Electrophysiological Studies of Human Face Perception. II: Response Properties of Face-specific Potentials Generated in Occipitotemporal Cortex

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In the previous paper the locations and basic response properties of N200 and other face-specific event-related potentials (ERPs) were described. In this paper responsiveness of N200 and related ERPs to the perceptual features of faces and other images was assessed. N200 amplitude did not vary substantially, whether evoked by colored or grayscale faces; normal, blurred or line-drawing faces; or by faces of different sizes. Human hands evoked small N200s at face-specific sites, but evoked hand-specific ERPs at other sites. Cat and dog faces evoked N200s that were 73% as large as to human faces. Hemifield stimulation demonstrated that the right hemisphere is better at processing information about upright faces and transferring it to the left hemisphere, whereas the left hemisphere is better at processing information about inverted faces and transferring it to the right hemisphere. N200 amplitude was largest to full faces and decreased progressively to eyes, face contours, lips and noses viewed in isolation. A region just lateral to face-specific N200 sites was more responsive to internal face parts than to faces, and some sites in ventral occipitotemporal cortex were face-part-specific. Faces with eyes averted or closed evoked larger N200s than those evoked by faces with eyes forward. N200 amplitude and latency were affected by the joint effects of eye and head position in the right but not in the left hemisphere. Full and three-quarter views of faces evoked larger N200s than did profile views. The results are discussed in relation to behavioral studies in humans and single-cell recordings in monkeys.

Introduction

In the previous paper we described the locations and some response properties of several types of face-specific event-related potentials (ERPs) (Allison *et al.*,1999). This activity occurs in three different regions of occipitotemporal cortex, ranges in latency over several hundred milliseconds, and probably reflects different portions of the neural operations involved in perceiving and identifying faces.

In this paper we focus on N200 and N700 ERPs recorded from ventral and lateral face-specific sites in order to further describe the response properties of this neuronal activity. These experiments were based on behavioral studies in humans and on recordings from face-specific cells in monkey STS/IT cortex, and sought to determine whether this activity is: (i) sensitive to face color or size; (ii) affected by removing the high-frequency or low-frequency portions of the face image; (iii) responsive to animal faces; (iv) affected by face inversion; (v) responsive to internal and external face parts; (vi) sensitive to changes in head and eye position; (vii) responsive to human hands. Rather than reviewing their rationale here, the Results section will provide for each experiment a brief review of prior work and the predictions to be tested. Preliminary results of some of these experiments have been reported (Allison *et al.*, 1994b, 1996a,b).

Materials and Methods

Patients and recording methods were as described previously (Allison *et al.*, 1999). Standard image size (8.4° × 8.4° of visual angle) and luminance (29 ± 4 cd/m^2) were as described previously except in the following experiments. (i) Normal and blurred faces had a luminance of 41 ± 7 cd/m^2, and line-drawing faces had a luminance of 15 ± 2 cd/m^2; these images were 11.1° wide × 13.5° high. (ii) Small, medium, and large faces and gratings were of standard luminance and subtended 2.7° × 2.7°, 8.4° × 8.4° and 15.2° × 15.2° of visual angle respectively (the images were 2.8 × 2.8, 8.8 × 8.8 and 16 × 16 cm respectively). (iii) Upright and inverted faces were of standard size and luminance. Faces presented in the hemifields were offset by 6.1° from the central fixation point, thus the inside edge of the images was offset 1.9° from the fixation point. Stimulus duration was 150 ms in order to preclude eye movements toward the hemifield stimuli (Leehey *et al.*, 1978). All targets were presented centrally to minimize the occurrence of eye movements, which patients were instructed to avoid. In addition, one of the experimenters sat by the patient's bedside and watched for eye movements away from the fixation point. (iv) In experiments using faces, face parts, and varying head and eye position the luminance of the images was 51 ± 5 cd/m^2, and they were 11.1° wide × 13.5° high.

The individual experiments were initiated at different times during the 6 year duration of this study, hence the number of face-specific ERP sites encountered in each experiment differed. Face-specific electrode sites were first identified using the screening tasks described in the preceding paper (Allison *et al.*, 1999) and ERPs at these sites were then measured in the experiments described here. While this strategy maintained independence between the definition of face-specific sites and their measurement, it could result in ignoring sites specific for other stimulus categories. A second analysis was therefore constructed to search for sites that were specific for categories other than full faces. In these exploratory analyses, presumptive category-specific ERPs had to be at least 50 μV in amplitude and twice the amplitude evoked by other stimulus categories.

Results

Colored and Grayscale Faces

Single-cell, imaging and lesion studies in monkeys suggest that STS/IT cortex plays an important role in color discrimination [reviewed by Komatsu (Komatsu, 1998)]. The ventral face area probably receives input from the color-sensitive human homolog of area V4, which appears on the basis of anatomical (Clarke and Miklossy, 1990), ERP (Allison *et al.*, 1993) and imaging (Lueck *et al.*, 1989; Sakai *et al.*, 1995; Kleinschmidt *et al.*, 1996) studies to be located in the posterior portion of the fusiform gyrus and adjacent collateral sulcus and inferior lingual gyrus. A region that may be anterior to human V4, area V8 (Hadjikhani *et al.*, 1998), is also color sensitive. Although humans can recognize faces well in the absence of color (e.g. in grayscale photographs), face color provides useful information when categorizing the sex or ethnicity of faces (Hill *et al.*, 1995). For these reasons we predicted that ventral face-specific N200 amplitude would be larger to

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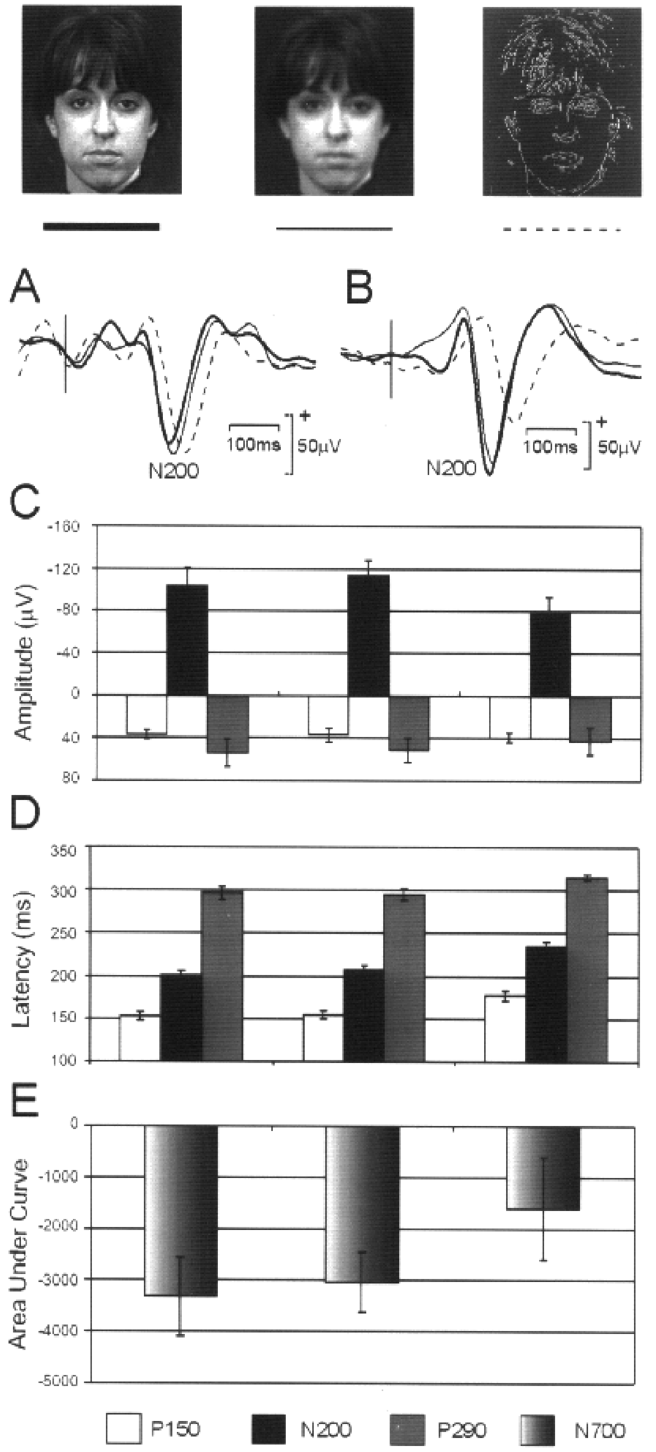

Figure 1. ERPs at ventral face-specific N200 sites to normal, blurred and line-drawing faces. (*A*,*B*) Examples of recordings. (*C*–*E*) Summaries of amplitude, latency and N700 AUC. Plotting conventions as described in Allison *et al.* [(Allison *et al.*, 1999) Fig. 2].

faces photographed in normal color than to equiluminant grayscale versions of the same faces.

There were 21 ventral face-specific N200 sites, 12 in the right and 9 in the left hemisphere. P150 latency, and N200 and P290 amplitude and latency, were not significantly different in colored versus grayscale faces. P150 amplitude was significantly larger [*F*(*df* 1,20) = 6.56, $P < 0.02$] to colored than to grayscale faces. N700 AUC was marginally ($P < 0.05$) larger to grayscale than to colored faces. At three lateral face-specific N200 sites P150, N200 and P290 amplitude and latency were not different to colored and grayscale faces. These results demonstrate that ventral and lateral face-specific N200s were not preferentially sensitive to colored faces.

Blurred and Line-drawing Faces

Humans can recognize faces when the high-frequency portion of the image is removed (blurred faces) or when low-frequency information is removed ('line-drawing' faces). Fiorentini *et al.* (Fiorentini *et al.*, 1983) found that spatial frequencies above or below 8 cycles/face width (c/fw) provide sufficient information to recognize individual faces. In monkeys Rolls (Rolls, 1985) found that face-selective cells responded well to blurred or line-drawing versions of the same faces. We asked whether face-specific N200s and related ERPs were sensitive to these manipulations. Line-drawing faces were created by applying an edge (Sobel) filter to the original faces. Blurred faces were created by applying a smoothing (average) filter using a kernel of 9 × 9 pixels. In both instances, the mean intensity of the resultant image was set equal to the original. The blurred and line-drawing faces approximately correspond respectively to the low-pass (<12 c/fw) and high-pass (>12 c/fw) filtered faces of Fiorentini *et al.* (Fiorentini *et al.*, 1983).

There were 18 ventral face-specific N200 sites, 6 in the right and 12 in the left hemisphere. Representative recordings are shown in Figure 1*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 1*C*–*E*. The overall ANOVA for N200 amplitude was significant [*F*(*df* 2,26) = 5.96, $P < 0.007$]. N200 amplitude to blurred or line-drawing faces was not significantly different than to normal faces, but N200 amplitude to blurred faces was marginally larger than to line-drawing faces ($P < 0.05$). The overall ANOVA for N200 latency was significant [*F*(*df* 2,26) = 155, $P < 0.0001$]. N200 latency increased progressively and significantly in the order normal, blurred and line-drawing faces ($P < 0.001$ in each case). The overall ANOVA for N700 AUC was significant ($P < 0.02$). N700 to line-drawing faces was significantly smaller than to normal and blurred faces ($P < 0.05$ in each case), which did not differ significantly between themselves. Similar results (not shown) were obtained at three lateral face-specific N200 sites. These results demonstrate that removing the high- or low-frequency components of faces had only moderate effects on N200 amplitude, but line-drawing faces evoked ventral and lateral N200s that were markedly later (34 ms on average) than those evoked by normal faces.

Face Size

Face-specific cells in monkey STS/IT cortex respond well to faces viewed over a range of sizes (Desimone *et al.*, 1984; Rolls and Baylis, 1986; Perrett *et al.*, 1992), suggesting that these cells generalize across face size. To determine the responsiveness of face-specific N200 and related ERPs to face size, patients viewed small, medium and large faces that varied in area by a factor of 32. Non-face stimuli were radial gratings of the same sizes.

There were nine ventral face-specific N200 sites, three in the right and six in the left hemisphere. Representative recordings are shown in Figure 2*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 2*C*–*E*. A two-way ANOVA for N200 amplitude (stimulus type × stimulus size) showed a significant main effect of stimulus type [*F*(*df* 1,7) = 8.06, $P < 0.03$]; faces evoked significantly larger N200s than

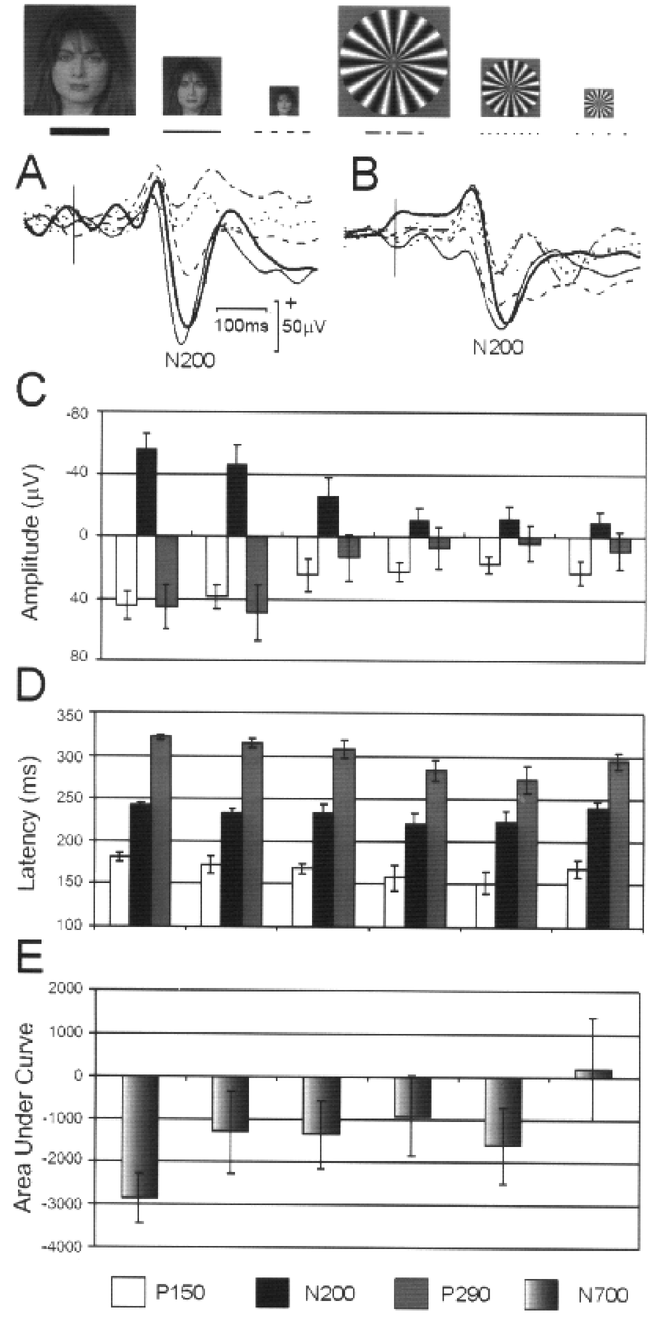

Figure 2. ERPs at ventral face-specific N200 sites to large, medium and small faces and radial gratings. (*A*,*B*) Examples of recordings. (*C*–*E*) Summaries of amplitude, latency and N700 AUC.

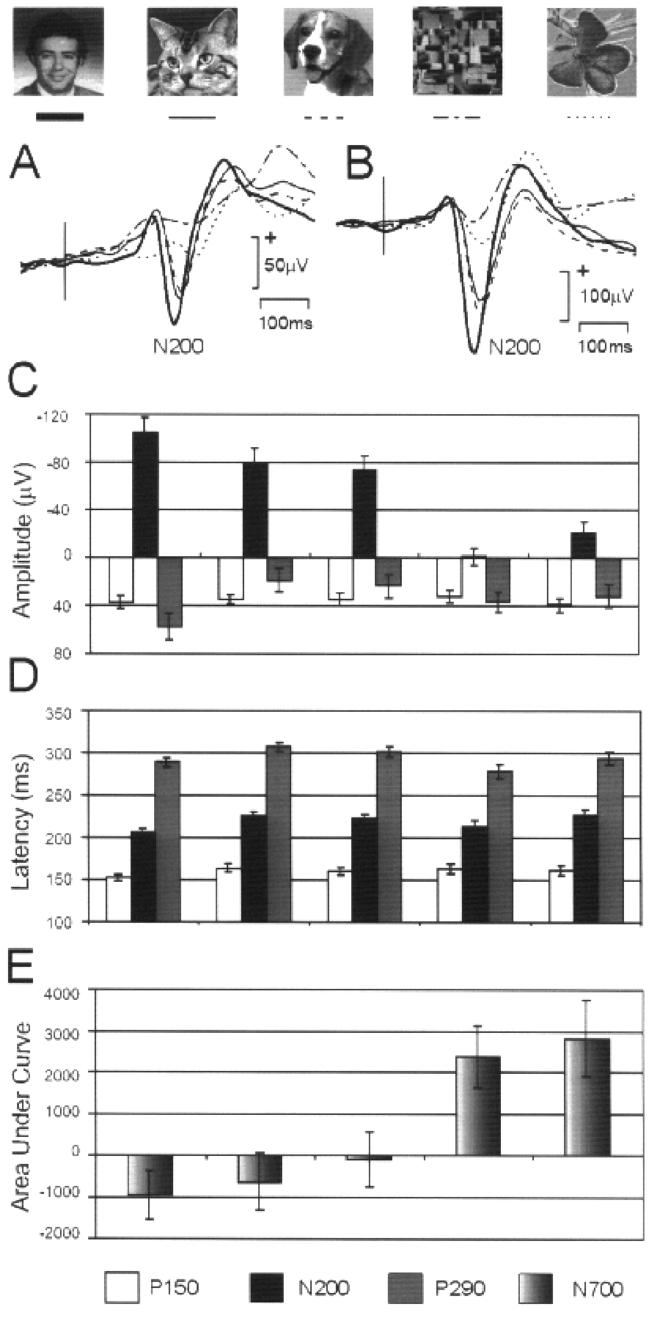

Figure 3. ERPs at ventral face-specific N200 sites to human, cat and dog faces. (*A*,*B*) Examples of recordings. (*C*–*E*) Summaries of amplitude, latency and N700 AUC.

gratings ($P < 0.02$ in each case). The main effect of size was not significant, but the stimulus type × stimulus size interaction was significant ($P < 0.04$); N200 amplitude showed a marginally significant effect of face size due to the fact that large faces evoked a significantly larger N200 than did small faces ($P < 0.03$). N200 amplitude to large or small faces was not significantly different than to medium faces. A two-way ANOVA for N700 AUC showed a significant main effect of stimulus size [$F(df\,2,14) = 6.52$, $P < 0.01$] and a significant stimulus type × stimulus size interaction ($P < 0.03$). N700 AUC was significantly larger to large faces than to medium and small faces ($P < 0.04$ in each case), which did not differ significantly from the N700 evoked by gratings. These results indicate that N200 amplitude was relatively invariant to face size, and that even small faces that were not easily discernible evoked N200s that were significantly larger than those evoked by gratings.

Cat and Dog Faces

Cat and dog faces are commonly viewed faces that have the same component parts as human faces, but with differences in the shape and arrangement of the parts. If face-specific N200 is tuned to the configuration of a prototypical human face, deviations from this arrangement should lead to a reduction of N200 amplitude. On the other hand, it is possible that N200 is responsive to the semantic category *faces* regardless of their

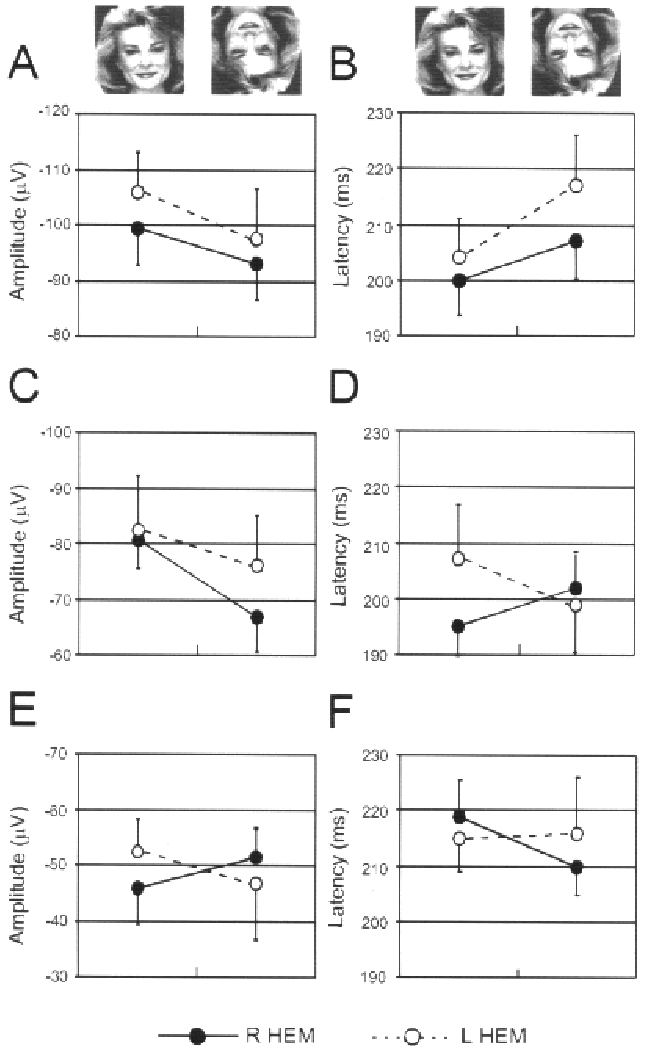

Figure 4. N200 amplitude (*A,C,E*) and latency (*B,D,F*) at ventral face-specific sites to upright and inverted faces presented in the central visual field (*A,B*), the contralateral visual field (*C,D*) and the ipsilateral visual field (*E,F*).

configuration, in which case animal and human faces should evoke N200s of similar amplitude and latency. Patients viewed equiluminant human, cat and dog faces, scrambled human faces and (target) butterflies.

There were 28 face-specific sites, 15 in the right and 13 in the left hemisphere. Representative recordings are shown in Figure 3*A,B*. Results for the right and left hemisphere were similar and are combined in Figure 3*C–E*. The overall ANOVA for N200 amplitude was significant [$F(df\,4{,}108) = 42.5$, $P < 0.0001$]. N200 amplitude to human faces was significantly larger than to cat or dog faces ($P < 0.003$ in each case), which did not differ significantly between themselves. N200 amplitude to cat or dog faces was significantly larger than to scrambled faces or targets ($P < 0.0001$ in each case). The overall ANOVA for N200 latency was significant ($P < 0.001$). N200 latency was significantly earlier to human faces than to cat or dog faces ($P < 0.0002$ in each case), which did not differ significantly between themselves. The overall ANOVA for N700 AUC was significant ($P < 0.0001$). N700 AUC did not differ significantly between human, cat or dog faces, but all face categories evoked significantly larger N700 AUCs than did scrambled faces or targets ($P < 0.0001$ in each case). There were four lateral face-specific N200 sites. N200 amplitude to cat and dog faces combined was 75% as large and 14 ms later than to human faces, results similar to those obtained at ventral sites. These results demonstrate that at ventral and lateral face-specific N200 sites, cat and dog faces evoked smaller and later N200s than did human faces.

Upright and Inverted Faces

It is well known that faces are more difficult to recognize when viewed upside down. The mechanisms responsible for the face inversion effect have been reviewed (Valentine, 1988; Rhodes *et al.*, 1993; Farah *et al.*, 1995). Discussion is usually framed in terms of 'holistic' as opposed to 'parts-based' or 'feature' modes of processing. Holistic processing refers to configurational processing in which the individual parts of the object are not separately processed (Bruce and Humphreys, 1994; Farah *et al.*, 1995). Because faces are such a homogeneous category of object, holistic processing is thought to be especially important for upright faces [reviewed by Rhodes (Rhodes, 1993) and Moscovitch *et al.* (Moscovitch *et al.*, 1997)]. By contrast, parts-based processing supposes that a complex object is broken down into its constituent parts. Evidence suggests that the right hemisphere is specialized for holistic processing, whereas the left hemisphere is specialized for parts-based processing (Bradshaw and Sherlock, 1981; Corballis, 1991; Rhodes, 1993). We therefore predicted that face inversion would have different effects on N200 and related ERPs recorded from the right and left hemisphere, and that the right hemisphere would be more sensitive to face inversion than the left hemisphere. Patients viewed upright and inverted faces presented centrally and in the left and right hemifields. There were 24 face-specific N200 sites, 13 in the right and 11 in the left hemisphere. The results of this experiment are best appreciated as plots of N200 amplitude and latency. Results for P150, P290 and N700 were not additionally informative and will not be described.

To central stimulation, right and left hemisphere N200 amplitude (Fig. 4*A*) was slightly but not significantly larger to upright than to inverted faces. In both hemispheres N200 latency (Fig. 4*B*) was significantly later (by 11 ms on average) to inverted than to upright faces ($P < 0.02$ in each case). While inverted faces evoked N200s that were later than those evoked by upright faces, the differences were approximately equal in both hemispheres and hence did not support the hypothesis that the right hemisphere is more sensitive to face inversion than is the left hemisphere.

Hemifield stimulation provides a more sensitive measure of processing performed in each hemisphere. Stimulation of the contralateral hemifield provides a measure of the amount (N200 amplitude) and rapidity (N200 latency) of processing of direct geniculocortical input. N200 amplitude was significantly larger ($P < 0.01$) to upright than to inverted faces in the right but not in the left hemisphere (Fig. 4*C*); the face-orientation × hemisphere interaction was significant [$F(df\,1{,}22) = 16.9$, $P < 0.0005$]. N200 latency in the right hemisphere was shorter to upright than to inverted faces, whereas in the left hemisphere the opposite pattern was seen (Fig. 4*D*); the face-orientation × hemisphere interaction was significant [$F(df\,1{,}22) = 22.9$, $P < 0.0001$].

In primates the responsiveness of visual cortex to stimulation of the ipsilateral hemifield is due entirely to interhemispheric transfer via the corpus callosum and anterior commissure (Zeki, 1973; Gross *et al.*, 1977). Thus stimulation of the ipsilateral hemifield provides a measure of the amount and rapidity of interhemispheric transfer of information from the directly

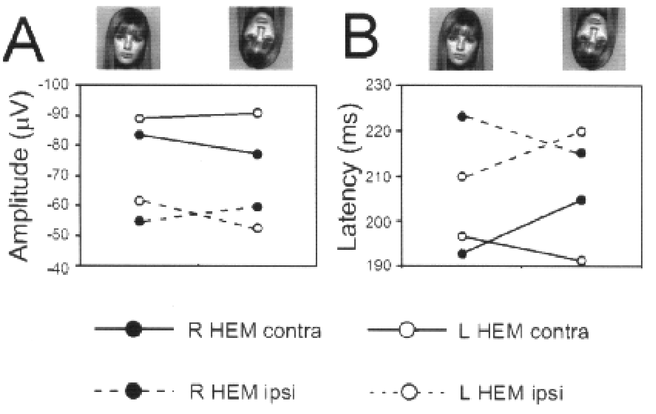

Figure 5. N200 at ventral face-specific N200 sites to upright and inverted faces presented in the contralateral and ipsilateral visual fields. (*A*,*B*) Summaries of amplitude and latency.

activated hemisphere. N200 amplitude in the right hemisphere appeared to be larger to inverted than to upright faces, whereas in the left hemisphere the opposite pattern was seen (Fig. 4*E*); however, the face-orientation × hemisphere interaction only approached significance ($P < 0.08$). N200 latency in the right hemisphere was longer to upright than to inverted faces, whereas in the left hemisphere there was no difference (Fig. 4*F*); however, the face-orientation × hemisphere interaction was not significant. This pattern of interaction was different than that obtained to stimulation of the contralateral hemifield (cf. Fig. 4*D* and *F*).

In the right hemisphere, upright faces presented in the contralateral hemifield evoked a larger N200 than did inverted faces, whereas inverted faces presented in the ipsilateral hemifield evoked a larger N200 than did upright faces; the face-orientation × hemifield interaction was marginally significant ($P < 0.06$). This pattern was not seen in the left hemisphere.

The hemifield latency changes were small relative to between-patient differences. To eliminate this source of variance we analyzed the subset of data of patients who had face-specific N200 sites in both the right and left hemisphere (Fig. 5). N200 latency effects were similar to those shown in Figure 4*D*,*F* but reveal more clearly the effects of face inversion on hemispheric responsiveness. To stimulation of the contralateral hemifield, N200 latency in the right hemisphere was shorter to upright than to inverted faces, whereas in the left hemisphere the opposite effect was seen; the face-orientation × hemisphere interaction was significant [$F(df\,1,9) = 18.2$, $P < 0.002$]. To stimulation of the ipsilateral hemifield the opposite pattern was seen. N200 latency in the right hemisphere was shorter to inverted than to upright faces, whereas in the left hemisphere it was shorter to upright than to inverted faces; the face-orientation × hemisphere interaction was significant ($P < 0.001$).

The difference in N200 latency to ipsilateral compared to contralateral stimulation yields a measure of interhemispheric transfer time (ITT). The longest ITT was 24.0 ms, reflecting the difference in the right hemisphere between N200 latency to upright faces presented contralaterally (195 ms) and ipsilaterally (219 ms); this difference was significant ($P < 0.0001$). The next longest ITT was 17.5 ms, reflecting the difference in the left hemisphere between N200 latency to inverted faces presented contralaterally (198.5 ms) and ipsilaterally (216 ms); this difference was significant ($P < 0.01$). The shortest ITT was 7.7 ms, reflecting the difference in the right hemisphere between N200 latency to inverted faces presented contralaterally (202.5 ms) and ipsilaterally (210.2 ms); this difference was significant ($P < 0.01$).

The results of hemifield stimulation can be summarized by saying that the right hemisphere responded more rapidly to upright faces and transferred such information rapidly to the left hemisphere, whereas the left hemisphere responded more rapidly to inverted faces and transferred such information rapidly to the right hemisphere. In addition, the right hemisphere responded with greater N200 amplitude to contralateral upright than inverted faces, an effect not apparent in the left hemisphere.

In both hemispheres, and to upright and inverted faces, N200 was significantly larger to faces presented centrally than to faces presented in either hemifield ($P < 0.03$ in each case) and was significantly larger to faces presented in the contralateral than in the ipsilateral hemifield ($P < 0.04$ in each case).

Face Parts

There are three reasons why it would be useful to know how face-specific and other sites respond to the component parts of a face. First, some theories of object recognition (Marr and Nishihara, 1978; Hoffman and Richards 1985; Biederman, 1987) assume that the visual system breaks down complex objects into simpler component parts. These primitive parts – 'geons' in the model of Biederman, for example – then provide the inputs for later stages of object processing. If face components are thought of as being analogous to primitive parts, they should activate the face perception system prior to activation by the full face. Second, some face cells in monkey STS/IT cortex respond well to face parts (Perrett *et al.*, 1982; Leonard *et al.*, 1985), and in the models of Perrett *et al.* (Perrett *et al.*, 1987) and Tovée and Cohen-Tovée (Tovée and Cohen-Tovée, 1993) face-parts processing provides the input to later stages of face processing. Third, recordings from the posterior temporal scalp showed that eyes viewed in isolation evoked an N170 that was larger than that evoked by a full face (Bentin *et al.*, 1996; Taylor *et al.*, 1997; Puce *et al.*, 1999), raising the possibility that N200 may respond preferentially to eyes or other face parts. ERPs were recorded in experiments that included faces; eyes, lips and noses viewed in isolation; and (target) butterflies or flowers.

There were 45 ventral face-specific N200 sites, 26 in the right and 19 in the left hemisphere. Representative recordings are shown in Figure 6*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 6*C*–*E*. The overall ANOVA for N200 amplitude was significant [$F(df\,4,140) = 33.4$, $P < 0.0001$]. N200 amplitude was significantly larger to faces than to face parts or targets ($P < 0.004$ in each case). N200 amplitude decreased progressively and significantly in the order eyes, lips, noses and targets ($P < 0.008$ in each case). Thus all face parts evoked an N200 that was significantly smaller than to faces but significantly larger than to non-face targets. The overall ANOVA for N200 latency was significant [$F(df\,4,140) = 39.3$, $P < 0.0001$]. N200 latency was significantly earlier to faces than to face parts ($P < 0.0001$ in each case). N200 latency increased progressively and significantly in the order faces, eyes, lips and noses ($P < 0.006$ in each case). The overall ANOVA for N700 AUC was significant [$F(df\,4,140) = 10.3$, $P < 0.0001$]. N700 was significantly larger to faces than to any other stimulus category ($P < 0.01$ in each case) and was significantly larger to eyes than to noses or targets ($P < 0.02$ in each case). There were six lateral face-specific N200 sites. The responsiveness of N200 and related

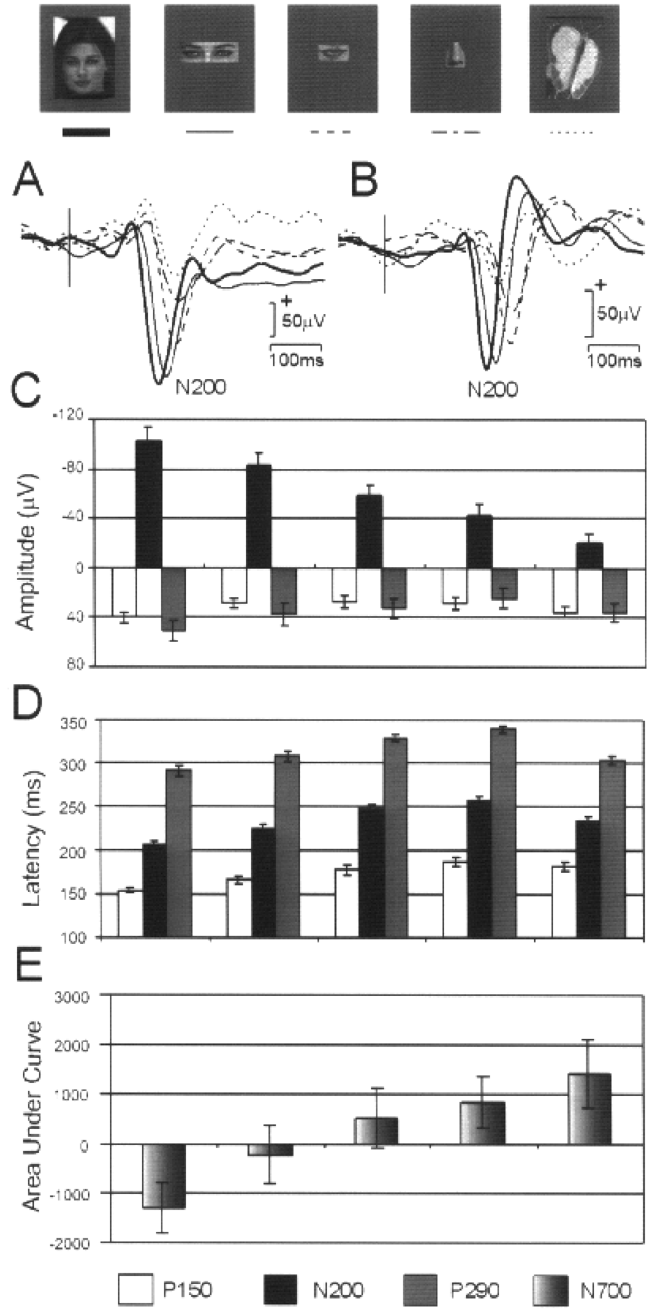

Figure 6. ERPs at ventral face-specific N200 sites to faces, eyes, lips and noses. (*A*,*B*) Examples of recordings. (*C*–*E*) Summaries of amplitude, latency and N700 AUC.

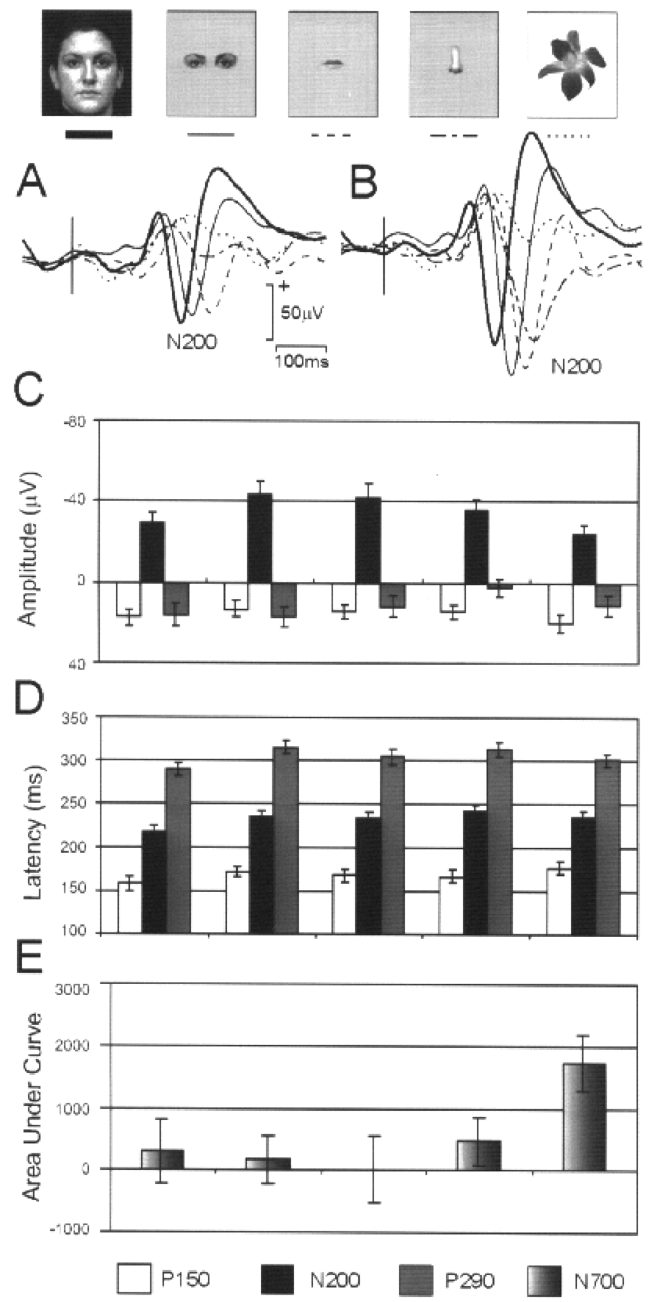

Figure 7. ERPs to faces and internal face parts at sites 1 cm lateral to ventral face-specific N200 sites. Recording from a ventral face-specific N200 site (*A*) and a site 1 cm lateral to it (*B*). (*C*–*E*) Summaries of amplitude, latency and N700 AUC.

ERPs (not shown) at these sites was similar to that seen at ventral face-specific N200 sites.

In another version of this experiment patients viewed faces and internal face parts and also viewed face contours (i.e. faces with the internal face parts removed). Contours consist of two parts, the hair and the shape of the face, both of which are useful in identifying faces (Shepherd *et al.*, 1981). There were 16 ventral face-specific N200 sites, 9 in the right and 7 in the left hemisphere. Results for the right and left hemisphere were similar and were combined for statistical analysis. The overall ANOVA for N200 amplitude was significant [$F(df\ 6{,}90) = 16.0$, $P < 0.0001$]. N200 amplitudes and latencies to faces and internal face parts were similar to those described above. N200 amplitude to contours was significantly smaller than to faces and eyes ($P < 0.04$ in each case), was not significantly different than to lips, and was significantly larger than to noses and targets ($P < 0.04$ in each case). The overall ANOVA for N200 latency was significant [$F(df\ 6{,}90) = 26.5$, $P < 0.0001$]. N200 latency to contours was significantly later than to faces ($P < 0.0001$), was not significantly different than to eyes, and was significantly earlier than to lips and noses ($P < 0.0001$ in each case). The overall ANOVA for N700 AUC was significant [$F(df\ 6{,}90) = 3.24$, $P < 0.006$]. N700 was significantly larger to faces than to noses ($P < 0.004$) but not to the other face parts.

At sites lateral to ventral face-specific N200 sites, internal face

Table 1

Centroids of active regions in the Talairach and Tournoux coordinate system (Talairach and Tournoux, 1988)

ERP	Right hemisphere				Left hemisphere			
	n	*x*	*y*	*z*	*n*	*x*	*y*	*z*
Ventrolateral face parts N200	29	47	–50	–14	26	–47	–50	–17
Ventral face-part-specific N200	3	31	–53	–14	7	–33	–54	–18
Lateral face-part-specific N200	1	39	–85	9	3	–49	–55	14
Ventral hand-specific N230	5	19	–68	–10	1	–27	–4	–35
Lateral hand-specific N230	0				6	–46	–50	16

parts evoked a relatively larger N200 than was evoked by faces. We analyzed the responsiveness of 57 sites, 31 in the right and 26 in the left hemisphere, 1 cm lateral to face-specific N200 sites. A recording is shown for a face-specific site in Figure 7*A* and for a site 1 cm lateral to it in Figure 7*B*. Results for the right and left hemisphere were similar and are combined for the ventrolateral sites in Figure 7*C–E*. N200 amplitude at the ventrolateral sites was significantly larger to all internal face parts than to faces and non-face targets ($P < 0.05$ in each case). This pattern of results is the opposite of that at face-specific N200 sites (cf. Figs 6*C* and 7*C*), as verified by a two-way ANOVA in which N200 amplitude to faces was compared to the average N200 amplitude to all face parts combined. The stimulus type × location interaction was significant [$F(df\ 1,31) = 52.1$, $P < 0.0001$], i.e. N200 amplitude was larger to face parts than to faces at the ventrolateral sites, whereas it was larger to faces than to face parts at face-specific N200 sites. At ventrolateral sites, like ventral sites, N200 latency was significantly later to all face parts than to faces ($P < 0.01$ in each case). There was no N700 at the ventrolateral sites (Fig. 7*E*). The centroids of the ventrolateral sites are listed in Table 1. Analysis of 29 sites 1 cm medial to face-specific N200 sites revealed that mean amplitudes were small (<30 μV) and that N200 amplitude to faces and combined face parts was not significantly different. That is, responsiveness at medial sites was minimal and non-specific. These results can be summarized by saying that N200 amplitude to internal face parts decreased rapidly medial to face-specific N200 sites but decreased less rapidly lateral to such sites.

In addition to the ventrolateral region just described there were 14 sites, 4 in the right and 10 in the left hemisphere, that were face part-specific. Face part-specificity was determined by first averaging N200 amplitudes evoked by eyes, lips and noses at every site. Similarly, N200 amplitudes evoked by non-face objects (hands and flowers) were averaged. A face-part-specific site was then defined as one that generated an averaged N200 to face parts that was at least twice as large as the averaged N200 to non-face objects and the N200 to full faces. Representative recordings are shown in Figure 8*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 8*C*,*D*. The overall ANOVA for N200 amplitude was significant [$F(df\ 2,24) = 16.9$, $P < 0.0001$]. N200 amplitude to combined face parts was significantly larger than to faces ($P < 0.0001$) or to combined objects ($P < 0.0008$). The sites from which face-part-specific N200s were recorded are shown in Figure 8*E*,*F*, and their centroids are given in Table 1. The ventral face-part-specific sites were in or near the ventral face area, but there was no discernible spatial relationship between face-part-specific and face-specific sites.

The major results of these experiments were: (i) internal face parts and face contours evoked a substantial N200 that was smaller and later than that evoked by full faces; (ii) N200 amplitude decreased progressively in the order faces, eyes, contours, lips and noses; (iii) N200 latency increased progressively in the order faces, contours, eyes, lips and noses; (iv) a region just lateral to ventral face-specific N200 sites was preferentially

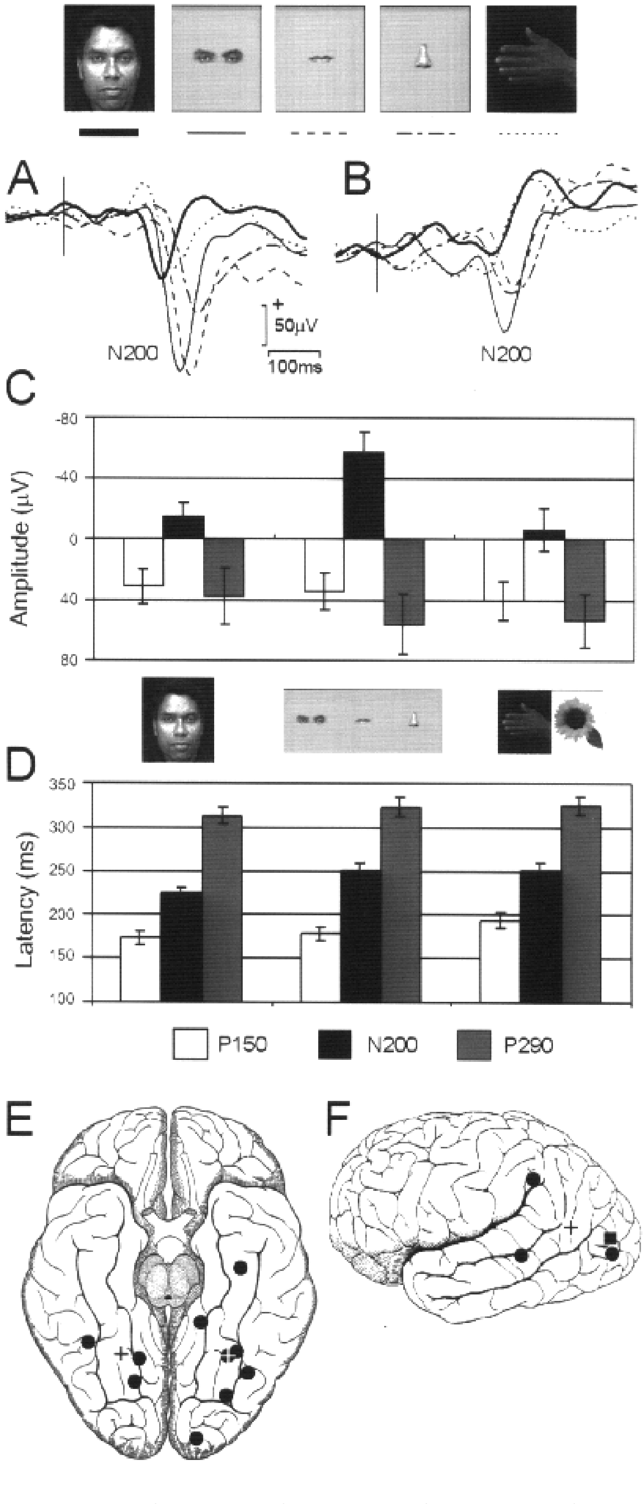

Figure 8. ERPs at face parts-specific N200 sites to faces and internal face parts. (*A*,*B*) Examples of recordings. (*C*,*D*) Summaries of amplitude and latency for faces (left), amplitude and latency averaged across internal face parts (center), and amplitude and latency averaged across non-face objects (right). (*E*,*F*) locations and centroids of face parts-specific sites. Maps constructed as described in Allison *et al.* (Allison *et al.*, 1999, Fig. 1).

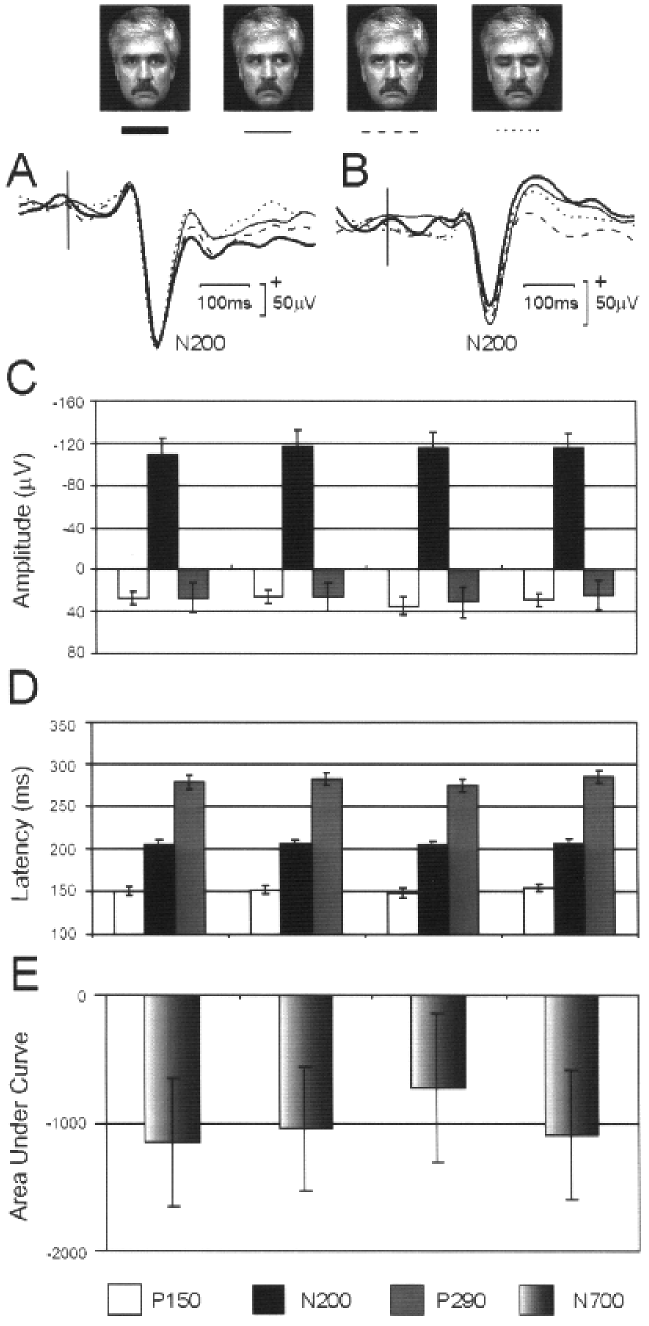

Figure 9. ERPs at ventral face-specific N200 sites to faces with eyes directed to the viewer, averted to the left, averted upward and closed. (*A*,*B*) Examples of recordings. (*C–E*) Summaries of amplitude, latency and N700 AUC.

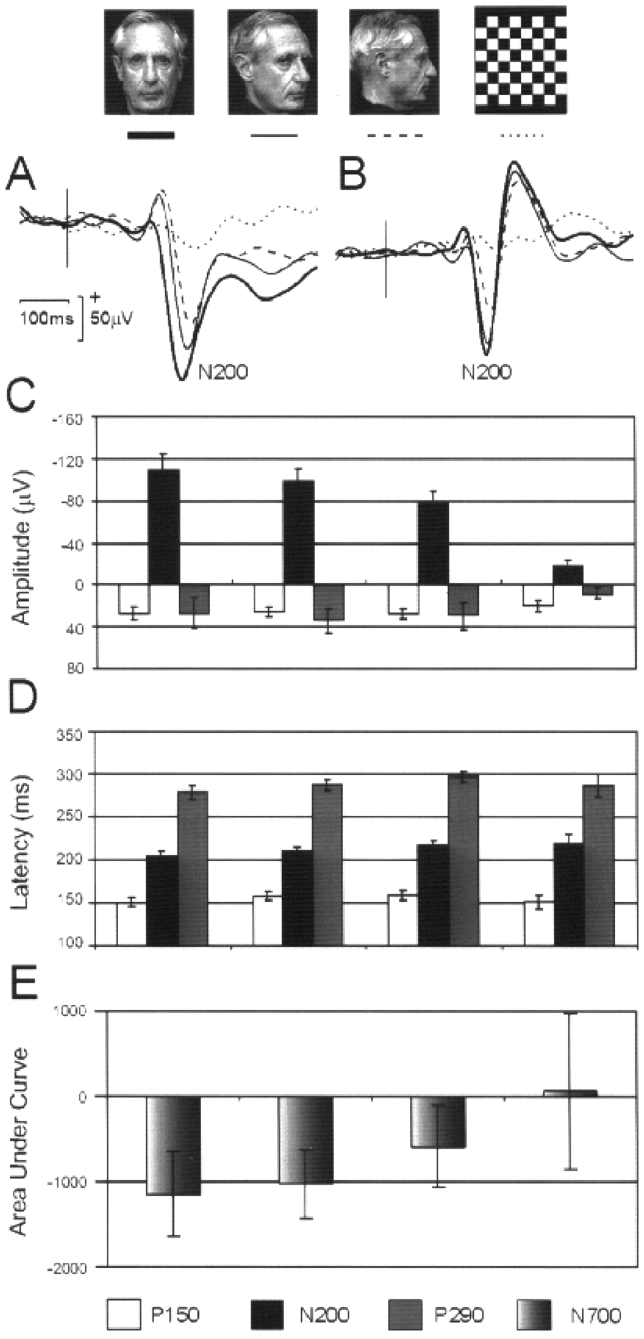

Figure 10. ERPs at ventral face-specific N200 sites to full-face, three-quarter and profile views. (*A*,*B*) Examples of recordings. (*C–E*) Summaries of amplitude, latency and N700 AUC.

responsive to internal face parts; (v) face-part-specific N200s were found at ventral and lateral sites.

Direction of Gaze and Head View

This set of experiments assessed the responsiveness of face-specific N200 and related ERPs to manipulations of head and/or eye position that have been shown in previous studies to affect human face recognition or the responsiveness of monkey face-specific cells. Patients viewed photographs, acquired for seven head and eye conditions, of 60 individuals of both sexes. Individuals were instructed to maintain the same neutral expression for each photograph. Targets were black and white checkerboards. There were 17 ventral face-specific N200 sites, 8 in the right and 9 in the left hemisphere. Because the stimuli varied along several dimensions it will be useful to make three sets of comparisons.

Direction of Gaze

In scalp recordings N170 was marginally larger when the eyes were averted than when the eyes looked directly at the viewer, suggesting that this activity was involved in the perception of cues related to social attention (Allison *et al.*, 1996a). Here we

Table 2

N200 amplitude and latency (± SEM) at face-specific sites as a function of head and eye position

Eyes	Right hemisphere		Left hemisphere	
Forward	126 ± 25 (202 ± 7)	111 ± 19 (213 ± 6)	94 ± 18 (207 ± 8)	93 ± 14 (206 ± 7)
Averted	138 ± 25 (206 ± 6)	102 ± 19 (214 ± 6)	97 ± 18 (206 ± 8)	96 ± 15 (207 ± 7)

Amplitudes are in µV, latencies (in parentheses) in ms.

used the same set of stimuli during intracranial recordings. Patients viewed faces in which the eyes were looking at the viewer or were averted to the left, averted upward or closed. Representative recordings are shown in Figure 9*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 9*C*–*E*. Overall ANOVAs for N200 amplitude and latency were not significant. All conditions in which the eyes were not looking at the viewer (either because they were averted or closed) evoked N200s that were larger than the N200 evoked when the eyes were directed to the viewer (Fig. 9*C*). Although this effect was consistent across conditions and hemispheres, N200 amplitude was not significantly larger ($P < 0.08$) for the averted conditions combined compared to the eyes directed at the viewer. The overall ANOVA for N700 AUC was not significant.

Head and Eye Position

Results of the combined effects of head and eye position are summarized in Table 2. In the right hemisphere there was a significant main effect of head position; N200 was larger ($P < 0.05$) and earlier ($P < 0.002$) when the head faced the viewer regardless of eye position. There was also a significant main effect of eye position; N200 was earlier ($P < 0.02$) when the eyes looked at the viewer than when they were averted regardless of head position. Head and eye aversion evoked the smallest N200, whereas N200 was largest when the head was directed to the viewer but the eyes were averted; this difference was significant ($P < 0.02$). By contrast, in the left hemisphere changes in head and eye position had no significant effects on N200 amplitude and latency. Thus N200 was sensitive to head and eye position only in the right hemisphere.

Head Views

Consider three views of a face and head: the head and eyes directly face the viewer, are at a 45° angle to the viewer, or are at a 90° angle to the viewer. These will be referred to as 'full-face', 'three-quarter' and 'profile' views respectively. Some behavioral studies found that the three-quarter view results in better recognition of unfamiliar faces than the full-face or profile views (Bruce *et al.*, 1987; Logie *et al.*, 1987), while others did not (Harries *et al.*, 1991; Troje and Bülthoff, 1996). We asked whether face-specific N200 and related ERPs were sensitive to head view.

Representative recordings are shown in Figure 10*A*,*B*. Results for the right and left hemisphere were similar and are combined in Figure 10*C*–*E*. The overall ANOVA for N200 amplitude was significant [$F(df\ 3{,}39) = 23.1$, $P < 0.0001$]. N200 amplitude was not significantly different for the full-face and three-quarter views, but both were significantly larger than for the profile view ($P < 0.01$ in each case). N200 amplitude to any head view was significantly larger than to checkerboards ($P < 0.001$ in each case). Checkerboards contained many high-contrast edges but evoked minimal N200s at face-specific sites (Fig. 10*A*–*C*),

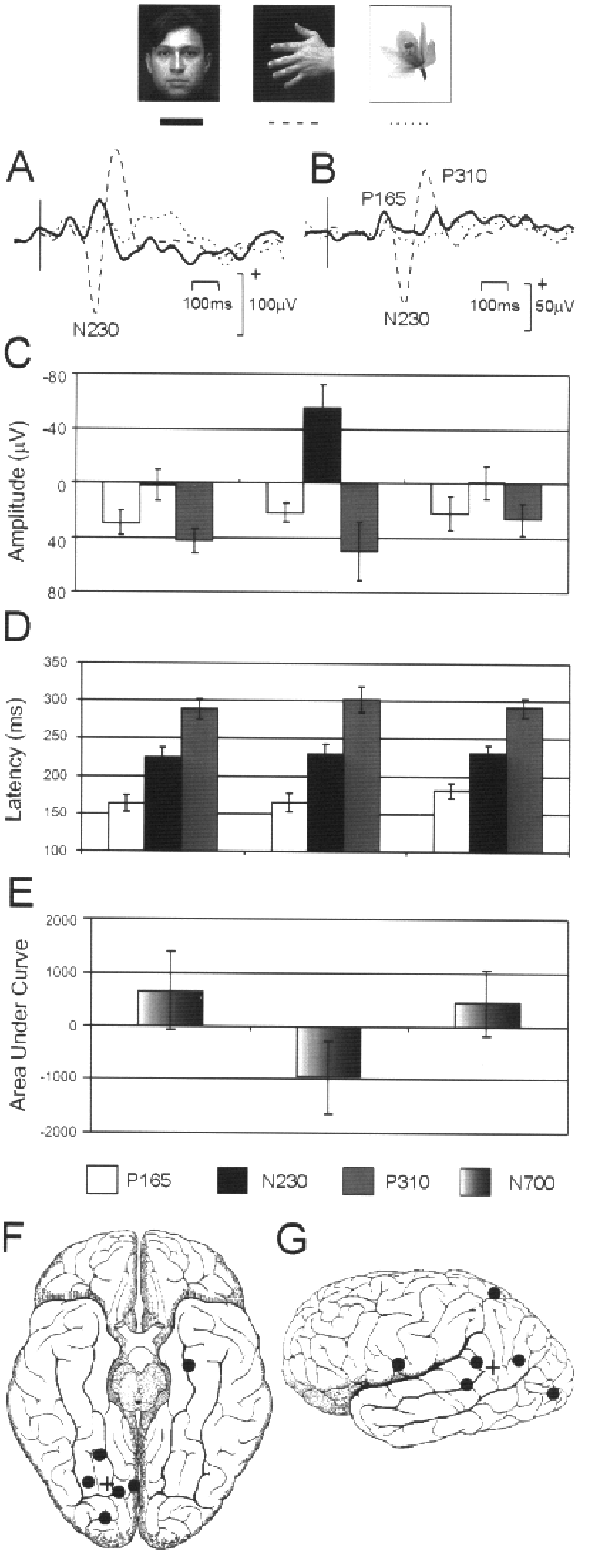

Figure 11. ERPs at hand-specific N230 sites. (A,*B*) Examples of recordings. (*C*–*E*) Summaries of amplitude, latency and N700 AUC. (*F*,*G*) Locations and centroids of hand-specific sites.

whereas such stimuli strongly activated striate and peristriate cortex (Allison *et al.*, 1999, Figs 2 and 3). The overall ANOVA for N200 latency was significant [$F(df\ 2,32) = 17.4$, $P < 0.0001$]. N200 latency increased progressively and significantly in the order full-face, three-quarter and profile views ($P < 0.02$ in each case). The overall ANOVA for N700 AUC was not significant. There were four lateral face-specific N200 sites. The responsiveness of lateral N200s (not shown) was similar to that of ventral N200s. Thus at ventral and lateral sites profile views evoked the smallest and latest N200s.

Harries *et al.* (Harries *et al.*, 1991) found that subjects, while learning to recognize model three-dimensional heads, did not distribute their time evenly between head views but tended to focus on full-face and profile views. They suggested that the three-quarter view is most efficiently recognized because it activates the representations of both the full-face and profile views. Ullman (Ullman, 1996) has made a similar argument on theoretical grounds. If this inference is correct we would predict that the largest N200s would be evoked by the three-quarter view; at face-specific N200 sites this prediction was not confirmed (Fig. 10*C*). Alternatively it might be predicted that more sites would respond best to full-face or profile views than to three-quarter views. We searched for locations that were view specific; none were found. We also searched for sites that responded at least 50% better to any view than to the average of the other two views; five such sites were found for the full-face view, four for the three-quarter view and two for the profile view.

Hands

The first hint that the primate temporal lobe contains cells responsive to complex objects was a cell that responded best to a monkey hand (Gross *et al.*, 1969; [see also Desimone (Desimone, 1991) and Gross (Gross, 1994)]. We included hands as stimuli to determine whether hand-specific ERPs could be recorded. In addition, it is possible that sites that appeared to respond selectively to faces or face parts were in fact responsive to any commonly viewed human body part. Patients viewed photographs of the upper side of hands in experiments that also included faces and objects (cars or flowers).

There were 25 ventral face-specific N200 sites, 16 in the right and 9 in the left hemisphere. Results for the right and left hemisphere were similar and were combined for statistical analysis. The overall ANOVA for N200 amplitude was significant [$F(df\ 2,46) = 41.0$, $P < 0.0001$]. N200 amplitude to faces was significantly larger than to hands or objects ($P < 0.0001$ in each case), which did not differ significantly between themselves. N200 amplitude to hands was 26% as large as to faces. The overall ANOVA for N700 AUC was significant [$F(df\ 2,48) = 15.8$, $P < 0.0001$]. N700 was significantly larger to faces than to hands or objects ($P < 0.0001$ in each case), which did not differ significantly between themselves. Similar results were seen at four lateral face-specific N200 sites. Hands were also used as stimuli at six face-part-specific sites. The overall ANOVA was significant [$F(df\ 3,15) = 7.18$, $P < 0.003$]. N200 amplitude to combined face parts was significantly larger than to hands ($P < 0.05$). N200 amplitude to hands, faces and objects did not differ significantly.

Hand-specific ERPs were recorded from 12 sites, 5 in the right and 7 in the left hemisphere. Examples are shown in Figure 11*A*,*B*. Hand-specific waveforms consisted of P165, N230 and P310 ERPs. Results for the right and left hemisphere were similar and are combined in Figure 11*C*–*E*. The overall ANOVA for N230 amplitude was significant [$F(df\ 2,11) = 6.30$, $P < 0.007$]. N230 amplitude to hands was significantly larger than to faces or objects ($P < 0.03$ in each case), which did not differ significantly between themselves. The overall ANOVA for N700 AUC was significant [$F(df\ 2,22) = 4.53$, $P < 0.02$]. N700 was significantly larger to hands than to faces or objects ($P < 0.03$ in each case), which did not differ significantly between themselves. Hand-specific ERPs were recorded from disparate regions of cortex (Fig. 11*F*,*G*); none of these sites were face-specific or face-part-specific. Thus hands evoked little activity at face-specific or face-part-specific N200 sites, but evoked hand-specific N230s and related ERPs at other sites.

Discussion

Colored and Grayscale Faces

The prediction that colored faces would evoke a larger N200 than grayscale faces was not confirmed, suggesting that the neural operations reflected by face-specific N200s are sensitive to the configuration of a face rather than to incidental features such as skin color. This result is consistent with the recordings of Perrett *et al.* (Perrett *et al.*, 1984) and Mikami *et al.* (Mikami *et al.*, 1994), who reported no difference in the response of face-specific cells to colored compared to grayscale faces. Desimone *et al.* (Desimone *et al.*, 1984) and Rolls and Baylis (Rolls and Baylis, 1986), however, reported that some face-specific cells responded better to colored than to grayscale monkey faces. P150 was significantly larger to colored faces at ventral face-specific N200 sites, suggesting that this early activity (which is rarely face specific) provides information about color to the ventral face area.

Blurred and Line-drawing Faces

Our results are similar to those reported for monkey face-specific cells, which respond well to normal and blurred faces but less well to line-drawing faces (Perrett *et al.*, 1984). These results agree with human behavioral results; blurred faces similar to those we used only slightly impair face recognition, whereas line-drawing faces similar to those we used produce a larger impairment (Fiorentini *et al.*, 1983). In that study the error rate for face recognition was about three times as large for the line-drawing (>12 c/fw) compared to blurred (<12 c/fw) faces. N700 was significantly smaller to line-drawing than to normal or blurred faces, suggesting that this activity is involved in (or affected by) face recognition processes. There was a 16% increase in N200 latency to line-drawing compared to normal faces (Fig. 1*D*), among the largest we encountered [(Puce *et al.*, 1999b), Fig. 9], suggesting that line-drawing faces require considerably more processing time.

Face Size

Small and large faces evoked N200s that were not significantly different than the N200 evoked by medium faces (Fig. 2). Thus N200 amplitude is relatively invariant across a wide range of face sizes, as is also the case for monkey face-specific cells (Desimone *et al.*, 1984; Rolls and Baylis, 1986; Perrett *et al.*, 1992). Large faces, like blurred faces, evoked N200s that were larger than those evoked by normal faces. These images are shifted toward the low-frequency portion of the spectrum, suggesting that N200 amplitude is preferentially sensitive to the low end of the face frequency spectrum.

Cat and Dog Faces

The results of this experiment support the conclusion that face-specific N200s are maximally sensitive to the configuration of human faces, and that deviations from this configuration evoke less activity (Fig. 3). Cat and dog faces evoked N200s that were respectively 76% and 70% as large as the N200 to human faces. N700 was also larger to human and animal faces than to non-face stimuli, but did not differ between human and animal faces. In a functional magnetic resonance imaging (fMRI) study of the face area of the fusiform gyrus, Kanwisher *et al.* (Kanwisher *et al.*, 1997) found that cat faces produced 82% as much activation in the fusiform face area as did human faces, a result similar to the 76% value we found in N200 amplitude.

Upright and Inverted Faces

The results of central stimulation demonstrate that face-specific N200s are almost as sensitive to inverted as to upright faces. For the right and left hemisphere combined, N200 to inverted faces was 93% as large and 5% later than to upright faces (Fig. 4*A*,*B*). These effects are small compared to changes seen to other stimulus manipulations [(Puce *et al.*, 1999b), Fig. 9]. Thus face-specific N200s clearly respond to inverted faces as face-like rather than object-like stimuli. Similarly, a fMRI study reported robust activation of the fusiform face area by inverted faces (Kanwisher *et al.*, 1998).

The results of hemifield stimulation provide several lines of evidence that the right and left hemisphere respond differently to face inversion.

Stimulation of the contralateral hemifield provides a measure of the amount (N200 amplitude) and rapidity (N200 latency) of processing of direct geniculocortical input. N200 amplitude was larger in the right hemisphere to upright than to inverted faces, and was affected more by face inversion in the right than in the left hemisphere (Figs 4*C* and 5*A*). In the right hemisphere N200 latency was earlier to upright than to inverted faces, whereas in the left hemisphere it was earlier to inverted than to upright faces (Figs 4*D* and 5*B*). Thus to direct geniculocortical input the right hemisphere responds more strongly and more rapidly to upright faces, whereas the left hemisphere responds relatively more strongly, and more rapidly, to inverted faces.

Stimulation of the ipsilateral hemifield provides a measure of the amount (N200 amplitude) and rapidity (N200 latency) of interhemispheric input from the directly activated hemisphere. Stimulation of the ipsilateral hemifield produced a pattern of results opposite to that produced by stimulation of the contralateral hemifield. In the right hemisphere N200 amplitude was larger to inverted than to upright faces, whereas in the left hemisphere it was larger to upright than to inverted faces (Figs 4*E* and 5*A*). In the right hemisphere N200 latency was shorter to inverted than to upright faces, whereas in the left hemisphere it was shorter to upright than to inverted faces (Figs 4*F* and 5*B*). Thus the left hemisphere transfers more information more rapidly about inverted faces to the right hemisphere, whereas the right hemisphere transfers more information more rapidly about upright faces to the left hemisphere.

These results demonstrate that the right hemisphere is better at processing information about upright faces and transferring it to the left hemisphere, whereas the left hemisphere is better at processing information about inverted faces and transferring it to the right hemisphere. The prediction that the right hemisphere would be sensitive to face inversion was confirmed, but not predicted was the finding that the left hemisphere responds better to inverted faces. The most parsimonious explanation of these results – and compatible with current theories about processing strategies in the right and left hemisphere as summarized in Results – is that the right hemisphere employs holistic processing on the normal upright configuration of a face. Inverting a face destroys the normal configuration, requiring the face to be assembled piecemeal, a task that these results suggest is carried out more efficiently by the left hemisphere.

Monkey STS/IT cortex cells have large receptive fields that include the fovea, often extend into the ipsilateral hemifield, and typically respond better to stimulation of the contralateral than the ipsilateral hemifield (Gross *et al.*, 1969, 1972; Desimone *et al.*, 1984). Assuming similar receptive fields in human face-specific cells, faces presented centrally should evoke the largest N200s, and faces presented in the contralateral hemifield should evoke larger N200s than faces presented in the ipsilateral hemifield, as in fact occurred (Figs 4*A*,*C*,*E* and 5*A*). To central stimulation, inverted faces evoked N200s in both hemispheres that were significantly later than to upright faces, suggesting that under normal viewing conditions inverted faces require additional processing time. Monkey face-specific cells also respond later to inverted than to upright faces (Perrett *et al.*, 1988).

Across hemispheres and stimulus conditions the mean ITT was 14.3 ms, less than the 20 ms ITT in somatosensory cortex (Allison *et al.*, 1989). Despite the fact that the interhemispheric pathway length is ~40% longer for visual than for somatosensory cortex [distances estimated from Talairach and Tournoux (Talairach and Tournoux, 1988)], the shorter ITT for visual cortex suggests that transcallosal fibers are on average larger in the visual than in the somatosensory system.

Face Parts

In behavioral studies the most salient internal face parts for face recognition are, in order of importance, eyes, mouth and nose [reviewed by Shepherd *et al.* (Shepherd *et al.*, 1981)]. N200 amplitude at face-specific N200 sites followed the same order (Fig. 6). Ellis *et al.* found that, for unfamiliar faces, face contours were as important for face recognition as were the internal face parts (Ellis *et al.*, 1979). N200 amplitude was larger to face contours than to any other face part except the eyes. Eye scanning studies in humans (Yarbus, 1967) [for similar results in monkeys see Nahm *et al.* (Nahm *et al.*, 1997)] show that eyes, hair/forehead and mouth are scanned more frequently than the nose. These results suggest that the amount of face processing as assessed by face-specific N200 amplitude is related to the relative importance of each face part in face recognition.

A clear conclusion that emerges from this experiment is that each face part, whether internal (eyes, lips, nose) or external (face contour), is treated by face-specific N200 as a face-like stimulus rather than as an object-like stimulus. That is, all face parts evoke a significantly larger N200 than does any category of non-face stimulus. However, N200 latencies to face parts are among the longest we encountered, suggesting that analysis of unusual or suboptimal views of a face – whether of face parts, animal faces, inverted faces or line-drawing faces, all of which evoked longer-latency N200s – requires additional processing time. The N200 evoked by a face is clearly not the linear sum of the response to the face parts, which would be much larger and later than the response to a face. Thus these results do not suggest a hierarchy of processing in which face-part cells send their output to the next stage of face processing, as proposed by Perrett *et al.* (Perrett *et al.*, 1987) and Tovée and Cohen-Tovée (Tovée and Cohen-Tovée, 1993). However, it is possible that the outputs from cortical processors of individual face parts are integrated by a single cortical region that could conclude on the basis of the accumulation of partial information that a face is present. This conclusion could be reached in less time than the full time required to process any individual face part.

A region just lateral to ventral face-specific N200 sites responds preferentially to internal face parts (Fig. 7), and scattered sites throughout the ventral face area respond selectively to one or more face parts (Fig. 8), suggesting analysis of face parts independent of analysis of the full face. The parts-sensitive ventrolateral sites are primarily located in the inferior temporal gyrus lateral to the occipitotemporal sulcus, at the border between ventral and lateral cortex. The activity generated in this region is probably recordable from scalp locations T5 and T6 and sites inferior to them, and may explain why the scalp-recorded N170 is larger to eyes than to full faces at these locations (Allison *et al.*, 1996a; Bentin *et al.*, 1996; Taylor *et al.*, 1997; Puce *et al.*, 1999a). Several lines of evidence including human lesion (Campbell *et al.*, 1986) and fMRI (Bonda *et al.*, 1996; Calvert *et al.*, 1997; Puce *et al.*, 1998) studies and monkey single-cell recordings (Perrett *et al.*, 1990; Oram and Perrett, 1994) implicate a region in or near the superior temporal sulcus in the analysis of facial and other biological motion. ERP (Allison *et al.*, 1999, Fig. 10) and fMRI (Puce *et al.*, 1996, 1997, 1998) studies demonstrate that the ventral and lateral face areas are separated by cortex (the superior portion of the inferior temporal gyrus) that is relatively uninvolved in face processing. Thus the ventrolateral parts-sensitive region appears to be anatomically, and perhaps functionally, separable from the ventral and lateral face areas and the superior temporal region. The ventrolateral region is also anatomically separable from the face-part-specific sites whose centroids are slightly *medial* to the centroids of face-specific sites (Fig. 8). The functionality of these two types of sites is unclear, but they may be involved in the perception of face parts independent of configural face perception presumed to occur at face-specific N200 sites.

Direction of Gaze and Head View

Attention has been given to aspects of face perception under the rubric of 'social attention' and 'theory of mind' (Brothers, 1990; Perrett *et al.*, 1990, 1992; Baron-Cohen, 1995; Cole, 1998). These discussions have in common the conviction that humans and other primates derive valuable information about the actions and intentions of other individuals by interpreting direction of gaze and facial gestures. Humans and other primates regard staring as aggressive and eye aversion as submissive (Perrett and Mistlin, 1990; Brothers and Ring, 1993); one might assume that eyes directed toward the viewer would evoke the largest N200. This was not the case. When the head was directed to the viewer, N200 was larger when the eyes were averted (Fig. 9). On the other hand, N200 was larger when the head was directed toward the viewer and decreased progressively as the head was rotated away from the viewer (Fig. 10). N200 amplitude in the right hemisphere was therefore a function of the joint effects of eye and head position. N200 amplitude was generally larger when eye and head position were incongruent, and smaller when they were congruent. These results suggest that congruent head and eye cues about another individual's direction of attention is the default condition, and that conflicting information requires more processing.

In a fMRI study Puce *et al.* (Puce *et al.*, 1998) found that a region of the superior temporal sulcus was activated by viewing moving eyes and lips. In scalp recordings eye movement away from the viewer evoked larger N170 amplitudes than when the eyes were moving toward the viewer (Puce *et al.*, 1999a). In intracranial recordings a region in or near the superior temporal sulcus generated ERPs to moving but not to static eyes or mouths, whereas ventral face-specific N200 sites often responded to moving eyes or mouths as well (Puce *et al.*, 1999a). These results, together with the results of this study, suggest that the superior temporal region is involved in analysis of social attention and facial movement from dynamic views of a face [see also Humphreys *et al.* (Humphreys *et al.*, 1993) and Calvert *et al.* (Calvert *et al.*, 1997)], whereas the ventral face area is involved in analysis of face identity and social attention from static and dynamic views of a face.

Ventral face-specific N200 amplitude was larger to full-face and three-quarter views than to the profile view (Fig. 10), similar to an early study of face-specific cell responsiveness (Perrett *et al.*, 1982). These results suggest that there is more processing of full-face and three-quarter views than of the profile view. However, the importance of particular views of the head in face recognition is unclear. Some studies found that the three-quarter view allows better recognition than do full-face or profile views (Bruce *et al.*, 1987; Logie *et al.*, 1987), whereas Harries *et al.* (Harries *et al.*, 1991) found that these views were equally good in a recognition task. Troje and Bülthoff (Troje and Bülthoff, 1996) found that for some types of face images the optimal learning view is close to the full-face view but that the results are dependent on the type of images shown during learning and testing. A search for sites that responded best to particular head views yielded five sites preferentially responsive to the full-face view, four to the three-quarter view and two to the profile view, results that do not support the hypothesis of Harries *et al.* (Harries *et al.*, 1991) that representations of full-face and profile views are preferentially constructed.

Hands

Hands evoked little activity at face-specific or face-part-specific sites, hence these sites are unresponsive to parts of the human body *per se*. Hands also evoked little activity in monkey face-specific cells (Desimone *et al.*, 1984). Hand-specific N230s suggest, however, that groups of cells are activated by the specific configuration of hands (Fig. 11). Hand-specific ERPs were encountered in disparate cortical regions (Fig. 11*F*,*G*), but all the lateral surface sites were in the left hemisphere and four of them were near the superior temporal or intraparietal sulci. These left hemisphere regions are activated by viewing moving hands (Bonda *et al.*, 1996; Rizzolatti *et al.*, 1996). Our results suggest that they are also activated (perhaps to a lesser extent) by viewing static hands. In primates hand movement provides social information to other individuals (Morris *et al.*, 1979; Brothers, 1990). The hand-specific sites may be part of a network that assesses another individual's actions and intentions as reflected by hand movement.

Note Added in Proof

We recently recorded two hand-specific N230s from posterior ventral sites. Thus this activity is to some extent bilateral, not unilateral as implied by Figure 11*F* of this paper and by Figure 10*C* of Puce *et al.* (Puce *et al.*, 1999b).

Notes

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