Face Perception, Neural Basis of

Intermediate article

Shlomo Bentin, Hebrew University of Jerusalem, Jerusalem, Israel

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There is neurophysiological evidence to support the existence of a specific neural mechanism in the extrastriate cortex, which is tuned to detect physiognomic information in the visual field and form a mental image, capturing those aspects of the face that enable us to distinguish it from other faces, a stage that is considered to precede personal identification.

INTRODUCTION

The outstanding expertise of humans in recognizing faces has led scientists to suspect that this perceptual process is based on dedicated neural structures. Indeed, face recognition in humans has often been paralleled to phonetic perception, as opposite poles on a hemispherical asymmetry continuum. Whereas the latter has been attributed to dedicated structures buried in the supra-temporal plane of the left hemisphere, the normal processing of faces has been assumed to engage primarily (but not exclusively) posterior-temporal structures in the right hemisphere. The view that the neural structures that are devoted to face perception are also *exclusively* dedicated to this process is controversial. In this article I shall review evidence suggesting that neural structures are implicated in face processing, and discuss their domain specificity. In particular, I shall focus on perceptual processes aimed at constructing a visual representation that is sufficiently detailed and complete to allow unequivocal categorization and identification of the face.

Current models of visual perception distinguish between levels of integration and representation in the visual system (Marr, 1982; Biederman, 1987, 1995; Ullman, 1995, 1996). Despite differences in emphasis and general approach, all of these models assume that the categorization of visually presented stimuli is based on the formation of a mental representation, which is reconstructed from changes in light energy impinging on the retina. Whereas the initial detection of these changes, in terms of edges between different levels of illumination, contrast, orientation and color, is performed in the striate and peristriate visual cortices, it is well accepted that the process of integrating the basic visual primitives into higher-level visual representations is a product of extrastriate neural mechanisms, most of which are distributed along the parvocellular ventral pathway of the visual system, the so-called 'what' pathway. To remind the reader, sensory information from the primary visual cortex reaches the temporal and parietal lobes to form two relatively (but not completely) separate pathways (Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989). One of these is the 'where' system, which passes dorsally in the extrastriate cortex to end in the posterior parietal lobule (and additional ramifications to the frontal lobe). This is the dorsal, magnocellular pathway, which contains cells that are particularly sensitive to the stimulus location in space, and to movement. The other pathway is the 'what' system, which passes ventrally in the extrastriate cortex to reach the inferior temporal cortex, which includes (among other structures) the inferotempral gyrus (IT), the occipito-temporal (fusiform) gyrus, the lingual gyrus and the superior temporal sulcus (STS). This is the parvocellular ventral pathway, which contains cells that are involved in the formation of object-oriented, category-specific visual representations (Van Essen and Deyoe, 1995).

NEUROPSYCHOLOGICAL EVIDENCE

Evidence that faces are processed by dedicated neural mechanisms located in the ventral and inferior-temporal regions comes from a number of different sources. The most notable of these are neuropsychological observations of patients with impaired face recognition (prosopagnosia), electrical activity of single cells recorded in monkeys and of cell assemblies recorded in humans (either directly from the cortical surface or on the scalp

surface), and imaging of brain activity using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI).

Although in most cases of acquired prosopagnosia (impaired face recognition due to brain damage) face-processing deficits are often the most conspicuous aspect of a more general visual agnosia (Gauthier *et al*., 1999a), there are a few reports of prosopagnosic patients whose ability to recognize objects remained intact (McNeil and Warrington, 1993; Farah *et al*., 1995, 2000; Bentin *et al*., 1999). Conversely, there are reports of patients suffering from associative object agnosia whose face recognition ability was spared (Moscovitch *et al*., 1997). The double dissociation between face and object recognition suggests that the two abilities may be neurologically as well as functionally distinct.

EVIDENCE FROM SINGLE-CELL STUDIES

Single-cell recordings in the monkey demonstrated the existence of cells in the temporal lobes that are tuned to respond selectively to monkey (as well as human) faces, but not to other complex and emotion-arousing stimuli such as snakes, spiders or food (Perrett *et al*., 1987, 1990; Desimone, 1991; Gross, 1992; Logothetis and Scheinberg, 1996). Face-selective cells were predominantly found in the superior temporal sulci (STS) and inferior temporal gyri (IT), as well as in the amygdala and the inferior convexity of the prefrontal cortex. Whereas some of these cells responded more vigorously to isolated eyes than to whole faces, other cells responded only to the entire face-view configuration – that is, they were sensitive to the holistic face shape rather than to the existence of individual features. The selectivity of these neurons for faces was maintained despite changes in stimulus size and position. Furthermore, many of these cells responded only to particular orientations of faces or particular directions of gaze. A detailed investigation revealed five types of face-specific cells in the STS, each being maximally responsive to one view of the head, namely full face, profile, back of the head, head up and head down. In addition, two subtypes have been discovered that respond only to left profile or only to right profile, which confirms that these cells are involved in the structural analysis of the face, rather than in representing specific social or emotional responses that faces might elicit (Perrett *et al*., 1985). In summary, the activity of single cells in the monkey suggests that with regard to visual analysis of faces, there is some specificity in the IT and STS. The sensitivity of different cells to different stimulus characteristics suggests a high degree of specialization, providing a complex mechanism of face encoding in the extrastriate cortex. However, the fact that the same cells respond to human faces as well as to within-species (monkey) faces also suggests a high degree of neural plasticity and susceptibility to visual experience.

NEUROIMAGING EVIDENCE

Suggestive as they are, data characterizing the visual system of the monkey cannot be immediately generalized to humans. Indeed, from a phylogenic perspective we see a continuous trend of *reduced* specialization of individual cells, at least in the primary visual cortex. Fortunately, modern technology has enabled the recording of stimulus-linked brain activity in humans. In particular, functional brain imaging using PET and fMRI, and the recording of event-related potentials (ERPs), have yielded pertinent data that suggest face-processing specificity.

The distribution of hemodynamic changes in brain tissue is correlated with neural activity, because elevated metabolism requires more oxygen. Since oxygen is transported to the tissue by hemoglobin cells, the amount of blood flowing through a particular region correlates with its relative activity. PET and fMRI are two techniques which may reveal task-related changes in regional cerebral blood-flow. A series of PET studies suggested that there is posterior-ventral localization of face-specific visual processing (Huxby *et al*., 1996). For example, in one of the first attempts to isolate components of face processing from the processing of objects and nonsense shapes it was found that, compared with nonsense gratings and sinusoid shapes, both faces and objects activate extensive areas in the occipito-temporal cortex. However, whereas this activation was more pronounced in the right hemisphere for faces, it was greater in the left hemisphere for objects (Sergent *et al*., 1992). More recently, fMRI studies have provided a more detailed description. Faces activated the fusiform and middle occipital gyri, the lateral occipital sulcus and more anteriorly the superior temporal sulcus (STS), and this activation was greater in the right than in the left hemisphere (Kanwisher *et al*., 1997; McCarthy *et al*., 1997) (see also Figure 2). In addition, fMRI studies showed distinct activation for perceptual categories other than faces in regions adjacent to the face areas. Although the neuroimaging studies were consistent in showing neuroanatomical specificity for face processing (but see

Gauthier *et al*., 1999b; Gauthier *et al*., 2000), they did not establish when such processing occurs. A tentative answer to the time-course question is provided by the ERP studies.

ELECTROPHYSIOLOGICAL EVIDENCE

The flow of ionic currents across the cell membranes of active neurons and glia cells produces electrical potentials that can be recorded from the cortical surface or from the scalp by disk electrodes (several millimeters in diameter) and represented in the electroencephalogram (EEG) as voltage as a function of time. ERPs are processing-induced changes in these potentials – changes that are time-locked to the brain event that elicited them. These changes become conspicuous on the background of the ongoing EEG following the averaging of designated time epochs that encompass the onset of the stimulus under investigation and are time locked to it. ERPs are usually defined in terms of polarity relative to a neutral reference, onset and peak latency, peak or mean amplitude, and scalp distribution. Recorded non-invasively on the scalp, this technique can be used to investigate normal functioning of the human brain. However, scalp recording does not allow firm conclusions to be drawn about the location of the relevant active structures in the brain. One way to (partly) overcome this limitation is to record the ERPs directly from the cortical surface (and/or from deeper structures) when such invasive recordings are clinically indicated. In a series of studies, investigators at the Yale New Haven Medical Center examined the neural specificity for face processing by recording the electrical activity directly from the ventral and lateral cortex of the temporal lobes. This procedure was possible in patients with medically refractory epilepsy who were implanted with electrodes for localizing the focus of the seizures.

Extensive and systematic electrophysiological investigation of about 100 patients revealed discrete regions in the human extrastriate cortex which were activated by faces but not by other categories of visual stimuli such as cars, flowers, human hands, butterflies or printed words (Allison *et al*., 1999; McCarthy *et al*., 1999; Puce *et al*., 1999). A region was considered to be face specific if the amplitude of any of the ERP components (or a combination of them) recorded at this site was at least twice as large in response to a face than in response to other stimulus categories (note that the same criterion was used to determine the face selectivity of single cells). From a total of more than 7500 recording sites (across patients), about 100 sites were face specific. Most importantly, whenever a component was significantly larger in response to faces, its amplitude was similar across all other stimulus categories (Figure 1). Consistent with the fMRI studies, the vast majority of these sites were clustered on the ventral occipito-temporal cortex, and some were found on the posterior lateral surface of the temporal lobes. A further differentiation of the face-specific ventral sites was between the posterior clusters and an anterior cluster, with no overlap between them. Whereas the posterior ventral and lateral face areas were bilaterally distributed, the anterior face area was only found in the right hemisphere.

Face specificity was evident during three latency windows (from stimulus onset). The earliest face-specific component was a robust negative (compared with the reference) potential that peaked at around 200 ms (N200). This component was elicited in the posterior ventral and lateral face areas. Its amplitude was similar in men and in women, and its latency was slightly more delayed in men than in women, probably reflecting the relatively larger brains in men. The second face-specific component was a positive potential with an average peak of about 350 ms (P350). It was recorded bilaterally from the posterior ventral face area, bilaterally from the lateral face area, and in the right hemisphere from the anterior ventral face area. The third face-specific component was a sustained negativity (N700) observed in the waveforms elicited at about half of the sites at which the N200 was face specific, but also at some sites where the N200 was not specific to faces.

The response properties of this neuronal activity were examined in a series of experiments. In general, the results of these investigations were similar to those obtained by recording face-specific activity of single cells. Neither the N200 nor the N700 were sensitive to the color of the face or to its size. Moreover, all face-specific components were similar in response to unfamiliar and famous faces. Face inversion (i.e. presenting the face upside down) had a complex effect, depending on the location of the face in the visual field. Compared with the face specificity of single cells in the monkey, the human N200 was more species-selective. Although faces of cats and dogs elicited an N200 response which was significantly larger than that elicited by non-face stimuli, the amplitude of this N200 was half the size and its latency was significantly delayed compared with the response to human faces. This pattern was replicated in scalp recordings, in which human and primate but not other animal faces elicited a distinctive component, the N170 (Bentin

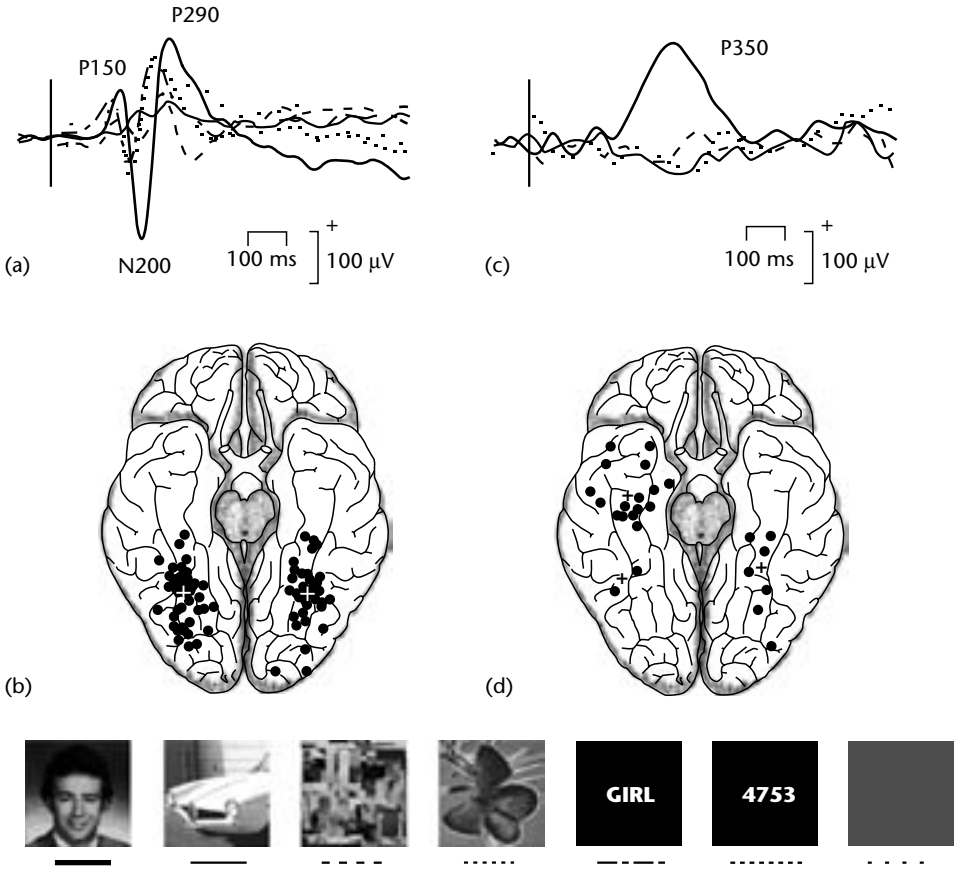

Figure 1. Face-specific ERP components recorded on the cortical surface. (a) N200 and its adjacent positive peaks. (b) Face-specific sites (black dots) in the posterior-ventral temporal lobes. (c) Face-specific P350. (d) Distribution of the P350. Note the unilateral right hemisphere distribution of the anterior sites. (Data provided courtesy of Dr Aina Puce.)

et al., 1996; Carmel and Bentin, 2002). Taken together, the ERP results suggest that the face-specific components recorded on the surface of the fusiform gyrus as well as those recorded from the posterior inferior temporal gyrus (IT) and those recorded on the scalp are associated with neuronal mechanisms that analyze the structural representation of the face, forming its internal representation, and that they are not involved in within-category face identification.

Additional results from intracranial as well as scalp recordings have revealed some characteristics of the face-encoding process. Behavioral and neuropsychological evidence strongly indicates that face identification is based on a holistic process – that is, the gestalt configuration of the face is analyzed first, whereas the analysis of individual face components (if necessary at all) is a late process, independent of face identification (Tanaka and Farah, 1993). Nonetheless, the possibility that the holistic process on which identification is based is only part of a more complex face-encoding mechanism that may also include the analysis of face parts has not been ruled out. Indeed, the finding that despite its significant detrimental effect on face identification, face inversion does not have dramatic effects on either the N200 or the N170 suggests that impeding configurative analysis of the face has only a minor influence on the activity of the face-encoding neuronal process with which these ERP components were associated. To investigate this hypothesis, the sensitivity of the N200 to face parts was directly examined. The results demonstrated that the N200s elicited by isolated eyes, lips, noses or face contours were significantly distinct from those elicited by objects such as cars, flowers and items of furniture, which suggests that the associated neuronal mechanism processed face parts (whether internal or external) as face-like rather than as object-like stimuli. Yet at all face-specific sites the N200 amplitude was reduced relative to that elicited by full-face gestalt. Moreover, as for inverted or degraded faces, the N200 latencies to face parts were significantly longer than those to full faces, suggesting

that analysis of unusual or partial views of a face requires additional processing time. However, the fact that neither the latency nor the amplitude of the N200 to faces is the linear sum of the response to face parts does not support a hierarchy of processing in which face-part cells send their output to a next stage of face processing. It is possible that individual face components are analyzed in parallel by other neuronal mechanisms, and that the accumulated information is integrated by the face-specific mechanism manifested in the N200. The latter hypothesis is supported by the finding of certain regions, lateral to the ventral face-specific N200 sites, which respond preferentially to face components, particularly eyes. These part-sensitive sites are primarily located in the inferior temporal gyrus, at the border between the ventral and lateral cortex. Given their location and the orientation of the cellular columns in that part of the cortex, their activity probably accounts for the modulation of the face-specific N170 recorded on the scalp. Indeed, one of the most consistent findings is that the amplitude of the N170 elicited by isolated eyes is significantly larger and its latency is longer than the N170 elicited by full faces.

Is the face-specific encoding modulated by top-down processes engaging previous knowledge, contextual information and expectations? A series of intracranial as well as scalp recordings designed to answer this question revealed a complex pattern of results. On the one hand, the intracranial recorded N200 was not significantly affected by

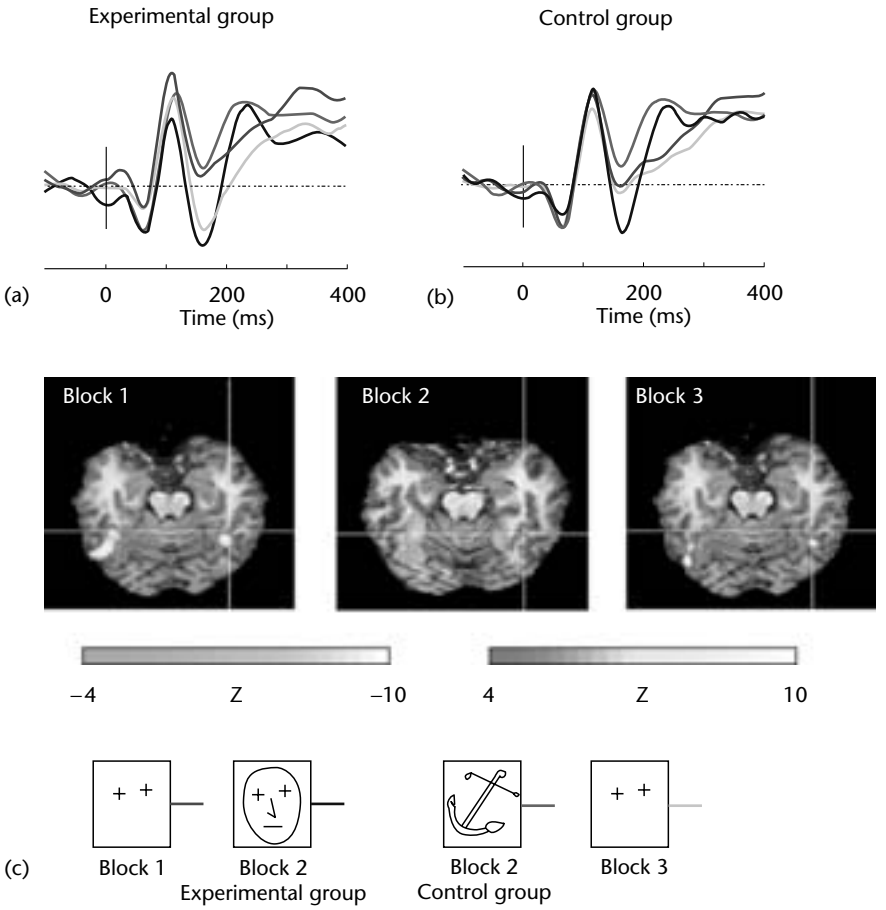

Figure 2. [*Figure is also reproduced in color section.*] Priming effects on face-specific neural activity. (a) The ERPs elicited by two crosses seen in block 1 resemble those elicited by objects. The same stimuli seen in block 3, after a face context was suggested, elicit an N170 similar to that elicited by faces. (b) If objects rather than faces are presented in block 2, the face-specific mechanism is not switched on. (c) Priming effects seen by fMRI. Note in the middle panel the right-hemisphere-lateralized activity elicited by faces (warm colors), and the bihemispheric activity elicited by objects. The two crosses shown in block 1 activate areas similar to those activated by objects. When provided with a face context, the same stimuli activate more restricted areas, albeit bilateral ones. (The fMRI data were collected at the Max-Planck Institute of Cognitive Neuroscience in collaboration with Axel Mecklinger, Yves von Cramon and Angela Friederici.)

stimulus repetition, showing no habituation. It was identical for familiar and unfamiliar faces, and it was not affected by semantic priming. On the other hand, the scalp N170 seems to be sensitive to conceptual influences. First, it is elicited as efficiently by schematic drawings of faces as by natural faces, provided that the schematic representation is simple and clear (Sagiv and Bentin, 2001). Secondly, whereas simple pairs of lines do not normally elicit an N170, they would do so if the subject was primed to interpret the lines as eyes in a schematic face (Figure 2) (*see* Bentin *et al*., 2002).

SUMMARY

The neurophysiological data suggest that faces are encoded in the human visual system by a specialized neural system located in the lateral posterior fusiform gyrus and inferotemporal gyrus. Some of these areas (particularly those located in the fusiform gyrus) probably process the face as a gestalt. The more lateral sites appear to be sensitive to face components, particularly the eyes. The shorter latency of the scalp-recorded N170 relative to the intracranial N200 suggests that the processing of the face parts starts slightly earlier than processing of the gestalt. Yet the exact relationships between these two components of the face-encoding system are unclear. Whether the face-specific activity is a manifestation of an innate module, as the visual preference of infants for faces suggests, whether it is imperative and domain specific, as is suggested by the insensitivity of the N170 to task-relevance of the face (Carmel and Bentin, 2002), or whether this is the manifestation of a change in visual processing induced by expertise (e.g. from an analytic, part-based strategy to a holistic strategy), as is suggested by some behavioral studies (Gauthier and Tarr, 1997) and ERP studies (Tanaka and Curran, 2001), has yet to be established.

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References

Allison T, Puce A, Spencer DD and McCarthy G (1999) Electrophysiological studies of human face perception. I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex* **9**: 415–430.

Bentin S, Allison T, Puce A, Perez E and McCarthy G (1996) Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience* **8**: 551–565.

Bentin S, Deouell LY and Soroker N (1999) Selective streaming of visual information in face recognition: evidence from congenital prosopagnosia. *Neuroreport* **10**: 823–827.

Bentin S, Sagiv N, Mecklinger A, Friederici A and von Cramon DY (2002) Conceptual priming in visual face-processing: electrophysiological evidence: *Psychological Science* **13**: 190–193.

Biederman I (1987) Recognition-by-components: a theory of human image interpretation. *Psychological Review* **94**: 115–147.

Biederman I (1995) Visual object recognition. In: Kosslyn M, Osherson DN (eds) *Visual Cognition*, pp. 121–166. Cambridge, MA: MIT Press.

Carmel D and Bentin S (2002) Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition* **83**: 1–29.

Desimone R (1991) Face-selective cells in the temporal cortex of monkeys. *Journal of Cognitive Neuroscience* **3**: 1–8.

Desimone R and Ungerleider LG (1989) Neural mechanisms for visual processing in monkeys. In: Boller F and Grafman J (eds) *Handbook of Neuropsychology*, pp. 267–299. Amsterdam: Elsevier.

Farah MJ, Levinson KL and Klein KL (1995) Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia* **33**: 661–674.

Farah MJ, Rabinowitz C, Quinn GE and Liu GT (2000) Early commitment of neural substrates for face recognition. *Cognitive Neuropsychology* **17**: 117–123.

Gauthier I and Tarr MJ (1997) Becoming a 'Greeble' expert: exploring mechanisms for face recognition. *Vision Research* **37**: 1673–1682.

Gauthier I, Behrmann M and Tarr MJ (1999a) Can face recognition be dissociated from object recognition? *Journal of Cognitive Neuroscience* **11**: 349–370.

Gauthier I, Tarr MJ, Anderson AW, Skudlarski P and Gore JC (1999b) Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience* **6**: 568–573.

Gauthier I, Skudlarski P, Gore JC and Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience* **3**: 191–197.

Gross CG (1992) Representation of visual stimuli in inferior temporal cortex. *Philosophical Transactions of the Royal Society of London* **B-335**: 3–10.

Huxby JV, Ungerleider LG, Horowitz B *et al*. (1996) Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences of the USA* **93**: 922–927.

Kanwisher N, McDermott J and Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience* **17**: 4302–4311.

Logothetis NK and Scheinberg DL (1996) Visual object recognition. *Annual Review of Neuroscience* **19**: 577–621.

McCarthy G, Puce A, Gore JC and Allison T (1997) Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience* **9**: 605–610.

McCarthy G, Puce A, Belger A and Allison T (1999) Electrophysiological studies of human face perception. II. Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex* **9**: 431–444.
McNeil JE and Warrington EK (1993) Prosopagnosia: a face-specific disorder. *Quarterly Journal of Experimental Psychology* **46A**: 1–10.
Marr D (1982) *Vision*. San Francisco, CA: WH Freeman.
Moscovitch M, Winocur G and Behrmann M (1997) What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience* **9**: 555–604.
Perrett DI, Smith PAJ, Potter DD *et al*. (1985) Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London* **B-223**: 293–317.
Perrett DI, Mistlin AJ and Chitty AJ (1987) Visual neurons responsive to faces. *Trends in Neuroscience* **10**: 358–364.
Perrett DI, Harries MH, Mistlin AJ *et al*. (1990) Social signals analyzed at the cell level: somone is looking at me, something touched me, something moved! *International Journal of Comparative Psychology* **4**: 25–54.
Puce A, Allison T and McCarthy G (1999) Studies of human face perception. III. Effects of top-down processing on face-specific potentials. *Cerebral Cortex* **9**: 445–458.
Sagiv N and Bentin S (2001) Structrual encoding of human and schematic faces: holistic and part-based processes. *Journal of Cognitive Neuroscience* **13**: 937–951.
Sergent J, Ohta S and MacDonald B (1992) Functional neuroanatomy of face and object processing: a positron emission tomography study. *Brain* **115**: 15–36.
Tanaka JW and Farah MJ (1993) Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology* **46A**: 225–245.
Tanaka JW and Curran T (2001) A neural basis for expert object recognition. *Psychological Science* **12**: 43–47.
Ullman S (1995) The visual analysis of shape and form. In: Gazzaniga MS (ed.) *The Cognitive Neurosciences*, pp. 339–350. Cambridge, MA: MIT Press.
Ullman S (1996) *High-Level Vision: Object Recognition and Visual Cognition*. Cambridge, MA: MIT Press.
Ungerleider LG and Mishkin M (1982) Two cortical visual systems. In: Ingle DJ (ed.) *Analysis of Visual Behavior*, pp. 549–586. Cambridge, MA: MIT Press.
Van Essen DC and Deyoe EA (1995) Concurrent processing in the primate visual cortex. In: Gazzaniga MS (ed.) *The Cognitive Neurosciences*, pp. 383–400. Cambridge, MA: MIT Press.

Face Perception, Psychology of

Intermediate article

Alice J O'Toole, University of Texas, Richardson, Texas, USA

CONTENTS

Perceptual information from the human face can be used to determine the identity, sex, race, age, and current mood of an individual. It may serve also as a guide for social interaction, providing us with continually changing feedback about the emotional state of the people with whom we interact.

INTRODUCTION

The number of different faces we must recognize as individuals makes the challenges associated with remembering faces nearly unique in the realm of visual memory. No other class of objects places such stringent requirements on visual memory, and simultaneously calls on human abilities to integrate information into a social context. To recognize and categorize faces, the facial 'features' useful for accomplishing these tasks must be extracted from a moving three-dimensional surface, encoded visually, and represented in memory. Evidence of the importance of face perception to human survival can be seen in the complex network of brain regions specialized for these functions (Haxby *et al*., 2000). (*See* **Face Perception, Neural Basis of**; **Face Cells**)

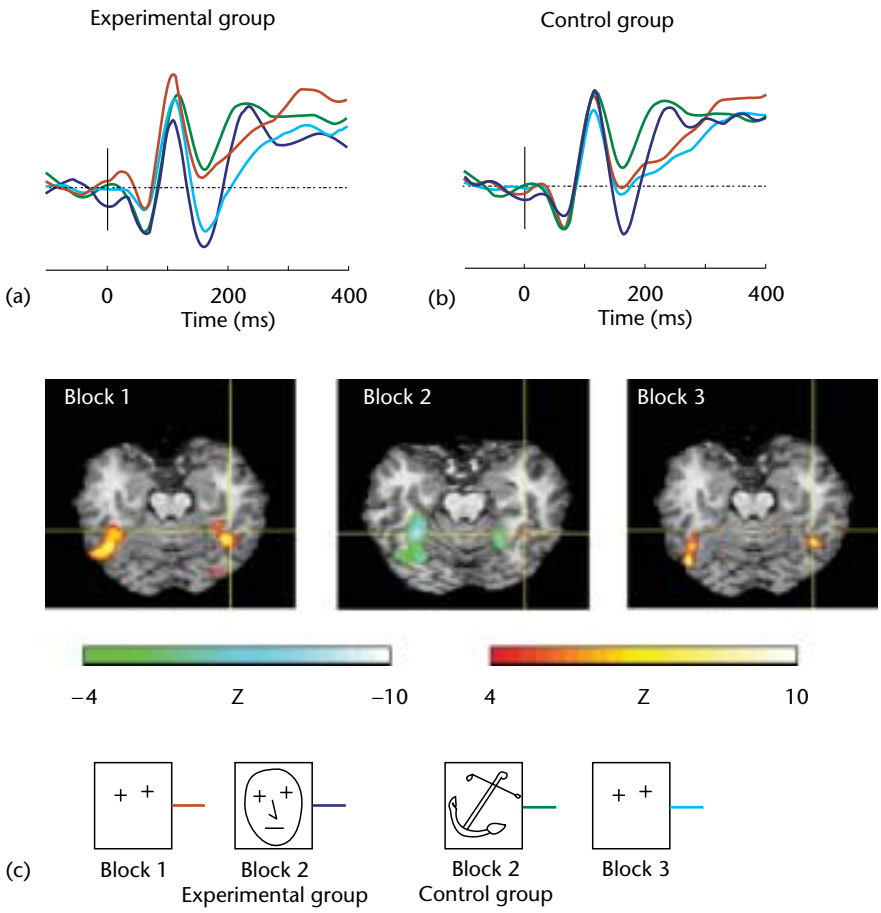

Plate 4 [Face Perception, Neural Basis of] Priming effects on face-specific neural activity. (a) The ERPs elicited by two crosses seen in block 1 resemble those elicited by objects. The same stimuli seen in block 3, after a face context was suggested, elicit an N170 similar to that elicited by faces. (b) If objects rather than faces are presented in block 2, the face-specific mechanism is not switched on. (c) Priming effects seen by fMRI. Note in the middle panel the right-hemisphere-lateralized activity elicited by faces (warm colors), and the bihemispheric activity elicited by objects. The two crosses shown in block 1 activate areas similar to those activated by objects. When provided with a face context, the same stimuli activate more restricted areas, albeit bilateral ones. (The fMRI data were collected at the Max-Planck Institute of Cognitive Neuroscience in collaboration with Axel Mecklinger, Yves von Cramon and Angela Friederici.)