest at occipitotemporal

pair 17–18 (Fig. 2a), $F(12,216)=37.92$, $\epsilon=.63$, $p<.001$, and larger over the right than left hemisphere, $F(1,18)=12.17$, $\epsilon=1$, $p<.005$. The analyses on the VPP site showed that the VPP was more positive to faces than to objects (VPP category effect), $F(1,18)=36.04$, $\epsilon=1$, $p<.001$ (Figs. 2a,b).

Later ERPs

Later components included an occipitotemporal N250 (for faces and objects; for objects, a polarity inverted P250 over frontocentral sites was also seen), and a frontocentral N400 (for faces; known as N350 for objects) that inverted polarity occipitotemporally to a P400 (for faces, and a P350 for objects). Both lateral and midline ANOVAs showed interactions between adaptor category and site from 200 to 300 ms, $F(12,216)=10.82$, $\epsilon=.20$, and $F(5,90)=12.36$, $\epsilon=.43$, respectively, and from 300 to 500 ms, $F(12,216)=8.36$, $\epsilon=.23$, and $F(5,90)=10.9$, $\epsilon=.37$, respectively (all $ps<.001$). The lateral ANOVAs also showed a 3-way interaction between adaptor category, site, and hemisphere, $F(12,216)=2.38$, $\epsilon=.56$, and $F(12,216)=2.85$, $\epsilon=.52$, for the 200–300 and 300–500 ms windows, respectively (both $ps<.05$).

Finally, the midline ANOVA from 200 to 300 ms also revealed a main effect of adaptor category, $F(1,18)=26.6$, $\epsilon=1$, $p<.001$.

Neural generators

Standardized Low Resolution Electrical Tomography Analysis (sLORETA) (Pascual-Marqui, 2002; Pascual-Marqui et al., 2002) was used to localize the neural generators of the N170/VPP complex in the ERP group average. Electrode coordinates were digitized using an infrared digitization system. The transformation matrix was calculated with a regularization parameter (smoothness) corresponding to a signal-to-noise (SNR) of 20 (Pascual-Marqui, 2002; Pascual-Marqui et al., 2002). This SNR was estimated from the N170 and VPP site data, as the ratio between signal power (mean square) in a 100 ms window centered around the N170/VPP peak and noise variance (calculated for the 100 ms in the baseline). To determine the stability of the inverse solution, the same analyses were repeated with smoothness optimized for SNR levels varying between 10 and 25, and the results were the same. First, we validated sLORETA methods (filter 0.01 to

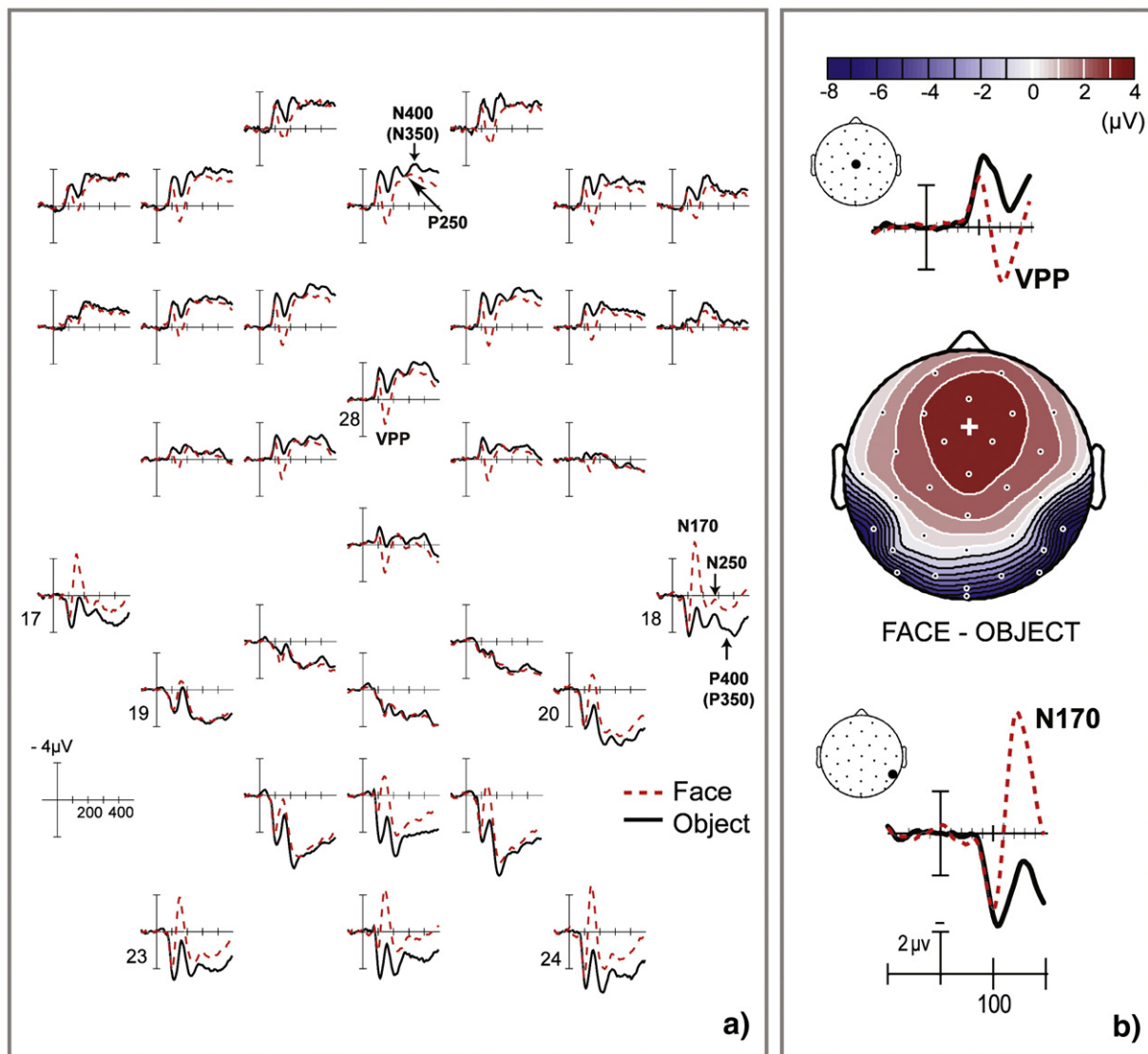


Fig. 2. Grand average ERPs elicited by adaptor faces (red dashed line) and objects (black solid line). (a) Plots of the ERPs between -100 and 500 ms (at all scalp recording sites). ERPs are shown negative up and referenced to the average of all sites. (b) An expanded view is shown of the ERPs between -100 and 200 ms at central site 28 (Cz) for the VPP (and N1) and occipitotemporal site 18 for the N170 (and P1), and the scalp distribution of the N170/VPP category difference (average ERPs to faces minus objects between 140 and 180 ms).

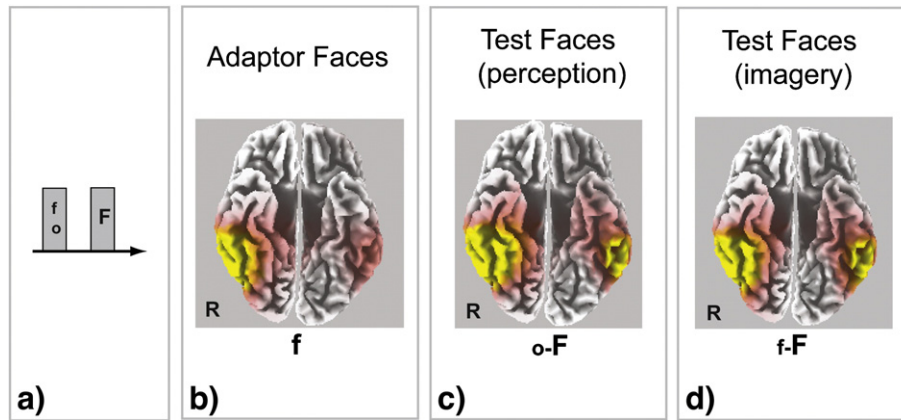


Fig. 3. The results are shown of the sLORETA inverse solutions on the N170/VPP to faces between 140 and 170 ms. Each depicted brain shows standardized cortical current density distributions, not statistical parametric maps (since they are derived from group data). Yellow represents maximal current density values. Note that these are (a) Schematic of the adaptation paradigm; (b) Data for adaptor faces (maximum at Talairach coordinates $x=55, y=-55, z=-10$); (c) Data for test faces preceded by adaptor objects (o-F) in the perception condition (maximum at Talairach coordinates $x=55, y=-45, z=-25$); (d) Data for faces preceded by adaptor faces (f-F) in the visual mental imagery condition (maximum at Talairach coordinates $x=50, y=-50, z=-20$); note that the f-F condition is shown in the mental imagery condition because it is associated with a larger N170/VPP complex than the o-F condition (the opposite of the perception condition).

20 Hz) by localizing the early visual C1 component (60 to 88 ms post-stimulus), since the sources have been determined previously (Di Russo et al., 2001). This component was correctly localized to Brodmann areas (BA) 17/18 (Talairach coordinates of maximum at $x=30, y=-95, z=-5$). These sLORETA methods then were used to estimate the sources of the N170/VPP complex for adaptor faces from 140 to 170 ms. In agreement with past findings (e.g., Deffke et al., 2007; Itier and Taylor, 2004), the results of the analysis showed neural generators in regions encompassing the mid fusiform gyrus, the middle and superior temporal gyrus and the middle occipital gyrus (Fig. 3b, Talairach coordinates of maximum at $x=55, y=-55, z=-10$).

Perceptual adaptation effects on test faces

The ERP adaptation data during the first 500 ms post-stimulus are shown in Fig. 4. First, we compared the ERPs to test faces preceded by adaptor faces (we will refer to this condition as f-F) with those of test faces preceded by adaptor objects (o-F) over the entire scalp. We will refer to the difference between the o-F and the f-F conditions as the *adaptor category effect*.

P1

There were no significant adaptor category effects or trends on the P1.

N170/VPP

The lateral ANOVA in the N170/VPP time window revealed interactions between adaptor category and site, $F(12,216)=10.75, \epsilon=.16, p<.001$, and adaptor category, site, and hemisphere, $F(12,216)=4.39, \epsilon=.30, p<.005$. The midline ANOVA also showed a main effect of adaptor category, $F(1,18)=8.23, \epsilon=1, p<.01$, and an interaction of adaptor category and site, $F(5,90)=8.94, \epsilon=.36, p<.001$.

The ANOVA on the N170 sites showed a main effect of adaptor category, $F(1,18)=18.38, \epsilon=1, p<.001$ (-3.02 and $-.71$ μV for the o-F and f-F conditions, respectively), and an interaction between adaptor category and site, $F(12,216)=21.1, \epsilon=.60, p<.001$, since the adaptor category effect was largest at pair 17–18 (3.53 μV). The analyses on the VPP site also showed an effect of adaptor category, $F(1,18)=12.21, \epsilon=1, p<.005$ (2.12 μV and .61 μV for the o-F and f-F conditions, respectively).

Later ERPs

Effects continued after the N170/VPP. Both lateral and midline ANOVAs revealed interactions between adaptor category and site from

200 to 300 ms, $F(12,216)=5.39, \epsilon=.21$, and $F(5,90)=4.31, \epsilon=.44$, respectively, and from 300 to 500 ms, $F(12,216)=3.89, \epsilon=.22$ and $F(5,90)=3.87, \epsilon=.38$, respectively (all $ps<.05$). Faces preceded by faces were less negative than faces preceded by objects for the occipito-temporal N250 and P400, whereas smaller effects in the opposite direction held at centrofrontal sites.

Direction relative to baseline

It is important to know whether the adaptor category effect on the N170/VPP to test faces corresponds to an amplitude decrease as a result of adaptor faces or to an increase as a result of adaptor objects. This was determined by comparing the amplitude of the N170/VPP to test faces with that of the ERPs evoked by the non-adapted, baseline face stimuli (i.e., the preceding faces used as adaptor stimuli). The analyses showed that adaptor faces suppressed the amplitude of the N170, relative to that elicited by the baseline face stimuli ($-.71$ and -3.26 μV , respectively), $F(1,18)=13.42, \epsilon=1, p<.005$, and this effect was modulated by site, $F(2,36)=20.51, \epsilon=.71, p<.001$. In contrast, adaptor objects did not affect the N170 elicited by test faces, compared to baseline face stimuli (-3.02 μV and -3.26 μV , respectively).

A similar pattern was found for the VPP: Adaptor faces reduced the amplitude of the VPP relative to baseline face stimuli (.61 μV and 2.38 μV , respectively), $F(1,18)=12.56, p<.005$, but adaptor objects did not (2.12 μV and 2.38 μV , respectively).

N170 onset latency

The onset of the adaptation effects was calculated by using a sliding window onset analysis on the N170 electrodes, following the recommended procedures (Picton et al., 2000). ANOVA were conducted on all time points between 0 and 200 ms (i.e., every 4 ms), and the onset was defined as the first time when 15 consecutive time points showed a significant effect of adaptation (main effect or interaction) at $p<.05$, a criterion providing sufficient protection against type I errors (Picton et al., 2000). The results showed that the onset time of adaptation effects for the perceptual condition was 120 ms, similar to the onset of the perceptual categorization effect for faces relative to objects (Schendan et al., 1998).

N170 peak latency

We measured the peak latency of the N170 at right occipitotemporal site 18, where this component is largest. Adaptor faces delayed the time of the peak latency of the N170 elicited by test faces (f-F, Fig. 5b), relative to that of baseline face stimuli (median peak latencies of

164 ms and 146 ms, respectively), $t(17)=3.62, p<.005$. Adaptor objects also delayed the peak latency of the N170 elicited by test faces (o-F, Fig. 5b), relative to that of baseline faces (median peak latencies of 156 ms vs. 146 ms, respectively), $t(17)=2.78, p<.05$. The difference in the N170 peak latency between test faces preceded by adaptor objects and faces was not significant, $t(17)=.75, p>.1$.

VPP peak latency

The same peak latency analyses were carried out on the VPP site (Cz). The results paralleled those found for the N170 (Fig. 5b). Adaptor faces increased the peak latency of the VPP elicited by test faces (f-F), relative to that of baseline face stimuli (median peak latencies of 160 ms and 146 ms, respectively), $t(17)=3.19, p<.005$. The same held true for adaptor objects (median peak latency of 156 ms), $t(17)=2.38, p<.05$. The difference in VPP peak latency between test faces preceded by adaptor objects and faces was not significant, $t(17)=.94, p>.1$.

Neural generators

Since adaptor faces produced a strong N170/VPP suppression for test faces, we localized only the neural generators of the large N170/VPP complex to test faces preceded by adaptor objects. The same

sLORETA methods used to localize the neural generators of the N170/VPP to adaptor faces were employed here. The results are shown in Fig. 3c. As for adaptor faces, neural generators were localized to the fusiform gyrus, extending into the lateral temporal cortex and the occipital cortex (mostly in the right hemisphere, maximum at Talairach coordinates $x=55, y=-45, z=-25$).

Imagery adaptation on test faces

The ERP imagery adaptation data are shown in Figs. 6 and 7. The same analyses conducted for the perceptual adaptation data were used to assess the effect of imagery adaptation.

P1

There were no significant category effects or trends on the P1.

N170/VPP

Results in the N170/VPP window showed adaptor category affected test faces, as indicated by the interaction of adaptor category and site in the lateral ANOVA, $F(12,216)=5.92, \epsilon=.19, p<.005$, and midline ANOVA, $F(5,90)=6.78, \epsilon=.33, p<.01$.

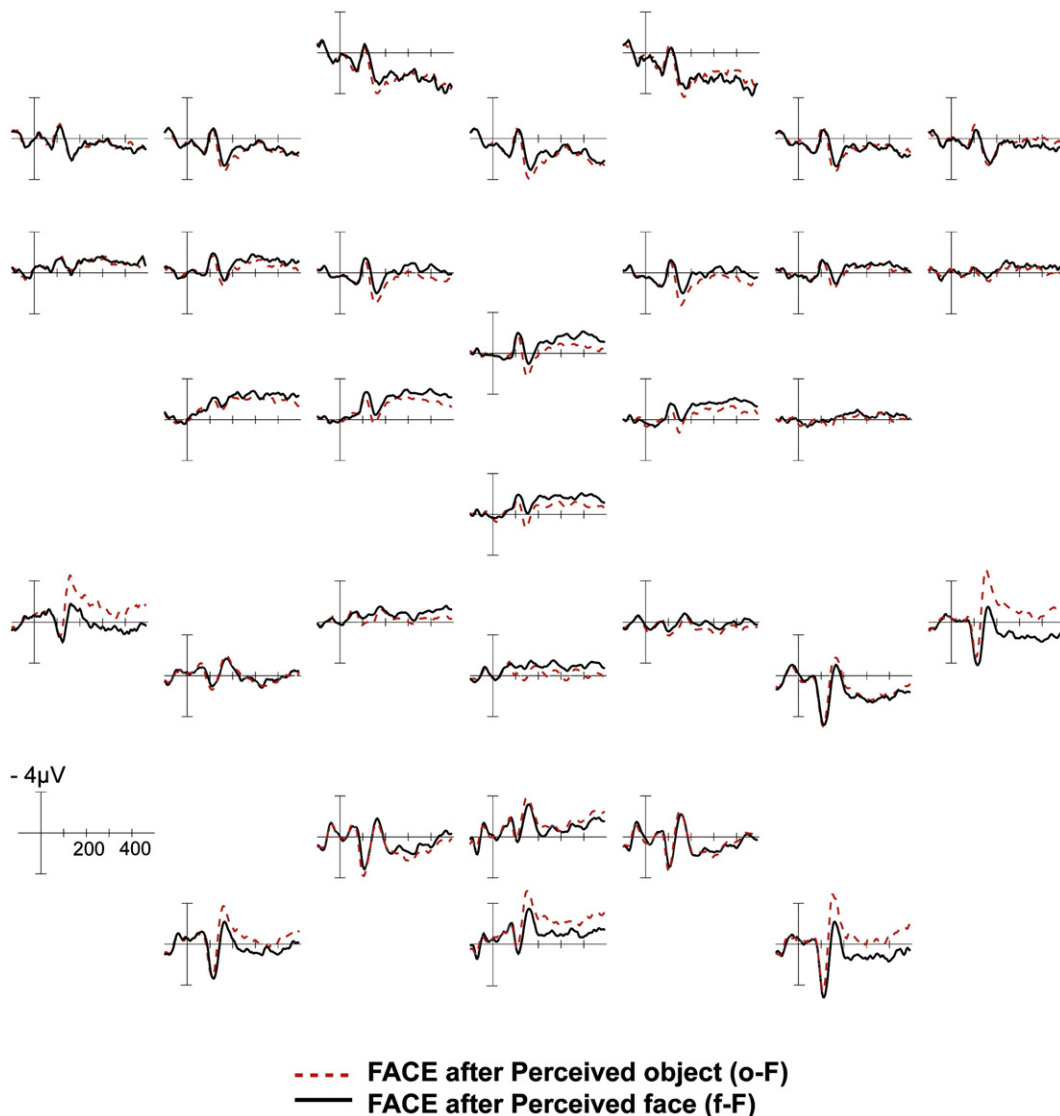


Fig. 4. Perceptual adaptation effects to test faces. Grand average ERP results, between -100 and 500 ms post-stimulus in the perception conditions, referenced to the average of all sites, and plotted negative voltage up. Data for faces following face adaptors (f-F) are depicted by the solid black line, whereas data for faces following object adaptors (o-F) are depicted by the dashed red line.

Follow-up analyses on the N170 sites showed a main effect of adaptor type, $F(1,18)=7.9$, $\epsilon=1$, $p<.01$ (-4.14 and -5.05 μV for o-F and f-F conditions, respectively), indicating that the amplitude of the N170 to test faces was *larger* when they were preceded by an adaptor face than object. This is the opposite of the direction of effects found for perceptual adaptation. Consistent with the N170 results, the analyses on the VPP site (Fig. 7) showed that test faces preceded by adaptor faces (f-F) enhanced the amplitude of the VPP, relative to faces preceded by adaptor objects (o-F), $F(1,18)=4.34$, $\epsilon=1$, $p<.05$.

Later ERPs

After the N170/VPP, test faces in the f-F condition were more negative than those in the o-F condition for the occipitotemporal N250 and P400, whereas the effect was in the opposite direction at centrofrontal sites (Fig. 6). The lateral ANOVAs showed interactions of adaptor category and site from 200 to 300 ms, $F(12,216)=14.25$, $\epsilon=.26$, and 300 to 500 ms, $F=12.61$, $\epsilon=.27$, $ps<.001$. The midline ANOVAs showed main effects of adaptor category from 200 to 300 ms, $F(1,18)=13.51$, $\epsilon=1$, $p<.005$, and 300 to 500 ms, $F=8.94$, $\epsilon=1$, $p<.01$, and interactions of adaptor category and site from 200 to 300 ms, $F(5,90)=12.13$, $\epsilon=.42$, and 300 to 500 ms, $F=10.85$, $\epsilon=.41$, $ps<.001$.

Direction relative to baseline

The same analyses conducted for the perceptual adaptation condition were carried out here (Fig. 7). The main effect of adaptor presence confirmed that adaptor faces increased the amplitude of the N170, relative to that elicited by non-adapted face stimuli (-5.05 μV and -3.26 μV , respectively), $F(1,18)=17.39$, $\epsilon=1$, $p<.001$. In contrast, there was only a nonsignificant trend for the N170 to test faces preceded by visualized objects to be larger than the N170 to adaptor faces (-4.14 μV and -3.26 μV , respectively), $F(1,18)=3.60$, $\epsilon=1$, $p=0.074$. Similar effects

were evident for the VPP: Adaptor faces increased the amplitude of the VPP, compared to baseline face stimuli (3.62 μV and 2.10 μV , respectively), $F(1,18)=5.57$, $\epsilon=1$, $p<.05$, but adaptor objects did not (2.72 μV and 2.10 μV , respectively), $F(1,18)=1.34$, $p>.1$.

Onset latency

The same onset analysis on the N170 electrodes conducted on the perceptual adaptation data were carried out on the imagery adaptation data. The results showed that the onset time of adaptation effects for imagery was also 120 ms.

N170 Peak latency

As for the perceptual condition, we measured the peak latency of the N170 at right occipitotemporal site 18, where this component is largest. Visualized adaptor faces slightly, but significantly, increased the peak latency of the N170 elicited by a subsequent test face, relative to that of baseline adaptor faces (with medians of 152 ms and 146 ms, respectively), $t(17)=2.24$, $p<.05$. Visualized adaptor objects also increased the peak latency of the N170 elicited by test faces (median peak latency of 156 ms), relative to that of baseline adaptor faces, $t(17)=3.55$, $p<.005$. The peak latency of the N170 to test faces was slightly longer when they were preceded by visualized objects than by visualized faces, $t(17)=2.67$, $p<.05$.

VPP peak latency

The same peak latency analyses on the VPP site (Cz) showed similar results. Visualized adaptor faces increased the peak latency of the VPP elicited by test faces (f-F), relative to that of baseline adaptor faces (median peak latencies of 154 ms and 146 ms, respectively), $t(17)=2.66$, $p<.05$. The same held for visualized adaptor objects (median peak latency of 156 ms), $t(17)=3.54$, $p<.005$. The VPP peak

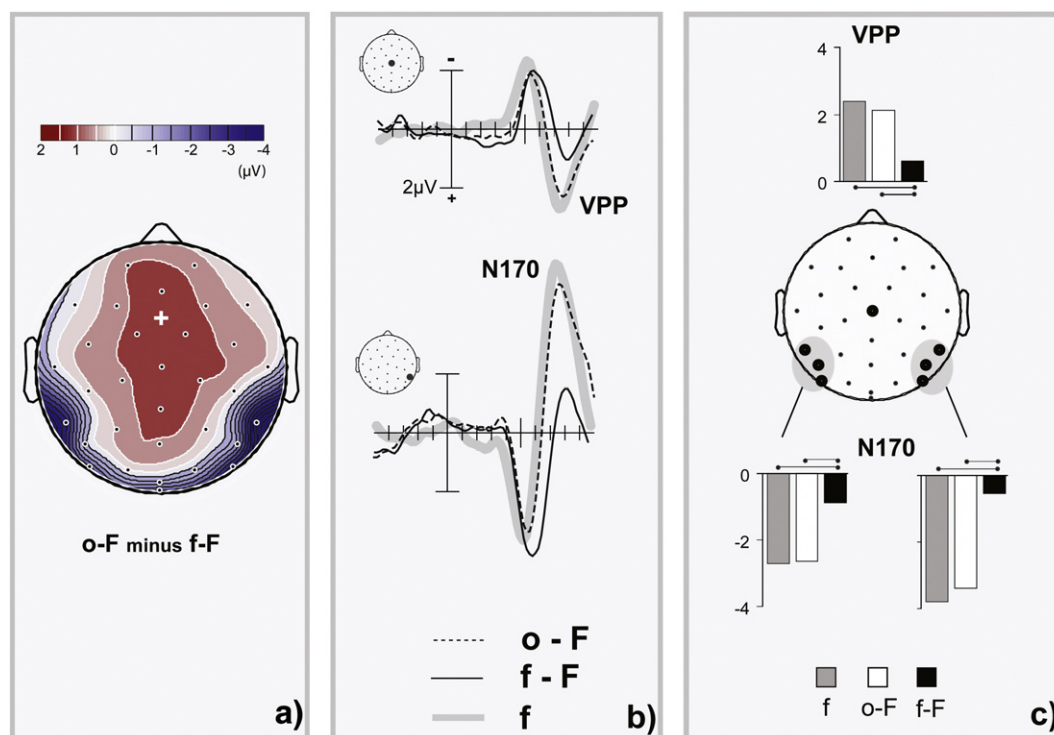


Fig. 5. Perceptual adaptation effects to test faces: Suppression of N170/VPP amplitude. Grand average ERP results in the perception conditions referenced to the average of all sites and plotted negative voltage up. (a) Scalp distribution of the ERP adaptation effect (ERPs to test faces preceded by object adaptors, o-F, minus ERPs to test faces preceded by face adaptors, f-F) between 140 and 170 ms in the perception conditions. (b) Grand average ERPs between -100 and 200 ms elicited by test faces preceded by object adaptors (o-F, dashed line), by test faces preceded by face adaptors (f-F, solid black line), and by adaptor faces (f, solid gray line). The N170 data are shown at the bottom (site 18), whereas VPP data (site 28) are shown on top. (c) N170 (bottom, mean of occipitotemporal sites 17, 18, 19, 20, 23, and 24) and VPP (top, site 28) amplitude data for perceived adaptor faces (f, gray bars), for test faces preceded by perceived adaptor objects (o-F, white bars), and for test faces preceded by perceived adaptor faces (f-F, black bars). Measurements taken from 140 to 170 ms. Significant differences are indicated with thin horizontal lines connecting the corresponding bars.

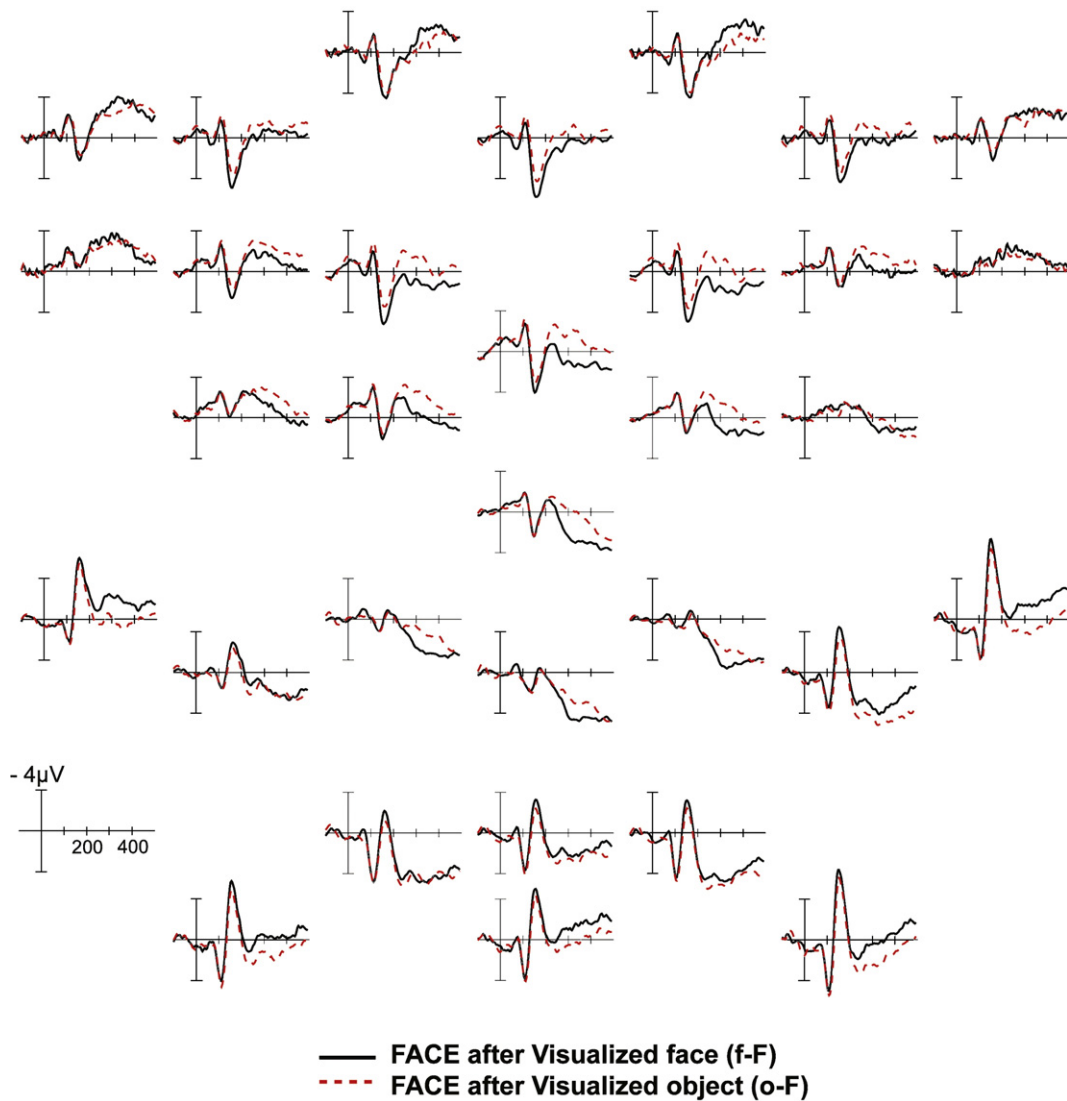


Fig. 6. Visual imagery adaptation effects to test faces. Grand average ERP results, between -100 and 500 ms post-stimulus in the visual imagery conditions, referenced to the average of all sites, and plotted negative voltage up. Data for faces preceded by visualized face adaptors (f-F) are depicted by the solid black line, whereas data for faces preceded by visualized object adaptors (o-F) are depicted by the dashed red line.

latency of test faces preceded by visualized object did not differ from that of test faces preceded by visualized faces, $t(17) = .93$, $p > .1$.

Neural generators

Given that adaptor faces produced a larger N170/VPP than adaptor objects, we localized only the neural generators of the N170/VPP complex to test faces preceded by adaptor faces. The same sLORETA methods used for the perception conditions were employed here. As shown in Fig. 3d, the results were remarkably similar to those found in the perception condition, with neural generators in the fusiform gyrus, extending into the lateral temporal cortex and the occipital cortex (mostly in the right hemisphere, maximum at Talairach coordinates $x=50$, $y=-50$, $z=-20$).

Imagery adaptation on test objects

Imagery adaptation effects on test objects were also analyzed to address two issues. First, visualizing faces could engage attention more strongly than visualizing objects, causing the relative enhancement effects for test faces. Second, the visual imagery enhancement effects could be specific to test faces and not generalize to other object categories. If the imagery adaptation effects were due to a salience

artifact associated with visualizing faces, then visualized adaptor faces should also produce stronger adaptation effects on test objects than visualized adaptor objects. Thus, the same analyses on the N170 and VPP sites were conducted for the test objects (in the 150 to 180 ms time window, since the N170 and VPP for objects peak around 165 ms). The results for the N170 showed a main effect of adaptor category, $F(1,18) = 15.92$, $\epsilon = 1$, $p < .001$ (-1.13 μV and -0.08 μV for visualized adaptor objects and faces, respectively), indicating that visualized adaptor objects enhanced the amplitude of the N170 to test objects more than visualized adaptor faces, ruling out a face saliency explanation for the enhancement effect. The results for the VPP paralleled those of the N170, with a main effect of adaptor category, $F(1,18) = 7.10$, $\epsilon = 1$, $p < .05$ (0.04 μV and -0.47 μV for visualized adaptor objects and faces, respectively). This evidence shows that relative face saliency was not the cause of the imagery adaptation effects. Furthermore, the effect found with test objects shows that the enhancement result is not restricted to test faces but generalizes to other objects as well.

Direct comparison between perception and imagery adaptation

Finally, we conducted a direct comparison between perception and imagery adaptation effects on the N170 and VPP sites by carrying out

an ANOVA including the data from both conditions. The results for the N170 confirmed that there were significant interactions between adaptor category and adaptation condition (imagery vs. perception), $F(1,18)=20.21$, $\epsilon=1$, $p<.001$, and between adaptor category, adaptation condition, and site, $F(2,36)=15.16$, $\epsilon=.74$, $p<.001$. The results for the VPP confirmed that there was a significant interaction between adaptor category and adaptation condition, $F(1,18)=7.88$, $\epsilon=1$, $p<.05$.

Discussion

We begin by summarizing the results. The most important and novel findings of this study are that i) both visualized and perceived adaptors affect the N170/VPP complex with a similar time course, and ii) remarkably, while perceived adaptors suppress the amplitude of the N170/VPP complex, visualized adaptors enhance it.

Non-adapted face stimuli (i.e., faces used as adaptors at the beginning of a trial) evoke a larger N170/VPP complex than non-adapted object stimuli, replicating previous ERP work on the perceptual categorization of faces and objects (e.g., Bentin et al., 1996; Jeffreys, 1989, 1996; Joyce and Rossion, 2005; Schendan et al., 1998). With an average reference, the amplitude of the N170 is maximal at occipitotemporal sites, and it is larger on the right than left hemisphere, whereas the amplitude of the VPP effect is maximal over centrofrontal sites. The distributed neural generators of the N170/VPP complex are localized in the fusiform gyrus, extending into the inferior, middle and superior temporal gyri and into the middle occipital gyrus (mostly on the right, Fig. 3), consistent with prior work (e.g., Deffke et al., 2007; Itier and Taylor, 2004).

The perceptual adaptation results confirm those found in studies reporting a *suppression* of the amplitude of the N170/VPP complex to

test faces preceded by adaptor faces (compared with adaptors from other categories, or no adaptors), at least with short ISIs (e.g., Harris and Nakayama, 2007b; Jeffreys, 1996; Kovacs et al., 2005; 2006). The perceptual adaptation effect on the N170 onsets around 120 ms post-stimulus, is maximal at occipitotemporal sites, and is larger over the right hemisphere, consistent with the N170 scalp distribution to faces relative to objects. Furthermore, the perceptual adaptation effect on the VPP is largest at centrofrontal sites, consistent with the scalp distribution of the VPP found in previous studies (Jeffreys, 1996; Joyce and Rossion, 2005; Schendan et al., 1998). The peak latency of the N170 and of the VPP to faces is increased by both perceived adaptor faces and objects, as reported in a previous study in which latency analyses were conducted (e.g., Kovacs et al., 2006). Finally, within the spatial resolution limits of ERP localization using LORETA, the neural generators of the N170/VPP to test faces in the perceptual adaptation condition are localized in similar temporal and occipital regions found for the non-adapted faces.

The imagery adaptation effect on the N170 starts at 120 ms post-stimulus, which is the same onset as the perceptual adaptation effect in this study, and perceptual categorization effects for faces relative to objects in our prior work (Schendan et al., 1998). Thus, the imagery adaptation results demonstrate that visualized adaptors, like perceived ones, affect early neural processes involved in the perceptual categorization of incoming faces. The N170 imagery adaptation effect is maximal at occipitotemporal sites, and tends to be larger on the right hemisphere, consistent with the scalp distribution of the N170 to faces and of the perceptual adaptation effects. Critically, adaptor faces cause an *enhancement* of the amplitude of the N170/VPP complex to test faces, the opposite of the direction found with perceptual adaptation, indicating that visual mental imagery and perception

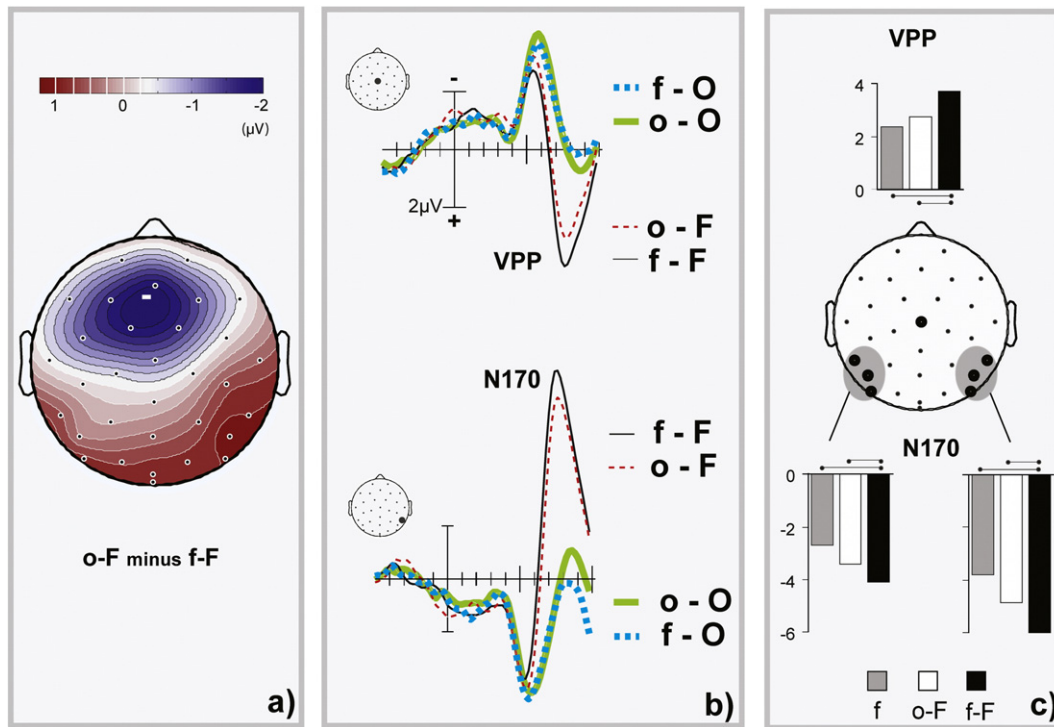


Fig. 7. Imagery adaptation effects to test faces and objects: Enhancement of N170/VPP Amplitude. Grand average ERP results in the imagery conditions referenced to the average of all sites, and plotted negative voltage up. (a) Scalp distribution of the adaptation effect (test faces preceded by adaptor objects, o-F, minus test faces preceded by visualized adaptor faces, f-F) for the imagery conditions. Note that, since visualized adaptor faces enhance the amplitude of the N170/VPP, the sign of the difference between o-F and f-F is reversed, compared to that of Fig. 5. (b) Grand average ERPs between -100 and 200 ms elicited by test faces preceded by visualized face adaptors (f-F, black solid line), by test faces preceded by visualized object adaptors (o-F, red dashed line), by test objects preceded by visualized object adaptors (o-O, green solid line), and by test objects preceded by visualized face adaptors (f-O, cyan dashed line). The N170 data are shown at the bottom (site 18), whereas VPP data (site 28) are shown on top. (c) N170 (bottom, mean of occipitotemporal sites 17, 18, 19, 20, 23, and 24) and VPP (top, site 28) amplitude data for perceived adaptor faces (f, gray bars), for test faces preceded by visualized object adaptors (o-F, white bars), and for test faces preceded by visualized adaptor faces (f-F, black bars). Significant differences are indicated with thin horizontal lines connecting the corresponding bars.

affect similar cortical areas but impact the underlying neural processes in different ways. Although the focus of this study was on faces, a parallel enhancement effect was also found for objects (i.e., a larger N170/VPP complex to test objects following visualized adaptor objects compared to adaptor faces), indicating that this effect generalizes to other object categories. Last, we note that later activity during the N250 and N400 to faces following both visualized and perceived adaptors largely continues the pattern of earlier N170/VPP effects (Figs. 4, 6), suggesting the earlier processing has continuing and analogous implications for the higher cognitive processing later on during the N250 and N400-like components. We will now discuss some of the implications of the N170/VPP findings that address our main aim of determining a possible role for imagery in early perceptual processing.

Visual mental imagery and visual perception

This is the first ERP study using visualized adaptors and directly comparing the effects with those of perceived adaptors. These data provide important evidence on the issue of whether key neural processes supporting visual mental imagery and visual perception rely on qualitatively similar neural mechanisms and on how to reconcile a fundamental dilemma facing image-percept equivalence theories: On the one hand, the strength of these theories is that they assume that visual mental imagery can use the neural machinery available for visual processing; on the other, they need to explain how the brain can easily distinguish between visual percepts and visual mental images. Our data suggest a simple solution. Visual mental imagery of faces does recruit the same general neural populations in the ventral stream that are engaged by early face perception, as shown by the similarity of the estimated neural generators and of the time course of modulation of the N170/VPP complex in the two cases. However, the opposite sign of the adaptation effects indicates that visual mental imagery and visual perception have different effects on these neural populations. This result complements the fMRI findings showing activation in the same temporal and occipitotemporal regions by visual mental imagery and perception of faces (Ishai et al., 2002; Mechelli et al., 2004; O'Craven and Kanwisher, 2000). In the following, we propose that the suppressive effects found with perceived adaptors reflect bottom-up processing pathway influences, whereas the enhancement effects found with visualized adaptors reflect top-down processing pathway influences (see for review, Ganis and Kosslyn, 2007).

Adaptation effects of perceptual suppression and imagery enhancement

Suppressive adaptation effects with short ISIs (a few hundred milliseconds) and without intervening stimuli are usually thought to be due to neural fatigue or to synaptic depression, and to be a form of habituation, which (unlike conditioning) is a type of non-associative memory (Squire and Zola-Morgan, 1991). Short-term suppressive effects with perceived adaptors have been found at many levels in the primate visual system, including in object-sensitive regions (see for reviews, Grill-Spector et al., 2006; Kourtzi and Grill-Spector, 2005). We propose that the suppressive effects brought about by the perceived adaptor faces on test faces reflect one of these neural suppression mechanisms in face-sensitive neural populations (the same idea would apply to the parallel case of other object categories).

To interpret the enhanced adaptation effects obtained with visualized adaptors, it is important to remember that visual mental imagery is thought to involve at least two supporting processes: i) Reactivating neural representations from explicit conscious long-term memory (Squire and Zola-Morgan, 1991), and ii) actively maintaining these representations in order to internally manipulate them in working memory. We propose that the reactivation process from long-term memory corresponds to the neural process described in the work in non-human primates by Tomita et al. (1999) showing that

prefrontal signals reach inferotemporal neurons in order to reactivate long-term visual memories (the representation of a paired associate, in their study) in the absence of the corresponding external stimulus. Once reactivated, these neural representations in inferotemporal cortex are kept alive by working memory processes, which have been studied in non-human primates using variants of the delayed matching-to-sample (DMS) task. In these paradigms, monkeys are shown a sample stimulus, which they must actively maintain in working memory in order to detect a matching stimulus in a subsequent stimulus series (Miller and Desimone, 1994; Miller et al., 1996). The results from these studies showed that, among the inferotemporal neurons showing memory effects, one subset exhibited non-specific suppression effects of the kind just discussed, that is, weaker responses to all repeated stimuli, including those matching the sample stimulus. In contrast, a second subset of inferotemporal neurons showed only enhancement effects, that is, stronger responses to stimuli matching the sample stimulus and no response suppression to stimulus repetition. This enhancement effect is thought to constitute a fundamental mechanism for working memory that is necessary to maintain neural representations actively over time. Although these studies investigated working memory processes used to maintain neural representations initially recruited by a perceived sample stimulus (Miller and Desimone, 1994), we propose that these same enhancement effects occur when maintaining inferotemporal neural representations reactivated by visualized stimuli, such as the ones used in our study. Note that the average size of the adaptation effect found in the visual mental imagery condition is about 1 μ V (Fig. 7), consistent with the size of ERP effects typically observed in visual tasks requiring top-down modulation, such as visual attention (e.g., Hillyard and Anllo-Vento, 1998).

To summarize, we hypothesize that the suppression effects found in our study with perceived adaptors reflect a passive suppression mechanism engaged by the immediate repetition of a visual stimulus at a very short delay. In contrast, the enhancement effects found with visualized adaptors reflect the neural sequelae of memory reactivation and maintenance processes during visual mental imagery. The inferotemporal representations for the visualized adaptor face are initially reactivated, and later maintained, by means of top-down signals, possibly originating in the prefrontal cortex (Miller et al., 1996; Tomita et al., 1999). Consistent with this proposal, using fMRI in humans, it has been found that object-sensitive cortex in ventral posterior cortex and ventrolateral prefrontal cortex are activated during object mental rotation (Schendan and Stern, 2007, 2008), a type of visuospatial mental imagery task, and for short-term maintenance during the delay period of a DMS task with well-studied visual images (Schon et al., 2008). Furthermore, one functional connectivity study using fMRI has reported evidence that prefrontal cortex modulates activation in posterior object- and face-sensitive regions during visual mental imagery (Mechelli et al., 2004).

Potential role of selective attention?

Enhancement effects in occipitotemporal cortex are found not only during working memory tasks, but also during selective attention tasks, when comparing neural activation to attended versus non-attended whole stimuli or stimulus features (e.g., Hillyard and Anllo-Vento, 1998). Thus, it is important to discuss the potential relationship between visual mental imagery and visual selective attention, defined here as a preparatory state to perceive an external stimulus (e.g., Neisser, 1976). A conceptual distinction between this definition of visual selective attention and visual mental imagery is that the main function of the former (attention) is to detect relevant information in the external world, whereas the main function of the latter (imagery) is to enable the manipulation of internal representations. Although it is not easy to disentangle empirically the effects of visual imagery and attention, there is good reason to believe that our enhancement effects

cannot be explained solely in terms of known mechanisms of visual selective attention. First, in order to minimize the preparatory aspects of the task, subjects were not asked to perform a detection or categorization task on the test stimuli. In fact, subjects were not performing any explicit tasks at all on the test stimuli, other than refraining from blinking and from moving their eyes. This is important because visual attention and visual imagery may be conflated by asking subjects to detect near-threshold, pre-specified target stimuli (e.g., Farah et al., 1988). Note that, if anything, the lack of a task on the test stimuli worked against our chances of finding any effects: The fact that reliable ERP effects were found shows that subjects were performing the tasks as instructed. In addition, the average time it took subjects to generate a vivid visual mental image (about 3.4 s) is consistent with image generation times for familiar visual stimuli found in other studies (e.g., D'Angiulli and Reeves, 2002). Second, the duration and contrast of the stimuli were well above the subject's perceptual thresholds and so using selective attention would hold little or no advantages. Third, as for the perceptual adaptation case, the visualized adaptor category had no value for predicting the category of the test stimuli: 50% of the time the test stimulus matched the visualized adaptor, and 50% of the time it did not. Therefore, there was no advantage to using the adapting phase to prepare for a specific test category. Fourth, the N170/VPP enhancement effect differs from the typical selection negativity (e.g., Hillyard and Anllo-Vento, 1998), a negativity starting around 150 ms that is larger for attended than non-attended visual ("non-spatial") attributes, such as color or shape. Although a direct comparison between visual attention and visual mental imagery of faces has not been conducted, the selection negativity has a clear occipitotemporal distribution with an *average mastoid reference* (e.g., Anllo-Vento and Hillyard, 1996; Anllo-Vento et al., 1998; Hillyard and Anllo-Vento, 1998). In contrast, in our study, when we re-referenced the ERPs to an average mastoid reference, ERP modulations due to visual mental imagery were not found at the occipitotemporal sites known to show a selection negativity (e.g., sites 18 and 24). Fifth, no reliable adaptor category effects were observed on the P1 component, usually found in spatial selection studies, suggesting that the N170/VPP modulations were not consequences of early effects of spatial attention.

Note that we are not claiming that selective attention played no role in the results, only that it was not the sole factor, as our analyses show. In fact, the N170/VPP to test faces tended to be enhanced also by adaptor objects (compared to faces not preceded by any adaptors), suggesting that imagined adaptor stimuli had not only a shape-specific, but also a marginal, non-specific enhancing role on the N170/VPP to test faces. This non-specific role may well be an attentional effect, consistent with fMRI findings of some non-specific top-down modulations of posterior visual cortex (Mechelli et al., 2004), but notably, it did not reach significance.

Potential confounds and limitations

One could argue that, at least part of the differences between the perceptual and imagery conditions may be due to the differential time subjects spent on the adaptors in the two cases, since this was a self-paced paradigm. On average, subjects spent more time on the imagery adaptor phase than on the perceptual adaptor phase. This difference was anticipated, since it is well-known that it takes a few seconds to generate a vivid visual image (e.g., D'Angiulli and Reeves, 2002, 2007). However, the timing difference between the two conditions is only apparent because most of the time spent on the adaptor phase when the name cue was presented in the visual mental imagery condition was used for the process of *generating* a vivid visual image. Since subjects were instructed to press the ready key as soon as they had generated such a vivid image, the actual time spent on actively experiencing the adaptors in the two conditions just prior to key press was comparable, by design. To further address this potential issue, we

correlated the amplitude of the N170 to test faces (at occipitotemporal site 18) preceded by adaptor faces with the time spent during the adaptor phase, separately for visual imagery and perception, over subjects. If spending more time on the adaptor results in a larger N170 modulation, then there should be a significant positive correlation. The analysis showed that there was virtually no correlation between the time spent on the adaptor and N170 modulation ($r=0.2$ and $r=.17$, for visual imagery and perception, respectively, $p>.4$).

One could also argue that trials where adaptation was expected (f-F and o-O) are also those in which there was a "match" between the adaptor and test stimuli; thus, the N170/VPP enhancement in the imagery conditions may reflect simply an adaptor-test stimulus "match" effect, even if the subjects were not performing an explicit matching task. It is unlikely that this factor can explain the full pattern of N170/VPP results for two reasons: First, f-F trials were "matches" in both the perception and imagery conditions (by identity and/or category), yet they led to opposite effects. Second, studies of face repetition with delays between the onset of adaptor and test stimuli comparable to those used in our visual mental imagery condition (1 s or longer) show adaptation effects only after about 200 ms post-stimulus, even when subjects perform explicit matching tasks (Bentin and McCarthy, 1994; Trenner et al., 2004); in our imagery condition, there wasn't even a picture of a face during the adaptor phase, only a word, presented seconds before the test stimulus, making it even more unlikely that a "match" factor can explain modulations in the N170/VPP window.

Finally, two limitations of this study are important for future work, although not directly relevant to the main goal of this study. First, the use of a small set of well-practiced photographs for the imagery condition, which is standard for imagery research to ensure vivid visualization, leaves open the possibility that the effects might differ for more ecological or everyday types of visual imagery from long-term memory (e.g., visualizing the face of a celebrity from memory without experimental exposure to specific photographs of the celebrity). Second, this study does not pinpoint the exact representations affected by adaptation (see for discussion, Fox and Barton, 2007). Since this was the first attempt to determine the effect of visualized adaptors on test stimuli, an extreme comparison was used to maximize the chance of observing any effect at all: Faces were overlearned, and each was preceded by visualization of the same face image versus visualization of an object. This comparison leaves open important questions about the representational level of these adaptation effects: Do the effects require visualizing exactly the same face image? Can they be elicited also by visualizing other pictures of the same celebrity, or even by visualizing any face (e.g., Schweinberger et al., 2007)? Future work will need to address these issues, as well as other important issues such as the relationship between adaptation and repetition priming (Huber, 2008).

Summary and conclusions

This is the first ERP study to compare the effect of visualized and perceived adaptors on the early cortical processing of faces. An adaptation paradigm was used to probe the effect of perceived and visualized faces and objects on face-sensitive neural populations. The first finding is that both visualized and perceived adaptors have an effect on the N170/VPP complex elicited by test faces. This effect onsets at 120 ms post-stimulus, indicating that both visual perception and visual mental imagery affect neural populations involved in the early perceptual processing of faces, and at the same time as perceptual categorization effects occur for faces. This result is important because techniques based on hemodynamic signals cannot conclusively determine that effects of visual mental imagery evident in perceptual processing areas actually reflect early perceptual processes, as opposed to later processes, also taking place in these same cortical areas. The second finding is that the effects of visualized

and perceived adaptors have opposite signs: N170/VPP enhancement for imagery but suppression for perception. This result suggests that perceived adaptors influence neural populations that support early perceptual processing of faces by means of bottom-up mechanisms, whereas visualized adaptors influence these neural populations via top-down mechanisms. Although this work focused on test faces, a similar enhancement effect by visual mental imagery was also found for test objects, suggesting that this phenomenon is not unique to faces. Finally, these findings provide a potential explanation for why the brain does not routinely confuse visual percepts and visual mental images, even though both engage similar neural populations in the visual system.

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