Differential impact of attention on the early and late categorization related human brain potentials

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Previous human studies have shown that object-selective attention enhances neural activities evoked in response to target stimuli. However, it is not clear whether the magnitude of activity enhancement is constant or varies according to the level of stimulus visibility. To examine the effect of attentional modulation on different event-related potentials (ERPs) and the relationship between attentional modulation and level of stimulus visibility, subjects were instructed to perform face detection and leaf detection tasks in separate blocks while the level of stimulus visibility varied randomly from trial to trial. As a result of object-selective attention, N170 and P400 ERP components were both modulated in response to the task target category compared to when the same category was used as distracter. We found that the magnitude of modulation of the N170 component was independent of the stimulus visibility level, while the P400 ERP component showed increased enhancement as the level of stimulus visibility increased. These findings demonstrate that attention impacts the neural populations, indexed by early (N170) and late (P400) evoked potentials, differentially and that attentional modulation becomes increasingly dependent on the level of stimulus visibility through the course of brain activities.

Keywords: event-related potential (ERP), object-selective attention, visual backward masking, N170, P400

Introduction

In a complex environment, attention plays an important role in creating a saliency map, based on object's relevance to the task at hand. Attention affects neural processes underlying objects encoding in different ways. For instance, attention may enhance brain activities responsible for encoding task targets (Eimer, 2000a; Furey et al., 2006; Luck, Woodman, & Vogel, 2000; Okazaki, Abrahamyan, Stevens, & Ioannides, 2008) and/or prevent further processing of distracters by inhibiting neural representation of distracters from sensory and memory areas (Jacques & Rossion, 2007; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Nasr, Moeeny, & Esteky, 2008). In spite of these evidences, it is not clear whether target stimulus parameters, such as its level of visibility, influence the effect of attention or whether attention affects target stimulus encoding independent of stimulus parameters.

While several ERP (Eimer, 2000a; Luck et al., 2000), MEG (Furey et al., 2006), and fMRI (Wojciulick, Kanwisher, & Driver, 1998) studies have shown that task target category recruits greater processing resources and evokes greater brain activities, none of these studies have found any evidence that the level of stimulus visibility or any other stimulus parameter can influence attentional modulation. Although this relationship has not previously been observed at neural population level, single cell electrophysiological recordings in non-human primates have shown that attentional modulation can be influenced by stimulus contrast and/or visibility level. For instance, it has been shown that spatial attention increases sensory neurons firing rate and that the amount of this activity enhancement is not constant but varies depending on the level of stimulus contrast (Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000; Treue & Martinez-Trujillo, 1999).

In this study, we used ERP technique to assess the relationship between the level of stimulus visibility and the magnitude of attentional modulation. Human subjects were instructed to perform two different tasks of face and leaf detection. Previous studies have shown that subjects' brain activities within object-selective areas are modulated during similar tasks when the preferred stimulus is the task target rather than the task distracter (Furey et al., 2006; Okazaki et al., 2008; Wojciulick et al., 1998). Here we used the level of visibility as an independent stimulus parameter because many previous studies have shown that this parameter affects the amplitude of evoked brain activities at the level of single neurons (Keysers & Perrett,

2002; Keysers, Xiao, Foldiak, & Perrett, 2001; Kovacs, Vogels, & Orban, 1995; Rolls, Tovee, & Panzeri, 1999) and also neural populations (Jemel et al., 2003; Nasr & Esteky, 2009; Rousselet, Husk, Bennett, & Sekuler, 2008; Tanskanen, Nasanen, Montez, Paallysaho, & Hari, 2005; Tanskanen, Nasanen, Ojanpaa, & Hari, 2007). We controlled the level of stimulus visibility in each trial by using the backward masking paradigm (Breitmeyer & Ogmen, 2000; Grill-Spector & Kanwisher, 2005; Keysers & Perrett, 2002). In this paradigm, the level of stimulus visibility and eventually the amount of evoked activities are controlled by changing the degree of stimulus onset asynchrony (SOA) between the actual stimulus and a subsequent mask image (Bacon-Mace, Mace, Fabre-Thorpe, & Thorpe, 2005; Keysers & Perrett, 2002; Keysers et al., 2001; Kovacs et al., 1995; Rolls et al., 1999; Tanskanen et al., 2007).

We mainly focused on N170 and P400 ERP components as components of interest because their contributions to perceptual categorization tasks had been studied previously. The occipito-temporal N170 is a relatively early brain potential that shows its greatest response amplitude to face stimuli (Allison, Puce, Spencer, & McCarthy, 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004; Jeffreys, 1996). Other studies have shown that this ERP component is mainly linked to processes responsible for facial structure encoding (Eimer, 2000b; Jeffreys, 1996; Rossion et al., 1999; Sagiv & Bentin, 2001) and/or object categorization (Philiastides, Ratcliff, & Sadja, 2006; Philiastides & Sadja, 2006). N170 is usually followed by late potentials recorded by temporal, central, and parietal electrodes, occurring approximately 300 to 500 ms after the stimulus presentation (Bentin & Deouell, 2000; Bentin & McCarthy, 1994; Curran, Tanaka, & Weiskopf, 2002; Eimer, 2000c; Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000; Philiastides & Sadja, 2006; Puce, Allison, & McCarthy, 1999; Trenner, Schweinberger, Jentzsch, & Sommer, 2004). These late brain potentials seem to index high-level brain processes responsible for stimulus identification via memory access (Bentin & Deouell, 2000; Bentin & McCarthy, 1994; Curran et al., 2002; Paller et al., 2000; Trenner et al., 2004) and/or target detection (Knight & Scabini, 1998; Philiastides et al., 2006; Philiastides & Sadja, 2006; Soltani & Knight, 2000; Sutton, Baren, Zubin, & John, 1965). It has also been shown that amplitude of these late potentials is highly affected by the level of stimulus visibility (Nasr & Esteky, 2009) and can be predictive of decision accuracy in perceptual categorization tasks (Philiastides et al., 2006).

Methods and materials

In this study, we used the same data set as we used previously (Nasr & Esteky, 2009).

Participants

Thirteen right-handed male students aged 22.9 ± 2.8 (mean ± SD) with normal or corrected-to-normal vision were paid to participate in the experiment. Written informed consent in accordance with the principles of the Declaration of Helsinki was obtained from them before the experiments.

Stimuli

Stimuli were selected from a set of six different object categories (faces, leaves, hands, cars, fruits and chairs) and each category contained fifty high-contrast gray-scaled images (Figure 1). Images were all from frontal view except for cars, which were from side view. The stimulus size was adjusted so that their longest dimension was equal to 7.3 degrees of visual angle at 70-cm distance. Mask images were white noise random dot pattern, generated for each trial separately (Figure 1). Each dot subtended 0.01×0.01 degrees of visual angle and their color was selected randomly from 256 different possible gray colors (black and white colors included). To increase the effect of masking, sizes of mask images were larger than other images and subtended 10×10 degrees of the visual angle. Stimuli were presented on a gray background (14.8 cd/m²) using Matlab Psychophysics Toolbox.

Task and procedure

Subjects performed face and leaf detection tasks during separate experimental blocks within one recording session. Subjects' task did not vary in each block and they were informed of the task type from the beginning of each block. The task sequence was counterbalanced between subjects, and each subject participated in both tasks within one recording session.

In each block, stimuli were presented for 10 ms at the center of the screen, followed by a noise mask that remained visible for 300 ms. A 1500 ± 100 ms interval was used between the mask offset and the start of the next trial. In both tasks, stimuli were selected pseudorandomly with the constraint that stimuli from the face set were selected for 33.3% of trials, stimuli from the leaf set were selected for 33.3% of trials, and stimuli from the other four object categories were selected for the remaining trials. In each trial, stimulus visibility was controlled by controlling stimulus onset asynchrony (SOA) between the presented stimulus and the following mask. SOA was selected randomly on each trial and could be 0 (i.e., mask only trials), 10, 20, 30, or 500 ms (with a 20% probability for each SOA). During the two tasks, subjects were instructed to report whether the presented stimulus was a target or a distracter by pressing one of two keys on a
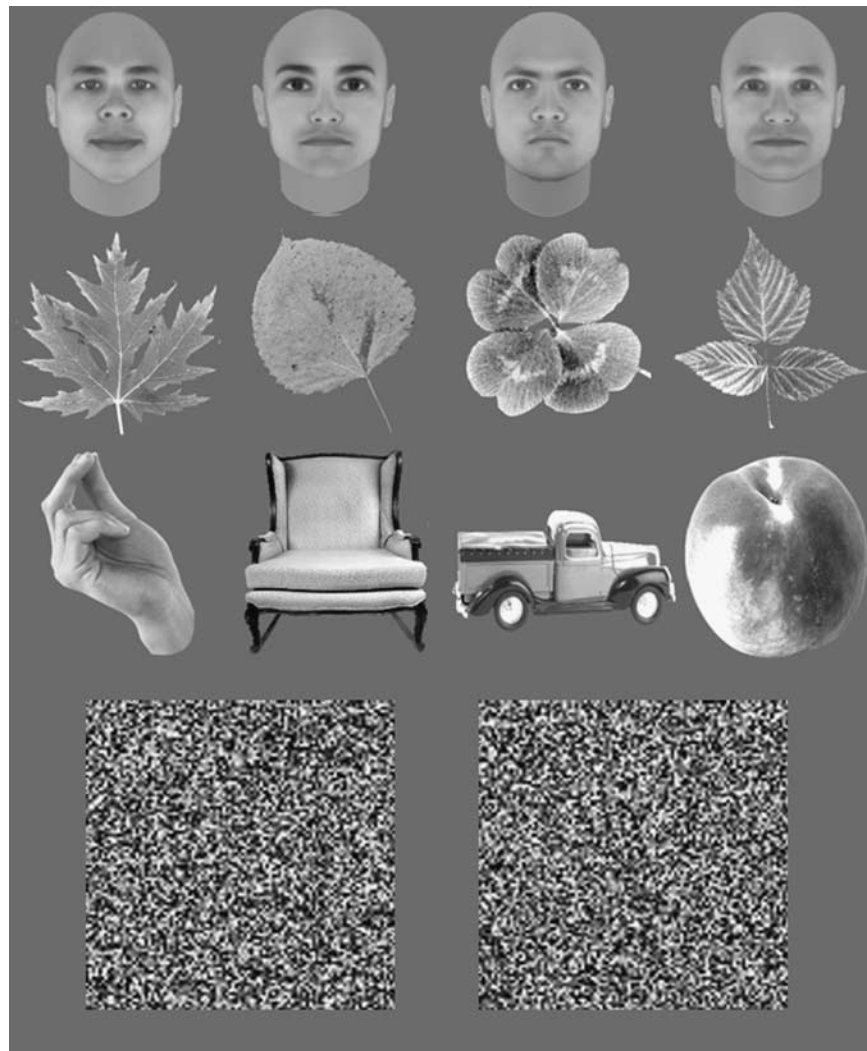
Figure 1. Example of stimuli used in this study. In the face and leaf detection tasks, 33.3% of the stimuli were face images (first row), 33.3% of the stimuli were leave images (second row), and the remaining stimuli were selected from images of four other object categories (third row). Mask stimuli were white noise random dot patterns that were generated for each trial separately. Their size was larger than other images to increase the masking effect. Two exemplar mask images are also presented in the fourth row.

keypad (i.e., two-alternative forced-choice task) and accuracy and speed were both stressed.

ERP recording

A Neuroscan system with 32 Ag/AgCl sintered electrodes was used for brain activity recording. Data were acquired continuously in AC mode (0.05–30 Hz) with a 1-kHz sampling rate. Reference electrodes were linked mastoids, grounded to AFz. Four electrodes monitored horizontal and vertical eye movements for offline artifact rejection. Channel impedance was kept at <5 kΩ. Data were further resampled at a 250-Hz sampling rate just to ease further data analysis. Baseline activity was corrected on a pre-sample stimulus interval of 100 ms. For all subjects, trials with eye blink (<10% of all trials) were eliminated by eliminating those trials on which the peak-to-peak voltage in the horizontal and vertical eye movement channels exceeded 30 μV.

Behavior data analysis

Subject's hit rate (HR) and correct reject rate (CRR) across different experimental conditions have been analyzed in detail in another article (Nasr & Esteky, 2009). Here, the method of signal detection theory (Green & Swets, 1966) was applied to measure subject's capability for discriminating target images from distracters and also to assess subject's bias in each task. On the basis of this method, subject's discrimination capability was indexed by adding the z-transformation of subject's HR and CRR. The amount of subject's bias was also measured separately by

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ERP data analysis

In this study, I focused on N170 and P400 as two ERP potentials that index early and late neural processes underlying object detection, respectively. N170 detected in occipital (recorded by O1, O2, and Oz electrodes) and occipito-temporal (recorded by P7 and P8 electrodes) sites were indexed by measuring the ERP peak activity during 150–250 ms after the stimulus onset for each subject separately. The P400 component was measured from the central (recorded by C3, C4, and Cz electrodes) and fronto-central (recorded by FC1, FC2, and FCz electrodes) sites. Since P400 component was a sustained rather than a sharp waveform, therefore, the averaged activity evoked during the 350–500 ms following stimulus onset was measured for each individual subject. For both N170 and P400 components, the target electrodes were selected on the basis of brain activity mappings, and since there was no significant lateral dominance for any of these ERPs (Figure 2), brain potentials recorded from the opposite hemispheres were averaged and used for all analyses.

The effect of attentional modulation, stimulus categories, level of stimulus visibility on P400, and also their possible interaction was assessed by applying a three-factor repeated measures ANOVA (stimulus category (face vs. leaf vs. other objects) × stimulus visibility (SOA = 10 vs. 20 vs. 30 vs. 500 ms) × task (face detection vs. leaf detection)) to each measured brain potential separately. All p-values were corrected for nonsphericity using the Greenhouse–Geisser correction method. For these analyses, brain potentials measured when the SOA was equal to zero (mask only trials) were excluded because no stimulus was presented in these trials. Further analyses were applied when necessary, and these analyses are described in the corresponding results sections.

Results

Behavioral results

Subjects' hit rate (HR) and correct rejection rate (CRR) performances are reported in Table 1. Subjects' HR and CRR improved with the level of stimulus visibility. In addition, subjects showed somewhat better performance during leaf detection trials compared with face detection trials. Subjects' discrimination capability and also their bias (toward either "target" or "distracter" response) was assessed on the basis of method of signal detection theory and by measuring d' and c-values, respectively. Consistent
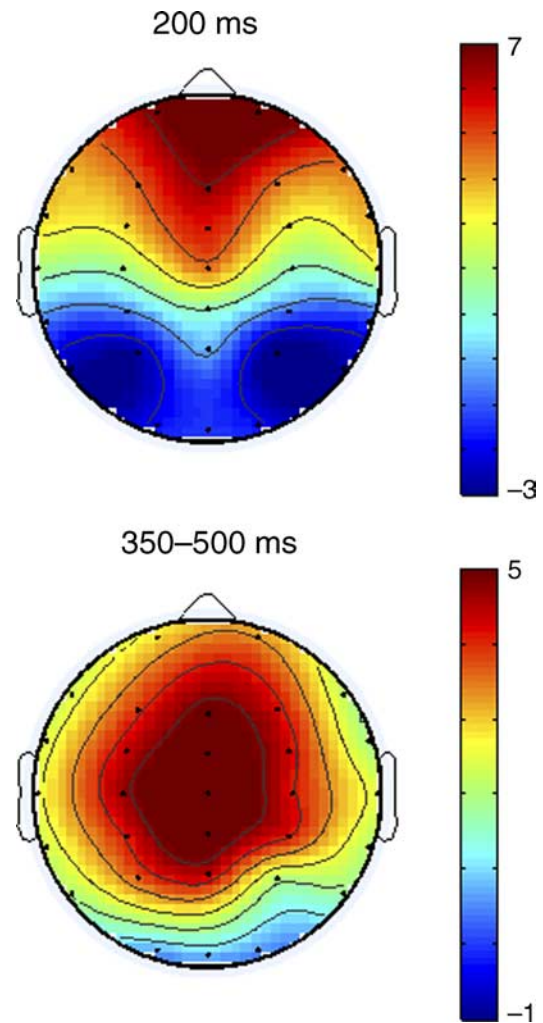

Figure 2. Mapping of brain activities evoked in response to a facial image (SOA = 500 ms) when it served as the task target; (top) 200 ms after the stimulus onset when N170 component reached its peak amplitude in occipito-temporal electrode sites and (bottom) averaged over 350–500 ms after stimulus onset when P400 was detected in the central and fronto-central electrode sites.

to their HR and CRR, subjects' performance at discriminating target and distracter stimuli (d') increased as the level of stimulus visibility increased (Figure 3). Application of a two-factor repeated measures ANOVA (stimulus visibility (SOA = 10 vs. 20 vs. 30 vs. 500 ms) × task (face detection vs. leaf detection)) to the calculated d' values revealed a significant effect of stimulus visibility ($F(1.32, 15.90) = 13.84$, $p < 0.001$). We also found a weak but still significant effect of task ($F(1, 12) = 5.06$, $p = 0.044$) but without any significant interaction between the two factors ($F(1.32, 15.80) = 2.18$, $p > 0.10$). Application of the same analysis to the measured subjects' bias (c-value) showed a significant effect of stimulus visibility ($F(1.69, 20.29) = 8.73$, $p < 0.01$) but no significant effect of task($F(1, 12) = 1.10$, $p > 0.10$). Rather, we found a significant interaction between the effects of task and level of stimulus visibility

	Face detection task				Leaf detection task			
	SOA				SOA			
	10 ms	20 ms	30 ms	500 ms	10 ms	20 ms	30 ms	500 ms
Hit rate	33.0 (25.9)	53.7 (23.9)	80.3 (15.9)	87.4 (21.7)	47.9 (25.7)	61.8 (25.5)	71.94 (22.5)	93.1 (7.3)
Correct rejection rate	85.2 (10.1)	87.7 (9.5)	92.5 (8.7)	95.9 (7.1)	74.6 (12.7)	80.2 (12.9)	87.6 (7.8)	93.7 (8.9)

Table 1. Subjects' hit rate and correct rejection rate (mean ($\pm SD$)) during face and leaf detection tasks.

$(F(1.25, 15.05) = 5.43, p < 0.01)$. It appears that in trials with low level of stimulus visibility, subjects hesitated to report "target" perception, which led to more negative c-values. This behavior was even more prominent during face detection trials (Figure 3).

We also analyzed subjects' reaction time (RT) during different experimental conditions to see whether response time also depended on experimental parameters, as subjects' performances, or not (Table 2). Although speed and accuracy were both stressed, application of the same analysis to subjects' RT did not show any effect of
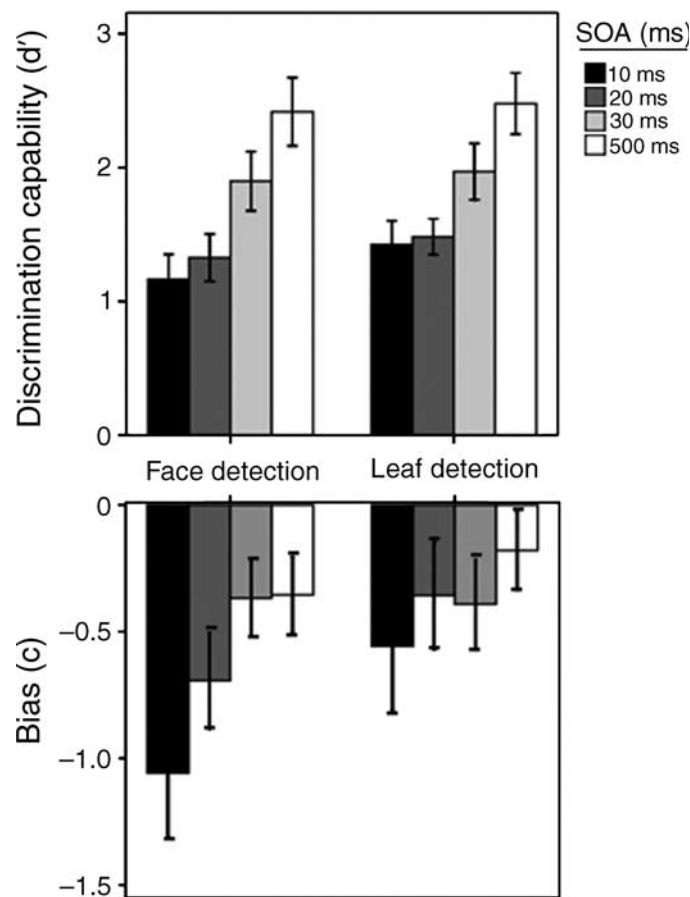

Figure 3. Subjects' behavioral performance across different SOA conditions. Top row demonstrates calculated subjects' discrimination capability (d') during (left) face and (right) leaf detection tasks. Bottom row shows subjects' bias (c) during the two tasks. Error bars represent one standard error of the mean.

experimental parameters ($F < 0.29, p > 0.90$). Separate comparison of subjects' RT during correct and wrong trials also did not yield any effect of experimental parameters on subjects' RT during either correct or wrong trials ($F < 0.30, p > 0.30$).

Lack of RT variation between experimental condition might seem to be strange with regard to previous studies that have shown longer RT during more difficult experimental conditions and also faster target detection compared to distracter rejection (for a review, see Ratcliff & Rouder, 1998). However, in all of these studies, target and distracter stimuli were presented with similar frequency. Here, lack of any difference between subjects' RT during target and distracter trials could be due to the fact that non-target stimuli were presented more frequently than target ones (see Methods and materials section). This difference could (a) reduce subjects' RT in response to distracters because non-target stimuli were more expected and/or (b) increase response time for target trials since these stimuli were presented less frequently. Using "fast guess" strategy could also improve subjects' RT, when less sensory information was available (Grice, Nullmeyer, & Spiker, 1982; Yellott, 1971).

ERP results

N170

N170 component was mainly detected in the occipital and occipito-temporal sites. Analysis of subjects' occipito-temporal N170 component showed that both stimulus visibility and subjects' task have affected evoked potentials. Here, application of three-factor repeated measures ANOVA (see Methods and materials section) showed that for the occipito-temporal N170 (recorded by P7 and P8 electrodes), the peak response amplitude was influenced by the level of stimulus visibility (Figure 4), as more visible stimuli evoked significantly larger (more negative) N170 potentials ($F(1.28, 15.39) = 11.96, p < 0.01$). In addition to this dependency on the level of stimulus visibility, there was also a significant interaction between stimulus category and task factors ($F(1.95, 23.34) = 7.74, p < 0.01$). This effect was due to the greater face- and leaf-related activities when face and leaf stimuli served as task targets rather than distracters (Figure 5). Here, we did not find any significant relationship between the level of stimulus visibility and the amount of task-dependent

	Face detection task				Leaf detection task			
	10 ms	20 ms	30 ms	500 ms	10 ms	20 ms	30 ms	500 ms
Face	762 (222)	761 (209)	753 (207)	750 (217)	759 (188)	763 (207)	756 (193)	778 (243)
Leaf	765 (233)	757 (221)	761 (217)	804 (281)	767 (180)	759 (180)	758 (189)	775 (216)
Object	763 (215)	764 (214)	748 (220)	811 (329)	768 (192)	755 (192)	742 (167)	787 (230)

Table 2. Subjects' reaction time (mean ($\pm SD$)) during face and leaf detection tasks.

activity modulation as the interaction between stimulus visibility and task ($F(1.58, 18.94) = 0.64$, $p = 0.51$) and also the interaction between stimulus visibility, stimulus category, and task ($F(3.80, 45.62) = 0.64$, $p = 0.63$) remained insignificant.

To assess the effect of attentional modulation more precisely, the amount of N170 enhancement was measured by subtracting the occipito-temporal activity when stimuli served as the task distracters from the evoked activity when the same stimuli served as the task target.
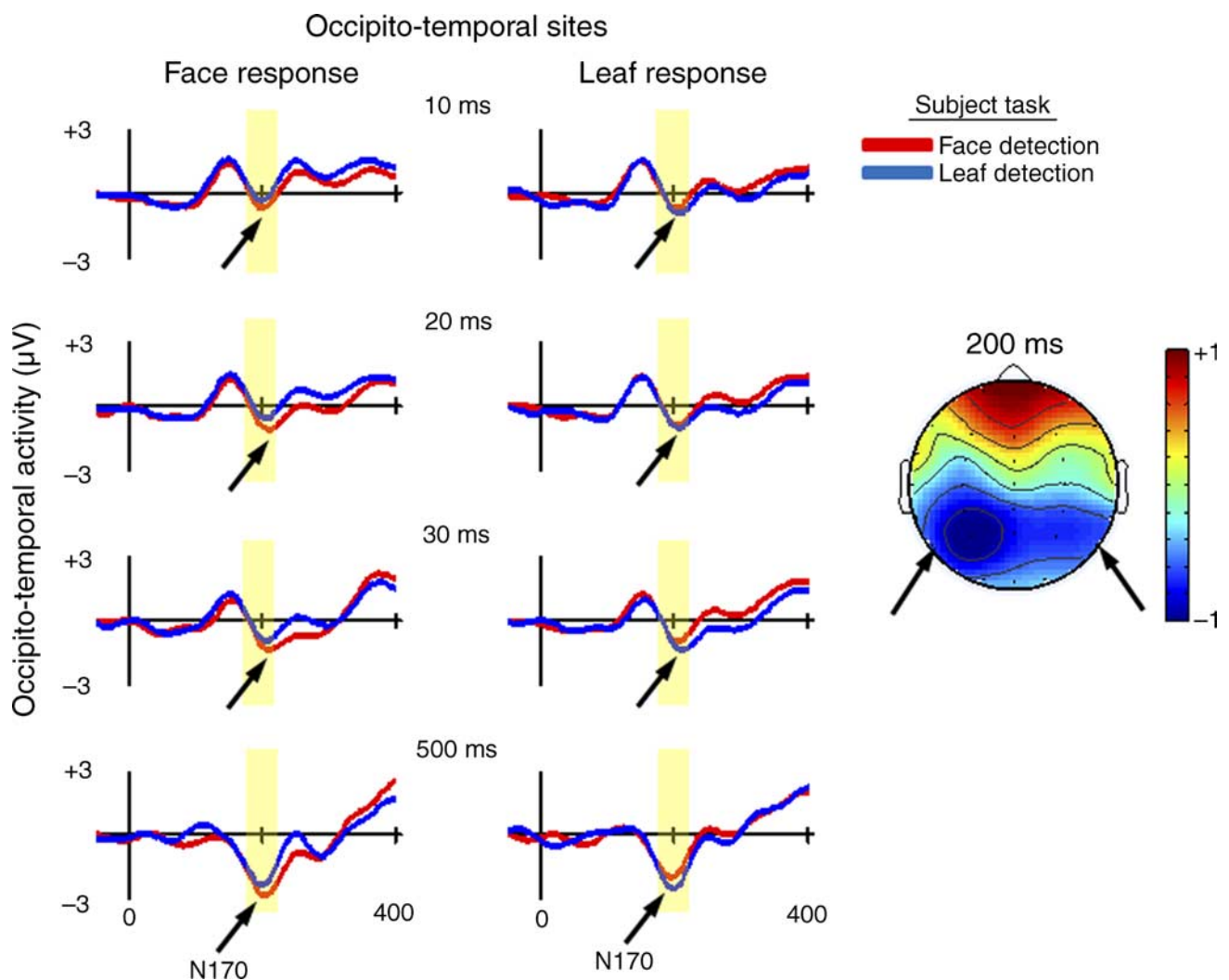

Figure 4. Occipito-temporal ERPs (recorded from P7 and P8 electrode sites) in response to the (left) face and (right) leaf stimuli across different SOA conditions. In each graph, blue and red lines demonstrate evoked activities during the face and leaf detection tasks, respectively, and arrows indicate the N170 ERP component. Shaded yellow areas represent 180–220 ms after stimulus onset used for detecting N170 peak amplitude and also for measuring N170 average amplitude. Brain activity mapping shows the distribution of differential (Target − Distracter) brain activities averaged over face and leaf trials (SOA = 500 ms), evoked 200 ms after the stimulus onset. Arrows indicate the location of the occipito-temporal electrodes.
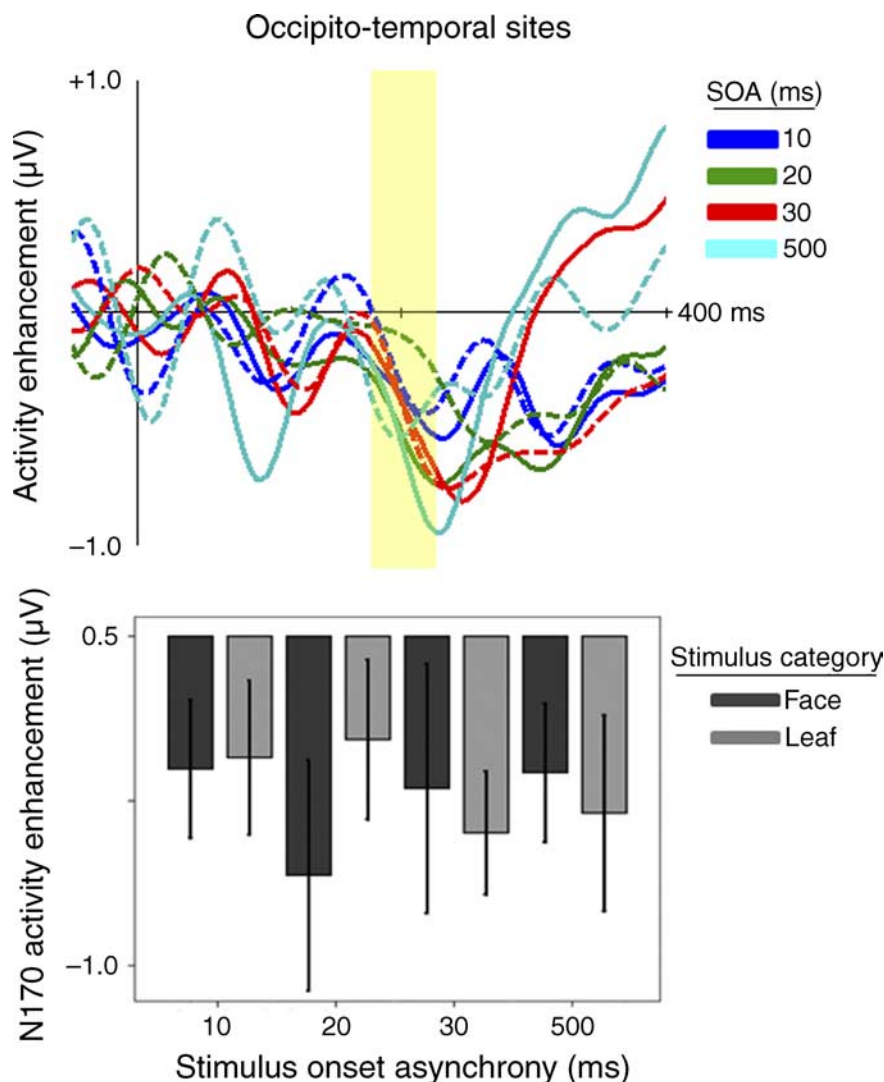
Figure 5. Amount of activity enhancement in the occipito-temporal site. In the top panel, this enhancement was measured by point-to-point subtraction of evoked activities when stimuli served as a distracter from evoked activity when the same stimuli served as the task target. Colored lines represent face (solid lines) and leaf (dashed lines) activity enhancements across different SOAs. In the bottom panel, peak amplitudes of N170 component were used for measuring the activity enhancement. In this panel, dark and light gray bars represent the amount of enhancement for face- and leaf-related ERPs, respectively. Error bars represent one standard error of the mean.

Here again although we found a prominent effect of attentional modulation on the occipito-temporal N170 amplitude, the amount of this activity modulation seemed to be independent of either stimulus visibility level (Figure 5) or stimulus categories (Figure 6). Application of a two-factor repeated measures ANOVA (stimulus category (face vs. leaf) × SOA (10 vs. 20 vs. 30 vs. 500 ms)) to the measured N170 peak amplitude enhancements did not show any effect of stimulus visibility ($F(1.87, 22.51) =$ 0.33, $p = 0.74$) or stimulus category ($F(1, 12) = 0.10$, $p =$ 0.78) or interaction between these two factors ($F(2.21,$ 26.53) = 1.03, $p = 0.35$). Measuring point-to-point activity enhancement, rather than comparing N170 peak amplitudes, also led to a similar result (Figure 5). So it seems that amplitude of occipito-temporal N170 component is

enhanced by the task-related attentional modulation independently of the level of stimulus visibility.

On the basis of subjects' performance, it seemed that subjects had more difficulty to perform face detection rather than leaf detection. Here we checked if this difference in the level of task difficulty have affected N170 component or not. We compared the amplitude of N170 component in response to objects other than faces and leaves between the two tasks by subtracting N170 amplitude evoked by these objects during the leaf detection task from the evoked N170 amplitude during the face detection task. Pairwise comparison did not show any significant difference between the occipito-temporal N170 evoked by objects during the two tasks ($t(51) =$ -0.15, $p = 0.10$). So it seems that the task-related
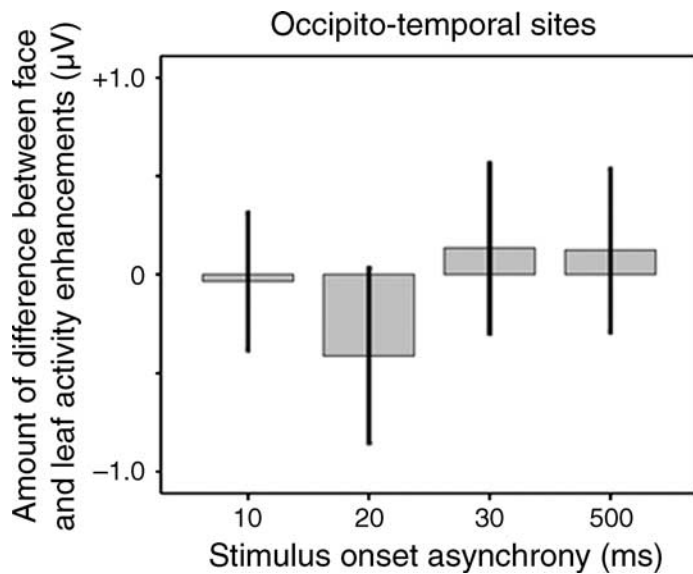
Figure 6. Amount of difference between face response enhancement and leaf response enhancement (Face Enhancement − Leaf Enhancement). Error bars represent one standard error of the mean.

attentional modulation has only affected target-related occipito-temporal N170 activity and N170 evoked by other objects has remained unaffected between the two tasks. Here again, application of one-factor repeated measures ANOVA (SOA (10 vs. 20 vs. 30 vs. 500 ms)) did not show any effect of stimulus visibility level on this object-related differential activity ($F(2.48, 29.71) = 0.83$, $p = 0.47$).

In addition to the effects mentioned above, there was also a significant interaction between effects of stimulus category and stimulus visibility ($F(3.43, 41.12) = 3.90$, $p = 0.01$), which was due to stronger face-selective N170 activity during trials with longer SOAs as it was reported previously by Bacon-Mace et al. (2005). Here, we further checked if N170 sensitivity to the level of stimulus visibility varied between stimulus categories or not as we did previously for the N250 component (Nasr & Esteky, 2009). We measured the range of N170 activity in response to the variation of stimulus visibility by subtracting the N170 amplitude when SOA = 10 ms from the N170 amplitude when SOA = 500 ms. It was found that manipulating the visibility level of facial images affected N170 amplitude to a greater extent compared to when the same manipulation was applied to non-facial images (Figure 7). Interestingly, this effect was similarly observed during both face and leaf detection trials, and increasing leaf relevance to the ongoing task during leaf detection trials did not increase the range of N170 activity in response to leaves. Here, pairwise comparison did not show any change in the range of N170 activity evoked by either face, leaf, or other objects between the two tasks ($t(12) < 1.04$, $p > 0.30$).

Besides occipito-temporal leads, N170 component was also detected in occipital sites (recorded by O1, O2, and Oz electrodes). Similar to the occipito-temporal N170, this component also had a larger amplitude during face trials compared to leaf and other objects trials and this face selectivity was more prominent during trials with longer SOAs (Figure 8). However, in contrast to the occipito-temporal N170, occipital N170 did not show any
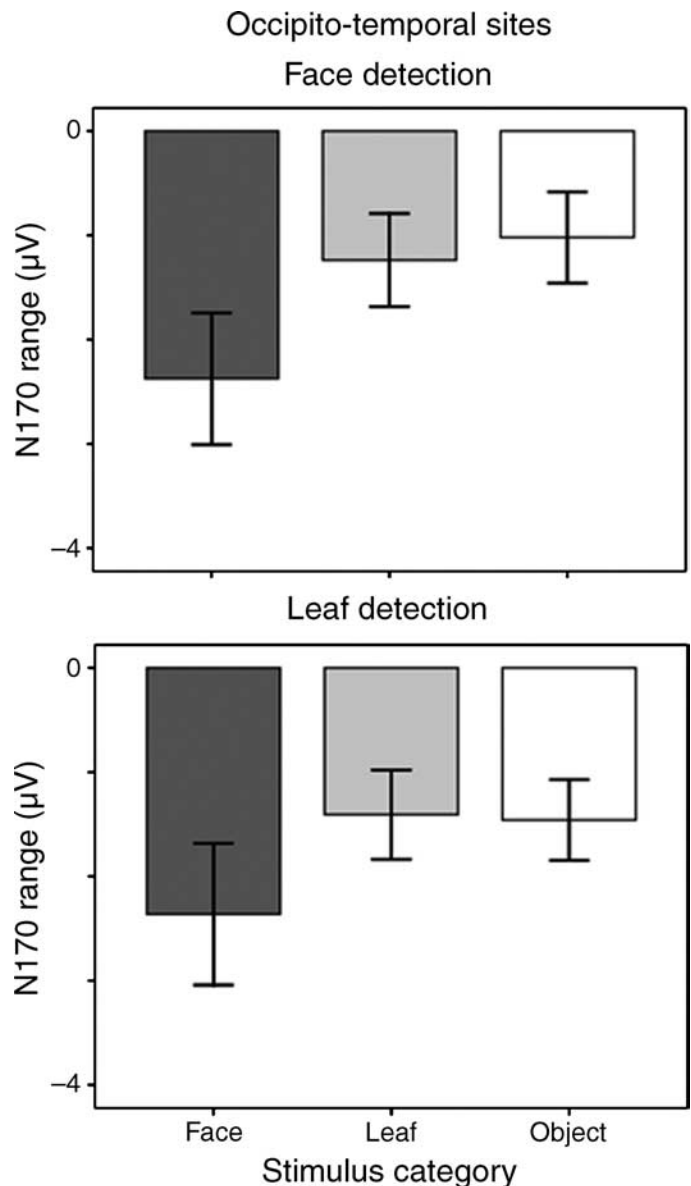

Figure 7. Range of the occipito-temporal N170 activity during (top) the face detection and (bottom) the leaf detection trials. Range of activity was measured by subtracting the amplitude of N170 potential evoked by the poorly visible stimuli (SOA = 10 ms) from the N170 potential evoked by the highly visible stimuli (SOA = 500 ms). In the bar graphs, dark gray, light gray, and white bars correspond to the range of N170 activity when stimuli belonged to the face, leaf, and other objects sets, respectively. Error bars represent one standard error of the mean.
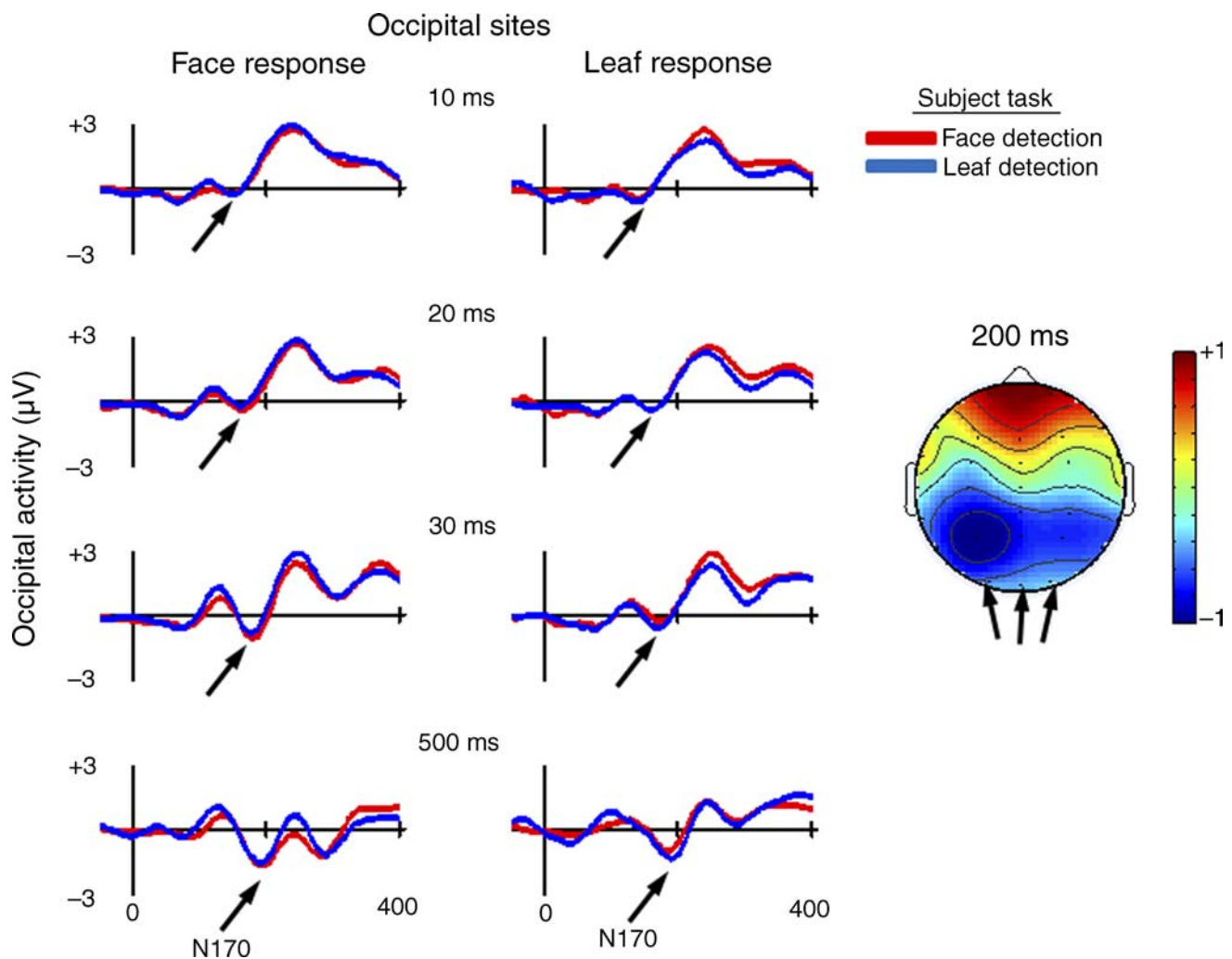
Figure 8. Occipital ERPs (recorded from O1, O2, and O3 electrode sites) in response to the (left) face and (right) leaf stimuli across different SOA conditions. Arrows indicate the location of occipital electrodes. Other figure details are the same as Figure 4.

sensitivity to the tasks. Here, application of a three-factor repeated measures ANOVA to the measured N170 peak amplitudes yielded a significant effect of stimulus categories ($F(1.38, 11.29) = 6.50$, $p = 0.01$) and also a significant interaction between the effects of stimulus category and SOA ($F(3.45, 41.40) = 6.17$, $p < 0.01$). Effect of task ($F(1,12) = 1.12$, $p = 0.35$) and also interaction between the effect of task and other independent factors remained non-significant ($F < 1.8$, $p > 0.20$). On the basis of these results, it appears that, compared to the occipito-temporal N170, the occipital N170 is generated by modules that are less influenced by task.

P400

The other component that was highly affected by the attentional modulation, due to the variation in task, was P400. This ERP component was mainly detected in central (recorded by C1, C2, and Cz electrodes) and

fronto-central (recorded by FC1, FC2, and FCz electrodes) sites (Figures 9 and 10). While no significant interaction between effect of attentional modulation and the stimulus visibility was found on evoked N170 response, application of the same analysis to the central and fronto-central P400 activities revealed a different effect in both sites. At the first glance, central and fronto-central P400 components, similar to occipito-temporal N170, were influenced significantly by the level of stimulus visibility ($F(1.39, 16.67) > 37.58$; $p < 0.01$) and also by the interaction between effects of stimulus category and task ($F(1.73, 21.30) > 15.04$, $p < 0.01$). We also found a significant interaction between the effects of stimulus category and stimulus visibility on the P400 amplitude in both central ($F(3.02, 36.18) = 6.08$, $p < 0.01$) and fronto-central ($F(2.98, 35.70) = 5.78$, $p < 0.01$) sites, as it was observed for the occipito-temporal N170. However, in contrast to the occipito-temporal N170, it appeared that the effect of attentional modulation on P400 component varied
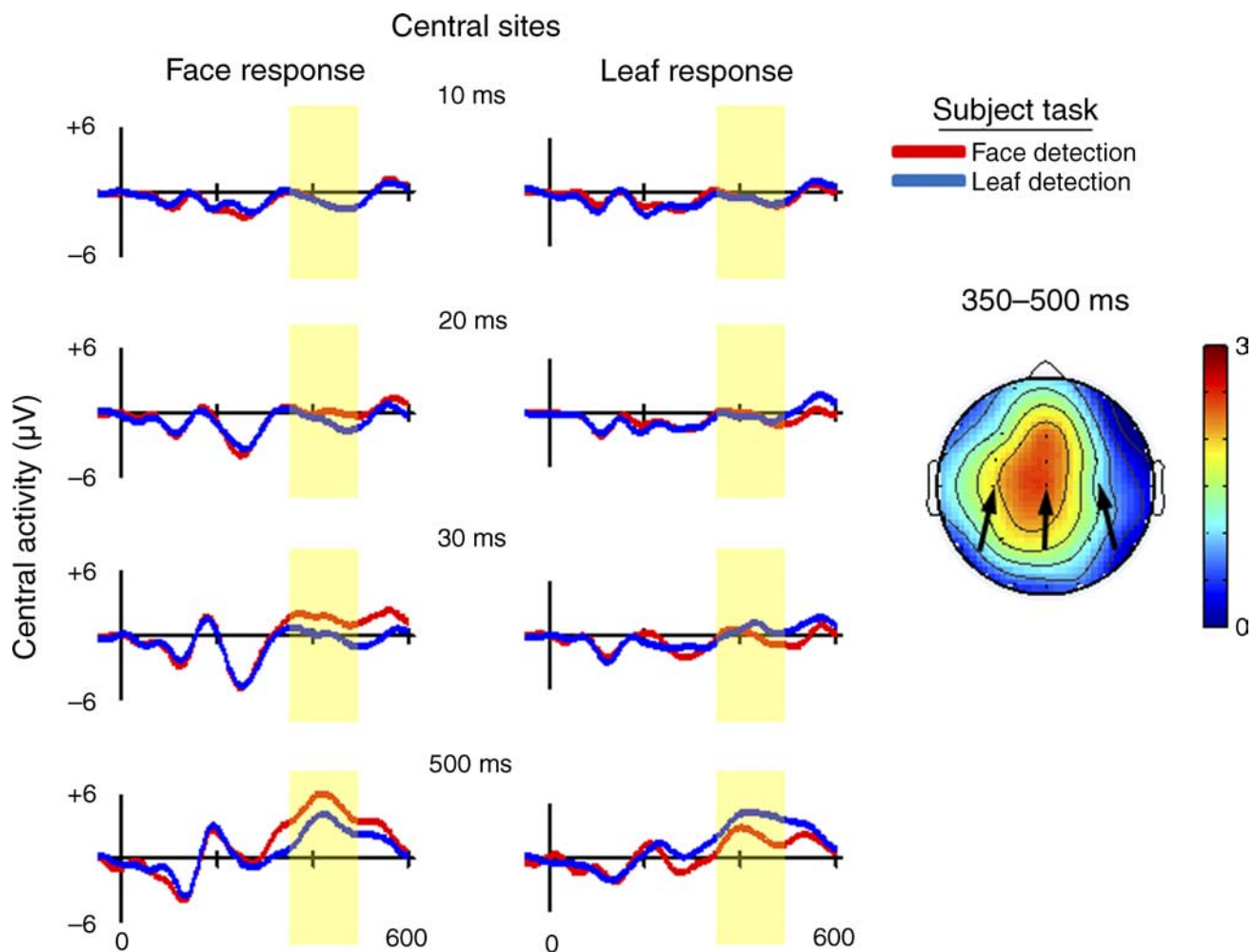
Figure 9. Central ERPs (recorded from C1, C2, and Cz electrode sites) in response to the (left) face and (right) leaf stimuli across different SOA conditions. In each graph, blue and red lines demonstrate the evoked activities during the face and leaf detection tasks, respectively. Yellow shaded areas show 350–500 ms after stimulus onset in which the P400 ERP component was measured. Brain activity mapping shows the distribution of differential (Target − Distracter) brain activities averaged over face and leaf trials (SOA = 500 ms), evoked 350–500 ms after the stimulus onset. Arrows indicate the location of central electrodes.

with the level of stimulus visibility and a significant interaction between effects of stimulus category, stimulus visibility, and task was found in both central ($F(2.37, 28.45) = 7.13$, $p < 0.01$) and fronto-central ($F(2.73, 32.80) = 6.97$, $p < 0.01$) sites.

To assess the nature of dependency between the amount of attentional modulation and the level of stimulus visibility, we measured the amount of face- and leaf-related P400 enhancements when these objects served as the task target compared to when they were used as distracters. In the central and fronto-central electrode sites, magnitude of P400 enhancement increased as the level of stimulus visibility increased (Figure 11). This effect was further assessed by applying two-factor repeated measures ANOVA (stimulus category (face vs. leaf) × stimulus visibility (SOA = 10 vs. 20 vs. 30 vs. 500 ms)) to the amount of P400 enhancement. In both sites,

results yielded a significant effect of stimulus visibility ($F(1.61, 19.35) > 8.29$, $p < 0.01$) but no significant effect of stimulus category ($F(1, 12) < 0.97$, $p > 0.30$) or interaction between effects of stimulus visibility and stimulus category ($F(1.94, 23.35) > 1.14$, $p > 0.30$).

Here again we checked whether the difference among levels of task difficulty, between face detection and leaf detection, has affected object-related P400 component or not. While no significant differential activity was found for N170 component, here we found greater P400 activity in response to objects when subjects performed face detection task compared to leaf detection (Figure 12). However, this effect was mainly confined to the trials with highly visible stimuli (SOA = 500). In central electrode sites, application of *t*-test to the measured object-related activities showed significant differential activity (face detection − leaf detection) during SOA = 500 ms trials
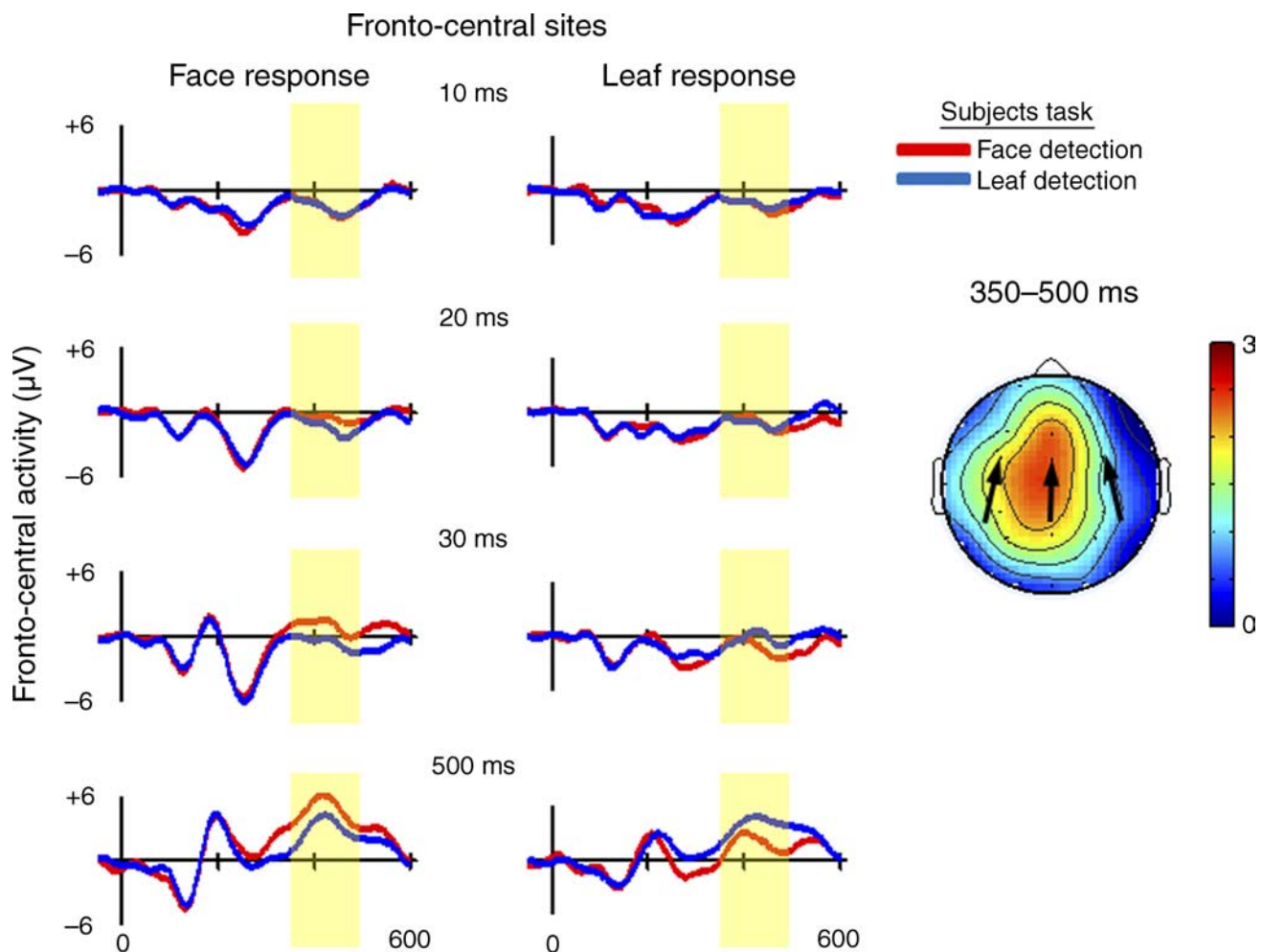
Figure 10. Fronto-central ERPs (recorded from FC1, FC2, and FCz electrode sites) in response to the (left) face and (right) leaf stimuli across different SOA conditions. Other figure details are the same as Figure 9. Brain activity mapping shows the distribution of differential (Target − Distracter) brain activities averaged over face and leaf trials (SOA = 500 ms), evoked 350–500 ms after the stimulus onset. Arrows indicate the location of fronto-central electrodes.

($t(12)$ = 2.26, p = 0.03) but not in other SOA conditions ($t(12)$ < 0.70, p > 0.20). In fronto-central electrode site, during SOA = 500 ms trials, this effect was only marginally significant ($t(12)$ = 1.87, p = 0.08) and we found no significant differential activity in other SOA conditions ($t(12)$ < 0.60, p > 0.20). Similar to face- and leaf-related P400, application of one-factor repeated measures ANOVA yielded a significant effect of stimulus visibility level on object-related P400 component evoked in central ($F(3, 36)$ = 9.68, p < 0.01) and fronto-central leads ($F(3, 36)$ = 4.05, p = 0.02). So, it seems that, for late P400 component, not only the amount of target-related modulations but also other, more general, task-related enhancements also vary with the level of stimulus visibility.

The other difference between effects of attentional modulation on N170 and P400 was clearly observed when the sensitivity of P400 component to the level of stimulus visibility was assessed (Figure 13). While N170 range of activity remained intact between the two tasks, pairwise

comparisons showed that the range of face- and leaf-related P400 was significantly greater when face and leaf stimuli served as the task target rather than distracter ($t(12)$ > 2.70, p < 0.05). So it seems that attentional modulation can change both amplitude and range of P400 component in responses to the stimulus of interest. P400 in response to objects (other than faces and leaves) also showed greater activity range during face detection task ($t(12)$ > 3.18, p < 0.01).

Although our findings demonstrated a significant interaction between effects of attentional modulation and the level of stimulus visibility on P400, the exact onset time of this effect was not clear. To assess onset time of the significant relationship between the attentional modulation and the level of stimulus visibility in the central leads, a two-factor repeated measures ANOVA (stimulus category (face vs. leaf) × stimulus visibility (SOA = 10 vs. 20 vs. 30 vs. 500 ms)) was applied to the measured activity enhancement calculated during different time windows
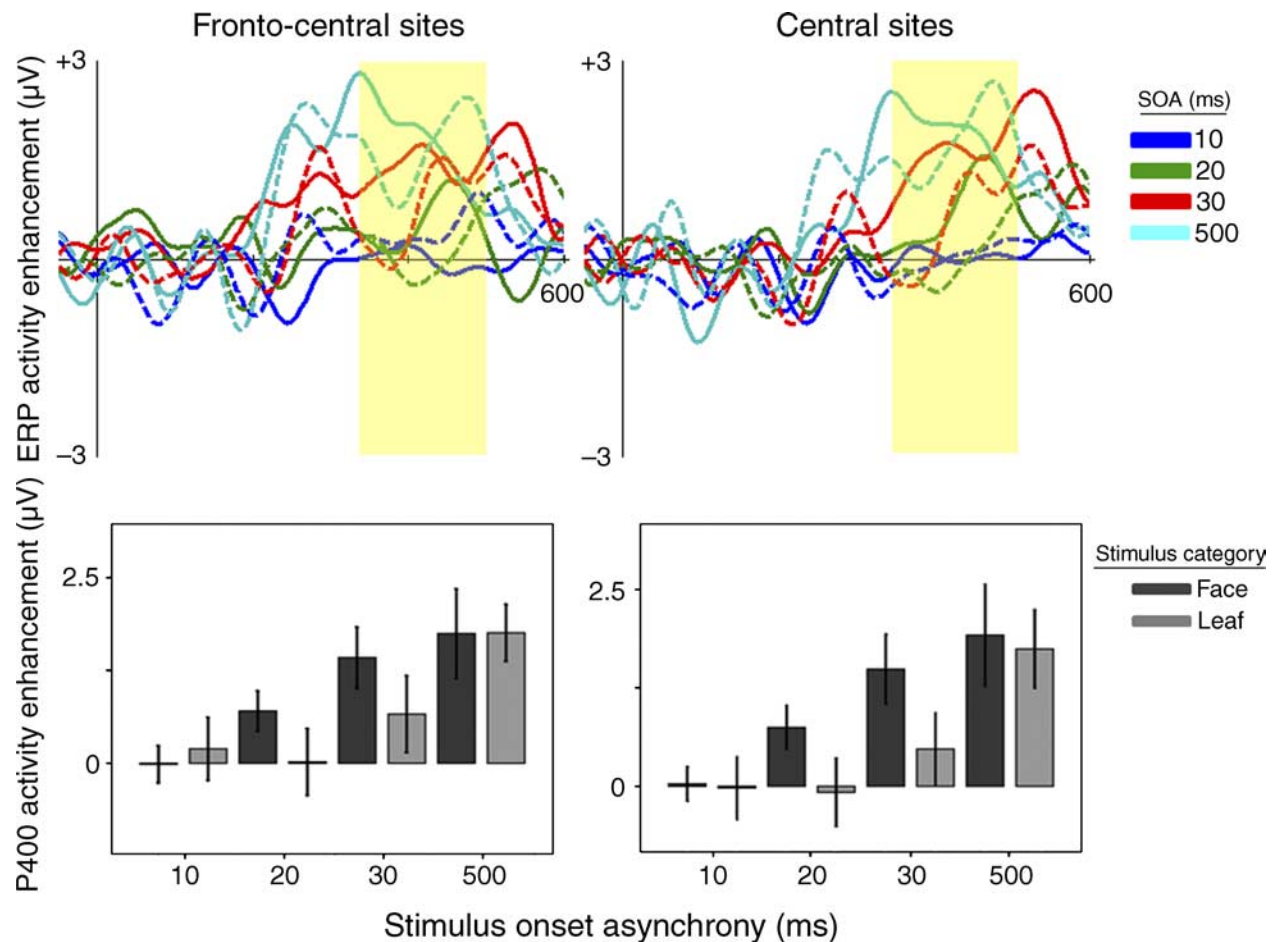
Figure 11. Amount of the P400 activity enhancement, in (left) central and (right) fronto-central sites, calculated by subtracting either (top) point-to-point stimulus-related activities or (bottom) averaged activity over 350–500 ms after stimulus onset when stimulus served as a task distracter from when the same stimulus served as a task target. Other figure details are the same as Figure 5.

between 0 and 800 ms after the stimulus onset (window length = 48 ms with 91.7% overlap between adjacent windows). This analysis showed that the earliest time window during which stimulus visibility significantly affected the magnitude of activity enhancement was the 284–332 ms interval, and enhancement persisted until the 524–572 ms interval following stimulus onset. In addition, a two-factor repeated measures ANOVA applied to brain activities measured from other electrode sites revealed no significant relationship between the level of stimulus visibility and the magnitude of activity enhancement due to attentional modulation earlier than the 284–324 ms interval.

To see if P400 better represents stimulus-dependent processes or decision-related ones, we checked the pattern of response-locked activities across different experimental conditions (Figure 14). Rearranging evoked brain activities relative to the subjects' response did not change the results and we found the same pattern of central and fronto-central modulations as we saw previously for stimulus-locked activities. We further compared the effect of the experimental parameters on stimulus-locked and response-locked activities. We averaged response-locked

activities during 300–450 ms before response onset in central and fronto-central electrodes and compared it with the averaged stimulus-locked activities within 350–500 ms after stimulus onset recorded from the same sites. Application of 4-way repeated measures ANOVA (measurement method (response-locked vs. stimulus-locked), SOA (10 vs. 20 vs. 30 vs. 500 ms), task (face vs. leaf detection), and stimulus category (face vs. leaf vs. objects)) did not yield any significant effect of measurement method and/or interaction between this parameter and effect of other factors ($F <$ 1.00, $p > 0.10$). Application of the same analysis to the activities measured in other electrode sites (within the same interval) yielded a similar result. So, as it was predictable from the lack of subjects' RT modulation, stimulus-locked and response-locked measurements of P400 component lead to very similar results. Finally, since subjects' performance varied across experimental conditions, we checked if we could see the same pattern of modulation in frontal and fronto-central electrode sites if we excluded wrong trials. Again, we did not find any prominent change in the pattern of activities within these electrode sites after excluding wrong trials.
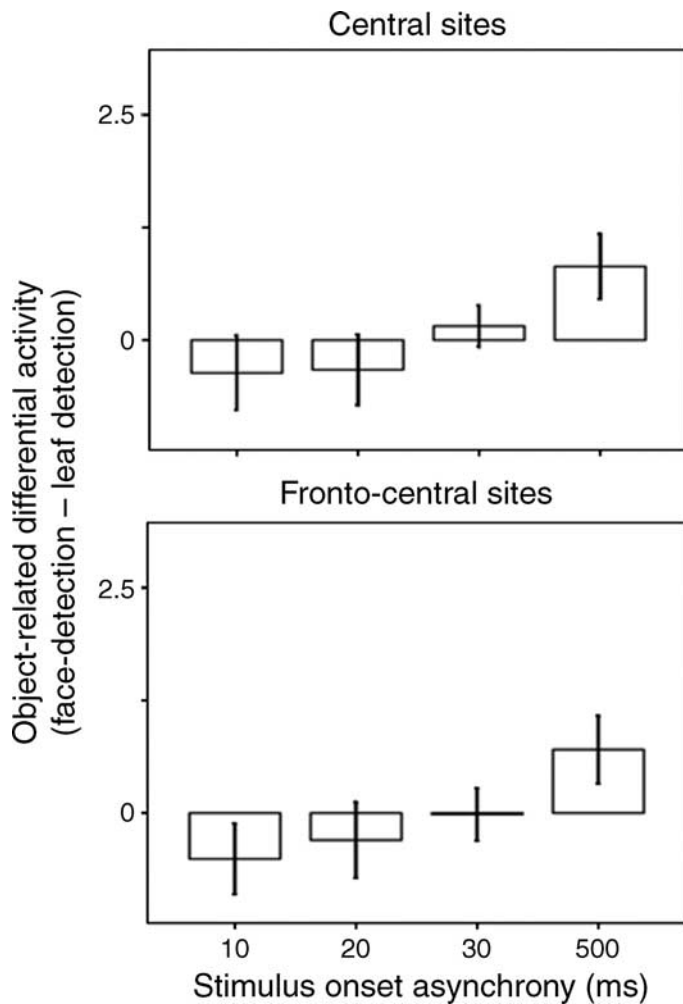
Figure 12. Object-related differential activities in (top) central and (bottom) fronto-central electrode sites, measured by subtracting evoked activities during the leaf detection trials from evoked activities during the face detection trials.

Since the N170 and P400 activity responses were measured by using two different methods (peak amplitude and averaged activity, respectively), the possibility remains that the differential effect of attention on the N170 and P400 components may be due to the different measurement methods employed. To address this possibility, the averaged activity for the N170 component was measured during the interval of 180–220 ms after the stimulus onset (±20 ms of the N170 peak time). Again, paired t-test revealed that N170 showed a significant attentional enhancement in response to face and leaf stimuli when they served as the task target ($t(51) < -2.32$, $p < 0.05$) and application of two-factor repeated measures ANOVA to the magnitude of N170 enhancement did not show any significant affect of the level of stimulus visibility level ($F(2.32, 27.9) = 0.42$, $p = 0.64$), the stimulus category ($F(1, 12) = 0.23$, $p = 0.61$), or the interaction between the two factors ($F(2.16, 26.0) = 0.43$,

$p = 0.67$). Thus, the differential effect of attention on N170 and P400 is likely not related to the method of ERP measurement.

Discussion

In this study, we showed the first evidences that attentional modulation due to switching between the two category detection tasks (face vs. leaf detection) could affect the amplitude of the N170 and P400 ERP components in two different ways. Here, the N170 and P400 ERP components were both enhanced when the stimulus was the task target relative to when the same stimulus served as a distracter. For the N170 potential, attentional modulation increases neural activities in response to the target categories independently of the level of stimulus visibility while the amount of P400 enhancement increased proportionally to the level of stimulus visibility. To the best of our knowledge, this is the first evidence in human studies showing a significant relationship between the level of stimulus visibility and the amount of activity enhancement due to attentional modulation at the neural population level (for reviews, see Kastner & Ungerleider, 2000; Luck et al., 2000).

The discrepancy between the effects of attentional modulation on early N170 and late P400 indicates that different top-down mechanism could be used to control sensory processing within one cognitive task. Previous ERP and MEG studies (Eimer, 2000a; Furey et al., 2006; Okazaki et al., 2008) only had shown that attentional modulation affects different time courses of brain activities in response to stimuli. In these studies, by directing object-based (Eimer, 2000a; Furey et al., 2006; Okazaki et al., 2008) and spatial-based (Eimer, 2000a) attentions toward face and non-face stimuli, both early and late brain activities were enhanced. In addition, attentional modulation had been found to be greater for late potentials (>190 ms) compared to earlier potentials (Eimer, 2000a, Furey et al., 2006). By showing that the magnitude of attentional modulation of P400, but not N170, varies with the level of stimulus visibility, our results extend these previous findings and suggest that not only the amount of modulation but also nature of attentional impact differs between early and late potentials.

Consistent to our findings, previous electrophysiological recordings in non-human primates have found a similar relationship between the amount of attentional modulation and stimulus physical properties at the level of single neurons. These studies have shown that the neural responses in the primate brain areas V1, MT, and V4 increase concomitant with parametric stimulus properties, such as image contrast, when attention is directed toward a stimulus within a neuron's receptive field (Martinez-
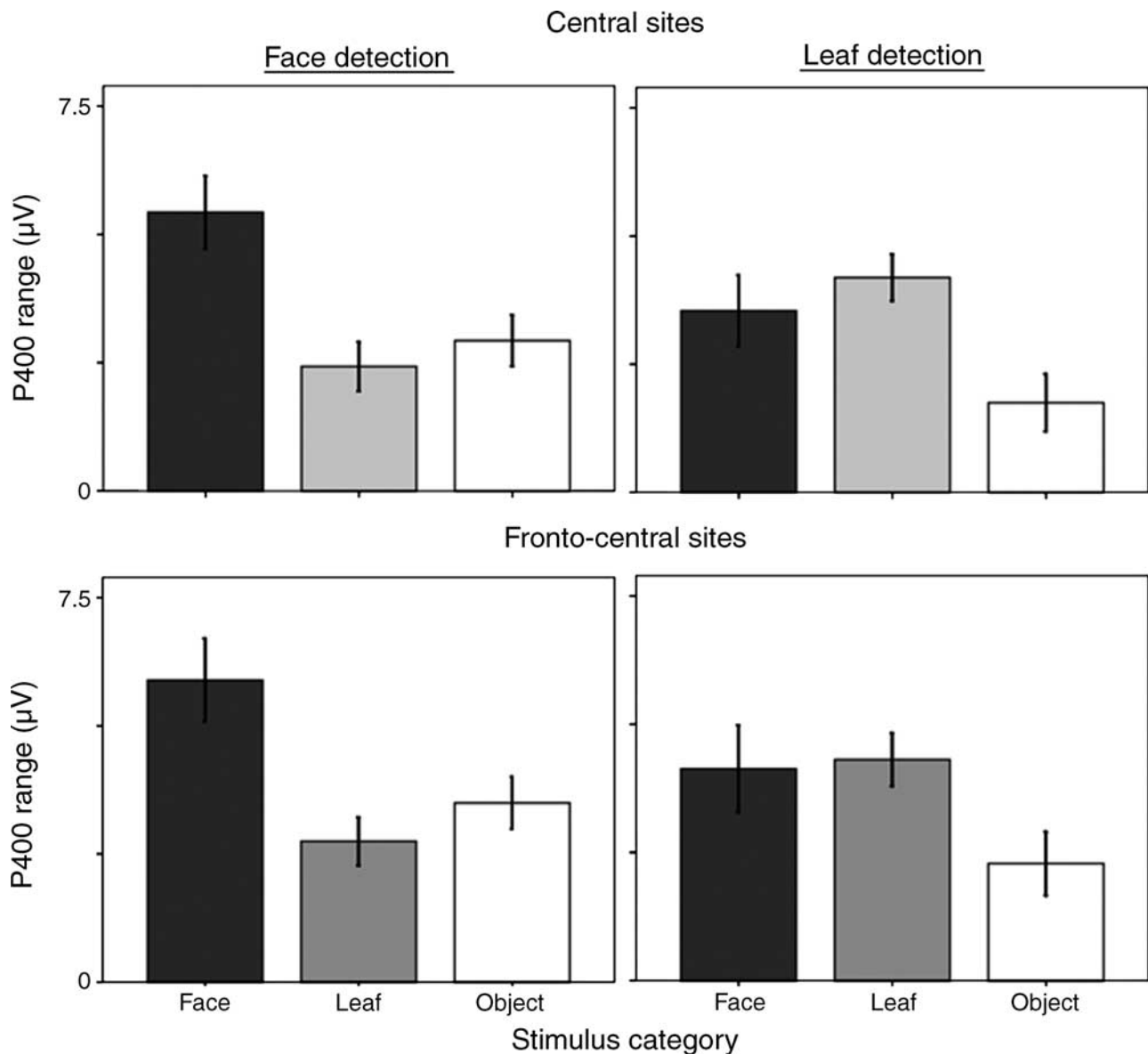
Figure 13. Range of the P400 ERP component recorded in the (top) central and (bottom) fronto-central electrode sites. In all panels, dark gray, light gray, and white bars correspond to the range of P400 activity when stimuli belonged to the face, leaf, and other objects sets, respectively. Error bars represent one standard error of the mean.

Trujillo & Treue, 2002; McAdams & Maunsell, 1999; Reynolds et al., 2000; Treue & Martinez-Trujillo, 1999). Although this multiplicative modulation could be observed in different brain areas (Martinez-Trujillo & Treue, 2002; McAdams & Maunsell, 1999), the exact mechanism responsible for producing such a modulation is not yet understood. For instance, some modeling studies have suggested that simple excitation and/or inhibition of neurons could result in the multiplicative modulation of neural activities (Murphy & Miller, 2003) while others have suggested a more complex mechanism, based on simultaneous neural inhibition and excitation, to be responsible for this type of activity modulation (Holt & Koch, 1997).

Regardless of the neuronal mechanism responsible for generating multiplicative modulation, it is still a matter of debate why two different types of activity modulation are observed and why only the amount of P400 activity enhancement varies with the level of stimulus visibility. This dichotomy could be due to the nature of processes linked to these ERP components. While earlier processes indexed by N170 component seems to be responsible for template matching, facial structure encoding, and/or category discrimination (Bentin et al., 1996; Curran et al., 2002; Eimer, 2000b; Philiastides & Sadja, 2006), later processes indexed by P400 are linked to processes such as object recognition and subordinate level object discrimination (Bentin & McCarthy, 1994; Curran et al., 2002; Trenner

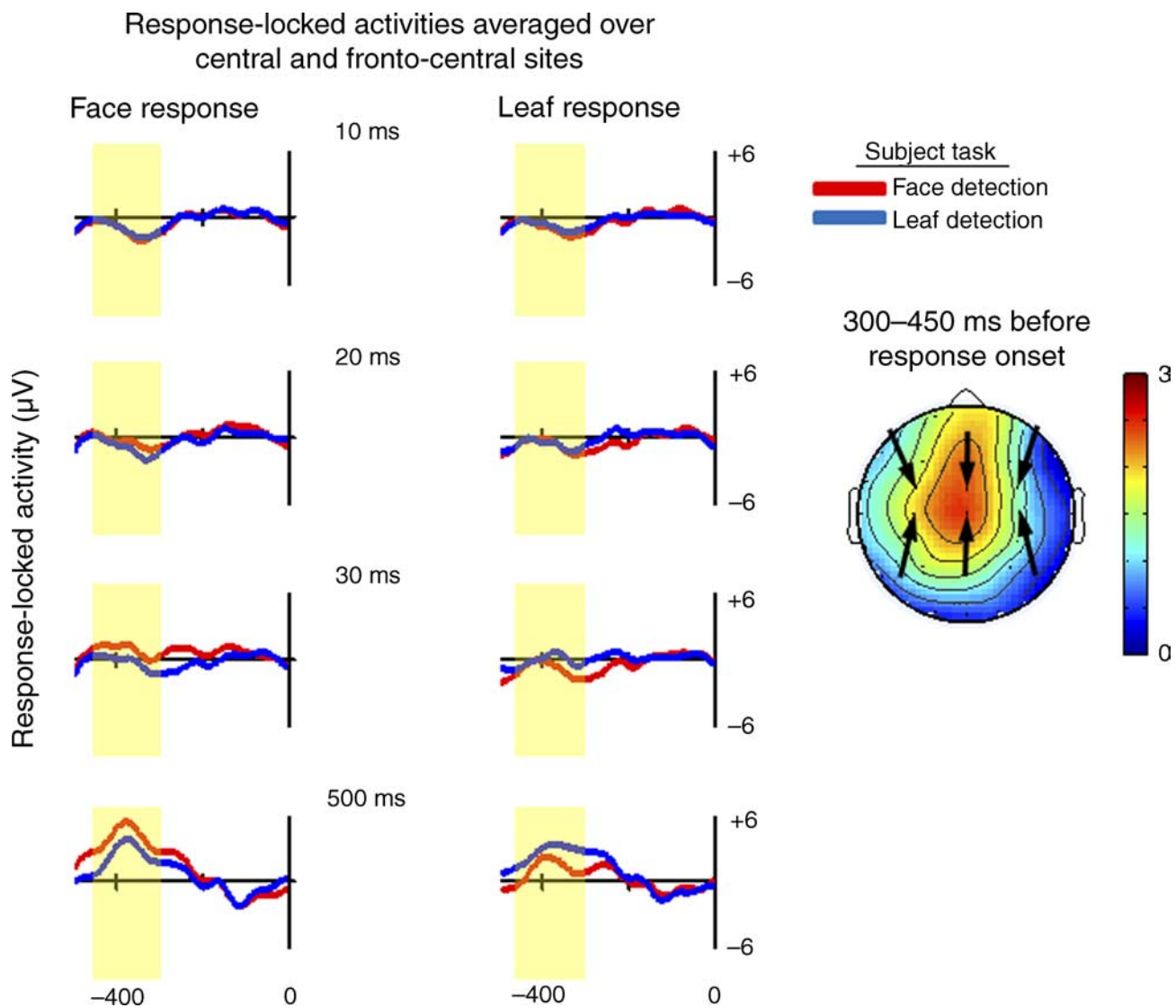## Response-locked activities averaged over central and fronto-central sites

Figure 14. Response-locked ERPs averaged over central and fronto-central electrode sites, in response to the (left) face and (right) leaf stimuli across different SOA conditions. Shaded areas show 300–450 ms before response onset, which were used for further comparisons of response-locked activities with stimulus-locked activities. Brain activity mapping shows the distribution of differential (Target − Distracter) response-locked brain activities averaged over face and leaf trials (SOA = 500 ms), evoked 300–450 ms before the response onset. Arrows indicate the location of central and fronto-central electrodes.

et al., 2004). It is also known from behavioral studies that object encoding and discrimination at the basic category level are less sensitive to the level of stimulus visibility compared to those processes responsible for encoding stimuli at subordinate levels (Grill-Spector & Kanwisher, 2005; Hegde, 2007).

Based on these electrophysiological and behavioral studies, it seems that attention enhances early potentials independently of the level of stimulus visibility, because processes underlying these activities encode basic aspects of a stimulus and this process can be done even when the presented stimulus is poorly visible. In contrast, attentional enhancement of late processes depends on the level of sensory information carried by stimuli. For these processes, indexed by late potentials, using constant activity enhancement seems not to be suitable because further processing of a visual object is only possible when this object is visible enough. Otherwise, modulation of brain activities with very low signal-to-noise ratio could lead to noise increase rather than signal enhancement.

Moreover, previous studies have suggested that late ERP components better represent those processes responsible for decision-making while earlier components represent purely stimulus-dependent processes (Philiastides et al., 2006). Although attention can modulate ERP components evoked as early as 100 ms after stimulus onset (Zhang & Luck, 2008), interactions between feedback processes and stimulus parameters are more expected

during later phases of evoked brain activities when stimuli are processed to some extent (i.e., early processes). These late processes usually show amplitude modulation correlated with the level of task difficulty (Philiastides et al., 2006) and/or onset time modulation correlated to subjects' response time (Makeig et al., 2004). Consequently, arranging evoked potentials relative to subjects' response onset could strengthen the amplitude of these late potentials and enhance the effect of experimental parameters. Here, although we have shown significant interaction between task and level of stimulus visibility, in late stages of brain activities (i.e., P400), we did not see any difference between stimulus-locked and response-locked activities. This lack of difference could be due to the fact that subjects' RT in our study remained invariant across experimental conditions and does not rule out the possibility that these potentials, at least partially, represent decision-related processes.

Besides effect of top-down control on target-related activities, our results also showed that general level of task difficulty can affect late potentials in response to non-target objects. In our experiment, subjects showed worse performance during face detection compared to leaf detection, indicating that the level of task difficulty was higher in the former. Although objects' (other than faces and leaves) relevancy to the subjects' task did not change between face and leaf detection trials, they evoked stronger P400 activity during face detection compared to leaf detection trials. Interestingly, the amount of this modulation also varied with the level of stimulus visibility. In other words, target-specific and general difficulty-dependent modulations of P400 seem to vary with the level of stimulus visibility. Although we have shown a clear effect of attention on occipito-temporal N170 component, two previous studies have suggested that object-selective attention has no effect on the amplitude of N170 ERP component. Using two different detection tasks, they have shown that object-selective attention modulates late ERP components but not N170 (Rousselet, Macé, Thorpe, & Fabre-Thorpe, 2007; Séverac-Cauquil, Edmonds, & Taylor, 2000). However, in those studies, authors have used high-contrast images with either long 400-ms presentation time (Séverac-Cauquil et al., 2000) or there has been a long blank interval after stimulus presentation (Rousselet et al., 2007), which increase the level of stimulus visibility and lower the task difficulty level in those studies. Eventually, it appears that subjects have detected target images among distracters easily and subjects' performances have been above 90% (Rousselet et al., 2007). In this condition, lack of N170 modulation is expected because attention does not affect neuronal activities of one sensory system unless that system was overloaded by the task demands (Luck et al., 2000). In total, these results support the notion that cortical generators underlying N170 component need to face more task demands in order to show any effect of attentional modulation compared to those generators whose activities generate later ERP components (Furey et al., 2006).

The other discrepancy between our results and other ERP studies of object detection tasks is that the brain mapping of P400 component in the current study seems to be slightly shifted toward more anterior electrode site while in previous studies, late target-related positive component (also known as P3b) usually has been detected in parietal and/or central electrode sites. On the basis of this mapping discrepancy, one may conclude that P400 could index other processes such as general motor preparation rather than those processes underlying target detection (e.g., see Makeig et al., 2004). However here, we have shown that the amplitude of P400 varies with the level of stimulus visibility and this variation was observed during both target and distracter trials. So, cortical generators indexed by P400 component seems to be sensitive to the stimulus visibility while motor activity was always the same within different trials and subjects had to respond by pressing one of two keys on a keypad independently of the level of stimulus visibility. Thus, motor preparation and/or other stimulus-independent processes are unlikely to be responsible for generating central and fronto-central P400. Moreover, response-locked activities showed a very similar pattern of activities, which means that motor-related activities could not be responsible for P400 modulation. Rather, shift in P400 activity distribution could be simply due to the mask presentation following each stimuli, which results in generating a slightly odd pattern of brain activity mapping not observed during paradigms with single stimulus presentation.

In conclusion, our results show that the mechanism of attentional modulation becomes increasingly dependent on the stimulus parameters through the course of brain activities. While earlier brain activities are modulated independent of the level of stimulus visibility, enhancement of later brain activities depends on this parameter as well as the level to which the stimuli are informative. This mechanism may avoid wasting processing resources for encoding those stimuli that are task relevant but not informative enough to be analyzed further.

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