

proposed. The former suggests the dysfunction of the dorsal (or M) pathway with sparing of the ventral (or P) pathway, which is related to the idea of “dorsal stream vulnerability” (Braddick, Atkinson, & Wattam-Bell, 2003). In contrast, the latter implies dysfunction of neurointegrative processing at a higher cortical level for both the dorsal and ventral pathways with preserved function of the lower level of dorsal and ventral pathways (before V1).

As mentioned above, our ERP results reveal that ASD adults have selective impairment of a higher level of the v-d (IPL) stream after V5/MT. Additionally, using visual evoked potentials (VEPs) with low contrast achromatic sinusoidal gratings, our recent study showed that the function of the lower level of dorsal pathways before V1 is preserved in ASD adults (4 out of 12 subjects also participated in the current study; Fujita, Yamasaki, Kamio, Hirose, & Tobimatsu, 2011). Therefore, our consecutive studies may partly support the “complexity-specific” hypothesis rather than the “pathway-specific” hypothesis, although we could not fully test these two hypotheses. Further VEP and ERP studies are needed to evaluate the function of the ventral pathway in ASD.

4.3. Methodological limitations

Although special care was taken when creating the coherent motion stimuli, our sample size was relatively small. Clinical diagnoses were performed based on extensive clinical interviews, and standard interview tools such as the ADI-R or ADOS-G were not used. Instead, we used a widely used scale (PARS) with high sensitivity and high specificity in Japanese populations to distinguish all ages of individuals with PDD (Kamio et al., 2006). Intellectual function was not assessed in control participants, but because they were recruited from college students and faculties and reported no developmental problems, their intellectual functioning was very likely to be within the normal range.

4.4. Conclusion

The current study indicates that the higher level of the dorsal motion pathway, particularly the v-d (IPL) pathway closely related to OF perception, is selectively impaired in ASD adults. Dysfunction of the v-d (IPL) stream may contribute to higher-level impairment of social cognition in ASD.

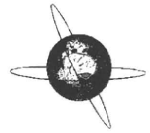
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Neural responses in the occipital cortex to unrecognizable faces

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ABSTRACT

Objective: Event-related potentials (ERPs) were recorded to examine neural responses to face stimuli in a masking paradigm.

Methods: Images of faces (neutral or fearful) and objects were presented in subthreshold, threshold, and suprathreshold conditions (exposure durations of approximately 20, 30 and 300 ms, respectively), followed by a 1000-ms pattern mask. We recorded ERP responses at Oz, T5, T6, Cz and Pz. The effects of physical stimulus features were examined by inverted stimuli.

Results: The occipital N1 amplitude (approximately 160 ms) was significantly smaller in response to faces than objects when presented at a subthreshold duration. In contrast, the occipitotemporal N170 amplitude was significantly greater in the threshold and suprathreshold conditions compared with the subthreshold condition for faces, but not for objects. The P1 amplitude (approximately 120 ms) elicited by upright faces in the subthreshold condition was significantly larger than for inverted faces.

Conclusions: P1 and N1 components at Oz were sensitive to subthreshold faces, which suggests the presence of fast face-specific process(es) prior to face-encoding. The N170 reflects the robustness of the face selective response in the occipitotemporal area.

Significance: Even when presented for a subthreshold duration, faces were processed differently to images of objects at an early stage of visual processing.

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1. Introduction

Faces are a source of extremely important social signals for humans, and contain complex visual information composed of various low-level visual features. Traditional models of face recognition have generally suggested three primary areas involved in face processing in the human brain (Haxby et al., 2000; Calder and Young, 2005). The fusiform gyrus (fusiform face area; FFA), the lateral occipital cortex (occipital face area; OFA), and the superior temporal sulcus (STS), are all considered to function as face-selective areas in the occipitotemporal cortices. Furthermore, evidence has emerged indicating that these areas exhibit functional specialization; the OFA for facial features, the FFA for identity, and the STS for changeable aspects of faces such as gaze direction (Tsao et al., 2008; Latinus and Taylor, 2006; Pitcher et al., 2007; Rhodes

et al., 2009). Several recent event-related potential (ERP) studies examined early face processing using manipulated face images. It was consistently reported that occipital P1/N1 responses occurring between 120 and 180 ms contributed to the detection of facial features, in experimental paradigms using spatially filtered images (Pourtois et al., 2005; Schyns et al., 2007; Nakashima et al., 2008a,b; Obayashi et al., 2009; van Rijsbergen and Schyns, 2009), mosaic faces (Goto et al., 2005), inverted faces (Itier and Taylor, 2002, 2004), and Mooney faces defined by shape-from-shading information (Latinus and Taylor, 2006; George et al., 2005). For faces to be fully recognized, output from several early visual information processing stages must already be integrated (Tarkiainen et al., 2002; Rossion et al., 2003; Latinus and Taylor, 2006). Hence, ERP signatures occurring approximately 100–180 ms after stimulus presentation that are distributed posterior to the N170 are related to ‘face categorization’ and appear to play a role in mediating holistic and configural face information (Liu et al., 2002; Herrmann et al., 2004).

To explore the early stages of face processing, it is necessary to quantitatively manipulate the level of stimulus recognizability. Various methods have been employed to control subjects’ ability to overtly perceive a visual stimulus, including binocular rivalry (Moutoussis and Zeki, 2002), interocular suppression (Jiang and

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He, 2006; Jiang et al., 2009) and perceptual masking (Bacon-Mace et al., 2005; Martens et al., 2006; Kouider et al., 2008). Perceptual masking has been used to differentiate between automatic and controlled (top-down) processes, and to interrupt higher processing and prevent the overt recognition of stimuli. Recent ERP and functional magnetic resonance imaging (fMRI) studies have reported that viewing masked faces that could not be overtly perceived elicits activity in occipitotemporal areas (Trenner et al., 2004; Martens et al., 2006; Henson et al., 2008; Kouider et al., 2008; Jiang and He, 2006). These studies reported the suppression or enhancement of masked faces was observed in the FFA and OFA, suggesting that neural activity in the occipital cortex does not always correlate with the overt recognition of stimuli as faces.

To address this issue, we examined the role of occipital visual areas in the recognition of briefly presented faces followed by a pattern mask, using different presentation durations to manipulate whether subjects were able to recognize them as faces or not. We systematically presented faces at durations that were under or over the threshold of subjective visibility (determined by adjusting stimulus duration) followed by the presentation of a pattern mask. ERPs from occipital and temporal areas were recorded simultaneously to examine visual activity at early stages of face processing. The study involved two main manipulations: first, to determine the effects of stimulus duration on ERP components, we used subthreshold, threshold, and suprathreshold presentation durations of approximately 20, 30 and 300 ms, respectively. Second, stimulus orientation was inverted to examine whether the physical similarity of the stimuli affected the results.

2. Methods

2.1. Subjects

Eleven healthy volunteers (five females, aged 20–27 years) participated in two experiments. All subjects were right handed and had normal or corrected-to-normal vision. Written informed consent was obtained from each subject after an explanation of the purpose and procedures to be used in the experiment. The experimental procedures were approved by the Ethics Committee of the Graduate School of Medical Sciences, Kyushu University.

2.2. Stimuli and apparatus

Photographs of eight fearful and eight neutral faces from 16 individuals (eight men and eight women) were taken from Matsumoto and Ekman (1988)'s standardized set of Japanese and Caucasian Facial Expressions of Emotion and Neutral Faces (JACFEE and JACNeuF; Fig. 1a). Half of the photographs depicted Asian faces, while the other half were Caucasian faces. All photographs showed a full-frontal view of the face. Eight objects were used as object stimuli (Fig. 1a). We used fearful faces, neutral faces, and non-face objects (as non-target stimuli) with three different stimulus durations in Experiment 1, to study the effect of stimulus duration. In Experiment 2, we used upright and inverted images of fearful faces, neutral faces, and objects presented at a subthreshold duration, to study the effect of inversion. A line drawing of a train was used as a target stimulus (Fig. 1b). All photographs were grayscale, sized 1000 × 660 pixels (visual angle of 17.6° horizontally and 11.7° vertically), and had an average stimulus luminance of 14.8 cd/m². For a pattern mask, we used a 1024 × 768 pixel noise pattern generated with Adobe Photoshop 7.0. A DELL OptiPlex GX260 computer which mounted VSG2/5 (The Math Works, Cambridge Research Systems Ltd.) controlled stimulus presentation and exposure duration. A 17-inch CRT monitor (SONY Trinitron Multiscan G220) with a refresh rate of 100 Hz was used for

stimulus presentation. Electroencephalogram (EEG) and electrooculogram (EOG) data were analyzed using MTS Signal Basic Light 2100 in IBM NetVista A40p (6841-EEJ).

2.3. Tasks and procedures

The experiment was conducted in a dimly lit, electrically shielded room. Subjects sat in front of the monitor at a viewing distance of 114 cm. The stimuli were preceded and followed by pattern masks of 1000 ms in duration (Fig. 1b). The target, which appeared in 10% of the trials in each block, was presented for 600 ms to shift subjects' attention away from the non-target stimuli (faces or objects). Subjects were instructed to respond by pressing the button as quickly and accurately as possible when the target stimulus was presented on the screen. Each experimental condition consisted of five blocks of 1000 trials, one block of 200 trials; 60 fearful faces, 60 neutral faces, 60 objects, and 20 targets. The stimuli were presented in a random order.

Experiment 1 was designed to examine whether ERPs elicited by faces that were presented too briefly to be recognizable as faces differed from ERPs elicited by faces presented for a recognizable duration. To this end, we presented images at three different durations: subthreshold (threshold minus 10 ms), threshold (the duration ranged from between 20 to 50 ms between subjects), and suprathreshold (300 ms). In addition, we used fearful faces as well as neutral faces to examine whether emotional content influenced early subthreshold ERP signatures. The order of presentation of the three conditions was fixed for all subjects; subthreshold, threshold and then suprathreshold. This order was used so that the content of the masked stimuli in the subthreshold condition would not have been revealed by allowing participants to experience the suprathreshold condition beforehand.

Experiment 2 was conducted to determine whether ERPs elicited by briefly presented unrecognizable faces resulted from face-specific neural responses rather than from the similarity of the physical features. To this end, we changed the stimulus orientation (upright and inverted) and presented them at the subthreshold duration level. The threshold was determined for each subject using the method of limits with an ascending series (see Table 1). The pattern mask was presented for 1000 ms. Subjects took part in the experiment for 3 days in total; 2 days for Experiment 1 and another 1 day for Experiment 2.

2.4. Threshold settings (Table 1)

The threshold setting experiment was conducted to determine the presentation duration at which subjects were able to recognize whether the masked stimuli were faces or objects. In this task, we use an ascending series of trials to prevent subjects from perceiving the content of masked stimuli, because a descending series with a duration exceeding threshold would allow subjects to see that the stimuli contained neutral faces, fearful faces and non-face objects. In each trial, subjects were randomly presented with a neutral face, a fearful face, or an object followed by a pattern mask, and verbally reported which type of stimulus had been presented. The stimulus presentation began with a duration of 10 ms, with duration increased thereafter in 10 ms steps. Stimuli were presented 20–30 times at each stimulus duration. This procedure was followed by Experiments 1 and 2. The threshold-setting stimuli were not used for the ERP experiments. In Table 1, threshold refers to the presentation duration threshold at which subjects first reported that they saw a human-like silhouette (e.g., a silhouette of a human head and shoulders). The total mean and SD represent the average of two measurements.

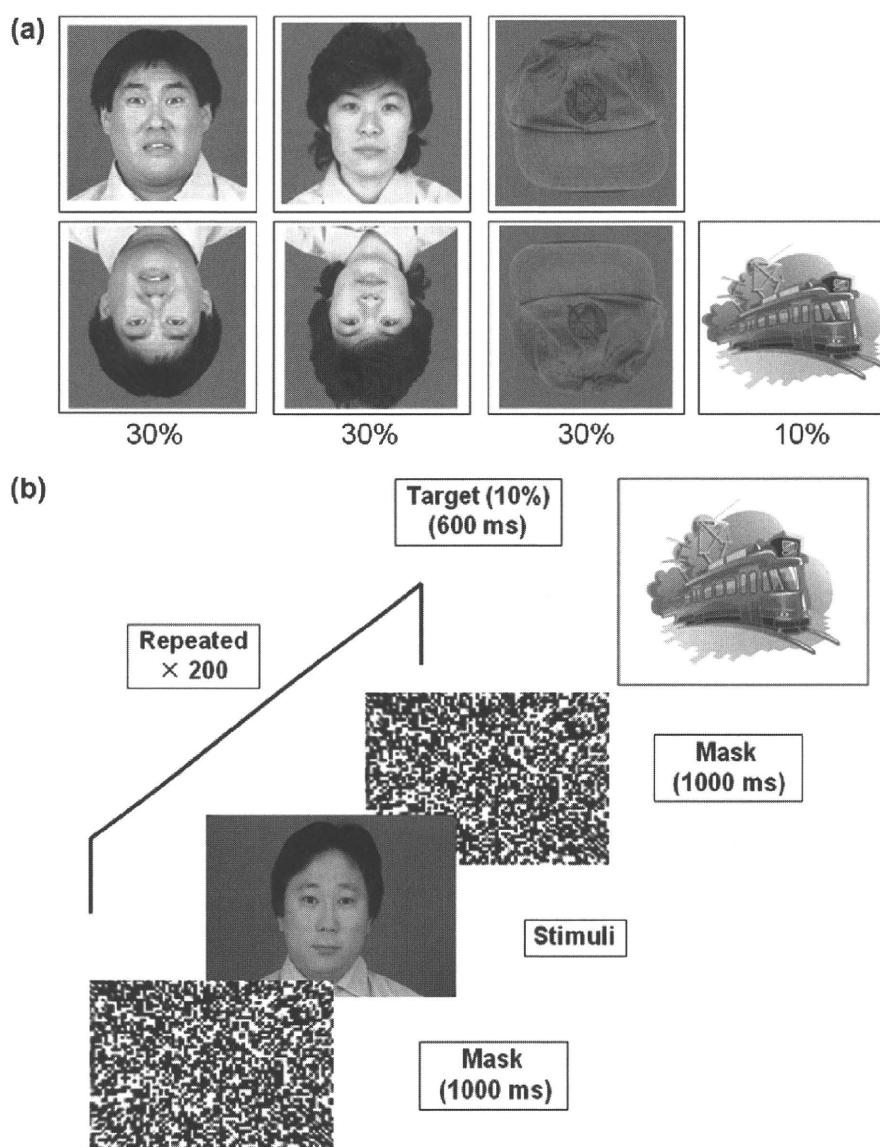


Fig. 1. (a) Representative examples of neutral face, fearful face, and object stimuli used in the experiment. (b) Experimental procedures. The faces and objects were followed by a 1000 ms pattern mask without a blank. The target appeared in 10% of the trials in each block, and was presented for 600 ms to draw subjects' attention away from the non-target stimuli.

2.5. ERP recordings and data analysis

Because we sought to extract ERP responses from early-stage visual processing areas, we selected five scalp locations (Oz, Cz, Pz, T5 and T6 according to the international 10–20 system) for ERP recording. An electrode on the nose tip was used as a reference. Horizontal and vertical EOG was also recorded, using four electrodes placed over the outer canthi and in the superior and inferior areas of the orbit. Electrode impedance was kept below 5 k Ω throughout recording. ERP and EOG data were filtered with a band-pass filter of 0.05–200 Hz, and sampled at a rate of 1.67 kHz. Averaged waveforms were then low-pass filtered at 30 Hz without phase shifting. For the ERP analysis, stimulus epochs began 60 ms prior to stimulus onset, and continued for 560 ms after. Trials in which eye blinks or other artifacts such as α waves (defined as a wave for which voltage exceeded $\pm 50 \mu\text{V}$ at any electrode) were excluded from the analysis.

We first focused on ERP components measured over occipital areas. At Oz, the first negative peak at about 80 ms after stimulus onset was defined as an 'early negativity' (eN) and the following positive peak at approximately 100 ms after the stimulus onset was defined as the occipital P1. The negative peak at approximately 150 ms following the P1 was defined as the occipital N1. We defined the N170 as a negative peak occurring at approximately 170 ms at the occipitotemporal site after stimulus onset. The amplitudes and latencies of the P1 and N1 at Oz and N170 at T5 and T6 were measured using a 60 ms pre-stimulus period as a baseline.

To analyze the latency of electrophysiological responses in Experiment 1, we conducted a three-way repeated measures ANOVA (3 [electrodes: Oz, T5 and T6] \times 3 [stimulus types: neutral faces, fearful faces and objects] \times 3 [stimulus duration: subthreshold, threshold and suprathreshold]) to ensure that the component recorded at Oz differed from that recorded at T5 and T6. For the

Table 1
Results of threshold setting in each subject.

Exp 1		Exp 2	
	Threshold		Threshold
S 1	40	S 1	30
S 2	30	S 2	40
S 3	30	S 3	30
S 4	30	S 4	40
S 5	40	S 5	30
S 6	30	S 6	30
S 7	20	S 7	40
S 8	30	S 8	30
S 9	50	S 9	20
S 10	30	S 10	40
S 11	40	S 11	20
Mean	33.6	Mean	31.8
SD	8.1	SD	7.5
Total mean	32.7		
Total SD	7.8		

S: subject.

amplitude analysis, we conducted a two-way repeated measures ANOVA (3 [stimulus type: neutral faces, fearful faces and objects] \times 3 [stimulus duration: subthreshold, threshold and suprathreshold]) for the P1, N1 and the N170, respectively. In Experiment 2, we measured the amplitude and latency of the P1 in each orientation. For the latency and amplitude analyses, we conducted two-way repeated measures ANOVAs for the P1, N1 and N170 (3 [stimulus type: neutral faces, fearful faces and objects] \times 2 [stimulus orientation: upright, inverted]). Bonferroni's correction was used for multiple comparisons in a *post hoc t*-test.

We further evaluated the time-course of the differences in responses to faces and objects systematically to determine the onset of the face effects. Thus, we analyzed the confidence intervals of ERP differences of faces (neutral/fearful) and objects over time, in accord with the methods of Rousselet et al. (2008). Analyses were performed on the mean amplitudes of responses to faces ((neutral + fearful)/2) and objects of Oz, T5 and T6 in Experiment 1,

and the response to upright faces and inverted faces at Oz in Experiment 2. These responses were examined over 51 successive time windows (20 sampling points per 0.6 ms, resulted in 11.4 ms each) across subjects, from the beginning (–60 ms) to the end (560 ms) of each epoch. The differences between the mean response amplitudes for face and object stimuli (or upright and inverted faces in Experiment 2) were calculated across subjects independently for each time-window and condition. The 95% percent confidence interval was then computed ($\alpha = 0.05$). The difference between the two sample means in each time window was considered significant if the 95% confidence interval did not include zero.

In addition, the reproducibility of responses in the subthreshold presentation was examined in five subjects over two recording sessions.

3. Results

3.1. Subjects' attention

In all experimental conditions, the P300 was exhibited only in response to the target stimulus. This finding confirmed that subjects' attention was not directed to non-target stimuli in either experiment (Fig. 2).

3.2. Durations of the subthreshold and threshold levels

Subjects' thresholds differed from 20 to 50 ms. The mean durations were 33.6 ms (SD = 8.1 ms) in Experiment 1 and 31.8 ms (SD = 7.5 ms) in Experiment 2, respectively. The mean subthreshold durations across subjects were 23.6 ms in Experiment 1, and 21.8 ms in Experiment 2 (see Table 1 for details).

3.3. Experiment 1

Fig. 3a shows the grand averaged waveforms of the occipital P1 and N1, while Fig. 3b and c represent the grand averaged waveforms of the N170 recorded at T5 and T6. At Oz, the eN, P1 and

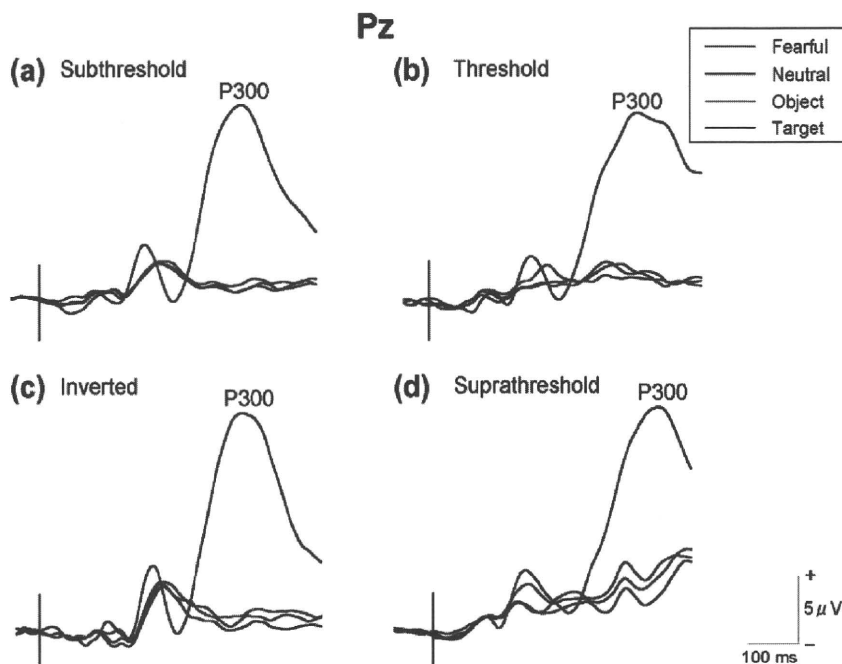
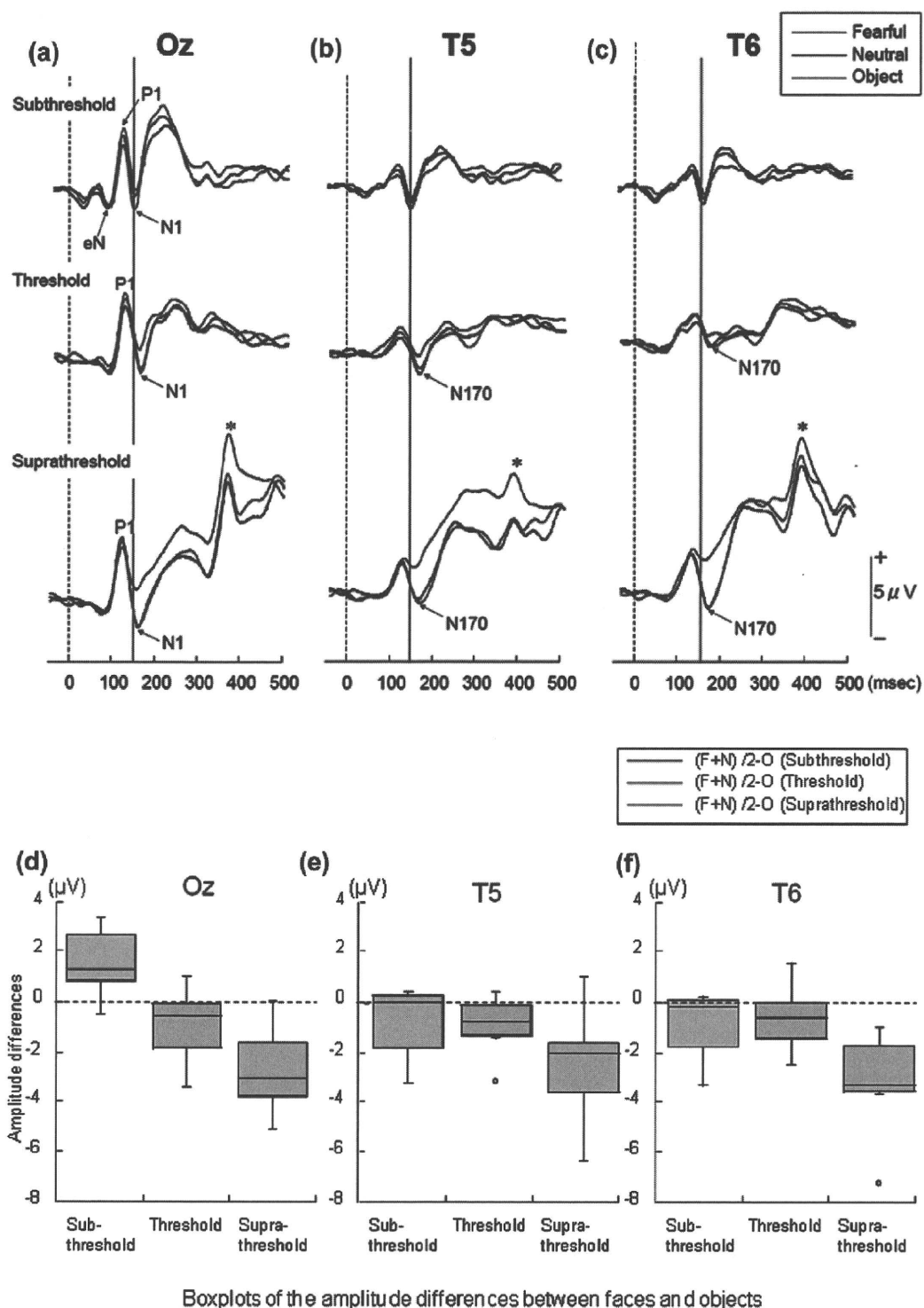


Fig. 2. ERP responses to the target stimuli at Pz across the two experimental conditions. The P300 appeared only in response to the target in all stimulus conditions.



Boxplots of the amplitude differences between faces and objects

Fig. 3. Grand averaged waveforms of the responses at Oz (a), T5 (b) and T6 (c) for neutral faces, fearful faces and objects in the subthreshold, threshold and suprathreshold conditions ($n = 11$). The black line indicates the peak of the occipital N1 response elicited by subthreshold stimuli. The off-response (asterisks) of the visual stimuli was observed at approximately 400 ms (i.e., about 100 ms after the stimulus offset) in the suprathreshold condition. Boxplots of ERP amplitude differences between faces (i.e., (fearful + neutral)/2) and objects in the occipital N1 at Oz (d) and in the temporal N170 at T5 (e) and T6 (f) ($n = 11$). The horizontal line indicates the median values. The boxes extend from the upper to the lower quartile values. The whiskers show the most extreme points within 1.5 times the inter-quartile range. Blue circles indicate outliers. The black dotted lines indicate the point where no amplitude differences between faces and objects were present. The 'faces-objects' difference in the N1 amplitude in the subthreshold condition only appeared at Oz (d). In contrast, 'faces-objects' difference for the N170 amplitude was only evident in the suprathreshold condition. Abbreviations: (F + N)/2-O = (fearful + neutral)/2-object. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

N1 were examined for the three stimulus durations. The P1 amplitude was not significantly affected by the stimulus type ($F[2, 20] = 3.027, p = .096$) or stimulus duration ($F[2, 20] = 2.403, p = .134$). Although the interaction did not reach significance ($F[2, 20] = 1.743, p = .185$), P1 amplitudes elicited by neutral faces and fearful faces tended to be larger than those elicited by objects in the subthreshold condition (neutral faces vs. objects [$p = .013$], fearful faces vs. objects [$p = .023$]). N1 amplitude differed significantly between faces and objects in the subthreshold condition ($F[2, 20] = 17.275, p = .00087$). The N1 amplitude elicited by objects was larger than that for neutral faces and fearful faces in the subthreshold durations (neutral faces vs. objects [$p = .021$], fearful faces vs. objects [$p = .022$]), whereas the N1 for neutral faces and fearful faces was larger than that elicited by objects with presentations at threshold and suprathreshold durations (threshold: neutral faces vs. objects [$p = .031$], fearful faces vs. objects [$p = .034$], suprathreshold: neutral faces vs. objects [$p = .002$], fearful faces vs. objects [$p = .006$], Fig. 3a and Table 2).

For N1 and N170 latencies, the main effect of stimulus duration was significant ($F[2, 20] = 6.107, p = .011$). Multiple comparisons revealed that the duration of the N1 in the subthreshold condition was significantly shorter than in the threshold and suprathreshold conditions (subthreshold vs. threshold [$p = .025$], subthreshold vs. suprathreshold [$p = .031$], respectively, See Fig. 3, Tables 2 and 3). Neither the effect of electrode position ($F[2, 20] = 3.224, p = .072$) or stimulus type ($F[2, 20] = 1.923, p = .177$) were significant. The N170 amplitude did not differ significantly between faces and objects in the subthreshold condition at T5 or T6. However, significant face-object differences appeared when the duration levels increased, shown in the results of the ANOVA given in Tables 2 and 3. Boxplots of the amplitude differences between faces ((fearful + neutral)/2) and objects at Oz, T5 and T6 are shown in Fig. 3d–f. The ‘faces-objects’ difference for N1 amplitude in the subthreshold condition only appeared at Oz (Fig. 3d). In contrast, the ‘faces-objects’ difference for the N170 amplitude was only evident in the suprathreshold condition (Fig. 3e and f).

3.4. Experiment 2

Grand averaged waveforms of occipital P1 and N1 are shown in Fig 4a. From the waveforms, it can be seen that face-object differences were evident for both the P1 and N1. Interestingly, P1 activity was markedly different to N1 activity, with faces eliciting a larger P1 than object stimuli. ANOVA confirmed the effects on the P1 and N1 of upright stimuli, revealing a significant main effect of orientation on P1 amplitude ($F[2, 20] = 10.293, p = .009$, Fig. 4a and b), such that the P1 was significantly larger for the upright condition than for the inverted condition ($p = .009$). In addition,

there was a significant interaction of stimulus type \times orientation ($F[2, 20] = 7.982, p = .014$), such that P1 amplitudes for neutral faces and fearful faces significantly differed between the upright and inverted conditions (neutral faces; $p = .004$, fearful faces; $p = .003$). However, P1 amplitude for the objects was not significantly different between the upright and inverted conditions ($p = .351$). The results revealed no significant main effect of either face orientation or stimulus type on P1 latency.

We found a significant main effect of stimulus orientation on N1 amplitude ($F[1, 10] = 5.433, p = .042$, Fig. 4c), such that N1 amplitude was significantly smaller in the upright than the inverted condition ($p = .042$). There was a significant interaction of stimulus type \times orientation ($F[2, 20] = 4.874, p = .033$). Upright faces and fearful faces elicited smaller amplitudes than inverted faces (neutral faces; $p = .013$, fearful faces; $p = .028$), whereas the N1 amplitude for the objects was not significantly different between upright and inverted conditions ($p = .56$). There was no significant main effect of either image orientation or stimulus type on the latency of responses. In addition, there was no effect of stimulus type or orientation on the N170 amplitude. Finally, there was no significant main effect of electrode on N170 latency. Boxplots of the amplitude differences between faces ((fearful + neutral)/2) and objects of P1 and N1 are shown in Fig. 4b and c. The P1 amplitude difference between faces and objects was only present for the upright stimuli (Fig. 4b). Similarly, the N1 amplitude difference between faces and objects was only present for upright stimuli (Fig. 4c).

3.5. Time-course analysis of ERP differences between faces and objects

In Experiment 1, the amplitude of the face-object differences began at 158 ms (time windows of 19) after stimulus onset in the subthreshold and suprathreshold conditions, and 170 ms (time windows of 20) in the threshold condition (Fig. 5). Face-object differences did not appear at any time-windows before N1 or N170 (from approximately 158 to 170 ms), suggesting that the pattern mask totally blocked the perception of faces up to about 160 ms (see Discussion). In Experiment 2, significant differences between upright and inverted faces appeared from 110 to 145 ms after the stimulus onset in the subthreshold condition (Fig. 6). In the subthreshold duration, face orientation had a significant effect on occipital responses from 110 ms, approximately 30 ms earlier than the effect of stimulus duration.

3.6. Reproducibility of the responses in the subthreshold presentation

In five subjects, we conducted two recording sessions with subthreshold stimulus presentation. The pattern of responses was highly similar between the two measurement sessions. Although

Table 2
Mean amplitudes (μV) and latencies (ms) of P1 and N1 for perception of faces (fearful and neutral) and objects.

Condition	Stimuli	P1		N1	
		Amplitude	Latency	Amplitude	Latency
Subthreshold	Fearful	5.4 ± 1.5^a	127.2 ± 5.8	-2.7 ± 1.3^a	158.6 ± 7.6
	Neutral	5.2 ± 1.5^b	127.3 ± 6.3	-2.8 ± 1.4^b	156.4 ± 11.4
	Object	3.7 ± 1.1^{ab}	125.2 ± 5.9	-3.6 ± 0.9^{ab}	163.0 ± 10.1
Threshold	Fearful	5.1 ± 1.8	121.3 ± 8.6	-1.4 ± 1.3^a	169.5 ± 6.4
	Neutral	4.7 ± 1.5	120.9 ± 8.0	-1.3 ± 0.9^b	169.8 ± 6.0
	Object	5.2 ± 1.9	120.6 ± 7.9	-0.4 ± 1.1^{ab}	169.0 ± 8.1
Suprathreshold	Fearful	5 ± 1.7	134.1 ± 10.0	-3.1 ± 2.6^a	172.1 ± 7.0
	Neutral	4.9 ± 1.3	124.5 ± 3.3	-2.6 ± 2.1^b	172.7 ± 8.1
	Object	4.7 ± 0.9	126.5 ± 5.4	0.3 ± 2.0^{ab}	173.2 ± 12.1

Values are means \pm SD. $n = 11$.

^a Significant effects of multiple comparisons between fearful vs. object ($p < .05$).

^b Significant effects of multiple comparisons between neutral vs. object ($p < .05$).

Table 3
Mean amplitudes (μV) and latencies (ms) of N170 for perception of faces (fearful and neutral) and objects.

Condition	Stimuli	T5		T6	
		Amplitude	Latency	Amplitude	Latency
Subthreshold	Fearful	-2.1 ± 0.7	159.8 ± 5.8	-2.3 ± 0.7	159.4 ± 5.0
	Neutral	-2.3 ± 0.6	157.4 ± 6.1	-2.4 ± 0.7	160.3 ± 7.4
	Object	-2.5 ± 0.8	158.4 ± 7.0	-2.9 ± 0.8	159.9 ± 7.4
Threshold	Fearful	-1.8 ± 0.6	175.7 ± 6.9	-2.1 ± 1.6^a	176.6 ± 8.7
	Neutral	-1.9 ± 0.4	176.7 ± 6.4	-1.8 ± 1.1^b	172.7 ± 8.2
	Object	-1 ± 0.4	176.9 ± 9.1	$-0.6 \pm 0.8^{a,b}$	174.6 ± 9.0
Suprathreshold	Fearful	-2.6 ± 1.9^a	174.3 ± 7.5	-2.5 ± 1.6^a	174.1 ± 9.0
	Neutral	-1.7 ± 1.4^b	174.3 ± 7.6	-2.1 ± 1.1^b	177.8 ± 7.2
	Object	$0.6 \pm 1.4^{a,b}$	182.1 ± 9.7	$0.5 \pm 1.1^{a,b}$	185.3 ± 10.2

Values are means \pm SD. $n = 11$.

^a Significant effects of multiple comparisons between fearful vs. object ($p < .05$).

^b Significant effects of multiple comparisons between neutral vs. object ($p < .05$).

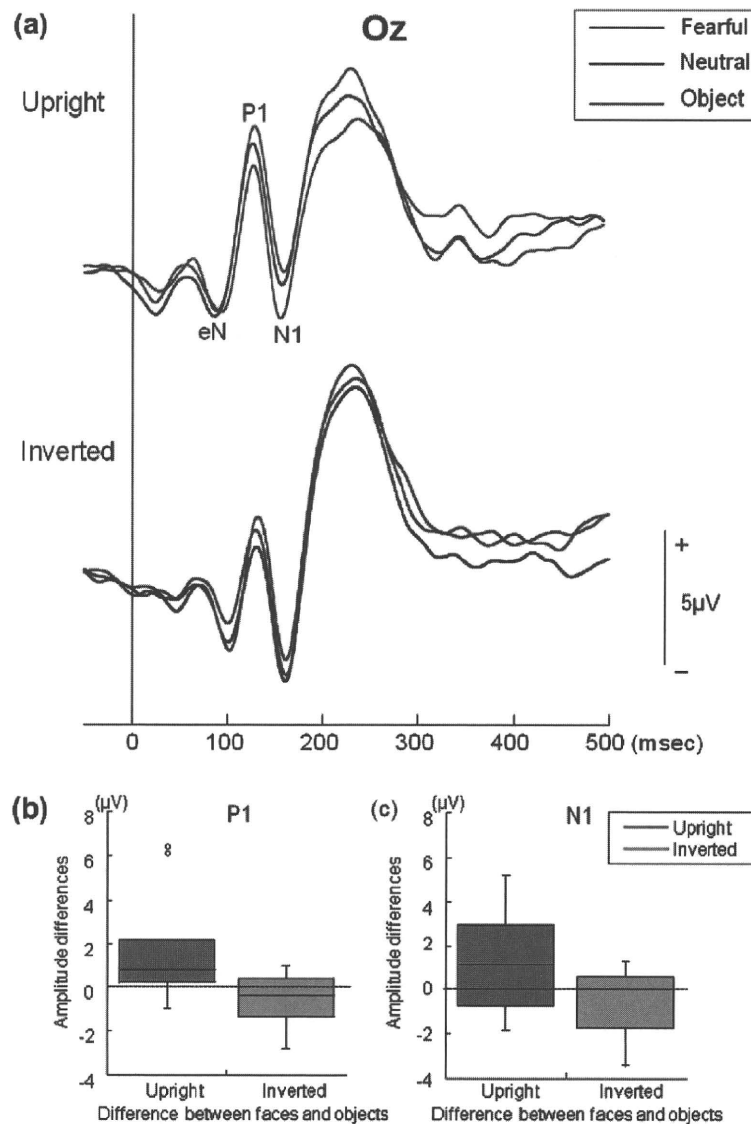


Fig. 4. (a) Grand averaged waveforms of the ERP responses for the faces, the fearful faces, and the objects at Oz in the subthreshold upright and inverted conditions in Experiment 2. (b) Boxplots of the ERP amplitude differences between faces (i.e., (fearful + neutral)/2) and objects at occipital P1 ($n = 11$). The P1 amplitude difference between faces and objects was only present for upright stimuli. (c) Boxplots of the ERP amplitude difference between faces (i.e., (fearful + neutral)/2) and objects at occipital N1 ($n = 11$). The N1 amplitude difference between faces and objects was only significant for upright stimuli.

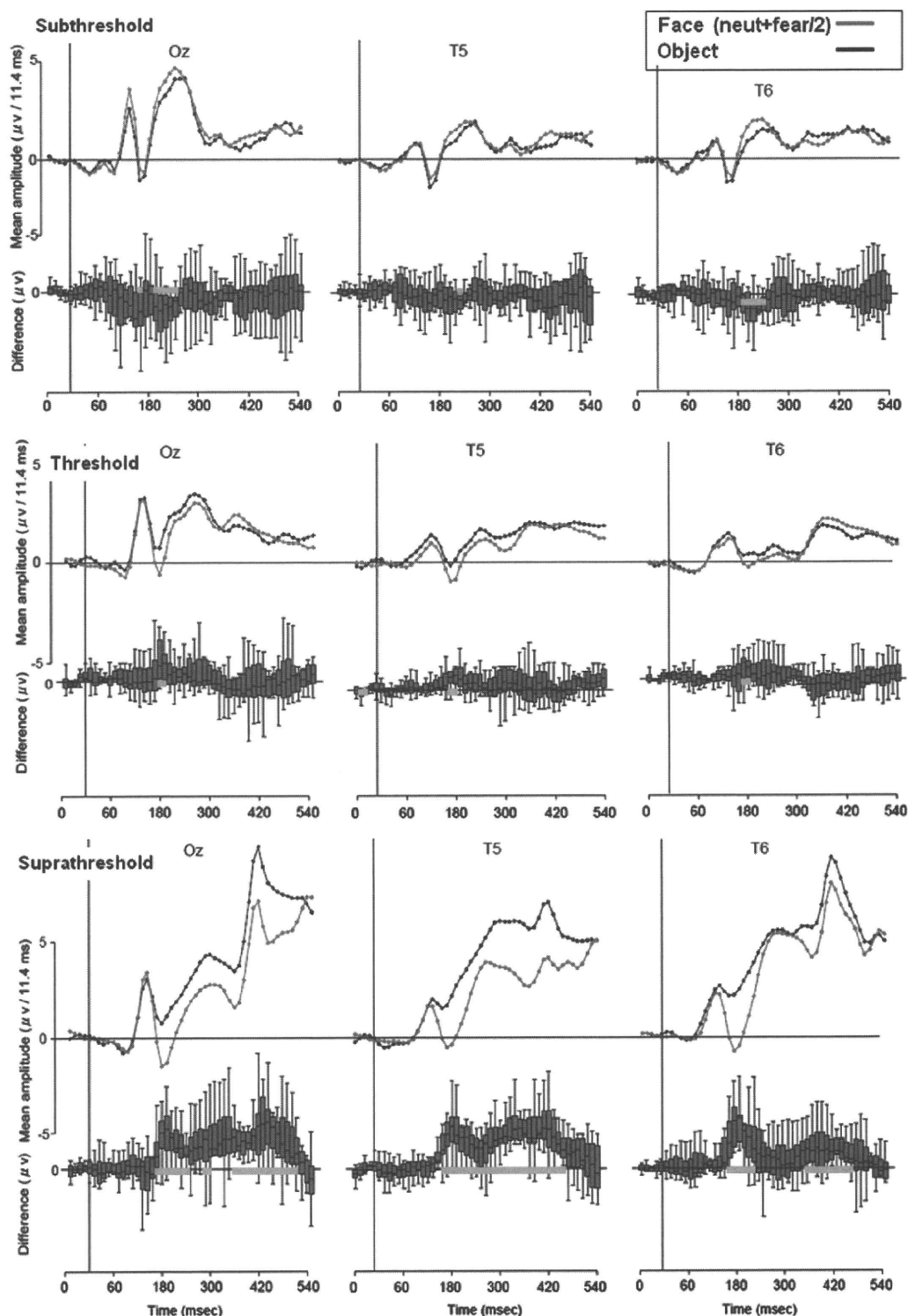


Fig. 5. Time-course analysis of the face-object differences among each condition in Experiment 1. For each cell, the red boxplots show the difference between the conditions plotted in red and black circles (each represents the time windows of the mean amplitudes per 20-samplepoints (approximately 11.4 ms) faces and the objects, respectively). The shaded gray area around the red difference boxplots shows the confidence interval of the difference between the two conditions. For each subplot, the horizontal black line indicates the median value. The boxes extend from the upper to the lower quartile values, and each bar represents the minimum and the maximum values. When the confidence interval does not include zero, the difference was significant, as indicated by the thick horizontal bright blue lines. Overall, the time-course analysis indicated significant differences between responses to different image types that started at 158 ms after stimulus onset in the subthreshold and suprathreshold conditions, and at 170 ms in the threshold condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

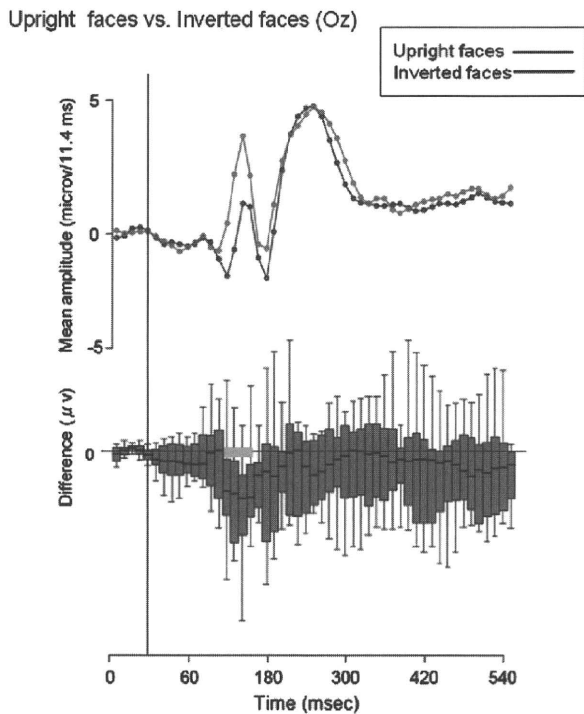


Fig. 6. Time-course analysis of the differences between upright and inverted faces in Experiment 2 (see legends of Fig. 5 for detailed explanations). Note that the significant differences between upright and inverted faces appeared from 110 to 145 ms after the stimulus onset in the subthreshold condition.

the sample size was too small to allow for statistical testing, visual inspection revealed only minor differences in amplitude between the two data sets (data not shown).

4. Discussion

In the current study, we employed a visual masking paradigm with briefly presented masked faces and objects to examine the role of occipital areas at an early stage of face-specific processing. By presenting faces below and above the threshold of recognition for each subject, we found that two major ERP components, the P1 and N1 (which reflect early face processing in occipital areas) were sensitive to masked faces that were presented at durations below the threshold at which they could be distinguished from objects.

4.1. P1 augmentation for invisible masked faces

When images were presented below the threshold duration of recognition, P1 amplitude was augmented for upright faces, but not for objects. This difference between faces and objects disappeared when stimuli were inverted. Time-course analyses further confirmed that face orientation affected responses from 110 to 145 ms over occipital areas, even when face stimuli were presented below the threshold of recognition. To our knowledge, this is the first report of occipital P1 sensitivity to inversion in subthreshold faces. The face inversion effect, delayed P1 latency and prolonged and enhanced N170 amplitude we observed are in accord with previous reports (Bentin et al., 1996; Rossion et al., 1999; Itier and Taylor, 2002, 2004). The orientation sensitivity of the P1 appeared to be opposite to the face inversion effects found

in the N170 over occipitotemporal regions for images presented for a recognizable duration. The face inversion effect is conventionally explained as resulting from a disruption of configural information processing, principally at the encoding stages of face processing (Yin, 1969; Tanaka and Farah, 1993). However, the inversion effect has not been found to occur when pictorial face images (e.g., Mooney faces, schematic faces, and pointillized faces) are used (Sagiv and Bentin, 2001; George et al., 2005; Linkenkaer-Hansen et al., 1998). The inversion of pictorial stimuli has been reported to disrupt processing of the meaning of the face representation, which alters subjects' recognition of the stimulus as a face. Moreover, psychophysical experiments have shown that upright and inverted faces are represented differently under subthreshold conditions, such that upright faces are more easily encoded into face representations than inverted faces (Jiang et al., 2007; Zhou et al., 2010). Taken together, these findings suggest that a conventional face inversion effect may not occur when stimuli are not detected as faces. We used a stimulus duration that was below the perceptual threshold, set for each subject. This brief duration did not allow sufficient face encoding for the overt recognition of the stimuli as faces or objects. Thus, under subthreshold conditions, the differences between the P1 and N1 amplitudes elicited by objects and those elicited by faces disappeared when stimuli were inverted.

Amplitude differences at the P1 level between faces and objects could be due to differences in low-level features. Itier and Taylor (2004) demonstrated that when all face stimuli presented in the experiment were superimposed, averaged faces were very similar to low-spatial frequency faces. They proposed that low-level spatial information itself is one of the critical factors for discriminating faces from objects. In the context of our study, this suggests that when faces are presented repeatedly even for a brief duration, vague, local contrast differences may have been introduced, changing the holistic information of the presented faces. The P1 augmentation for upright faces could be due to the high contrast patterns of eyes appearing in the upper visual field and mouths in the lower visual field for upright face stimuli. This first-order relation visual pattern information may act as a very early index differentiating faces from other objects. Hence, P1 differences between upright and inverted faces might represent the activity of a local contrast detector of face parts that can be used to discriminate faces from objects.

It has been suggested that holistic face perception relies on coarse visual cues transmitted by early spatial frequency filters (Sergent, 1984). Physiological findings indicate that visual information is processed in parallel via the magnocellular and parvocellular pathways (Livingstone and Hubel, 1988; Tobimatsu and Celesia, 2006). The former is activated faster than the latter by coarse visual cues such as low-spatial frequency (LSF) information (Schiller et al., 1979; Liddell et al., 2005). Previous studies have reported that the P1 amplitude for faces using LSF filtering was augmented in healthy subjects (Nakashima et al., 2008b; Obayashi et al., 2009). These authors proposed that P1 enhancement elicited by LSF faces reflects the function of the magnocellular pathway (holistic processing). With brief presentations, faces are not fully recognized but it is possible to process vague, holistic visual information from them. We, therefore, assume that these rapid and transient signals primarily activate the magnocellular pathway, so that upright faces can be identified very rapidly. This, in turn, leads to the augmentation of the P1 response to briefly presented faces relative to objects.

4.2. N1 suppression for subthreshold faces

In the current results, both the amplitude and latency of the N1 measured at Oz differed from those of the occipitotemporal N170 obtained at T5 and T6. The N1 was diminished for subthreshold

masked neutral face and fearful face stimuli, whereas it was augmented for the faces in the threshold and suprathreshold conditions. N170 amplitude did not differ between faces and objects in the subthreshold condition. An analysis of the time-course of responses to faces and objects, however, revealed significant differences between the three duration conditions at 158 or 170 ms after the stimulus onset, roughly corresponding to the peak latency of the N1 and N170, respectively. This finding is in accord with previous reports (Nakashima et al., 2008b; Bentin et al., 1996). These results indicate that the N1 reflects distinct activity that precedes face recognition (i.e., the N170). A small number of studies have focused on the occipital N1 (or N2) response in face perception (Goto et al., 2005; Nakashima et al., 2008b; Jiang and He, 2006). The N1 suppression for subthreshold face images in our results may be related to a recently reported early suppression effect for subthreshold faces at the OFA, which occurred even when subjects could not detect the masked faces (Trenner et al., 2004; Martens et al., 2006; Henson et al., 2008; Kouider et al., 2008; Jiang and He, 2006). Since the physical features of the neutral and fearful faces resemble each other but differ from the features of objects, it could be argued that this repetition sensitivity of similar object categories alone might cause the N1 decrement. However, in our second experiment, this ERP signature disappeared when faces were inverted. Thus, the sensitivity of similar object categories cannot account for the effect we observed.

4.3. What causes the face-sensitivity of neural activity in the occipital cortex?

The present results revealed that early ERP components (P1/N1) derived from the occipital region were sensitive to the briefly presented masked faces, in accord with other studies using manipulated face images (Itier and Taylor, 2002, 2004; Latinus and Taylor, 2006; George et al., 2005; Nakashima et al., 2008a,b; Obayashi et al., 2009; Jiang et al., 2009). Past studies have reported neural responses to facial information even when face stimuli are unrecognizable (Moutoussis and Zeki, 2002; Jiang and He, 2006; Jiang et al., 2009; Henson et al., 2008; Kouider et al., 2008). Such ERP responses have been observed in occipitotemporal areas between 100 and 150 ms (Martens et al., 2006; Henson et al., 2008), and between 120 and 200 ms (Jiang et al., 2009) post-stimulus. These findings are related to the pattern of P1/N1 activity in the present study.

Our results indicated that 'face-object' differences did not occur during mask presentation (see Figs. 5 and 6). If the difference in ERP responses between faces and objects is caused by differences in the contrast or white-black ratio between these stimuli, there would be some differences in lower-level ERP components such as the eN. However, we found no significant differences before 158 ms in Experiment 1, and 110 ms in Experiment 2. As such, we propose that the ERP difference between faces and objects cannot be explained by differences in the spatial distribution of elements between the image types (i.e., faces, objects, and mask stimuli) alone.

Because retinal responses are highly sensitive to physical stimulus characteristics, it is possible for ERP differences between faces and objects to result from differences in the spatial distribution of elements between pictures (Tobimatsu and Celesia, 2006; Yue et al., 2010). When natural images are used to study face recognition, it is difficult to completely control stimulus characteristics of this type. However, the P1 and N1 have been proposed to play a specific role in face recognition regardless of physical stimulus characteristics (Linkenkaer-Hansen et al., 1998; Liu et al., 2002; Itier and Taylor, 2002, 2004; Goto et al., 2005; Nakashima et al., 2008a,b).

4.4. N170 as an index of the overt face recognition

In the current study, electrophysiological differences between faces and objects in the occipitotemporal N170 were present in the above-threshold condition, and increased as the presentation duration lengthened. This indicates that the amplitude differences we observed were dependent on the subjects' level of face recognition. The gradual emergence of the N170 as stimulus duration increased thus appears to be due to the sensitivity of this component to the recognizability of stimuli as faces. These results are consistent with the notion that the N170 reflects perceptual integration processes, resulting from initial 'structural encoding' (Haxby et al., 2000; Jemel et al., 2003; Rousselet et al., 2008).

5. Conclusions

Overall, our results indicate that the processing of faces by early visual processing areas differs from the processing of objects, even when images were presented at a duration below the threshold of recognition. This finding suggests the existence of fast face-sensitive processes prior to the activity of advanced face-specific processing. We propose that the P1 reflects rapid detection in the visual system of information from faces based on the local contrast of the spatial alignment of face parts. In addition, we suggest that the N1 detects information regarding facial features, which is then transferred to the fusiform area. Thus, we believe that the P1 and N1 components reflect early sensitivity to facial features, that is predominantly supported by LSF information, operating before the face selective responses reflected by the occipitotemporal N170.

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