



**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.

(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 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 can-

not 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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