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Abstract: The aim of this study was to determine the extent to which the N170 event-related potential (ERP) is selective for processing faces. Although the N170 potential is greatest to images of faces, significant responses above baseline are also found to other object categories. Using an adaptation paradigm, we investigated the significance of the responses to faces and non-face objects. We compared ERP responses to repeated presentations of the same image or to the presentation of different images from a variety of object categories: (faces, inanimate objects, and places). We found a reduced N170 potential to repeated presentations of the same face image compared to different images of faces. This reduction in response was invariant to changes in the size of the stimulus, but was sensitive to changes in the viewpoint. In contrast, we found no adaptation to images of inanimate objects or places. These results suggest that the

N170 potential reflects face-specific neuronal activity and is not involved in the representation of inanimate objects or places.

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The Editor
Neuroimage

8 July, 2005

Dear Sir or Madam:

I would be grateful if you would consider our manuscript (ADAPTATION OF THE N170 POTENTIAL TO IMAGES OF FACES, BUT NOT TO INANIMATE OBJECTS OR PLACES) for publication in Neuroimage.

The paper addresses whether the N170 evoked potential is specific for faces or is involved in the processing of categories of object. Using an adaptation paradigm, we found that the N170 potential reflects face-specific neuronal activity and is not involved in the representation of inanimate objects or places.

Referees who would be qualified to review this work include:

Professor Shlomo Bentin (msbentin@mscc.huji.ac.il)
Professor Greg McCarthy (gregory.mccarthy@duke.edu)
Dr Bruno Rossion (Bruno_Rossion@brown.edu)

Yours sincerely,

Tim Andrews

ADAPTATION OF THE N170 POTENTIAL TO IMAGES OF FACES, BUT NOT TO INANIMATE OBJECTS OR PLACES

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ABSTRACT

The aim of this study was to determine the extent to which the N170 event-related potential (ERP) is selective for processing faces. Although the N170 potential is greatest to images of faces, significant responses above baseline are also found to other object categories. Using an adaptation paradigm, we investigated the significance of the responses to faces and non-face objects. We compared ERP responses to repeated presentations of the same image or to the presentation of different images from a variety of object categories: (faces, inanimate objects, and places). We found a reduced N170 potential to repeated presentations of the same face image compared to different images of faces. This reduction in response was invariant to changes in the size of the stimulus, but was sensitive to changes in the viewpoint. In contrast, we found no adaptation to images of inanimate objects or places. These results suggest that the N170 potential reflects face-specific neuronal activity and is not involved in the representation of inanimate objects or places.

INTRODUCTION

The perception and recognition of faces is a function of the ventral processing stream that projects toward the temporal lobe (Ungerleider and Mishkin, 1982; Milner and Goodale, 1995). Lesions to this region can result in perceptual deficits, such as prosopagnosia, where patients are unable to recognise and identify faces (McNeil and Warrington, 1993). Functional imaging studies have shown regions of ventral temporal cortex that are selectively activated during face processing. A region in the lateral part of the fusiform gyrus, known as the fusiform face area (FFA) (Kanwisher et al., 1997) or area pFs/LOa (Avidan et al., 2002; Grill-Spector et al., 1999) has consistently been implicated in face perception. Face selective activity has also been found on the lateral surface of the occipital lobe; a region variously termed the occipital face area (OFA) (Gauthier et al., 2000), or inferior occipital gyrus (Hoffman & Haxby, 2000). While a region in the superior temporal sulcus (STS) has been implicated in the perception of changeable aspects of faces, such as expression, eye gaze and speech related mouth movements (Hoffman and Haxby, 2000).

Event related potential (ERP) studies have also shown that faces can be distinguished by the pattern of electrical activity in regions of the occipitotemporal lobe (Allison et al. 1999). In particular, an early negative component, peaking between 140 and 200ms after stimulus onset, known as the N170, has consistently been found to be greater to faces than to other complex objects (Bentin et al., 1996, Eimer, 2000). The idea that the N170 potential is involved in face processing is also shown by studies of face-inversion, in which recognition is greatly impaired for inverted faces, but not other object categories, (Yin, 1969). ERP studies have shown that the latency and amplitude of the N170 for faces, but not objects, is affected by inverting the image (Rossion et al. 2000). Behavioural data shows that priming improves face recognition (Bruce et al., 1994). Such priming effects are also observed in ERP studies, with the N170 potential showing a reduction in amplitude following repeated presentations of the same face compared to different faces (Campanella et al., 2002; Itier & Taylor, 2004a). The idea that the N170 is related to processing faces is also supported in studies of prosopagnosia in which patients fail to demonstrate an enhanced N170 when viewing face stimuli (Eimer & McCarthy, 1999).

The neural source of the N170 potential remains unclear. The N170 is often found to be maximal in the right hemisphere (Bentin et al., 1996), consistent with both functional imaging and brain lesion studies (Kanwisher et al., 1997; McNeil and Warrington, 1993). Dipole localization studies have suggested that a region of the inferior temporal lobe, possibly corresponding to FFA, is the source of the potential (Itier & Taylor, 2002). However, other studies report that the N170 originates in the face-selective STS region (Itier & Taylor, 2004b). It is has also been suggested that the OFA might be the source of the N170 potential (Schweinberger et al., 2002a), although other evidence suggests that this region may generate an earlier face-selective potential with a latency of approximately 100 msec. (Liu et al, 2002).

The contribution of non-face selective regions to the N170 potential is similarly unresolved. Imaging studies have shown that regions in the occipitotemporal lobe are selectively activated by inanimate objects (Grill-Spector et al., 1998), places (Epstein and Kanwisher, 1998) and human body parts (Downing et al., 2001). Indeed, while the N170 potential is maximal to face stimuli, significant responses above baseline occur to non-face objects such as cars, houses and dogs (Eimer, 2000; Rossion et al., 2000).

The aim of the current study is to use adaptation to determine whether the N170 potential is selective for faces or whether it reflects the activity of neurons that are selective for other categories of object. Some ERP studies have found adaptation to faces (Campanella et al. 2002; Itier & Taylor, 2004a) with a decrease in the magnitude of the N170 potential, whereas other studies have failed to find any effect of repetition (Eimer, 2000; Schweinberger et al., 2002b). It is also uncertain whether adaptation of the N170 is sensitive to lower-level changes in the stimulus. Finally, it is not clear whether this potential will show an adaptation response to repeated images of other object categories. To answer these questions we measured the N170 potential during repeated presentations of the same or different images from different categories of object: faces, inanimate objects and places.

METHODS

Event-related potentials

Eighteen subjects (9 females) ranging from 20 and 54 years (mean age = 30.3 years) participated in the study. All observers had normal or corrected-to-normal visual acuity. Sixteen subjects were right-handed. ERPs were recorded from 32 electrodes mounted in an electrode cap (Quik-Cap). Electrodes were placed according to the standard international 10-20 system, referenced to left and right mastoid. To correct for eye blinks and non-stimulus related eye-movements, three ocular electrodes were used to monitor vertical and horizontal eye movement potentials. Impedances were kept below 5kΩ. Continuous EEG was recorded using Neuroscan 4.3 and amplified using a SymAmps system, with a gain of 500. Data were recorded with a sampling rate of 1000Hz through a band pass filter of 0.1-100Hz. Epochs were defined as the period 100ms prior to the stimulus and continuing for 500 ms after stimulus onset. ERPs were averaged according to stimulus type for each subject. Baseline correction was performed relative to a 100ms pre-stimulus baseline. Averages were then digitally filtered (0.1-30Hz).

Localiser scan

In order to identify electrodes that responded preferentially to images of faces, subjects viewed greyscale images from different object categories: (1) faces; (2) inanimate objects; (3) places (buildings, indoor and natural landscapes) and (4) textures. Photographs of faces were taken from a database of the Psychological Image Collection at Stirling (PICS: http://www.pics.psych.stir.ac.uk) and were unfamiliar to all subjects. Images of inanimate objects, places and textures were obtained from various sources including commercial clip-art collections (CorelDraw, Microsoft).

Each stimulus block contained 20 images. Each image was presented for a period of 300ms, and was followed by a blank screen containing a fixation cross for 1500ms. In each stimulus block, five images from each object category were randomly interleaved. A total of eight stimulus blocks were presented. A resting period was inserted in between each block, during which an equiluminant grey screen was presented for 10 seconds. Subjects were required to perform a one-back matching task to identify when two identical images were consecutively repeated.

Electrodes showing the largest face-selective response in each hemisphere were identified individually for each subject. The mean latency of the N170 response was obtained from an average of all subjects, the peak N170 amplitude for each subject was then taken within a $\pm$ 30 ms window centred on this mean latency. Repeated measures ANOVA was used to measure the significance of responses in each stimulus condition. Analysis of the adaptation response to different object categories was then restricted to these face-selective electrodes.

Adaptation scan

First, we determined whether the N170 potential would show a reduced response (adaptation), to repeated presentations of the same face image. Stimulus blocks contained 20 repetitions of the same face image or 20 different face images. Each image was presented for 300ms followed by a 1500ms blank screen containing a fixation cross. To determine whether adaptation to faces was size invariant, the dimensions of the face images were varied in some stimulus blocks ($3x3^o$, $6x6^o$ and $9x9^o$). We also asked whether the response to faces was view invariant by varying the direction of gaze and emotional expression of the images. Changes in gaze direction included frontal, 3/4 and side profiles, and the faces could convey a happy emotion or speech. Stimulus blocks were separated by periods of fixation when an equiluminant grey screen was presented for 10 seconds. Subjects were instructed to perform a contrast detection task using a response box, with two face images in each block being presented at a reduced contrast (25%). Each stimulus condition was repeated twice in a counterbalanced block-design, making a total of 12 stimulus blocks.

Finally, we determined whether the N170 peak would adapt to repeated images of inanimate objects and places. Images of inanimate objects and places were obtained using 3D design software (Strata 3D: http://www.strata.com). Exemplars of inanimate objects and places were balanced across all *same* image and *different* image conditions. In this way, we were able to control for any change in response that may be due to differences in object features or semantic attributes.

The peak N170 amplitude for each subject was taken within a ± 30 ms window centred on the average N170 latency. A multi-factorial ANOVA was used to determine the main effects of identity (same, different), category (face, inanimate object, place) and hemisphere (left, right). To assess whether the reduction in the N170 amplitude was statistically significant for particular categories in different conditions, we performed a two-sample t-test on the peak amplitudes across subjects. Finally, we calculated an adaptation index (AI) to quantify the reduction in the N170 amplitude during the same image blocks compared to different image blocks: AI = Response[same] / Response[different]. This ratio was used to give an indication of the effect of adaptation, but was not used in the analysis.

RESULTS

Localiser scan

First, we determined which electrodes showed selective responses to images of faces. Face-selective responses were found on electrodes P4 or P8 in the right hemisphere, and P7 in the left hemisphere (Fig. 1). Faces evoked a significantly greater response than inanimate objects (RH: $F = 32.41$, $P < 0.001$; LH: $F = 33.39$, $P < 0.0001$); places (RH: $F = 22.43$, $P < 0.001$; LH: $F = 50.73$, $P < 0.0001$) and textures (RH: $F = 48.37$, $P < 0.0001$; LH: $F = 35.93$, $P < 0.0001$). The mean latency of the face-selective N170 was 172 ± 2.6 ms in right hemisphere and 164 ± 3.5 ms in left hemisphere.

However, activation in these electrodes was not restricted to images of faces, as significant responses above baseline were also observed to images of inanimate objects (RH: $F = 10.09$, $P < 10e\text{-}5$; LH: $F = 4.04$, $P < 0.01$); places (RH: $F = 13.42$, $P < 10e\text{-}6$; LH: $F = 6.56$, $P < 0.01$) and textures (RH: $F = 8.61$, $P < 0.001$; LH: $F = 6.94$, $P < 0.001$). Behavioural data indicated that subjects were performing the one-back matching task successfully during the localiser experiment (90.5 ± 3.6 % correct).

[Figure 1 near here]

Adaptation scan

A 3-factor ANOVA 2x2x3 (Identity, Hemisphere, Category) revealed a significant effect of category ($F = 5.73$, $P < 0.05$). Although there was no main effect of identity ($P = 0.58$) or hemisphere ($P = 0.24$), there was a significant interaction between identity and hemisphere ($F = 69.91$, $P < 0.01$). This implies that there are differences in levels of adaptation between hemispheres.

[Figure 2 near here]

Next, we compared responses in face-selective electrodes during the presentation of the same face or different faces (Fig. 2). Our prediction was that face-selective electrodes would show a reduced response to images of the same face compared to different faces. We found that the peak N170 response to the same face was significantly lower than the response to different faces in face-selective electrodes in the right hemisphere (AI = 0.7 ± 0.31; $t(12) = 2.41$, $P < 0.05$), but not in the left hemisphere ($t(12) = -0.05$, $P = 0.96$). There was no difference in the latency of the N170 response between conditions in either the left ($t(12) = 0.62$, $P = 0.54$) or right hemisphere ($t(12) = -0.24$, $P = 0.81$).

[Figure 3 near here]

To determine whether adaptation to faces was sensitive to changes in low-level features, we varied the size of the face images (Fig 3). The results revealed a significantly reduced response to images of the same face shown at different sizes compared to different faces shown at different sizes, in the right hemisphere (AI = 0.62 ± 0.25; $t(12) = 2.3$, $P < 0.05$), but not in the left hemisphere ($t(12) =0.25$, $P = 0.80$). No latency differences were found in the right hemisphere ($t(12) = -0.5$, $P = 0.63$), however there was a small but significant latency difference in the left hemisphere (different - same = 4 ± 1.3 msec; $t(12) = 2.39$, $P < 0.05$). To determine the extent of size-invariance in the right hemisphere, we performed a 2-way ANOVA (*same-identity same-size, different-identity same-size* x s*ame-identity vary-size, different-identity vary-size*). The results revealed a significant effect for identity (F =

9.5, $P < 0.01$), but not for size ($F = 1.12$, $P = 0.31$); there was also no interaction between size and identity ($F = 0.06$, $P = 0.82$).

[Figure 4 near here]

We then determined whether this adaptation was invariant to changes in viewpoint and expression of the face (Fig 4). The results revealed no reduction in the N170 response to the same face shown at different viewpoints compared to different faces shown at different viewpoints (RH: $t(12) = -1.5$, $P = 0.14$; LH: ($t(12) = -1.42$, $P = 0.17$). The latency of the N170 did not differ between conditions (RH: $t(12) = -1.6$, $P = 0.12$; LH: $t(12) = -1.54$, $P = 0.15$).

[Figures 5 and 6 near here]

Finally, we investigated the N170 response to the presentation of images of inanimate objects (Fig. 5) and places (Fig. 6). We predicted that if the N170 response to inanimate objects and places represented the activity of non face-selective neurons, then the peak N170 should show a reduction in amplitude to presentations of the same image compared to different images. We found no reduction in response to presentations of the same object compared to different objects, (RH: $t(12) = 0.6$, $P = 0.55$; LH: $t(12) = -0.36$, $P = 0.72$), or to images of the same place compared to different places (RH: $t(12) = -1.39$, $P = 0.18$; LH: $t(12) = -.63$, $P = 0.53$). No difference in the latency of the N170 between the *same* and *different* conditions was found in either the object experiment (RH: $t(12) = -0.65$, $P = 0.53$; LH: $t(12) = 1.96$, $P = 0.07$) or place experiment (RH: $t(12) = -0.6$, $P = 0.55$; LH: $t(12) = 1.1$, $P =0.29$).

Behavioural results indicated that subjects were performing the contrast detection task successfully during each adaptation scan, faces: (92.8 ± 2.1 % correct); inanimate objects: (95.1 ± 1.7 % correct); places: (96.6 ± 0.9 % correct).

DISCUSSION

The aim of this study was to determine whether the N170 event-related-potential reflects face-specific neural activity or also contributes to the perception of other object categories. We addressed this issue by investigating whether face-selective potentials would show a significant reduction in amplitude (adaptation) following the repeated presentation of different categories of object: (faces, inanimate objects and places). We report that the N170 potential shows adaptation to faces, but not other object categories, and that this adaptation is invariant to changes in the size of the image, but not to changes in viewpoint.

Consistent with previous studies, we located electrodes in occipitotemporal regions that showed a face-selective potential, peaking approximately 170 ms after stimulus onset (Bentin et al. 1996, George et al., 1996). We found adaptation to the repeated presentation of the same face in face-selective electrodes in the right-hemisphere, but not in the left hemisphere. A right-hemisphere bias is consistent with functional imaging studies, which have shown stronger face-selective activity occurring in right hemisphere regions (Kanwisher et al. 1997). Studies presenting faces to different visual fields have also revealed a right hemisphere advantage in face processing (Hillger & Koenig, 1991). The finding of adaptation is consistent with previous ERP studies revealing repetition effects for unfamiliar faces in the right hemisphere (Campanella et al., 2000), but contrasts with other studies that failed to find adaptation to identical faces (Eimer, 2000; Schweinberger et al. 2002b). By varying low-level attributes, we also revealed that adaptation to faces was invariant to changes in the size of the face image. This suggests that the N170 reflects the neural representation of facial identity, and not simply an early structural encoding stage. The reason for the lack of N170 adaptation in previous studies may be due to the number of intervening stimuli or the number of repetitions. For example, early face-selective potentials have been found to show greatest adaptation effects after short delays or numerous image repetitions (Guillaume & Tiberghien, 2001; Itier & Taylor, 2004a).

We failed to find adaptation when the same face was shown from different viewpoints. This result is consistent with previous fMR-adaptation studies (Grill-Spector et al., 1999; Andrews & Ewbank, 2004) and concurs with single-unit studies that have shown the majority of face-selective neurons in monkey inferior-temporal cortex are relatively invariant to changes in the size of the stimulus, but are sensitive to changes in viewpoint (Rolls & Baylis, 1986; Perrett et al., 1985). Behavioural evidence shows that recognition performance for faces falls off with increasing angle of rotation from a familiar view, implying that face-selective neurons are tuned to specific viewing angles (Hill et al., 1997; Fang & He, 2005). However, our ability to recognise individual faces, despite changes in viewing angle and expression, suggests that the neural representation of faces retains some degree of viewpoint-invariance. In this study, we employed large changes in viewpoint, and used faces that were unfamiliar to subjects. It is possible that viewpoint-invariant adaptation may be found when using smaller changes in viewing angle, or when presenting familiar faces.

In a previous fMR-adaptation study (Andrews & Ewbank, 2004), we reported size-, but not viewpoint-invariant adaptation to faces in the face-selective FFA and OFA. In contrast, the STS face-selective region did not show adaptation to faces (Andrews & Ewbank, 2004). Because we find adaptation to faces in the N170 potential, we suggest that the FFA or OFA, rather than the STS face-selective region, are the likely source of the N170 potential.

We also investigated the N170 response to repeated images of objects or places. We found no adaptation of the N170 potential during the presentation of identical object images compared to different object images, or identical place images compared to different place images. This finding is consistent with previous MEG studies showing that the M170 response is not correlated with successful identification of either images of houses (Liu et al., 2002) or cars (Xu, et al., 2005). In a recent study, we reported fMR-adaptation to inanimate objects within FFA (Ewbank et al., 2005). A possible reason for the discrepancy between the N170 and the fMR responses in the FFA could simply be that the N170 reflects the activity of a wider network of visual areas. For example, although OFA shows face-selective adaptation (Andrews and Ewbank, 2004), we failed to find adaptation to inanimate objects within this region (Ewbank et al., 2005).

In conclusion, these findings support the theory that the N170 reflects a face-specific neural response (Bentin et al., 1996, Rossion et al., 2000, Itier & Taylor, 2004a). Furthermore, this representation appears invariant to changes in the size, but not the viewpoint of the face, suggesting that the N170 potential represents an early stage in the perceptual representation of facial identity. This finding largely correlates with MR activity observed in the FFA, however other face-selective regions may also contribute. The N170 potential also failed to adapt to repeated images of identical inanimate objects or places, suggesting that the N170 does not reflect neural activity involved in the representation of either of these categories.

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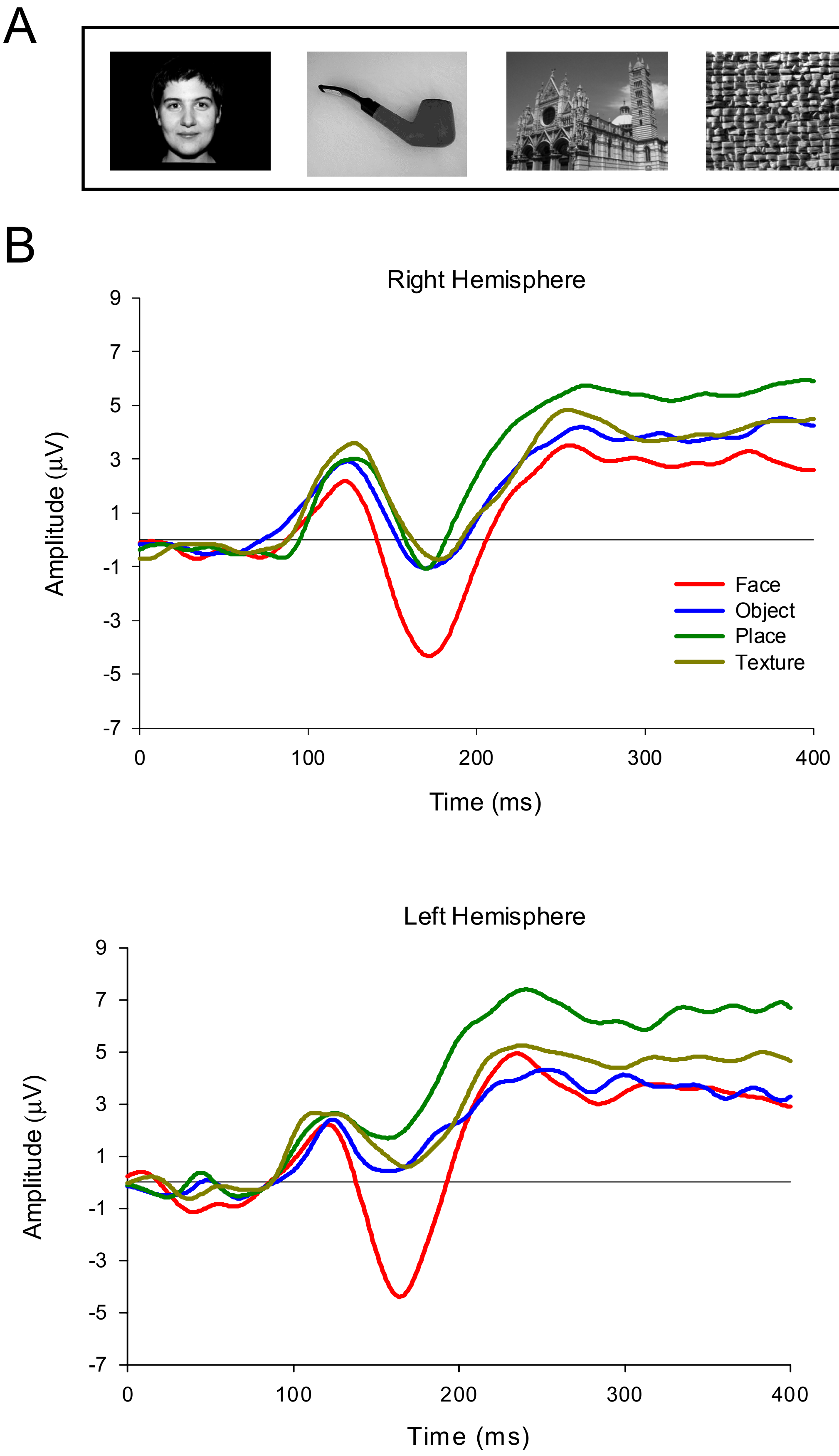
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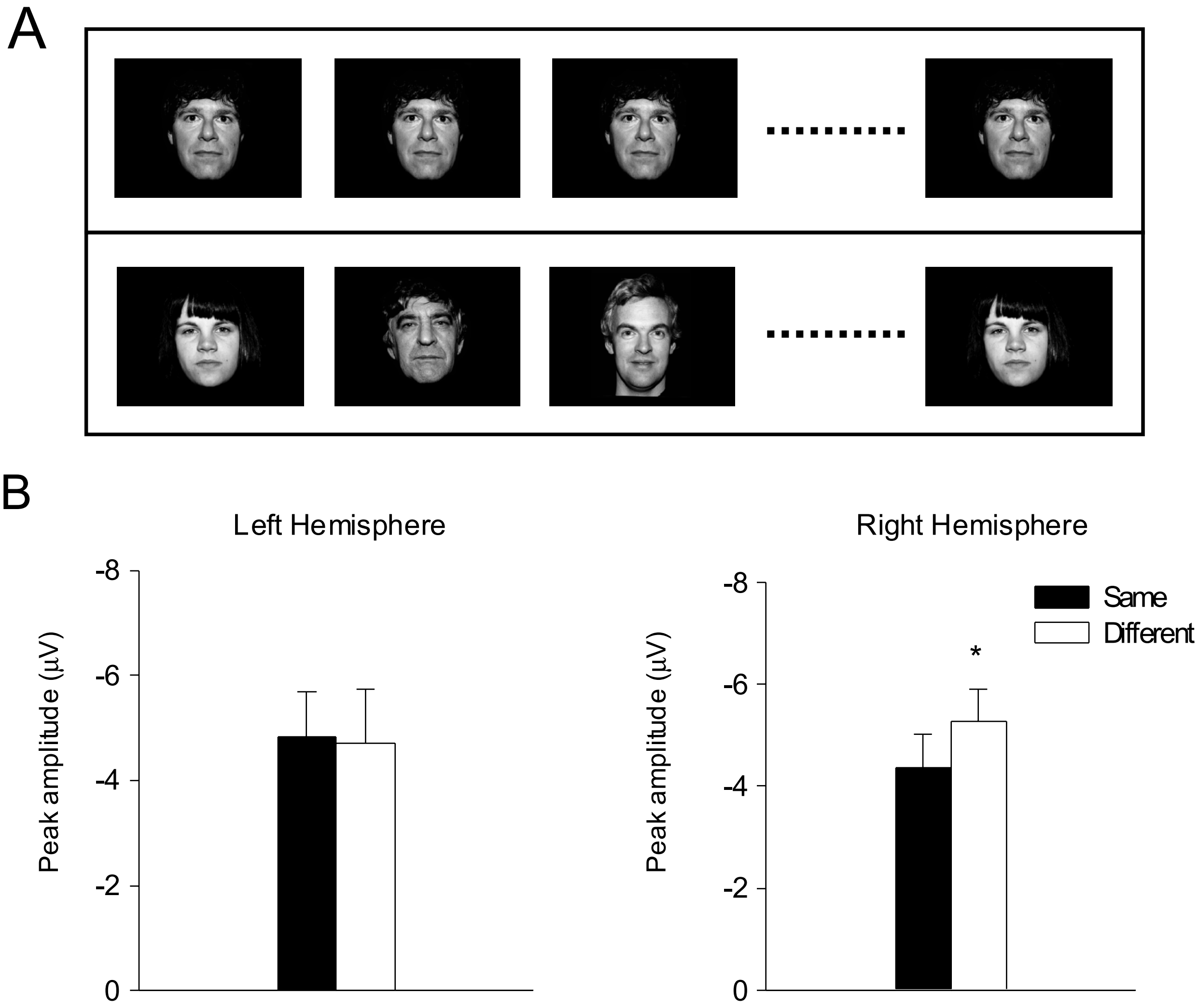
Figure 1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-4
-2
0
Same
Different
*

Figure 2

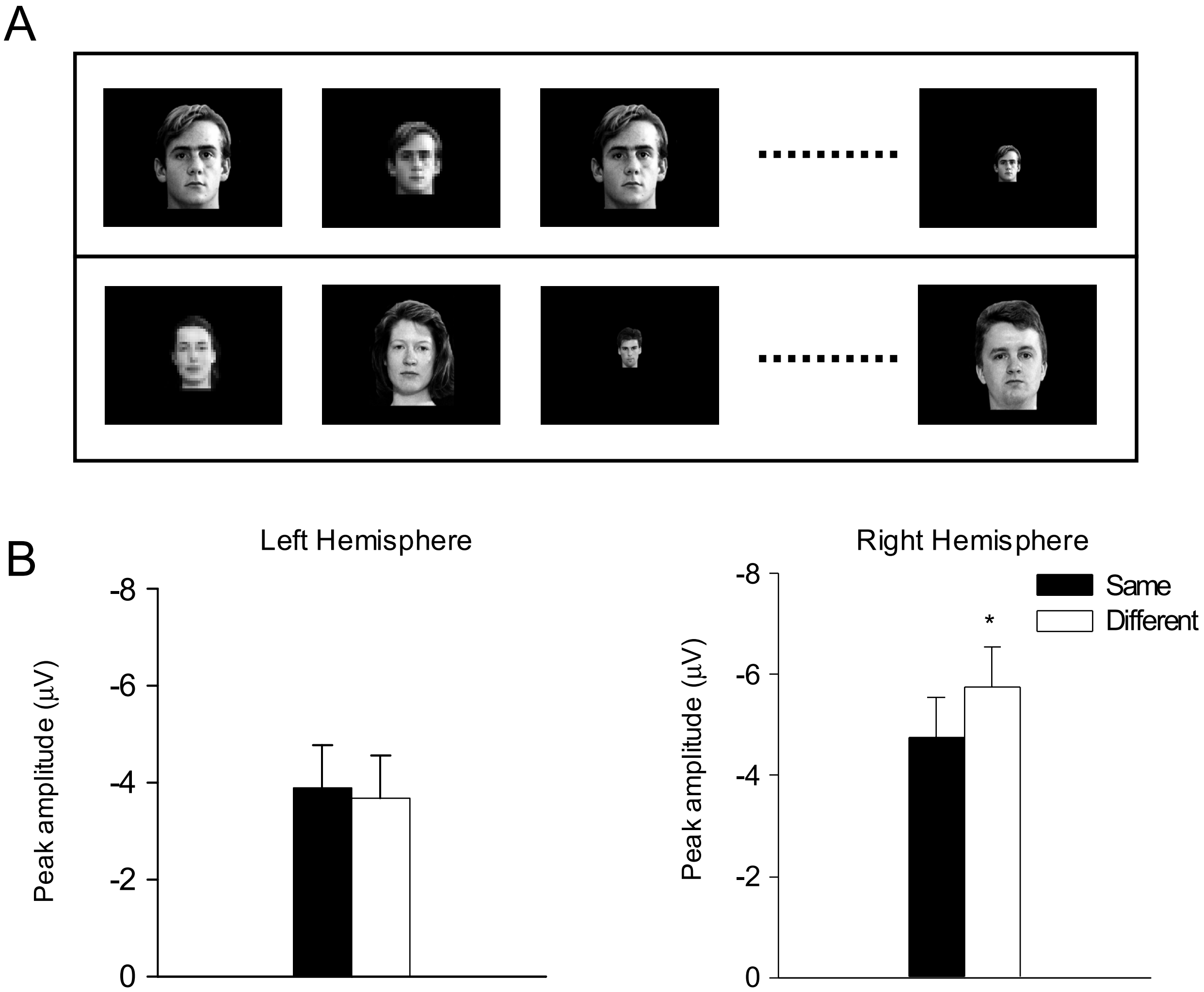

A
B
Left Hemisphere
Right Hemisphere
Peak amplitude (µV)
-8
-6
-4
-2
0
Same
Different
*

Figure 3

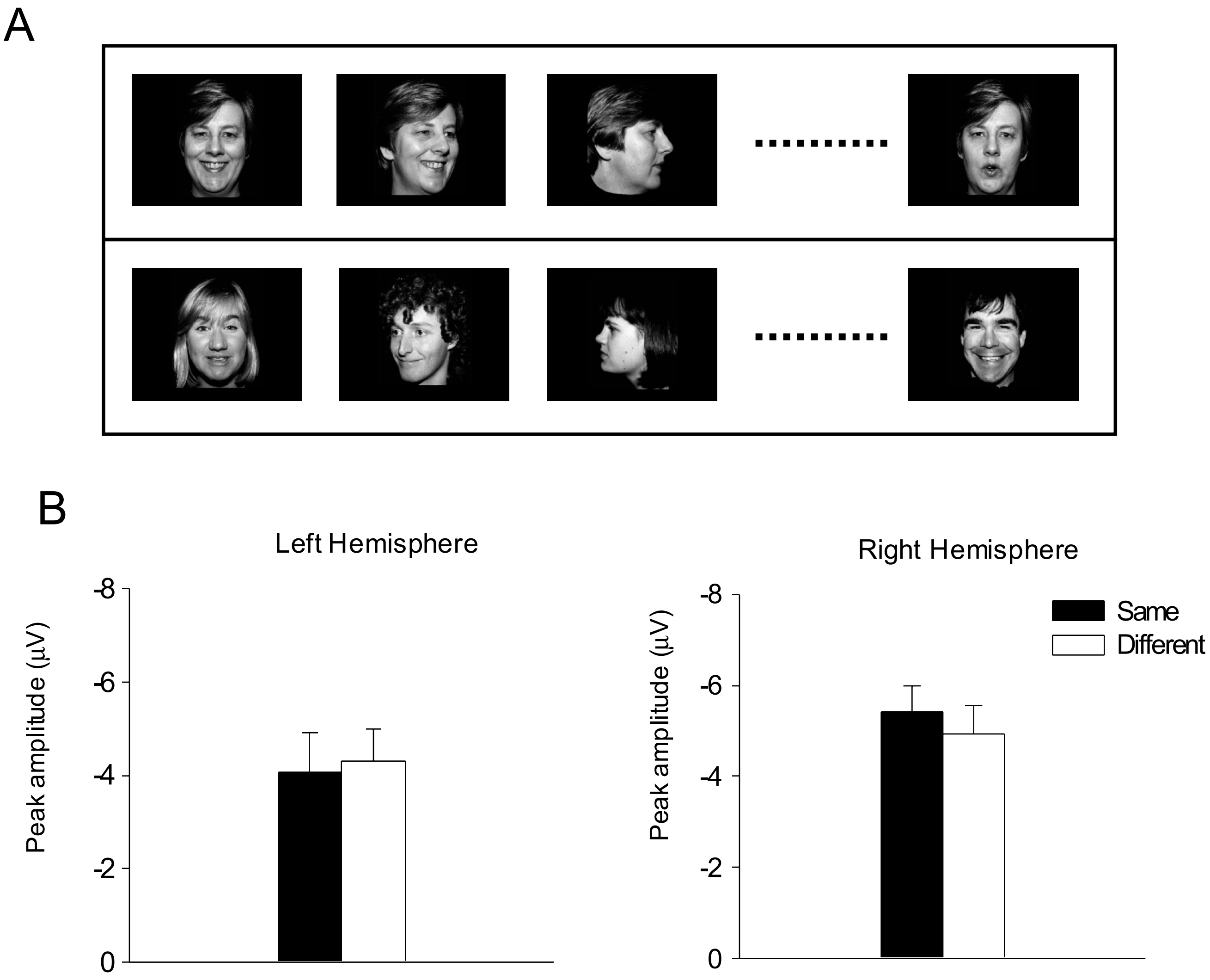
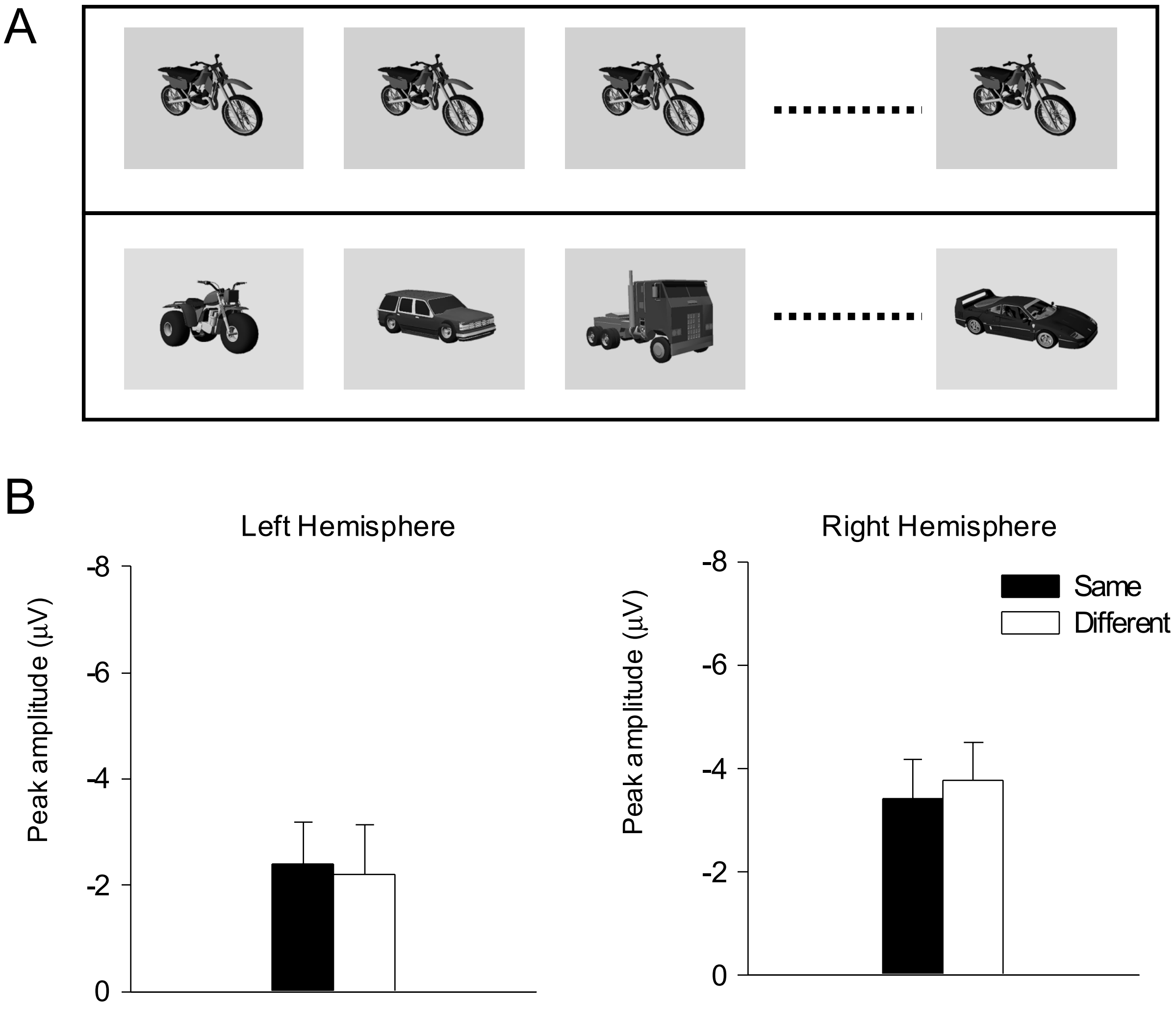

A
B
Left Hemisphere
Right Hemisphere
Peak amplitude (μV)
-8
-6
-4
-2
0
Same
Different

Figure 4


A
B
Left Hemisphere
Right Hemisphere
Peak amplitude (μV)
-8
-6
-4
-2
0
Same
Different

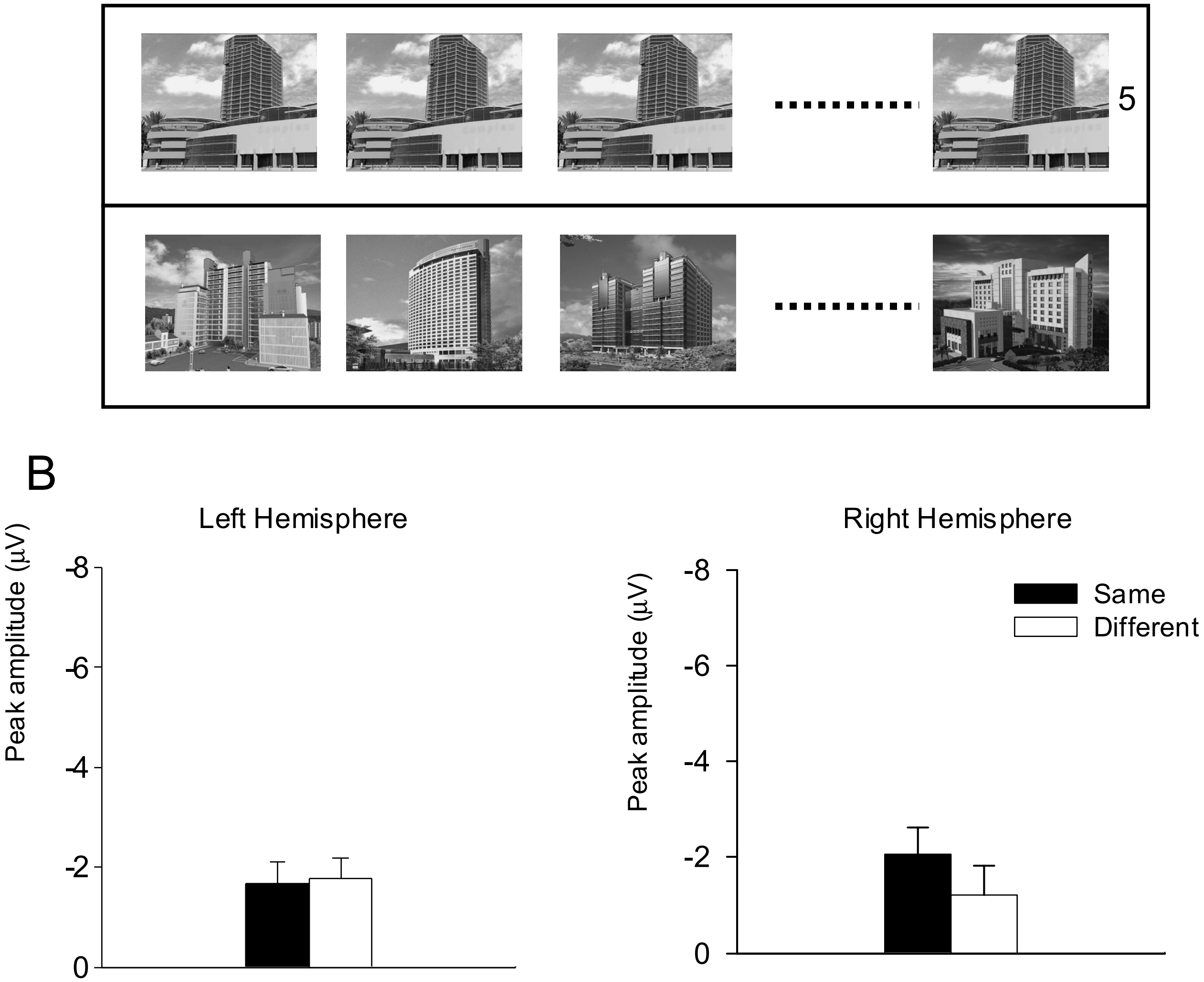

5
B
Left Hemisphere
Peak amplitude (µV)
-8
-6
-4
-2
0
Right Hemisphere
Peak amplitude (µV)
-8
-6
-4
-2
0
Same
Different

Figure 6

Fig. 1. Localiser experiment. (A) Examples of images from each of the four categories used in the localiser experiment: Faces, Inanimate objects, Places, Textures. (B) Average ERP waveforms recorded for each category during the localiser experiment. Waveforms for face-selective electrodes are shown in right and left hemispheres across subjects. Face-selective electrodes were defined as those electrodes demonstrating the largest N170 potential elicited by faces in comparison to other stimuli.

Fig. 2. Face adaptation experiment. (A) Examples of images from the *same-face* (top) and *different-face* (bottom) conditions. (B) Bar graphs representing the average peak N170 amplitude in both left and right hemispheres across subjects. Error bars represent ± 1 standard error. * $P < 0.05$.

Fig 3. Face-size adaptation experiment. (A) Examples of images from the *same-face vary-size* (top) and *different-face vary-size* (bottom) conditions. (B) Bar graphs representing the average peak N170 amplitude in both left and right hemispheres across subjects. Error bars represent ± 1 standard error. * $P < 0.05$.

Fig 4. Face-viewpoint adaptation experiment. (A) Examples of images from the *same-face vary-viewpoint* (top) and *different-face vary-viewpoint* (bottom) conditions. (B) Bar graphs representing the average peak N170 amplitude in both left and right hemispheres across subjects. Error bars represent ± 1 standard error.

Fig 5. Object adaptation experiment. (A) Examples of images from the *same-object* (top) and *different-object* (bottom) conditions. (B) Bar graphs representing the average peak N170 amplitude in both left and right hemispheres across subjects. Error bars represent ± 1 standard error.

Fig 6. Place adaptation experiment. (A) Examples of images from the *same-place* (top) and *different-place* (bottom) conditions. (B) Bar graphs representing the average peak N170 amplitude in both left and right hemispheres across subjects. Error bars represent + 1 standard error.

*** Reviewer Suggestions**

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