COGNITIVE NEUROPSYCHOLOGY, 2000, 17 (1/2/3), 1–11

# THE COGNITIVE NEUROSCIENCE OF FACE PROCESSING: AN INTRODUCTION

**Nancy Kanwisher**
*Massachusetts Institute of Technology, Cambridge, USA*

**Morris Moscovitch**
*University of Toronto at Mississauga, and Rotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, Canada*

Faces are extraordinarily rich sources of information. From one glance, you can determine the person's age and sex. You know where he or she is looking. You can read mood. If the person is familiar, you know who it is. For most of us, faces are a unique class of visual stimulus: What else do we look at more often or care about more deeply? The very fact that faces have been so special to us and to our primate ancestors makes them a fascinating test case for many of the central questions in cognitive neuroscience. To what extent does visual cognition rely on domain-specific processing mechanisms? How do these specialised cognitive mechanisms arise? How autonomous are they, and how do they interact with other cognitive systems?

The centrality of faces in our lives, however, poses a thorny problem for researchers. What visual stimuli can serve as adequate controls, matched for interest, biological relevance, and visual expertise? Few investigators would disagree that faces are visually special, but it's not easy to discover exactly how and why they are unique.

Not easy, but worth the effort. Exploiting the gamut of techniques from cognitive neuroscience, research on face processing is now making substantial progress. The articles in the present issue use single-unit recording, event-related potentials (ERPS), fMRI, cortical microstimulation, and behavioural testing of patients with brain damage. These studies, together with recent related studies published elsewhere, have helped us gain traction on the long-standing questions of how faces are perceived, how their processing differs from that of nonface stimuli, and how the interaction of evolutionary and experiential forces has produced a neural mechanism that still outperforms the best computer vision algorithms. Here we synopsise the main advances that have been made by the research reported in this volume.

## RECENT PROGRESS IN UNDERSTANDING FACE PROCESSING

### The Multiple Components of Face Processing

Given the diversity of information that can be extracted from a face, we might expect face perception to be accomplished by a system with multiple components (Bruce & Young, 1986). Indeed, evidence from neuropsychology suggests that dissociable neural systems exist for the recognition of individual faces, the discrimination of emotional expressions, and the discrimination of the direction of overt attention (i.e. gaze). The articles in the present issue advance this story further in several respects.

Requests for reprints should be addressed to Morris Moscovitch, Department of Psychology, University of Toronto at Mississauga, Mississauga, Ontario, Canada L5L 1C6 (Email: momos@credit.erin.utoronto.ca).

MM was supported by NSERC grant A8437 and NK was supported my NIMH grant 56037 and a Human Frontiers grant.



http://www.tandf.co.uk/journals/pp/02643294.html

Two papers investigate an ERP marker of face-specific processing called the N170, described earlier by Bentin, Allison, Puce, Perez, and McCarthy (1996; see also Jeffreys, 1996). Bentin, Deouell, and Soroker (1999) demonstrate that the N170 is unaffected by the familiarity of the face presented (see also Rossion et al., 1999), although later ERPs occurring 250msec to 500msec after stimulus presentation are sensitive to face familiarity. These results are taken as evidence that the N170 reflects a fairly early stage of the visual analysis of faces rather than the recognition process itself. Puce et al. (this issue) investigated the ERP responses to moving eyes and moving mouths, and found that the N170 was greater over the left hemisphere for open mouth stimuli (relative to closed mouths), whereas the N170 was greater over the right hemisphere for averted gaze than directed gaze. These findings may reflect the recruitment of left-hemisphere lip-reading mechanisms by moving mouths and the recruitment of specialised gaze mechanisms of the right hemisphere. Related results reported recently by Puce, Allison, Bentin, Gore, and McCarthy (1998) using fMRI suggest that the neural mechanisms in both cases may lie in the region of the superior temporal sulcus (STS), a region that has been implicated in several prior studies in the analysis of biological motion (Bonda, Petrides, Ostry, & Evans, 1996).

Two papers in this volume use behavioural evidence from patients with neurological disorders to provide new information about the functional organisation of the face processing system. Tippet et al. (this issue) provide evidence for a dissociation between the learning of new faces, and the recognition of old faces. They studied patient CT who exhibits an impairment of face learning, or "prosopamnesia," while retaining near normal performance on tasks requiring recognition of previously-learned faces and tasks requiring learning of other visual forms. Although many theorists might assume that mechanisms involved in learning new faces would largely overlap with those involved in recognising and remembering known faces (Dubois et al., 1999; Gorno Tempini et al., 1998), the evidence from this patient suggests otherwise. As such it provides an interesting parallel to neuropsychological patients who lose the ability to learn the appearance of new places despite retaining the ability to recognise old places and the ability to learn new faces (Habib & Sirigu, 1987; Landis, Cummings, Benson, & Palmer, 1986). Collectively, these cases demonstrate a surprising degree of domain specificity in the mechanisms involved in visual learning. One possibility is that these category-specific learning deficits arise from disconnections between visual recognition systems and the hippocampal formation.

Calder et al. (this issue) investigated three patients with Möbius syndrome, a congenital disorder producing facial paralysis. After finding that these patients showed little or no impairment in the recognition of facial expressions, these authors conclude that the ability to produce facial expressions is not a necessary prerequisite for their recognition.

Two paired papers report the results from several different techniques applied to an intriguing single case of an epilepsy patient who had depth electrodes implanted for presurgical mapping. Marinkovic et al. (this issue) report large face-specific potentials from several different electrode sites in the patient's right ventrolateral prefrontal cortex. These results are consistent with the face-specific reponses reported recently in the frontal cortex of macaques (Ó Scalaidhe, Wilson, & Goldman-Rakic, 1997). Interestingly, these sites appear to be very focal, as similar responses were not found in electrode loci only 1.5mm medial or lateral to the active site. As Marinkovic et al. (this issue) note, this pattern of multiple, very small, face-selective regions would probably not be resolvable with current PET and fMRI techniques. Vignal et al. (this issue) further report the stunning result that when the frontal electrode sites showing face-specific responses were subsequently stimulated, the subject reported seeing a series of faces! Further, after surgical excision of the cortex surrounding the same right prefrontal sites, the patient was found to have a deficit in the recognition of emotional expressions, particularly fear. This deficit, however, had largely disappeared when the patient was retested 3 years later. Although these tantalising results do not resolve the precise role of the right ventrolateral prefrontal cortex in face processing, they do

demonstrate that very small foci within this region are selectively involved in some aspects of face processing. Grady et al. (this issue) also report evidence for frontal involvement in face recognition tasks; see following.

Finally, the paper by Breen et al. (this issue) considers several accounts that have been proposed for covert face recognition in prosopagnosia and delusional misidentification syndromes such as Capgras syndrome (a condition in which the patient has a delusional belief that someone they know has been replaced by an impostor). Breen et al. (this issue) argue that both syndromes can be accounted for in terms of a model of face processing in which both covert and overt recognition are mediated by the ventral stream, after which the system bifurcates into one stream that processes semantic and biographical information about the seen face, and another stream responsible for generating the affective response to faces.

Thus the papers in this section provide evidence for a number of distinct components of the face processing system: (1) an early N170 response to faces whether familiar or unfamiliar, probably originating in ventral occipitotemporal cortex; (2) lateral cortical responses to face motion probably in the vicinity of the STS; (3) a functional dissociation of face recognition from face learning; (4) another dissociation between the production and the recognition of emotional expressions; (5) multiple discrete focal regions in right prefrontal cortex involved in working memory for faces and/or in extracting or responding to emotional expressions in faces; and (6) a dissociation between two different ventral pathways involved in face processing, one for extracting semantic and biological information about faces, and the other for producing appropriate affective responses to faces.

## Face-specific Processing vs. Individuation of Within-class Exemplars

The impression gained from the papers discussed above is that cognitive neuroscientists have been generally successful at identifying the neural substrates involved in extracting the different types of information conveyed by faces. One conclusion that may be drawn from these studies is that each of these neural substrates are face-specific processing components that together form a system which is itself face-specific. This conclusion is endorsed by many investigators but it is by no means universally accepted. Other investigators take the view that the function of the system, and by implication its components, is to discriminate between similar exemplars of the same category. According to these investigators, faces are the prototypical stimuli on which this system operates, but not the exclusive ones.

Although in principle the debate applies equally to all the subcomponents of the system, its focus has been on the early components of face recognition centred on the mid-fusiform gyrus, designated the fusiform face area (FFA) by Kanwisher, McDermott, and Chun (1997; see also McCarthy, Puce, Gore, & Allison, 1997). Tong et al. (this issue) show that this area is activated by a wide variety of face stimuli (including cartoon faces and cat faces) compared to other nonface objects. They argue that this region is selectively involved in some aspect of the perceptual analysis of faces such as the detection of a face in an image or the structural encoding of the information necessary for face recognition.

By contrast, Gauthier et al. (this issue) argue that the FFA is more active when subjects make subordinate-level classifications than basic-level classifications (e.g. classifying a particular canine as a beagle rather than a dog). It is not immediately apparent how to reconcile these data with prior studies showing a response in the FFA that was at least twice as great during discriminations between faces as during within-class discriminations between hands (Kanwisher et al., 1997), houses, and backs of human heads (Tong et al., this issue). One possibility is that the large region activated by subordinate-level categorisation in Gauthier et al.'s (this issue) study reflects in part the greater difficulty of the subordinate-level task. Another possibility is that the discrepancy arises because Gauthier et al. used a different technique to identify the FFA from that originally proposed by Kanwisher et al. (1997). For example, they assumed that the FFA occupies a square-shaped region of

cortex. It is therefore possible that the region/s identified in their study are partially or completely nonoverlapping with the FFA as originally defined by Kanwisher et al. (1997) and as identified in subsequent studies by Kanwisher and colleagues (Kanwisher, Tong, & Nakayama, 1998; Kanwisher, Stanley, & Harris, 1999; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Tong et al., this issue).

## Development of Recognition Systems

Two of the papers concerned with the development of face and object recognition systems are also concerned with the problem of specificity. Farah and her colleagues (this issue) present a single-case study of Adam, a 16-year-old boy who became prosopagnosic following bilateral infarction in the occipital lobes at one day of age. Formal testing revealed that Adam could recognise objects much better than faces, leading Farah et al. to conclude that this case provides evidence for an innate face-specific mechanism whose function cannot be assumed by other structures despite ample opportunity and time to do so (but see Ballantyne & Trauner, 1999). Farah et al.'s argument would have carried more weight had they tested Adam on within category discriminations, especially in light of the observation that his recognition of living things is impaired. In support of Farah et al.'s conclusion, however, Bentin et al. (1999) report a case of a developmental prosopagnosic whose N170 response to faces is severely reduced but who has no difficulty making within-class discriminations on various nonface categories (see also Eimer & McCarthy, 1999).

Taking their lead from the seminal studies by Diamond and Carey (1986) on development of expertise in recognising dogs, Gauthier and Logothetis (this issue) argue that through extensive training, specialised mechanisms can be acquired whose characteristics will resemble, and may even overlap or be identical with, those used to recognise faces. As evidence, they cite Gauthier and Tarr's work on recognising "greebles" (artificially created creatures whose members bear a family resemblance to one another), and Logothetis' work on training monkeys to recognise paperclip figures. In both cases, Gauthier and Logothetis show that regions in inferotemporal cortex "learn" to respond to items on which the individual has recently been trained. However, it is not clear whether the regions responsive to "greebles" in humans are the same as those claimed to be selectively involved in the perception of faces (Kanwisher et al., 1997; McCarthy et al., 1997) because of the differences in the techniques used to localise face-selective regions (as discussed earlier). In monkeys, the region responsive to newly learned objects is well anterior to the regions typically found to be responsive to faces. Further, no cells have yet been found that are strongly responsive to both paperclips (after training) and faces. The existence of such cells is predicted by the hypothesis that common mechanisms are involved in all expert subordinate-level categorisation. Future work using fMRI in monkeys should provide an excellent way to survey a large cortical territory at a variety of stages during the acquisition of extensive expertise with novel objects. This work, in combination with studies of the deficits that result from brain damage, will be crucial in resolving the debate about the specificity of visual recognition systems. They may also help answer the even more fundamental question: why is the inferotemporal cortex such a fertile ground for cultivating modules that are specialised for processing complex visual stimuli ranging from words to faces?

## Configural and Part-based Processes in Face and Object Recognition

As difficult as it is to resolve the debate concerning the existence of face-specific neural mechanisms, it is even more difficult to determine what processes might distinguish recognition of faces from that of objects. A popular hypothesis is that object recognition is analytic and part-based whereas face recognition is holistic and configural. Yin's (1969) finding that inversion impairs recognition of faces more than that of other objects supported this hypothesis because inversion impairs the percep-

tion of the spatial configuration among features on which face recognition depends more than identification of the features themselves, which would suffice for much of object recognition. This finding also established inversion as a marker of face-specific processes and a tool for investigating what makes face-recognition special. Building on this tradition, de Gelder and Rouw (this issue) replicated Farah's observation of an "inverted inversion effect" in prosopagnosic patients, that is, better performance on inverted than upright faces. Like Farah, Wilson, Drain, and Tanaka (1995), de Gelder and Rouw account for this effect in terms of the mandatory operation of a damaged holistic processing system, which is engaged by upright but not inverted faces. However, de Gelder and Rouw further show a similar benefit in prosopagnosics for inverted compared to upright stimuli even for animal faces and objects. They account for this result by arguing that the holistic system is also engaged by upright objects and when it is damaged in prosopagnosia it interferes with the operation of the part-based system necessary for object recognition.

Moscovitch and Moscovitch (this issue) discovered that requiring subjects to identify people from photos of inverted internal or external features and from those of inverted fractured faces lead to a "super inversion effect", in which performance dropped to about 20% correct compared to about 70% for intact inverted faces. The super inversion effect in controls resembles the inversion effect for intact faces in CK, a person with object agnosia but otherwise normal recognition of intact upright faces. If the object system is needed for recognition of intact inverted faces, as CK's performance indicates, then the super inversion effects in normal people suggest that some type of configural, orientation-specific information is also needed for recognising intact inverted faces, and possibly also objects. Moscovitch and Moscovitch conclude that both the face and object system use configural and orientation-specific information, but of different types. The face system works on representations of orientation-specific global configurations formed primarily by internal facial features. The object system, on the other hand, integrates information about individual features which themselves may be orientation-specific, with information about local or categorical relations among those features.

One would expect that inversion effects for faces that are so apparent at the behavioural level would have a clear neural correlate. Moreover, if inverted faces are indeed processed as objects as many claim, then they should activate brain regions involved in object processing more than would upright faces. Ashbridge et al. (this issue), recording from single units in a STS, found orientation-selective cells (as well as size-selective cells), the majority of which responded to upright faces and bodies whose size was in the normal range. Ashbridge et al. concluded that the ease of recognising upright over inverted faces is a statistical phenomenon based on the number of neurons involved in processing faces in one or the other orientation. Although this interpretation may account for some of the inversion effect, it does not explain why recognition of inverted faces is related to the integrity of the object recognition system, rather than simply to damage to the face system.

In examining the effects of face inversion on the FFA, Tong et al. (this issue; as well as Kanwisher et al., 1998) found only a slight reduction in activation, with the response to inverted faces remaining much higher than that to objects (see also Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999). If inverted faces are treated as objects, why should the two engage the FFA to such different degrees? A solution suggested by Moscovitch and Moscovitch is that the object system forms a representation of the face based on information congruent with its operating characteristics, which it then transfers to the FFA for further processing. The FFA, in turn, sends its output to more anterior regions for identification. Thus, even inverted faces should activate the FFA, though not as strongly, and at a delay, compared to upright faces. Consistent with this hypothesis, Haxby et al. (1999) found that inverted faces activated object processing regions more than upright faces did, and they activated the face system including the FFA at a longer delay than did upright faces.

### System Wide Distributed Networks in Face Recognition

The study by Grady et al. (this issue) demonstrates that regions not traditionally considered part of the posterior neocortical face system contribute to face recognition, and that their activity levels, as well as the levels of the posterior recognition system, vary with the clarity of the stimulus and the age of the individual. For example, increasing degradation of face stimuli was associated with greater activity in prefrontal cortex in both age groups, presumably because the frontal lobes were recruited in order to allocate additional cognitive resources to stimulus analysis. The old and young, however, differed in a number of ways. In the undegraded condition, the older adults showed greater activity than the young in prefrontal cortex, suggesting that sensory loss in the elderly may have led to some loss in clarity even for the undegraded stimulus. By contrast, the young showed greater activity in parietal and prestriate cortex, reflecting their greater reliance on posterior perceptual mechanisms for stimulus analysis. When the stimuli were degraded, there were striking differences between the young and old adults in the correlations between brain activity and recognition, both in posterior neocortex and in the hippocampus and the thalamus.

Grady et al.'s results indicate that face recognition is not as automatic as a modular account would have one believe. This view is reinforced by Eimer's finding that attention affects even the early N1 components that are specifically sensitive to faces. As in Grady et al.'s study, attentional influences interacted with stimulus properties such that attention affected N1 amplitude in posterior sites for centrally presented faces, but not for peripheral ones. One possible account of the lack of attentional effects for peripherally presented faces is that foveal projections may have preferential access to the ventral visual system where the FFA is located. Another possibility is that peripherally-presented faces may act as exogenous cues such that all peripheral stimuli are maximally attended, swamping any effect of the task.

Both Grady et al.'s and Eimer's (this issue) findings support and extend previous findings by Wojciulik, Kanwisher, and Driver (1998) that the FFA is not a passive system but one whose activity is modulated by attention that is either internally generated or elicited by external factors such as stimulus quality and location. It is interesting to speculate whether the frontal system recruited in Grady et al.'s study acts on posterior face-specific sites directly, or indirectly through the face-specific regions in prefrontal cortex that were identified by Marinkovic et al. (this issue) and Vignal et al. (this issue, corresponding to the face-specific neurons in macaques discovered by Ó Scalaidhe et al., 1997).

## FUTURE DIRECTIONS

The articles in this issue advance our understanding on many of the key questions in the cognitive neuroscience of face processing. Yet many of the core questions in this area are still largely unanswered. We conclude by suggesting several critical areas where future research on face processing may be able to make the most headway.

### The Functional Organisation of Face Processing

The central task of the cognitive neuroscience of face processing is to characterise the functional organisation of the face processing system, including an enumeration of the components of that system, a precise description of what each component does and how it works, and an understanding of how the components interact in real-world face processing tasks.

The increased involvement of new cognitive neuroscience techniques has provided a wealth of new candidate components of the face processing system. The present issue illustrates this progress with articles that provide evidence for different roles for left and right hemisphere STS systems involved in processing face movements (Puce et al., this issue; Ashbridge et al., this issue), frontal areas involved in face processing (Marinkovic et al., this issue; Vignal et al., this issue; Grady et al., this issue), a posterior mechanism for the structural encoding of faces (Bentin & Deouell, this issue; see

also George et al., 1999), different systems involved in the production and perception of emotional expressions (Calder et al., this issue), and others in the emotional responses to faces (Breen et al., this issue), as well as evidence that non-face-specific mechanisms may play an important role in processing inverted faces (Aguirre et al., 1999; Haxby et al., 1999; Moscovitch & Moscovitch, this issue). Although the research in each of these areas is making substantial progress, we are still far from having a definitive account of the precise processes that are involved in each. To take just one example, despite the extensive recent research on the fusiform face area, it is not yet clear whether this region is involved simply in the detection of faces (Tong et al., this issue), the structural encoding of faces (George et al., 1999), or the subordinate-level categorisation of nonface objects (Gauthier et al., this issue). Thus one obviously important direction for future research is to determine more precisely the role of each of the functional components of face processing.

The proliferation of new cognitive neuroscience techniques for studying face processing, however, raises a new challenge: How are we to relate the findings collected from different techniques? Is the generator of the N170 observed with ERPs the same as that for the face-selective N200 observed with subdural strip electrodes (McCarthy, Puce, Belger, & Allison, 1999)? (Bentin et al., 1996, argue that it is not.) Does prosopagnosia result from the loss of the FFA, or rather from some other part of the face-processing system? Answers to these questions will be crucial if any effort to bring coherence and unity to this field is to succeed. One way to approach this question is to run closely matched experiments on the same individuals using two or more of these techniques, enabling a qualitative comparison of the functional properties of each neural marker. It will also be important to conduct similar studies in people with neurological disorders to determine whether damage to these areas produce the types of deficits predicted from functional studies in normal subjects. As yet, there are only a few studies that have applied the new techniques to investigate individuals with brain damage (e.g. Eimer & McCarthy, 1999).

An even greater challenge arises in relating data across species. Is the STS region in monkeys homologous to the human FFA, STS, or neither? Do monkeys have a region of face-selectivity in ventral cortex homologous to the FFA? A major limitation in answering this question has been the difficulty of recording from many cortical regions simultaneously in monkeys. However, the advent in the last year of techniques for running fMRI experiments on monkeys (Logothetis, Guggenberger, Peled, & Pauls, 1999) greatly improves the prospect for progress in this area by providing a way to run closely matched studies in monkeys and humans, enabling a direct comparison of the data collected across species.

Thus a major direction for future research will be to attempt to bridge across techniques, different human populations, and species. This effort is bound to provide a much richer and more precise picture of the involvement and function of each of the functional components in face processing.

## Lessons from Machine Vision

Although our special issue did not include papers on this topic, a wealth of recent research in computer vision has been directed toward the development of algorithms for machine face recognition (Hallinan, Gordon, Yuille, Giblin, & Mumford, 1999). This work is relevant to our efforts to understand human face recognition in two ways. First, machine vision has long informed the study of human vision by providing counterintuitive insights about just which aspects of a visual task pose the greatest computational challenge. To the extent that any aspect of face perception poses special computational demands, we might expect the brain to exhibit a greater degree of cortical specialisation in its solution to that problem. Second, computer vision algorithms can be thought of as candidate theories of human recognition, specified with unusual precision and therefore eminently testable by behavioural and other techniques. In the long run the goal of a cognitive theory of face recognition should be to transcend the vague terminology now in use (e.g. "holistic processing") by achieving a precise characterisation of each compo-

nent of face processing in terms of the actual algorithms involved. Thus one important direction for the cognitive neuroscience of face processing in the future will be a greater integration of the field with computational approaches to face perception.

## Face Processing: How Selective and How Special?

Many of the articles in this issue address the selectivity of different neural mechanisms for face processing. Demonstrating a greater response to one stimulus class than to another is not sufficient to make the case for selectivity; a large number of noninstances of the stimulus class must be shown to produce a much lower response. Single-unit physiologists have made the greatest progress toward this goal, as they have tested the response of individual "face cells" to a wide variety of stimuli (Gross, Roche-Miranda, & Bender, 1972; Perrett et al., 1991). ERP work (Bentin et al., 1996; Jeffreys et al., 1996) and fMRI studies (Kanwisher et al., 1999; McCarthy et al., 1999; Tong et al., this issue) are catching up, with substantial evidence for face-selectivity of both the N170 and the FFA. However, note that claims of face selectivity amount to hypotheses that none of the infinite number of as-yet-untested stimulus categories will produce a response as great as that observed to faces. Any such claim may be refuted whenever a new stimulus category is tested and shown to produce a response as great as (or greater than!) faces. Given this situation it will be important for all neural markers of supposed face-specific processes to be tested on a wide range of nonface stimuli.

Nonetheless, even substantial evidence for face selectivity need not imply that faces are unique. After all, the brain could be populated by hundreds of discrete regions, each specialised to analyse a different class of stimuli. Thus one important direction for future research is to test a wider range of stimulus categories to see whether any other similarly selective responses to distinct categories can be found. Neuropsychological evidence for category-specific impairments suggests that faces may not be the only domain of specialisation; it will be important in the future to supplement this evidence with fMRI and other neural measures in normal subjects (Downing & Kanwisher, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996).

A wider exploration of the range of stimulus selectivities found in the brain should provide a broader context in which to view the implications of face-selective mechanisms. Further, this enterprise may shed some light on the more fundamental question of the origins of cortical specialisation (Downing & Kanwisher, 1999). If the experience of the individual is important in shaping the organisation of visual cortex, then we might expect to find selective responses to stimulus classes with which modern individuals (but not their primate ancestors) have frequent daily experience (e.g. cars and chairs). However, if the evolutionary experience of the species is the critical determinant, then we might expect to find cortical regions specialised for the visual analysis of stimulus classes (e.g. predators and flowers) critical to the survival of our primate ancestors but not to modern humans.

The type of representation that is used by a particular specialised cortical system may also depend on whether evolution or experience plays the more prominent role in its origin. For stimuli such as faces, which are likely to be encountered by every member of the species, configural representations or templates may be most effective because the basic stimulus configuration is invariant across the environments in which individuals may live. Thus the predictability of species-specific stimuli may allow for the creation through evolution of complex pattern recognition systems. These systems are likely to be based on templates or configurational properties that are tuned at birth to the relevant stimulus properties but that remain plastic through development (Johnson, 1999; Maurer, 1985; Valenza, Simion, Cassia, & Umilta, 1996).

A different type of recognition system would be needed for dealing with complex patterns whose presence in the environment is accidental and whose identification would depend on experience. Manufactured objects would be one such stimulus class. Further, animals, plants, and objects may be so different from one another that no single template or handful of templates could capture the stimulus characteristics of all of them. For these

kinds of complex patterns, a part-based system would allow the necessary flexibility to represent heterogeneous classes of stimuli.

It may be significant that several category-specific representation systems are found in ventral extrastriate cortex in the lingual, fusiform, and parahippocampal gyri. Located between posterior regions that code for primary sensory features and anterior and lateral regions concerned with semantics and memory, the inferotemporal cortex is ideally situated to serve as a convergence zone for binding information across distributed sensory networks under the guidance of higher-order systems. Regions within this ventral pathway appear to be distinguished from each other by their location, by the type of information that is bound, and perhaps by the algorithms underlying the binding operations. Recent neuroimaging and single unit studies on repetition priming suggest that inferotemporal cortex is also rapidly modified by experience (Grill-Spector et al., in press; Wiggs and Martin, 1998), a feature that may be crucial for the creation of structural representation systems.

If different representational systems exist that are structurally separate and operate according to different principles, how do they share information with each other? Moscovitch and Moscovitch addressed this problem with regard to sharing of information between the face and object system. One possible solution is to use translation codes for communicating between two systems, and another is to form associations between coactivated systems so as to create new, inter-related units that embody information about both. Apart from some computational modelling, few studies have attacked this problem directly.

## Origins of Cortical Specialisation

A final and crucial area for future research will be the effort to explore the origins of cortical specialisation. We have discussed several methods for tracking the effect of individual experience on cortical specialisation. An important complement to this work will be to investigate possible innate bases for specialised face recognition mechanisms. Advances in imaging technology may make it possible in the future to safely scan young children and infants, enabling the origins of cortical specialisations to be tracked directly throughout the development of the individual. fMRI studies of developing primates may also allow us to address closely related questions. In a similar vein, longitudinal imaging studies during recovery from brain damage should provide a better understanding of the mechanisms that cause cortex to become specialised.

## REFERENCES


Aguirre, G.K., Singh, R., & D'Esposito, M. (1998). Timing and intensity of fusiform face area (FFA) responses to upright and inverted faces. *Society of Neuroscience Abstracts,* #355.8.

Aguirre, G.K., Singh, R., & D'Esposito, M. (1999). Stimulus inversion and the responses of face and object-sensitive cortical areas. *Neuroreport, 10,* 189-194.

Ashbridge, E., Perrett, D.I., Oram, M.W., & Jellema, T. (this issue). Effect of image orientation and size on object recognition: Responses of single units in the macaque monkey temporal cortex. *Cognitive Neuropsychology, 17,* 13–33.

Ballantyne, A.O., & Trauner, D.A. (1999). Facial recognition in children after perinatal stroke. *Neuropsychiatry, Neuropsychology and Behavioural Neurology, 12,* 82–87.

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

Bentin, S., & Deouell, L.Y. (this issue). Structural encoding and identification in face processing: ERP Evidence for separate mechanisms. *Cognitive Neuropsychology, 17,* 35–54.

Bentin, S., Deouell, L.Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *Neuroreport, 10,* 823–827.

Bonda, E., Petrides, M., Ostry, D., & Evans, A., (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *The Journal of Neuroscience, 16,* 3737–3744.

Breen, N., Caine, D., & Coltheart, M. (this issue). Models of face recognition and delusional

misidentification: A critical review. *Cognitive Neuropsychology, 17,* 55–71.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77,* 305–327.

Calder, A.J., Keane, J., Cole, J., Campbell, R., & Young, A.W. (this issue). Facial expression recognition by people with Möbius syndrome. *Cognitive Neuropsychology, 17,* 73–87.

de Gelder, B., & Rouw, R. (this issue). Structural encoding precludes recognition of face parts in prosopagnosia. *Cognitive Neuropsychology, 17,* 89–102.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General, 115,* 107–117.

Downing, P., & Kanwisher, N. (1999). Where do critical modules come from? *Poster to be presented at the Annual Meeting of the Cognitive Neuroscience Society*.

Dubois, S., Rossion, B., Schiltz, C., Bodart , J.M., Michel, C., Bruyer, R., & Crommelinck, M. (1999). Effect of familiarity on the processing of human faces. *Neuroimage, 9,* 278–289.

Eimer, M. (this issue). Attentional modulations of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology, 17*, 103–116.

Eimer, M., & McCarthy, R.A. (1999). Prosopagnosia and structural encoding of faces: Evidence from event- related potentials. *Neuroreport, 10,* 255–259.

Farah, M.J., Rabinowitz, C., Quinn, G.E., & Liu, G.T. (this issue). Early commitment of neural substrates for face recognition. *Cognitive Neuropsychology, 17,* 117–123.

Farah, M.J., Wilson, K.D., Drain, H.M., & Tanaka, J.R. (1995). The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Vision Research, 35,* 2089–2093.

Gauthier, I., & Logothetis, N.K. (this issue). Is face recognition not so unique after all? *Cognitive Neuropsychology, 17,* 125–142.

Gauthier, I., Tarr, M.J., Moylan, J., Anderson, A.W., Skudlarski, P., & Gore, J.C. (this issue). Does visual subordinate-level categorisation engage the functionally-defined fusiform face area? *Cognitive Neuropsychology, 17,* 143–163.

George, N., Dolan, R., Fink, G.R., Baylis, G.C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus, *Nature Neuroscience, 2*, 574-580.

Gorno Tempini, M.L., Price, C.J., Josephs, O., Vandenberghe, R., Cappa, S.F., Kapur, N., & Frackowiak, R.S.J. (1998). The neural systems sustaining face and proper-name association. *Brain, 121,* 2130–2118.

Grady, C.L., McIntosh, A.R., Horowitz, B., & Rapoport, S.I. (this issue). Age-related changes in the neural correlates of degraded and non-degraded face processing. *Cognitive Neuropsychology, 17,* 165–186.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (in press). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*.

Gross, C.G., Roche-Miranda, G.E., & Bender, D.B. (1972). Visual properties of neurons in the inferotemporal cortex of the macaque. *Journal of Neurophysiology, 35,* 96–111.

Habib, M., & Sirigu, A. (1987). Pure topographical disorientation: A definition and anatomical basis. *Cortex, 23,* 73–85.

Hallinan, P.L., Gordon, G.G., Yuille, A.L., Giblin, P.J., & Mumford, D.B. (1999). Two- and three-dimensional patterns of the face. Wellesley, MA: A.K. Peters.

Haxby, J.V., Ungerleider, L.G., Clark, V.P., Schouten, J.L., Hoffman, E.A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron, 22,* 189–199.

Jeffreys, D.A. (1996). Evoked potential studies of face and object processing. *Visual Cognition, 3,* 1–38.

Johnson, M.H. (1999). Ontogenetic constraints on neural and behavioural plasticity: Evidence from imprinting and face processing. *Canadian Journal of Experimental Psychology, 53,* 77–90.

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

Kanwisher, N., Stanley, D., & Harris, A. (1999). The fusiform face area is selective for faces not animals. *Neuroreport, 10,* 183–187.

Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition, 68,* B1--B11.

Landis, T., Cummings, J.L., Benson, D.F., & Palmer, E.P. (1986). Loss of topographic familiarity: An environmental agnosia. *Archives of Neurology, 43,* 132–136.

Leung, T.K., Burl, M.C., & Perona, P. (1995). Finding faces in cluttered scenes using random graph match-

ing. *International Conference on Computer Vision, Cambridge, MA.*

Logothesis, N.K., Guggenberger, H., Peled, S., & Pauls, J. (1999). Functional imaging of the monkey brain. *Nature Neuroscience, 2,* 555–562.

Marinkovic, K., Trebon, P., Chauvel, P., & Halgren, E. (this issue). Localized face-processing by the human prefrontal cortex: Face-selective intracerebral potentials and post-lesion deficits. *Cognitive Neuropsychology, 17*, 187–199.

Martin, A., Wiggs, C., Ungerleider, L., & Haxby, J. (1996). Neural Correlates of Category-Specific Knowledge. *Nature, 379,* 649–652.

Maurer, D. (1985). Infants' perception of facedness. In T.N. Field & N. Fox ( Eds.) *Social perception in infants*. Norwood, NJ: Ablex.

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. *Cerebral Cortex, 9,* 431–444.

McCarthy, G., Puce, A., Gore, J.C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 9*, 604–609.

Moscovitch, M., & Moscovitch, D.A. (this issue). Super face-inversion effects for isolated internal or external features, and fractured faces. *Cognitive Neuropsychology, 17,* 201–219.

Ó Scalaidhe, S.P., Wilson, F.A., & Goldman-Rakic, P.S. (1997). Areal segregation of face-processing neurons in prefrontal cortex. *Science, 278,* 1135–1138.

Perrett, D.I., Oram, M.W., Harries, M.H., Bevan, R., Hietanen, J.K., Benson, P.J., & Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research, 86,* 159–173.

Puce, A., Allison, T., Bentin, S., Gore, J.C., & McCarthy, G. (1998). Temporal cortex activation in human subjects viewing eye and mouth movements. *Journal of Neuroscience, 18,* 2188–2199.

Puce, A., Smith, A., & Allison, T. (this issue). ERPs evoked by viewing facial movements. *Cognitive Neuropsychology, 17,* 221–239.

Rossion, B., Campanella, S., Gomez, C.M., Delinte, A., Debatisse, D., Liard, L., Dubois, S., Bruyer, R., Crommelinck, M., & Guerit, J.M. (1999). Task modulation of brain activity related to familiar and unfamiliar face processing: An ERP study. *Clinical Neurophysiology, 110,* 449–62.

Tippett, L.J., Miller, L.A., & Farah, M.J. (this issue). Prosopamnesia: A selective impairment in face learning. *Cognitive Neuropsychology, 17,* 241–255.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. (this issue). Response properties of the human fusiform face area. *Cognitive Neuropsychology,* 17, 257–279.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21,* 753–759.

Valenza, E., Simion, F., Cassia, V.M., & Umilta, C. (1996). Face preference at birth. *Journal of Experimental Psychology: Human Perception and Performance, 22,* 892–903.

Vignal, J.P., Chauvel, P., & Halgren, E. (this issue). Localized face-processing by the human prefrontal cortex: Stimulation-evoked hallucinations of faces. *Cognitive Neuropsychology, 17,* 281–291.

Wiggs, C.L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology, 8*, 227–233.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Modulation of activity in the fusiform face area by covert attention: An fMRI study. *Journal of Neurophysiology, 79,* 1574–1579.

Yin, R.K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81,* 141–145.