Electrophysiological Studies of Human Face Perception. I: Potentials Generated in Occipitotemporal Cortex by Face and Non-face Stimuli

This and the following two papers describe event-related potentials (ERPs) evoked by visual stimuli in 98 patients in whom electrodes were placed directly upon the cortical surface to monitor medically intractable seizures. Patients viewed pictures of faces, scrambled faces, letter-strings, number-strings, and animate and inanimate objects. This paper describes ERPs generated in striate and peristriate cortex, evoked by faces, and evoked by sinusoidal gratings, objects and letter-strings. Short-latency ERPs generated in striate and peristriate cortex were sensitive to elementary stimulus features such as luminance. Three types of face-specific ERPs were found: (i) a surface-negative potential with a peak latency of ~200 ms (N200) recorded from ventral occipitotemporal cortex, (ii) a lateral surface N200 recorded primarily from the middle temporal gyrus, and (iii) a late positive potential (P350) recorded from posterior ventral occipitotemporal, posterior lateral temporal and anterior ventral temporal cortex. Face-specific N200s were preceded by P150 and followed by P290 and N700 ERPs. N200 reflects initial face-specific processing, while P290, N700 and P350 reflect later face processing at or near N200 sites and in anterior ventral temporal cortex. Face-specific N200 amplitude was not significantly different in males and females, in the normal and abnormal hemisphere, or in the right and left hemisphere. However, cortical patches generating ventral face-specific N200s were larger in the right hemisphere. Other cortical patches in the same region of extrastriate cortex generated grating-sensitive N180s and objectspecific or letter-string-specific N200s, suggesting that the human ventral object recognition system is segregated into functionally discrete regions.

Introduction

The recognition of faces and other complex objects is so accurate and effortless that it is easy to discount the complexity of the neuronal mechanisms that are involved. These mechanisms are revealed by brain damage that produces specific deficits of visual recognition. Perhaps the most striking and interesting of these is face agnosia, or prosopagnosia (Bodamer, 1947), the inability to recognize familiar faces [this has been reviewed by a number of authors (Hecaen and Angelergues, 1962; Meadows, 1974; Whitely and Warrington, 1977; Damasio et al., 1982, 1990; Farah, 1990)]. Prosopagnosia often occurs together with other visual deficits, but when it occurs in isolation it is difficult to avoid the inference that specialized brain regions or processes are involved in face recognition. Despite this, the evidence for specificity of face processing is equivocal, and other interpretations have been considered, including a face-specific memory impairment (Ellis and Young, 1988), right versus left hemisphere processing (Young, 1988), differences in depth of processing (Damasio et al., 1990), holistic versus feature-based processing (Farah, 1990), the development of perceptual expertise (Carey and Diamond, 1994), and local versus global processing (Rentschler et al., 1994).

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Evidence for face-specific processing also comes from single-cell recordings in monkeys, which demonstrate that some cells in the temporal lobe respond selectively to faces, to particular views of faces, to face parts, or to the direction of gaze [reviewed by Perrett et al. (Perrett et al., 1987, 1990), Desimone (Desimone, 1991), Gross (Gross, 1992) and Logothetis and Scheinberg (Logothetis and Scheinberg, 1996)]. The portion of the monkey temporal lobe in which face-specific cells are encountered comprises cortex of the upper wall, fundus, and lower wall of the superior temporal sulcus and contiguous inferotemporal cortex, and will be referred to hereafter as STS/IT cortex. Some cells in the amygdala (Rolls, 1992) and frontal lobe (Wilson et al., 1993; Ó Scalaidhe et al., 1997) are also face specific. In humans, scalp recordings of event-related potentials (ERPs) demonstrate neuronal activity sensitive to faces (Grüsser et al., 1990; Bentin et al., 1996; George et al., 1996; Jeffreys, 1996; Schendan et al., 1998), although this technique does not allow strong inferences about the locations of the active structures. This limitation can be partly overcome by recording directly from the surface of the human brain when such invasive recordings are clinically justified.

ERPs have been recorded from the cortical surface or deep brain structures of patients with medically refractory epilepsy who were implanted with electrodes for seizure focus localization. We have used this technique to localize sensorimotor cortex (Wood et al., 1988), to determine the cytoarchitectonic areas generating specific somatosensory ERPs (Allison et al., 1991), and to record task-related ERPs generated in the anterior medial temporal lobe (McCarthy et al., 1989, 1995; Nobre and McCarthy, 1995). More recently electrodes have been placed on posterior regions of the brain to evaluate seizures of possible posterior temporal, parietal or occipital origin (Williamson et al., 1992). Recordings from the surface of occipitotemporal extrastriate cortex revealed that discrete regions were activated by faces but not by other categories of visual stimuli (Allison et al., 1994a,c), suggesting that faces are processed by a dedicated subsystem of the ventral visual pathway known to be involved in object recognition (Ungerleider and Mishkin, 1982; Merigan and Maunsell, 1993). The most consistent face-related activity was a surface-negative field potential with a peak latency of ~200 ms (N200). Longer-latency face-specific potentials were also recorded from the ventral surface of the anterior temporal lobe, suggesting a posterior-to-anterior sequence of processing stages (Allison et al., 1994c) [for analogous evidence related to letter-string processing, see Nobre et al. (Nobre et al., 1994)].

The purpose of this and the following two papers is to provide a systematic account of these and other face-related ERPs, to compare face-related ERPs with ERPs evoked by non-face stimuli, and to review the implications of these recordings for understanding the locations and properties of the systems involved in face perception. In addition to the papers cited, preliminary Figure 1. Illustration of electrode localization. (A) Coronal slice of an MRI. An electrode strip was inserted subdurally from the lower margin of the craniotomy and extended across the right ventral surface and onto the right mesial wall. Electrode 1 was just anterior to the marginal sulcus, electrodes 2-6 were on the precuneus, posterior cingulate gyrus, and retrosplenial cortex, electrode 7 was on the lingual gyrus, electrode 8 was on the medial fusiform gyrus medial to the midfusiform sulcus, and electrodes 9 and 10 were on the lateral fusiform gyrus. An 8 \times 8 grid of electrodes was placed subdurally on the right parietal and temporal lobes; the electrodes of column 4 are seen in this image. Electrodes 1 and 2 were on the inferior temporal gyrus, electrodes 3 and 4 were on the middle temporal gyrus, and electrodes 5-8 were on the superior temporal and angular gyri. The locations of these electrodes are shown on lateral (B), mesial (C) and inferior (D) views of a brain. The extent of the grid is indicated by dashed lines in (B), and its inferior margin is indicated in (D). In this and later maps electrodes were spaced 10 mm apart, but do not always appear to be linearly spaced due to placement of each electrode in relation to sulci and gyri of the illustrative brain. The susceptibility artifact created by each electrode was larger than the electrode itself (4 mm diameter, 2.2 mm diameter in contact with the brain). Abbreviations: C, cuneus; CaS, calcarine sulcus; CoS, collateral sulcus; EC, entorhinal cortex; FOG, fourth occipital gyrus of Duvernoy (Duvernoy, 1991); ILG, inferior lingual gyrus; ITG, inferior temporal gyrus; LFG, lateral fusiform gyrus; MFG, medial fusiform gyrus; MFS, midfusiform sulcus; MTG, middle temporal gyrus; OTS, occipitotemporal sulcus; PC, precuneus; PG, parahippocampal gyrus; POF, parieto-occipital fissure; SLG, superior lingual gyrus; STG, superior temporal gyrus.

reports of other parts of this work have appeared (Allison *et al.*, 1994b, 1996a,b).

Materials and Methods

Recordings were obtained from 98 patients (44 males, 54 females, 10–55 years of age) with medically intractable epilepsy who were being evaluated for possible surgery (Spencer *et al.*, 1982). All patients were on anticonvulsant medications during testing, but were in various stages of dosage reduction to facilitate seizures. Their full-scale IQ was 89 ± 14 . As assessed by the Wada test, 80% were left-hemisphere dominant for language, 11% were right-hemisphere dominant, and 9% were mixed dominant. With two exceptions they scored within normal limits on the Benton face-matching test (Benton *et al.*, 1983). The protocols used in this study were approved by the Human Investigation Committees of the West Haven VA Medical Center and Yale University School of Medicine. Informed consent was obtained.

Under general anesthesia, strips of electrodes were placed subdurally on the cortical surface. In many patients 8 × 8 grids of electrodes were also placed on the lateral surface. The exposed surface of each stainless steel electrode was 2.2 mm in diameter; interelectrode spacing was 10 mm (5 mm in a few cases). The electrodes are maximally sensitive to field potentials generated within the 3.8 mm² area in contact with the brain, but are less sensitive to activity generated in surface cortex more than a few millimeters distant from the electrode, or to activity generated deep within sulci. In addition to the subdural electrodes, multi-contact depth probes were often targeted at the hippocampus and other temporal and frontal lobe structures. The procedure used to determine and illustrate surface electrode locations is shown in Figure 1. T₁-weighted magnetic resonance images (Fig. 1A) were obtained the day following implantation. The location of each electrode was calculated in the coordinates of Talairach and Tournoux (Talairach and Tournoux, 1988). However, only the y-axis (anterior-posterior) coordinates were used to plot locations in Figure 1 and similar maps. There is considerable inter- and intrahemispheric variation in the location and configuration of gyri and sulci, hence the use of Talairach coordinates in the x-axis (medial-lateral) and z-axis (inferior-superior) would lead to errors in apparent location. In these axes, locations were plotted according to their position in relation to sulci and gyri, as illustrated in Figure 1.

ERP recordings were obtained concurrently with EEG and behavioral video recording used to determine the location and behavioral correlates of seizure onset. The ERP recordings reported here were not obtained immediately before or after seizures, and the EEG was usually normal at recording sites of interest for these studies. ERPs were time-locked to images displayed on a computer screen placed 60 cm from the patient's face. An experimenter sat at the patient's bedside to monitor fixation and alertness. Several experiments were used to search for face-specific activity. In early experiments we used the following digitally scanned



grayscale photographs. (i) Faces from college yearbooks. Females and clean-shaven males were equally represented, and none had extraneous features such as spectacles or jewelry. (ii) Scrambled faces made by rearranging each face such that all elements of the original image were retained (thus the scrambled image was equiluminant with the original image) but their location and orientation was modified until the face and its parts were unrecognizable. This method of scrambling produces many edges, and increases the high-frequency portion of the image spectrum. (iii) The front ends of cars from automotive magazines. (iv) Cars scrambled in the same manner as for faces. (v) Butterflies from a field guide.

Later experiments used improved grayscale stimuli. (i) Faces from books prepared by model agencies. (ii) Phase-scrambled faces created by computing a two-dimensional Fourier transform of each face, randomly scrambling its phase spectrum while preserving its frequency spectrum, and then performing an inverse transform and correcting for luminance. This method of scrambling produces images with luminance and spatial frequency comparable to the corresponding face. (iii) Flowers obtained from digital stock images. (iv) Phase-scrambled flowers made in the same manner as for faces. (v) Letter-strings (concrete nouns) and Arabic number-strings viewed as white characters against a black background. (vi) Phase-scrambled nouns and numbers made in the same manner as for faces. (vii) Blank gray rectangles of the same size and mean luminance of the object or letter-string stimuli.

In all experiments stimulus duration was 250 or 500 ms and the interstimulus interval varied randomly between 1.5 and 2.2 s. Stimulus order was randomized. Face, object and scrambled images had a luminance of 29 ± 4 cd/m² and subtended $8.4^{\circ} \times 8.4^{\circ}$ of visual angle. Sinusoidal gratings had a luminance of 31 ± 4 cd/m² and subtended $7.3^{\circ} \times 7.3^{\circ}$ of visual angle. Nouns and Arabic numbers had a luminance of 11 ± 3 cd/m², subtended $2.4-7.2^{\circ}$ of visual angle horizontally and 1.5° vertically, and had a length of 5.6 ± 1.4 characters. Butterflies, flowers or gray rectangles were targets to which the patient pressed a button; faces were not task relevant and were unfamiliar. The requirement to make button presses to the targets provided a measure of the patient's attention to the stimuli and allowed assessment of the relationship, if any, between stimulus-related and target-related ERPs. Each experiment consisted of 40-75 stimuli of each category and 20-30 target stimuli (target probability 5-15%). Patients performed target detection at >90% accuracy.

Local field potentials generated by these stimuli were recorded simultaneously from 32 or 64 locations using a gain of 10 000, filter settings of 0.1-100 Hz (-3 dB points), and digitized at a rate of 250 Hz. Recordings were referential to a mastoid and were obtained 3-14 days following implantation. A computer algorithm was written to identify and measure amplitude, latency and area under the curve (AUC) of ERP peaks and troughs within specified latency windows. The resulting measurements for each ERP for each stimulus category were stored in a database that also contained the Talairach coordinates of each electrode location. A face-specific ERP was defined as one that was at least twice as large to faces than to any other category of stimulus tested. This criterion is the same as that used in some single-cell recordings of face-specific activity (Perrett et al., 1982; Baylis et al., 1985; Leonard et al., 1985; Ó Scalaidhe et al., 1997). A letter-string-specific ERP was defined as one that was at least twice as large to letter-strings (in the experiments of this study, concrete nouns) than to any other category of stimulus tested. An objectspecific site was defined as one at which the mean ERP amplitude across object categories (any combination of cars, butterflies, flowers and faces) was at least twice as large as the mean amplitude across scrambled object categories (any combination of scrambled cars, flowers and faces).

The influence of stimulus category upon the amplitude and latency of face-specific ERPs was assessed by ANOVA. Because of volume conduction, adjacent electrode sites may have partially sampled the same neural activity. Therefore, if adjacent electrodes were determined to be face specific, only measurements from the site having the largest face-specific ERP were entered into the statistical analysis.

Because each electrode site entered into the ANOVA for a given experiment experienced each of several stimulus categories, a repeatedmeasures ANOVA design was employed. The significance of the stimulus category factor is reported throughout as the overall ANOVA. Although a significant overall ANOVA indicates that a difference in N200 amplitude or latency existed among the categories, additional *post-hoc* contrasts



Figure 2. ERPs from striate and peristriate cortex. (*A*–*D*) examples of recordings. In these and following waveform plots: stimulus onset is at solid vertical line; stimulus offset is at dashed vertical line; time and voltage calibrations apply to all waveforms unless separate calibrations are given; positive voltage is recorded upward; stimulus categories and line types are identified by exemplars. (*E*,*F*) locations and centroids of sites generating N100 and P100. Dorsal occipital pole sites were near the midline and are shown on the mesial maps. This and following maps were prepared as described in Figure 1; electrode locations are shown as solid circles or squares; centroids (geometric means) of locations are shown as black or white crosses.

were also performed to determine which categories differed from each other. Mixed ANOVA designs were used when the influence of stratifying variables such as sex or hemisphere was evaluated. This same analytic approach was used to evaluate other category-specific ERPs.

Results

ERPs Recorded from Striate and Peristriate Cortex

Although the focus of this paper is on face-specific ERPs, it is useful to contrast the face-specific activity with earlier ERPs recorded from electrodes on or near striate cortex. We encountered 37 such sites that generated large ERPs, 14 in the right and

Table 1

Centroids of face-specific and other active regions in the Talairach and Tournoux coordinate system (Talairach and Tournoux, 1988)

ERP	Right hemisphere				Left h	Left hemisphere			
	n	Х	y	Ζ	n	Х	y	Ζ	
N100/P100	14	6	-90	5	22	-14	-83	-3	
Ventral face-specific N200	41	37	-55	-14	34	-38	-53	-17	
Lateral face-specific N200	4	51	-64	9	3	-48	-73	7	
Ventral face-specific VP350	2	39	-45	-18	7	-25	-47	-13	
Lateral face-specific LP350	6	47	-67	8	8	-53	-55	12	
Anterior face-specific AP350	16	34	-10	-30	0				
Ventral gratings N180	5	22	-73	-8	7	-19	-79	-12	
Lateral gratings N180	1	34	-87	-3	1	-32	-88	-11	
Ventral object-specific N200	6	29	-63	-9	9	-33	-64	-18	
Lateral object-specific N200	3	32	-83	14	2	-49	-85	14	
Ventral letter-string-specific N200	7	33	-80	_4	11	-34	-78	-7	
Ventral non-specific N200	9	17	-54	-5	11	-28	-57	-13	

23 in the left hemisphere. These ERPs often began with a surface-negative potential (N100) with a latency of 90–120 ms. (In this and following papers latency refers to peak latency unless specified otherwise.) Representative recordings are shown in Figure 2*A*,*B*. In other cases these ERPs began with an initial positivity (P100) in the 90–120 ms latency range; examples are shown in Figure 2*C*,*D*. P100 sites tended to be on the dorsal surface of the occipital pole. The largest N100 and P100 ERPs were evoked by scrambled faces, checkerboards or other images with sharp edges (Fig. 2*A*–*D*). The locations of these sites are shown in Figure 2*E*,*F*. The centroids of this and other functionally active regions are listed in Table 1. The preponderance of left hemisphere sites was due to increased electrode coverage necessary for language mapping in the event of resections of the left temporal lobe.

Many cells in V1 and V2 respond to stimulus offset (Hubel and Wiesel, 1959; Duysens *et al.*, 1996), and in humans visual ERPs recorded from the occipital scalp contain an off-potential (Kriss and Halliday, 1980). ERPs recorded from striate and peristriate cortex contained an off-potential. That the later potentials were off-potentials, rather than longer-latency potentials to stimulus onset, was demonstrated by the fact that they were time-locked to the offset of the stimulus, as in Figure 2A,B, in which stimulus duration was 250 ms, and in Figure 2C,D, in which stimulus duration was 500 ms.

An electrode located on left striate cortex just inferior to the calcarine sulcus recorded much larger onset potentials to checkerboards presented in the right than in the left visual field (Fig. 3*A*). In an experiment using letter-strings and phasescrambled letter-strings, and larger and brighter non-letter-string images, the latter images evoked a larger N100 (Fig. 3*B*). In an experiment in which patients viewed gratings and an equiluminant blank field, gratings evoked a much larger N100 than did non-patterned stimuli (Fig. 3*C*). Likewise, larger gratings evoked a larger N100 than did smaller gratings (Fig. 3*D*). Thus N100s and P100s recorded from striate and peristriate cortex were not sensitive to stimulus category, but rather were sensitive to stimulation of the contralateral visual field, luminance, luminance contrast and size.

Ventral Face-specific N200 and Related ERPs

N200

N200 is the only face-specific ERP described previously in any detail (Allison *et al.*, 1994a,c), and it continues to be the most



Figure 3. ERPs from striate and peristriate cortex. Recordings from the left striate cortex to checkerboards (either white–black or gray–black) presented in the right and left hemifields (A), to stimuli of varying luminance (B), to gratings and blank stimuli (C), and to gratings of varying size (D).



Figure 4. ERPs at ventral face-specific N200 sites. (*A*,*B*) Examples of recordings. (*C*,*D*) Summaries of amplitude and latency. These and following histogram plots show means \pm SEM; histograms for each stimulus category are in the same order as the exemplars at top.

common face-specific ERP encountered in these recordings. A number of experiments included faces and other categories of stimuli. To illustrate the major features of these recordings we will describe the ERPs obtained in one such experiment.

In this experiment patients viewed faces, cars, scrambled faces, nouns, Arabic numbers and (target) gray rectangles. There were 21 face-specific N200 sites, 13 in the right and 8 in the left hemisphere. Representative recordings are shown in Figure 4A,B. As illustrated in Figure 4B, the earlier portion of the waveform at face-specific sites was usually triphasic and consisted of P150, N200 and P290 ERPs. Results for the right and left hemisphere were similar and are combined in Figure $4C_{,D}$. The overall ANOVA for N200 amplitude was significant [F(df 6,120) = 20.9, P < 0.0001]. Faces evoked a significantly larger N200 than did any other stimulus category (P < 0.0001 in each case). The overall ANOVA for N200 latency was not significant. The degree of specificity of N200 to faces was variable. For example, in the recording of Figure 4B N200 amplitude to number-strings was $\sim 40\%$ as large as to faces, whereas in the recording of Figure 4A there was little response to the other stimulus categories.

P150 and P290

As illustrated in Figure 4B, N200 was often preceded by a



Figure 5. N700 at a ventral face-specific N200 site. The early fraction of N700 is indicated by the black arrow, the late fraction by the gray arrow.

positivity with a mean latency of 154 ms (P150) and followed by a positivity with a mean latency of 288 ms (P290). At all face-specific N200 sites, P150 was rarely (7%) face specific, was often (77%) present but not face specific, and was occasionally (16%) absent. At the same sites, P290 was sometimes (12%) face specific, often (67%) present but not face specific and sometimes (21%) absent. Thus face-specific N200s were often preceded and followed by positivities of variable specificity. P150 and P290 amplitude and latency often showed changes like those seen for N200, but usually not as robust.

N700

P290 was often followed by one or two slow negative ERPs with a mean latency of 690 ms (N700). In Figure 5 both the early fraction (black arrow) and late fraction (gray arrow) were seen. In some recordings only the early or late fraction was seen. One or both fractions of N700 were face-specific at 49% of all face-specific N200 sites. Face-specific N700s were also recorded from 25 sites that did not generate a face-specific N200.

Summary of Responsiveness at Ventral Face-specific N200 Sites

Overview

For all experiments designed to identify face-specific ERPs, a total of 75 face-specific N200 sites were encountered on ventral occipitotemporal cortex. The experiments used for this summary analysis had in common faces, objects (cars or flowers), scrambled or phase-scrambled faces, and targets (butterflies or gray rectangles). Results for the right and left hemisphere were similar and are combined in Figure 6A-C. The overall ANOVA for N200 amplitude was significant [*F*(*df* 3,213) = 150, *P* < 0.0001]. N200 amplitude was significantly larger to faces than to the other stimulus categories (P < 0.0001 in each case), which did not differ significantly among themselves. P150 and P290 amplitudes were significantly larger to faces than to the other stimulus categories (P < 0.01 in each case), which did not differ significantly among themselves. Overall ANOVAs for P150, N200 and P290 latency were not significant. N700 was sometimes composed of more than one fraction (Fig. 5), hence peak amplitude



Figure 6. ERPs at ventral face-specific N200 sites. (A–C) Summaries of amplitude, latency and N700 AUC. (D) Locations and centroids of ventral face-specific N200 sites.

was a poor measure of this activity. The AUC was a better estimate. Calculated AUCs could be positive or negative; a negative AUC means that net voltage was negative in the latency range within which AUC was determined. N700 AUC measurements were made within a latency range of 450–924 ms, which captured most of this activity. N700 at face-specific N200 sites was present only to faces, whereas the other stimulus categories



Figure 7. N200s evoked by faces are shown at a face-specific site and at sites 10 mm medial and lateral to it. Recordings from the right (*A*) and left (*B*) hemisphere. (*C*) Frequency histograms of half-power width.

evoked a broad late potential that on average remained positive (Fig. 6*C*). The overall ANOVA for N700 AUC was significant [*F*(*df* 3,99) = 20.9, *P* < 0.0001]. N700 to faces was significantly larger than to the other stimulus categories (*P* < 0.001 in each case), which did not differ significantly among themselves.

The locations of the ventral face-specific N200 sites are shown in Figure 6D. There were 41 right and 34 left hemisphere sites. Fifty-three sites were on the temporal lobe and 22 were on the occipital lobe, defined as sites posterior to the occipitotemporal notch. Most (75%) sites were on the fusiform or fourth occipital gyri, and 25% were on the inferior temporal or occipital gyri just lateral to the occipitotemporal or inferior occipital sulci. Within the fusiform gyrus 73% of the sites were on the lateral fusiform gyrus and 27% were on the medial fusiform gyrus medial to the midfusiform sulcus. Across patients the most anterior site was at y = -24 and the most posterior site was at y = -91, spanning the posterior two-thirds of the fusiform gyrus and extending into the fourth occipital gyrus. The most medial site was at Talairach |x| = 15, and the most lateral site (excluding the lateral face area, see below) was at |x| = 57. For convenience the region encompassing these face-specific N200 sites will be referred to as the ventral face area.

Intrahemispheric Comparisons

There could be processing stages within the large ventral face area that might be reflected by systematic changes in facespecific N200 amplitude or latency. For each hemisphere, N200 amplitude and latency were plotted as a function of Talairach *x* and *y* coordinates. In no case was the linear trend significant, and in no case did changes in amplitude or latency account for >6% of the variance in these measures. Thus there was no evidence of anterior-posterior or medial-lateral differences in N200 amplitude and latency within the ventral face area of either hemisphere.



Figure 8. Locations of ventral face-specific N200 sites (solid circles) and other sites (open circles) in six patients (A-F).

Interhemispheric Comparisons

The right hemisphere is considered to be more important than the left hemisphere in processing facial information. Behavioral studies show a right hemisphere advantage for face recognition [reviewed by Sergent (Sergent, 1988) and Rhodes (Rhodes, 1993)]. Prosopagnosia always involves the right hemisphere, and can sometimes be produced by damage to the right hemisphere alone (Landis et al., 1986; Sergent and Villemure, 1989; Damasio et al., 1990; DeRenzi et al., 1994; Puce et al., 1997). Positron emission tomography (Horwitz et al., 1992; Sergent et al., 1992, 1994; Haxby et al., 1995) and functional magnetic resonance imaging (fMRI) (Puce et al., 1996; Kanwisher et al., 1997; McCarthy et al., 1997) studies demonstrate that the right hemisphere is more strongly activated by faces than is the left hemisphere. In scalp-recorded ERPs evoked by faces, a facespecific N170 was usually larger over the right than the left posterior temporal region (Bentin et al., 1996; George et al., 1996). We therefore predicted that face-specific N200 sites would generate larger N200s, or would be more numerous, in the right than in the left hemisphere.

Faces evoked no significant differences between the right and left hemisphere for P150, N200 and P290 amplitude and latency or for N700 AUC. To determine whether the 41 right hemisphere

and 34 left hemisphere face-specific N200 sites were secondary to better right hemisphere coverage we counted the total number of electrodes on ventral cortex posterior to the most anterior N200 site; there were 720 right and 785 left hemisphere sites. Although there were proportionally more face-specific N200 sites in the right than in the left ventral face area, the difference in laterality was not significant ($\chi^2 = 1.20$, P = 0.15).

The Size of Ventral Face-responsive Cortex

Figure 6D demonstrated that a large region of ventral occipitotemporal cortex can be involved in face processing. However, those results tell us little about the size and shape of cortex activated by faces in individual hemispheres. Medial and lateral to ventral face-specific N200 sites were sites that were not face specific by our amplitude criterion but were responsive to faces. Face-specific and adjacent cortex will be referred to as face-responsive cortex. Of the 75 ventral face-specific N200 sites, 41 (20 right, 21 left hemisphere) had enough electrodes both lateral and medial to the face-specific site to allow determination of the falloff of N200 amplitude about the peak. A recording from the right hemisphere is shown in Figure 7A and from the left hemisphere in Figure 7B. A common measure of bandwidth is the half-power (0.707 amplitude) width. As calculated from recordings like those in Figure 7A,B, the half-power width was 16.2 ± 5.9 mm (mean \pm SD) in the right hemisphere and 11.8 ± 3.2 mm in the left hemisphere; this difference was significant (P < 0.02). Frequency histograms of half-power width are shown in Figure 7C and indicate, in addition to a main peak at ~12 mm, a smaller peak at ~20 mm, and a tendency for the right hemisphere to have larger and more variable half-power widths.

The length of face-responsive cortex in the anteroposterior dimension was difficult to assess because in most hemispheres only a single electrode strip was placed appropriately to record a face-specific N200. However, exceptions to this rule provided some insight into the possible length and number of faceresponsive regions. In Figure 8A,B, face-specific sites 15-25 mm apart were found. Figure 8C shows the largest putative facespecific cortex we encountered. In both hemispheres anterior face-specific sites were separated from posterior face-specific sites by 23 mm (right hemisphere) and 36 mm (left hemisphere). In these recordings the half-power widths ranged from 10 to 14 mm, suggesting face-responsive regions ~10-15 mm wide and ~35-48 mm long. However, this conclusion assumes that cortex between the anterior and posterior face-specific sites was also face specific. The recordings of Figure 8D-F suggest that this is not necessarily a valid assumption; the anterior and posterior face-specific N200 sites were separated by cortex unresponsive to faces, suggesting the presence of anatomically separate face-specific regions.

Sex Differences

There is little evidence that females and males respond differently to faces, although females may be better than males in face recognition memory [reviewed by Shepherd (Shepherd, 1981)] and discrimination of facial expression [reviewed by Vermeire and Hamilton (Vermeire and Hamilton, 1998)]. To test for possible ERP differences we queried the 75 ventral facespecific N200 sites, 45 in females and 30 in males. Results for the right and left hemisphere were similar and were combined for statistical analysis. P150, N200 and P290 amplitudes, P150 and P290 latency, and N700 AUC were not significantly different for males and females. N200 latency was significantly (P < 0.05) later



Figure 9. ERPs at lateral face-specific N200 sites. (A,B) Examples of recordings. (C-E) Summaries of amplitude, latency and N700 AUC. (F) Locations of lateral N200 sites in the left hemisphere (solid squares projected onto a right hemisphere view) and right hemisphere (solid circles), and centroid of left and right hemisphere sites combined.



Figure 10. Simultaneous recording of face-specific N200s from ventral and lateral sites. (*A*) Recording from the right hemisphere. (*B*) Ventral view of locations. (*C*) Coronal view of locations. Electrode 5 was on the border of the middle temporal gyrus and the middle occipital gyrus (MOG). FG, fusiform gyrus; ITS, inferior temporal sulcus; LOS, lateral occipital sulcus.

in males than in females; the ratio of male/female latency was 1.06. Male/female latency ratios of 1.06 or less can be attributed to male/female differences in brain size and corresponding differences in pathway length (Allison *et al.*, 1983). Thus the sex difference in N200 latency was probably secondary to the sex difference in brain size.

ERPs Recorded from the Normal and Abnormal Hemisphere

All the patients of this study had seizures not adequately controlled by anticonvulsant medication, and most had epilepsy of >5 years duration. The question arises whether their ERPs are representative of those that would be recorded from normal brains. The most direct approach to this question is to determine whether there were systematic differences in ERP amplitude or latency in the normal compared to the abnormal hemisphere, defined as the presence of a unilateral epileptogenic focus as determined by intracranial EEG recording and, in the great majority of patients, subsequent resection of the abnormal tissue.

Fifty-three face-specific N200 sites were in the abnormal hemisphere, and 18 were in the normal hemisphere. (This bias reflects the fact that previous information often suggested which hemisphere was abnormal prior to electrode implantation. Four sites were in patients with bilateral abnormality and were not included in this analysis.) Faces evoked no significant differences between the normal and abnormal hemisphere for P150, N200 and P290 amplitude and latency or for N700 AUC. Thus the patients' epilepsy did not significantly affect the face-specific N200 and related ERPs described in this study.

Lateral Face-specific N200 and Related ERPs

Seven face-specific N200 sites were encountered on the lateral surface of the temporal lobe, four in the right and three in the left hemisphere. Representative recordings are shown in Figure 9A,B. Results for the right and left hemisphere were similar and are combined in Figure 9C-E. The overall ANOVA for N200 amplitude was significant [F(df 3, 15) = 9.59, P < 0.001]. N200 amplitude to faces was significantly larger than to the other stimulus categories (P < 0.02 in each case), which did not differ significantly among themselves. P290 amplitude was also significantly larger to faces than to the other stimulus categories (P < 0.02 in each case), which did not differ significantly among themselves. The overall ANOVAs for P150 amplitude and P150, N200 and P290 latency were not significant. N700 AUC was marginally larger to faces than to the other stimulus categories (P < 0.06 in each case), which did not differ significantly among themselves. Thus the responsiveness of lateral face-specific N200 and related ERPs to face and non-face stimuli was similar to that at ventral sites. P150 latency was significantly (P < 0.02) earlier at lateral compared to ventral sites. N200 latency to faces at lateral sites was 16 ms earlier than at ventral N200 sites, but this difference did not reach significance (P < 0.11). The locations of these sites are shown in Figure 9F; they were centered on the middle temporal gyrus. This area will be referred to as the lateral face area.

The lateral and ventral face areas were anatomically separate (Fig. 10). From electrode 1 a ventral face-specific N200 was recorded from the lateral fusiform gyrus, no face-specific ERPs were recorded from electrodes 2–4, and a lateral face-specific N200 was recorded from electrode 5 located on the middle temporal or middle occipital gyrus. This recording also demonstrates that face-specific N200s were focal in the medial-lateral dimension; in this case they were recorded from more than two adjacent electrodes. Lateral face-specific N200 sites were encountered during the final portion of this study, when we recorded more systematically from the lateral temporal lobe; they were found in 6 of the later 13 patients studied. It is therefore highly probable that the lateral face area generates face-specific N200s more frequently than the overall results would suggest.

P350

A face-specific positivity with a mean latency of 344 ms (P350) was recorded from 39 sites, 24 in the right and 15 in the left hemisphere. P350 was recorded in several experiments that included faces, objects (cars or flowers), scrambled or phasescrambled faces, and targets (butterflies or gray rectangles). Representative recordings are shown in Figure 11A, B. P350 was a broad potential sometimes containing subpeaks (e.g. Fig. 11B), hence AUC measurement was used over the latency range 200-600 ms, which captured most of the P350 waveform. Results for the right and left hemisphere were similar and are combined in Figure 11C. The overall ANOVA for P350 AUC was significant [F(df 3,84) = 33.2, P < 0.0001]. P350s evoked by faces were significantly larger than to any other stimulus category (P <0.0001 in each case). P350s were recorded from three regions (Fig. $11D_{E}$); bilaterally from the ventral face area, bilaterally from the lateral face area, and in the right hemisphere from the anterior ventral temporal lobe. P350s recorded from these regions will be referred to respectively as VP350, LP350 and AP350.

AP350s were recorded only from the right hemisphere (Fig. 11*D*); this region will be referred to as the anterior face area. To



Figure 11. ERPs at face-specific P350 sites. (*A*,*B*) Examples of recordings. (*C*) P350 AUC. (*D*) Locations and centroids of VP350 and AP350 sites. (*E*) Locations of LP350 sites in the right hemisphere (solid squares projected onto a left hemisphere view) and left hemisphere (solid circles), and centroid of right and left hemisphere sites combined.

determine whether this laterality might be secondary to better electrode coverage in the right hemisphere, we counted all



Figure 12. ERPs at sites that generated the largest N180 to gratings. (*A*,*B*) Examples of recordings. (*C*,*D*) Summaries of amplitude and latency. Cartesian vertical gratings (not shown) evoked ERPs similar to those evoked by Cartesian horizontal gratings. Gratings are, from left to right, Cartesian horizontal, hyperbolic, polar, radial and spiral. (*E*,*F*) locations and centroids of N180 sites; in the lateral view a right hemisphere site (solid square) is projected onto the left hemisphere.

electrode sites on the ventral surface of the temporal lobe anterior to the most posterior AP350 site (Talairach coordinate y = -23). There were 485 right and 623 left hemisphere sites, thus AP350 was lateralized to the right hemisphere. There was no anatomical overlap between AP350 and VP350 sites. In two recordings (not shown) N350s were recorded from depth probes superior to the medial ventral surface; they were probably the polarity-inverted counterparts of AP350. Not shown in the maps of Figures 6*D*, 9*F* and 11*D*,*E* are negative sites, i.e. locations recorded from that did not generate a face-specific ERP. Such sites numbered >7000 and covered the ventral, lateral and mesial surfaces of the brain. No face-specific ERPs were recorded from mesial temporal lobe structures, including the hippocampus and parahippocampus, nor from white matter of the temporal and occipital lobes. It is unlikely that additional recordings will reveal any appreciable expansion of the ventral and anterior face areas beyond the regions shown. The lateral face area could be larger than indicated by Figure 9*F* and may approximate the region shown in Figure 11*E*.

A total of ~7500 locations were recorded from in the experiments of this study, and each experiment contained 4–8 stimulus categories. It is possible that some N200s were adventitious and reflected random EEG changes. To determine the number of apparent category-specific N200s recorded by chance, we searched all locations for N200s evoked by scrambled faces, which would not be expected to generate scrambled facespecific activity; three such sites were found. This result provides strong evidence that the N200s described in this and the following papers reflect valid category-specific neuronal activity rather than biological or non-biological noise.

Grating-sensitive ERPs

Following initial processing in areas V1 and V2, subsequent stages of form processing occur in areas including V4 and STS/IT. Some cells in these areas respond to complex features that do not form identifiable objects (Desimone and Schein, 1987; Gallant *et al.*, 1993; Tanaka, 1993; Ghose and Ts'o, 1997). ERP recordings to test the responsiveness of face-specific sites to complex non-objects and to search for form processing sites were based on a study by Gallant *et al.* (Gallant *et al.*, 1993). We used the following grayscale subset of their sinusoidally modulated gratings: Cartesian horizontal and vertical; polar concentric, radial and spiral; and hyperbolic. Targets were gray circles of the same size and mean luminance as the gratings.

There were 11 ventral face-specific N200 sites, 6 in the right and 5 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(df7, 63) = 21.4, P < 0.0001]. N200 amplitude was significantly larger to faces than to any grating (P < 0.0004 in each case), which did not differ significantly among themselves. Gratings evoked N200s that were 9–18% as large as to faces. There were three lateral face-specific N200 sites; their responsiveness was similar to that at ventral sites.

The site in each hemisphere that generated the largest ERPs to gratings was determined. There were 14 such sites, 6 in the right and 8 in the left hemisphere. Representative recordings are shown in Figure 12*A*,*B*. Waveforms were triphasic and consisted of a positivity with a mean latency of 117 ms (P120), a negativity at 179 ms (N180) and a positivity at 258 ms (P260). Results for the right and left hemisphere were similar and are combined in Figure 12*C*,*D*. The overall ANOVA for N180 amplitude was significant [*F*(*df* 6,78) = 5.61, *P* < 0.0001]. All types of non-Cartesian gratings evoked N180s that were significantly larger than those evoked by (target) gray circles (*P* < 0.02 in each case); this was not the case for either type of Cartesian gratings than to any type of non-Cartesian grating (*P* < 0.02 in each case), which did not differ significantly among themselves. The locations of

these sites are shown in Figure 12E,F, and summarized in Table 1.

Object-specific N200 and Related ERPs

To determine whether occipitotemporal cortex contains sites responsive to recognizable complex objects in addition to their possible responsiveness to faces, we searched for sites that were object-specific using the amplitude criterion defined in Materials and Methods. There were 24 object-specific sites, 11 in the right and 13 in the left hemisphere. Representative recordings are shown in Figure 13A.B. Object-specific waveforms consisted of P150, N200 and P290 ERPs. Results for the right and left hemisphere were similar and are combined in Figure 13C,D. N200 amplitude to objects was significantly larger than to scrambled objects (P < 0.001). P150 and P290 amplitude, and P150, N200 and P290 latency were not significantly different to objects than to scrambled objects. The locations of these sites are shown in Figure 13E,F, and summarized in Table 1. They occupied the inferior lingual, fusiform and inferior occipital gyri and extended laterally onto the surface of the occipital pole.

Cars are commonly viewed complex objects. Front views of cars are similar to faces in the arrangement of their component parts (eye-like headlights, etc.) and are easy to anthropomorphize, as in cartoons. Cars thus provide a useful inanimate control for faces. At face-specific N200 sites, cars evoked small N200s (e.g. Fig. 4). Averaged over all experiments in which cars were used, N200 amplitude to cars was 12% as large as to faces. Thus cars did not evoke appreciable activity at face-specific N200 sites. Two car-specific N200 sites were found; this number did not exceed the number of scrambled face-specific sites (see above), hence there was no evidence that cars evoked category-specific N200s.

Occipitotemporal lesions reveal a dichotomy in the recognition of living versus non-living objects (Warrington and Shallice, 1984; Farah *et al.*, 1991; Newcombe *et al.*, 1994), and some of the factors that produce this effect have been investigated (Tranel *et al.*, 1997b; Caramazza and Shelton, 1998). It is possible that putative face-specific N200 sites are responsive to other living things as well.

Butterflies served as a category of animate living things because animal recognition appears to be particularly affected (Newcombe *et al.*, 1994; Caramazza and Shelton, 1998). Averaged over all experiments in which butterflies were used, N200 amplitude to butterflies was 5% as large as to faces at facespecific N200 sites. In these experiments butterflies were targets to which the patient pressed a button. In none of the experiments described in this paper were faces explicitly attended, whereas attended target stimuli did not evoke an N200 but evoked target-related P300s [reviewed by Donchin and Coles (Donchin and Coles, 1988)] at some sites, demonstrating that attention to a stimulus did not *per se* evoke an N200.

Flowers were used to determine responsiveness to a category of inanimate living things. At face-specific N200 sites, and averaged over all experiments in which flowers were used, N200 amplitude to flowers was 4% as large as to faces. Thus living objects *per se* did not evoke appreciable N200s at face-specific N200 sites. Three flower-specific N200 sites were found, not enough to suggest flower-specific processing.

Letter-string-specific N200 and Related ERPs

Some ventral sites generate letter-string-specific N200s that are larger to nouns, pseudowords and other types of letter-strings than to faces and other categories of stimuli (Allison *et al.*,



Figure 13. ERPs at object-specific N200 sites. (*A*,*B*) Examples of recordings. (*C*,*D*) Summaries of amplitude and latency combined across all object and all scrambled-object categories. (*E*,*F*) Ventral and lateral locations and centroids of object-specific sites.

1994c; Nobre *et al.*, 1994). In this study some experiments contained faces, flowers, letter-strings, phase-scrambled letter-strings and (target) gray rectangles. There were 18 letter-string-specific sites, 7 in the right and 11 in the left hemisphere. Representative recordings are shown in Figure 14*A*,*B*. The waveform at letter-string-specific sites consisted of P150, N200,



Figure 14. ERPs at letter-string-specific N200 sites. (A,B) Examples of recordings. (C-E) Summaries of amplitude, latency and N700 AUC. (F) Locations and centroids of letter-string-specific sites.

P290 and N700 ERPs. Results for the right and left hemisphere were similar and are combined in Figure 14C-E. The overall ANOVA for N200 amplitude was significant [F(df 4, 64) = 36.3, P < 0.0001]. N200 was significantly larger to letter-strings than to any other category of stimuli (P < 0.0001 in each case), which did not differ significantly among themselves. The overall ANOVA for N200 latency was not significant. The overall ANOVA for N700 AUC was significant (P < 0.004). N700 was significantly larger to letter-strings than to any other stimulus category (P <0.02 in each case). Letter-string-specific sites occupied the fusiform, fourth occipital, and inferior temporal and occipital gyri (Fig. 13F) except for two sites (not shown) on the middle occipital gyri. More sites were in the left than in the right hemisphere, but electrode coverage was better in the left hemisphere as described above; the difference in laterality was not significant.

Face-specific ERPs in the Frontal Lobe

This study focused on ERPs generated in occipitotemporal cortex. However, Wilson *et al.* (Wilson *et al.*, 1993) found face-specific cells in monkey inferior prefrontal cortex. This led us to record from the frontal lobe when possible. There were 752 frontal lobe sites including locations on the mesial wall (superior frontal and anterior cingulate gyri), orbitofrontal cortex and cortex of the lateral frontal lobe. We found no face-specific N200 sites in the frontal lobe. However, we encountered 11 sites, 4 in the right and 7 in the left hemisphere, that generated small (20–40 μ V) face-specific positivities in the 200–400 ms latency range, with a mean latency of ~250 ms. Two sites were on orbitofrontal cortex and the others were on the lateral frontal lobe inferior to the middle frontal gyrus. These results suggest that some inferior prefrontal cortex sites generate small but face-specific ERPs.

Discussion

The Functional Organization of Human Visual Cortex

Early ERPs

The earliest activity evoked in visual cortex is reflected by N100 and P100 (Fig. 2). This activity is sensitive to elementary stimulus features such as luminance (Fig. 3), and is thus distinguishable from category-specific ERPs, which are sensitive to stimuli of a particular category but not to equiluminant stimuli of another category. Most N100/P100 sites were located on the cuneate and superior lingual gyri corresponding approximately to striate cortex or area V1. Most of the other sites were located on the inferior cuneus and inferior lingual gyrus corresponding approximately to area V2. A few lateral sites on the dorsal and ventral occipital pole were probably on areas V3 and VP as judged by comparison with retinotopic maps (Sereno *et al.*, 1995; De Yoe *et al.*, 1996; Engel *et al.*, 1997; Van Essen and Drury, 1997). The centroid of this activity was in the medial occipital pole (Fig. 2*E*,*F*; Table 1).

Intermediate ERPs

At ventral face-specific sites sinusoidal gratings evoked N180s that were 13% as large as the N200 to faces, thus face-specific N200s are insensitive to this category of stimuli. Similarly, Desimone *et al.* (1984) reported that sinusoidal gratings evoked

little or no response from monkey face-specific STS/IT cells. By contrast, gratings evoked large N180s from sites that were on average posterior to ventral face-specific N200 sites. N180 was generally larger to non-Cartesian than to Cartesian gratings, responded well to all types of gratings, but occasionally responded better to one type of grating, results similar to those reported by Gallant et al. (Gallant et al., 1993). Thus these sites are probably involved in a stage of form processing similar to that in monkey area V4 (Desimone and Schein, 1987; Gallant et al., 1993; Ghose and Ts'o, 1997). The latencies of the P120-N180-P260 ERPs generated at grating sites were on average 20-30 ms earlier than the P150-N200-P290 ERPs generated at face-specific, object-specific and letter-string-specific sites, and were later than the N100 and P100 ERPs initially generated in striate and peristriate cortex. These results suggest that grating ERPs reflect processing that is temporally intermediate between initial processing in V1 and V2 and category-specific processing.

Face-specific ERPs

Face-specific processing occurs in three cortical regions: the ventral face area, which generates N200, its related P150, P290 and N700 ERPs, and VP350 (Figs 6D, 11D); the lateral face area, which generates N200, its related P150, P290 and N700 ERPs, and LP350 (Figs 9F, 11E); and the anterior face area, which generates AP350 (Fig. 11D). N200s reflect the earliest clear evidence of face-specific processing, and may reflect postulated early stages of face processing such as 'template formation' (Damasio et al., 1982) or 'structural encoding' (Bruce and Young, 1986; Perrett et al., 1987). Some P150s were face specific, suggesting that face-specific processing could begin as early as P150 onset, 130-140 ms after stimulus onset and 40-50 ms after onset of activation of striate cortex at ~90 ms. This estimate differs from that of Seeck et al. (Seeck et al., 1997), who concluded that face-specific processing begins as early as 50 ms after stimulus onset.

Ventral face-specific N200 sites are located primarily in the lateral fusiform and adjacent inferior temporal gyri, and less frequently in the medial fusiform and fourth occipital gyri. The fusiform gyrus is ~20 mm wide (Lang and Belz, 1981), suggesting (together with the results of Fig. 7) that a typical face-responsive patch of cortex occupies the lateral 50-75% of the fusiform gyrus, or the lateral half of the fusiform gyrus and adjacent inferior temporal gyrus. Face-specific VP350s reflect a later and presumably different type of neuronal activity than N200, yet they were recorded from the same ventral area from which face-specific N200s were recorded. In some cases VP350 sites were adjacent to N200 sites, suggesting that later face processing may be carried out near the initial processing reflected by face-specific N200s. Face-specific processing as assessed by fMRI was also localized primarily to the lateral fusiform gyrus (Kanwisher et al., 1997; McCarthy et al., 1997; Halgren et al., 1999). fMRI studies suggest that cortex within the midfusiform and occipitotemporal sulci is also activated by faces (Clark et al., 1996; Puce et al., 1996; Halgren et al., 1999). This cortex probably generates face-specific ERPs, but cortical surface recordings are relatively insensitive to generators within sulci.

The lateral face area is centered in the middle temporal gyri. Like the ventral face area, the lateral face area generates early (N200) and late (P350) face-specific ERPs. Activation of this region by faces, as detected by fMRI (Puce *et al.*, 1996), is probably the summation of neuronal activity reflected by face-specific N200 and related ERPs, and by LP350.

The anterior face area consists of the anterior fusiform gyrus, cortex of the ventral temporal pole and entorhinal cortex (Fig. 11*D*). McCarthy *et al.* (McCarthy *et al.*, 1995) found that words evoked P400s from the surface of this region and N400s from depth probes superior to it. This spatial distribution of voltage suggested generators mainly in the collateral sulcus and anterior fusiform gyrus. Face-specific AP350s showed a similar spatial distribution, suggesting similar generators.

Object-specific ERPs

Object-specific N200s were evoked by complex objects but not by scrambled objects (Fig. 13). This activity may reflect general object processing. Object-specific N200s were recorded from sites that extended from the inferior lingual gyrus medially to the middle occipital gyrus laterally (Fig. 13*E*,*F*). Not enough objectspecific sites were encountered to draw strong conclusions about the borders of the object-related region; it included, but was not confined to, the 'lateral occipital complex' (LO) activated by objects and faces in the fMRI study of Malach *et al.* (Malach *et al.*, 1995). Ventrally the centroid of this activity was in the posterolateral fusiform gyrus; the lateral surface sites were centered in the middle occipital gyrus (Fig. 13*E*,*F*; Table 1).

Cars did not evoke large N200s or related ERPs at face-specific N200 sites despite the fact that front views of cars resemble faces in the arrangement of headlights ('eyes'), grill ('nose') and bumper ('mouth'). Butterflies and flowers did not evoke an appreciable N200 or related ERPs at face-specific N200 sites. These results demonstrate that face-specific N200 sites are not responsive to complex inanimate and living objects *per se*, but are responsive only to faces.

Letter-string-specific ERPs

Letter-string-specific N200s were evoked by nouns but not by phase-scrambled nouns or other categories of stimuli (Fig. 14). Letter-string-specific N200s suggest a separate subsystem for letter-string recognition that may be involved in the prelexical grouping of letters into recognizable word forms (Nobre *et al.*, 1994). The centroids of this activity were in the fourth occipital gyri near the occipitotemporal sulci (Fig. 14*F*).

Laterality of Face-specific ERPs

Face-specific N200s and related ERPs were recorded bilaterally from the ventral face area, and their amplitude, latency and AUC did not differ significantly between hemispheres. Thus the right and left hemisphere are engaged more or less equally in the initial stages of face processing. This conclusion is similar to that of Moscovitch et al. (Moscovitch et al., 1976), who argued from behavioral results that hemispheric differences are not seen in the early stages of face processing, but rather are seen in higher-order mnemonic processes. However, two differences were found. (i) Face-responsive cortex was significantly wider in the right than in the left ventral face area (Fig. 7). More face-specific N200 sites were encountered in the right than the left ventral face area (Fig. 6D) despite better electrode coverage in the left hemisphere. This result is probably secondary to the larger face-responsive patches of cortex in the right hemisphere; a particular electrode is somewhat more likely to be placed over face-specific cortex in the right than in the left hemisphere. (ii) Comparison of right and left hemisphere sites shows that N200 latency to faces in the right hemisphere was on average 5.6 ms earlier than in the left hemisphere. Conversely, N200 latency to objects was on average 11.8 ms earlier in the left than in the right hemisphere; this interaction was significant [F(df 1,59) = 4.04],

P < 0.05]. These differences are small, but if one assumes that the hemisphere that first responds to a stimulus pre-empts processing in the other, such differences may be amplified when both faces and objects are simultaneously present in the visual scene. Greater right hemisphere lateralization for face processing and left hemisphere lateralization for object processing may result when face and object stimuli are presented in competition than in isolation (McCarthy *et al.*, 1997).

Face-specific AP350s were encountered only in the right hemisphere (Fig. 11D). This was unexpected because Nobre et al. (Nobre et al., 1994) encountered word-specific P400 sites bilaterally (five in the right and six in the left hemisphere). However, in their study P400s were identified by their sensitivity to semantic priming, not by category specificity. To assess word-specific P400s using the same criterion used in this study to define face-specific P350s (i.e. the P400 to words was at least twice as large as to faces and other stimuli in a screening experiment, independent of its responsiveness in priming experiments) we reviewed all recordings made since the Nobre et al. study. We found 4 right hemisphere and 14 left hemisphere sites. Thus we reach the surprising conclusion that face-specific AP350s are lateralized to the right hemisphere, whereas word-specific P400s are less strongly lateralized (by the current definition) to the left hemisphere. This difference was significant (χ^2 = 21.2, P < 0.0005) and may be part of the reason for the superiority of the right and left hemisphere in processing information about faces and words respectively (Young, 1988).

Relevance to Prosopagnosia

These ERP results are pertinent to the difficult question of the neuroanatomical correlates of prosopagnosia. Damasio et al. (Damasio et al., 1990) distinguish between 'apperceptive', 'associative' and 'amnesic associative' types of prosopagnosia. In their view apperceptive prosopagnosia is due to right hemisphere damage involving both ventral and lateral occipitotemporal cortex; in our terminology both the right ventral and lateral face areas would be involved. Prosopagnosia of the associative type is thought to be due to bilateral damage to ventral occipitotemporal cortex; in our terminology both ventral face areas would be involved. Prosopagnosia of the amnesic associative type is thought to be due to damage to the anterior temporal lobe; in our terminology the anterior face area would be involved. Perhaps prosopagnosia of the amnesic type could also be produced by lesions that disconnected the ventral and anterior face areas. Prosopagnosic patient 2 of Clarke et al. (Clarke et al., 1997) might be an example of such a case, although the lesion also involved part of the anterior face area. Damasio et al. (Damasio et al., 1990) concluded that the associative types of prosopagnosia require bilateral lesions, although this conclusion is controversial (De Renzi et al., 1994; Landis et al., 1986; Sergent and Villemure, 1989). If the anterior face area is as highly lateralized as our results suggest, damage to the right anterior face area alone might be sufficient to produce an amnesic associative prosopagnosia. Tranel et al. (Tranel et al., 1997a) found that brain-damaged patients with defective recognition of famous faces had right hemisphere lesions that maximally involved the right anterior ventral temporal pole. This region appears to be coextensive with the anterior face area. Furthermore, these regions are roughly coextensive with anterior ventromedial temporal (aVMT) cortex, which has been implicated in object recognition and memory in monkeys and humans [reviewed by Nakamura and Kubota (Nakamura and Kubota, 1996)]. Thus converging lines of evidence implicate

aVMT cortex, particularly in the right hemisphere, in the retrieval of knowledge about faces and other objects.

Most prosopagnosics can recognize facial expressions despite their inability to recognize familiar faces (Sergent and Villemure, 1989). Conversely, patients with right hemisphere lesions who are deficient in discriminating facial expressions are not necessarily prosopagnosic (Humphreys et al., 1993). Thus Bruce and Young (Bruce and Young, 1986) proposed parallel systems for recognition of facial identity and facial expression. Our results also suggest parallel pathways to the ventral and lateral face areas, which may be involved preferentially in recognition of face identity and expression, respectively. P150 was significantly earlier (P < 0.02), and N200 latency marginally earlier (P = 0.11), in the lateral face area than in the ventral face area, hence the assumption of a serial pathway from the ventral to the lateral face area is not tenable. Lateral face-specific N200 and LP350 may reflect activity in the 'expression analysis' and 'facial speech analysis' stages of face processing in the model of Bruce and Young (Bruce and Young, 1986).

Conclusions

This paper has described some of the complex neuronal events that occur in human visual cortex following the onset of complex visual stimuli. Initial activation of striate and peristriate cortex is followed by category-specific processing, detected by the presence of a surface-negative field potential with a peak latency of ~200 ms (N200). Three types of category-specific processing can be inferred that deal with faces, objects and letter-strings. Face processing, the focus of this study, is complex and is reflected by at least four types of ERPs (N200, P290, N700 and P350). The earliest face-specific activity is bilateral and appears to perform the same neuronal operations in both hemispheres, whereas one later type of activity (AP350) was recorded only from the right hemisphere. The description of these ERPs sets the stage for the additional studies of their response properties described in the following two papers.

Notes

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