The distributed human neural system for face perception

James V. Haxby, Elizabeth A. Hoffman and M. Ida Gobbini

Face perception, perhaps the most highly developed visual skill in humans, is mediated by a distributed neural system in humans that is comprised of multiple, bilateral regions. We propose a model for the organization of this system that emphasizes a distinction between the representation of invariant and changeable aspects of faces. The representation of invariant aspects of faces underlies the recognition of individuals, whereas the representation of changeable aspects of faces, such as eye gaze, expression, and lip movement, underlies the perception of information that facilitates social communication. The model is also hierarchical insofar as it is divided into a core system and an extended system. The core system is comprised of occipitotemporal regions in extrastriate visual cortex that mediate the visual analysis of faces. In the core system, the representation of invariant aspects is mediated more by the face-responsive region in the fusiform gyrus, whereas the representation of changeable aspects is mediated more by the face-responsive region in the superior temporal sulcus. The extended system is comprised of regions from neural systems for other cognitive functions that can be recruited to act in concert with the regions in the core system to extract meaning from faces.

Face perception may be the most developed visual perceptual skill in humans. Infants prefer to look at faces at a very early age[1] and, across the lifespan, most people spend more time looking at faces than at any other type of object. People seem to have the capacity to perceive the unique identity of a virtually unlimited number of different faces, and much of the cognitive and neuroscience research into face perception has focused on this ability to recognize individuals. Recognition of identity, however, is clearly not the reason humans spend so much time looking at faces. Most face viewing occurs in the context of social interactions. Faces provide a wealth of information that facilitates social communication, and the ability to process such information may represent a more highly developed visual perceptual skill than the recognition of identity.

The recognition of identity is based on the perception of aspects of facial structure that are invariant across changes in expression and other movements of the eyes and mouth. Although perception of identity is important for social communication insofar as we interact differently with different people, perception of the changeable aspects of the face (e.g. expression and eye gaze) plays a far greater role in facilitating social communication. The face perception system must represent both the invariant aspects of a face that specify identity, as well as the changeable aspects of a face that facilitate social communication. The representation of identity must be relatively independent of the representation of the changeable aspects of a face, otherwise a change in expression or a speech-related movement of the mouth could be misinterpreted as a change of identity.

An influential cognitive model of face perception by Bruce and Young[2] emphasized a distinction between processes involved in the recognition of identity and those involved in the recognition of expression and speech-related movements of the mouth. This distinction is supported by behavioral studies that show that the recognition of identity and expression appear to proceed relatively independently. For example, familiarity and repetition priming facilitate performance on face perception tasks that involve processing the identity of faces, but not on tasks that involve processing face expression[3,4].

In this review, we will discuss the human neural systems that mediate face perception and attempt to show how cognitively distinct aspects of face perception are mediated by distinct neural representations. We will present evidence, primarily from functional brain imaging studies, that face perception is mediated by a distributed neural system in the human brain, comprised of multiple bilateral regions. The core of the human neural system for face perception consists of three bilateral regions in occipitotemporal visual extrastriate cortex[5–10]. These regions are in the inferior occipital gyri,

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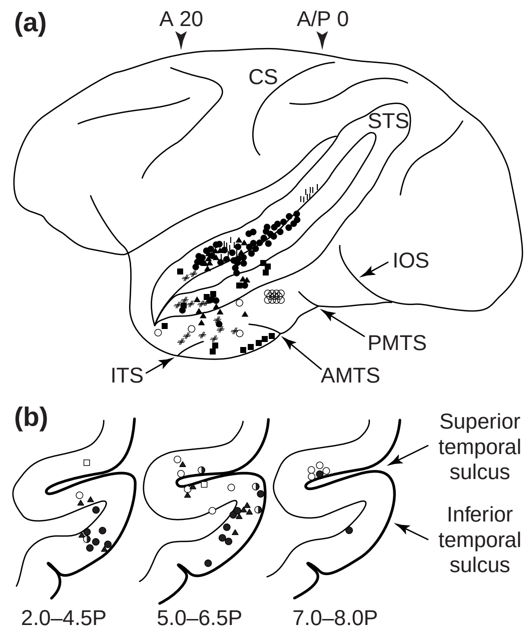

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Fig. 1. Locations of face-selective neurons identified in single-unit recording studies in the macaque. (a) Summary of eight studies (reproduced, with permission, from Ref. 49). Each symbol represents the work of a different investigator. (See original article for references.) **(b)** Locations of neurons that were selective for facial expressions (open circles), identity (closed circles), both expression and identity (half-filled circles), showed an interaction between expression and identity (squares), or were selective for neither (triangles) in the study by Hasselmo *et al.*[29] Locations are plotted on three coronal sections and are from two monkeys. The numbers below each section represent distances posterior to the sphenoid reference. (Reproduced, with permission, from Ref. 29.) Abbreviations: A, anterior; AMTS, anterior middle temporal sulcus; CS, central sulcus; IOS, inferior occipital sulcus; ITS, inferior temporal sulcus; P, posterior; PMTS, posterior middle temporal sulcus; STS, superior temporal sulcus.

the lateral fusiform gyrus, and the superior temporal sulcus. These regions are presumed to perform the visual analysis of faces and appear to participate differentially in different types of face perception. The region in the lateral fusiform gyrus appears to be involved more in the representation of identity[9,11,12], whereas the region in the superior temporal sulcus appears to be involved more in the representation of changeable aspects of faces[9,13]. The anatomical location of the region in the inferior occipital gyri suggests that it may provide input to both the lateral fusiform and superior temporal sulcal regions. Additional regions in other parts of the brain also participate in face perception insofar as they are recruited to process the significance of information gleaned from the face. For example, lip-reading elicits activity in regions that are associated with auditory processing of speech sounds[14]. Similarly, the perception of facial expression elicits activity in limbic regions that are associated with processing emotion[15–18], and the perception of eye gaze direction elicits activity in parietal regions that are associated with spatial attention[9]. Although these additional regions are parts of neural systems involved in other cognitive functions, such as auditory verbal comprehension, emotion processing, and spatial attention, they facilitate the accurate recognition of speech-related mouth movements, expression and eye gaze direction when acting in concert with the core face perception system.

A human neural system for face perception

The existence of a specialized neural system for face perception in the human brain was suggested first by the observation of patients with focal brain damage who had a selectively impaired ability to recognize familiar faces, but a relatively unimpaired ability to recognize other objects. This syndrome is called prosopagnosia[19,20]. Prosopagnosia is associated with lesions in ventral occipitotemporal cortex that are usually bilateral[21–23], although a few well-documented cases have been reported following right unilateral lesions[24,25].

Further evidence of a specialized neural system for face perception came from studies of non-human primates. Single unit recording studies in macaques have identified neurons in the superior temporal sulcus and the inferior temporal cortex that respond selectively to faces[26–31] (Fig. 1). These results suggested that similar clusters of face-selective neurons may exist in homologous regions in the human brain, but the locations of these homologous regions were not obvious.

Identification of face-responsive regions in the human brain with functional brain imaging

With the development of functional brain imaging, the brain regions that participate in face perception could be studied non-invasively in the intact human brain with greater anatomical precision than is possible in patients with naturally occurring brain lesions. The perception of faces has consistently been found to evoke activity in a region in the lateral fusiform gyrus that is usually bilateral, but more consistently found on the right[5–10,12,32,33] (Fig. 2). In this region, the activity in response to faces is greater than that evoked by the perception of nonsense (control) stimuli or by non-face objects. Some investigators have proposed that this region is a module that is specialized for face perception[6,7] (see Boxes 1 and 2), and it has been termed the 'fusiform face area'[6]. The location of this region has been highly consistent across numerous studies. The position of this face-responsive region relative to nearby regions that respond more to other categories of objects (e.g. houses[5,10,34], chairs[10] and tools[35]) or to other visual stimuli (e.g. landscapes and indoor layouts[36]) has also been clearly established. The consistency of the topological arrangement of these regions across numerous studies of individual subjects illustrates the power of fMRI to reveal the detailed functional neuroanatomy of the ventral object vision pathway. However, a recent meta-analysis of data from earlier imaging studies failed to find such consistency[37], suggesting that the detection of functional specialization at this level of detail requires imaging methods with greater resolution and sensitivity, which allow reliable within-subject comparisons.

The functional brain imaging studies that have identified the face-responsive region in the lateral fusiform gyrus all used either passive viewing tasks or tasks that focus attention on invariant aspects of the facial configuration. These tasks have included simultaneous and delayed matching of identical or different pictures of the same individual[5,6,9,10,32,33] and identifying the gender or profession (which requires recognition of identity) of pictured individuals[12]. However, attending to a changeable aspect of the face, namely eye gaze direction, reduces the magnitude of the response to faces in the fusiform face-responsive region[9]. This suggests that this

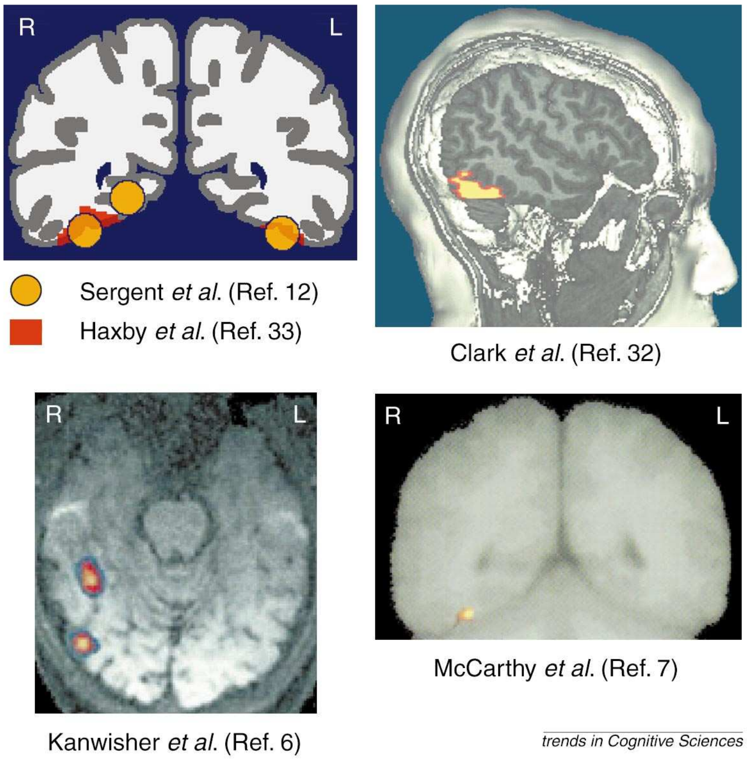

Fig. 2. Locations of face-responsive regions in the fusiform gyrus from five functional neuroimaging studies. The PET–rCBF study by Haxby *et al.*[33] and the fMRI study by Clark *et al.*[32] contrasted activation while viewing faces with activation while viewing nonsense pictures. The PET–rCBF study by Sergent *et al.*[12] contrasted activation during a facial identity discrimination task (actor versus non-actor) with activation during a gender discrimination task (male versus female). The fMRI studies by Kanwisher *et al.*[6] and McCarthy *et al.*[7] contrasted activation while viewing faces with activation while viewing non-face objects. Note that the figure from Kanwisher *et al.*[6] also shows the location of the inferior occipital face-responsive region. (Reproduced, with permission, from Refs 6,7.)

region may not play a central role in all aspects of face perception but, rather, may be involved more in the perception of invariant aspects of faces.

In addition to the face-responsive fusiform region, functional imaging studies have identified other face-responsive regions, usually consistently located in the lateral inferior occipital gyri and the posterior superior temporal sulcus[5,6,8,9,13,35] (Fig. 3). The inferior occipital region often abuts the lateral fusiform region ventrally and the superior temporal sulcal region dorsally, which suggests that it may provide input to both of these face-responsive regions in temporal cortex[5,9].

Evoked potential studies of face-responsive regions in human cortex

The existence of multiple regions that participate in face perception is corroborated by studies of evoked potentials recorded with electrodes placed on the cortical surface in patients undergoing brain surgery for the treatment of epilepsy[38–40]. Face-specific potentials [a sharp negative potential with a latency of 200 ms (N200) and a slower and broader negative potential with a latency of 690 ms (N700)], were recorded from electrodes placed on ventral occipitotemporal and lateral temporal cortex. In ventral occipitotemporal cortex, face-specific sites were found bilaterally and most commonly over the lateral fusiform gyrus. Some sites, however, were lateral to the fusiform gyrus, in the inferior temporal or inferior occipital gyri. The lateral temporal sites were over the posterior middle temporal gyrus, very near the location of the face-responsive region in the posterior superior temporal sulcus identified by functional brain imaging[5,6,8,9,13,35]. Usually, face-specific N200 and N700 potentials were recorded from the same electrodes. Another face-specific potential, a broad positive potential with a latency of 344 ms (P350), was recorded at different electrode sites, including an additional face-responsive region in right anterior ventral temporal cortex, which may correspond to sites of activation in studies of the retrieval of biographical information associated with faces[12,41,42].

Functional specialization in the face perception system

The finding that multiple regions in visual extrastriate cortex participate in face perception presents the possibility that different aspects of face perception are mediated by different parts of this distributed neural system. Evidence from neuropsychological studies of patients with impaired face perception following brain damage and studies of non-human primates indicate that the recognition of identity can be anatomically dissociated from the perception of facial expression and eye gaze[29,43–47].

In the monkey, neurons that respond selectively to faces are found in patches of cortex in the superior temporal sulcus and in the inferior temporal gyrus[26–31,48] (Fig. 1). Recording in the superior temporal sulcus, Perrett and others have found neurons that respond selectively to different gaze angles and different angles of profile[27,48,49]. Most cells that responded to a particular gaze direction also responded to a compatible angle of profile. Perrett *et al.*[26–28,48] have also found cells in the superior temporal sulcus that respond selectively to different individuals and expressions. The clusters of cells in the superior temporal sulcus that respond to different aspects of faces are intermixed with clusters of cells that respond to other visual features, most notably movement of the face, head and body[50,51]. Hasselmo *et al.*[29] studied the selectivity of neuronal responses to identity and expression, comparing cells in the superior temporal sulcus and the convexity of the inferior temporal gyrus. They found a large proportion of face-selective cells that responded selectively either to identity or expression. Moreover, cells that responded differentially to different individuals did so across variations in expression, and cells that responded differentially to different expressions did so across individuals. Of greatest interest here is that cells that were tuned differentially to expression were found primarily in the superior temporal sulcus, whereas the cells that were tuned differentially to identity were found primarily in inferior temporal cortex (Fig. 1b).

Thus, the findings from single-neuron recording studies in the monkey suggest a dissociation between the roles of face-selective cells in the superior temporal sulcus and inferior temporal cortex. The superior temporal sulcus appears to be involved more in the perception of facial movement and static images of changeable aspects of the face, such as expression and the angle at which the eyes and head are oriented. Inferior temporal cortex, on the other hand, appears to be involved more in perceiving facial identity. With functional brain imaging, it is possible to examine whether a similar dissociation exists in human face-responsive regions and the most likely candidate regions for such a dissociation are the posterior superior temporal sulcus and the lateral fusiform gyrus.

Box 1. Is the face perception system specialized solely for face perception?

Although neuroimaging studies have consistently shown that certain occipitotemporal regions respond more to faces than other objects, it is not clear if these regions are specialized only for face perception. Patients with prosopagnosia have a disproportionate impairment of face recognition, but significant doubt remains as to whether they would show similar recognition impairments for other objects if the tasks were properly matched for level of categorization and expertise (Ref. a). Single unit recording studies in the monkey clearly demonstrate that some neurons are highly face-selective, but typically only 20% or fewer of these neurons are face-selective in the face-responsive regions in the superior temporal sulcus and inferior temporal cortex (Ref. b).

In functional imaging studies, face-responsive regions respond maximally to faces but also respond significantly to other object categories (Ref. c). In particular, the face-responsive regions in the lateral fusiform gyrus and superior temporal sulcus respond vigorously to animals (Fig. I, Ref. d, but see Ref. e). In fact, the maximal responses to animals, even with their faces obscured, are located in these face-responsive regions. The pattern of response to faceless animals does differ from the pattern of response to human faces insofar as animals evoke a smaller response in face-responsive regions and a greater response in regions that respond more to non-face objects. These results suggest that, if the human face-responsive regions contain neurons that respond exclusively to faces, these neurons are intermixed with neurons that respond to attributes of other objects, especially those of animals.

Gauthier and her colleagues (Ref. f) have proposed a different hypothesis. They suggest that face-responsive regions are specialized for visual expertise. They propose that these regions will respond to any objects that the subject perceives as distinct individuals, rather than as generic exemplars of a category. The fact that we are all experts at face recognition means that faces consistently activate these regions in all subjects. In an fMRI study of experts at bird and car recognition, Gauthier *et al.* (Ref. f) found that responses to these objects were augmented in the occipital and fusiform face-responsive regions in expert subjects, compared with non-experts (Fig. II, Ref. g). Cognitive studies have suggested that expert discrimination between members of homogeneous categories, such as faces or birds, involve similar underlying representations (Ref. h). These results suggest that the 'face-responsive' regions may be better characterized as regions that represent perceptual processes for recognizing objects at the subordinate level as unique individuals, rather than at the category level.

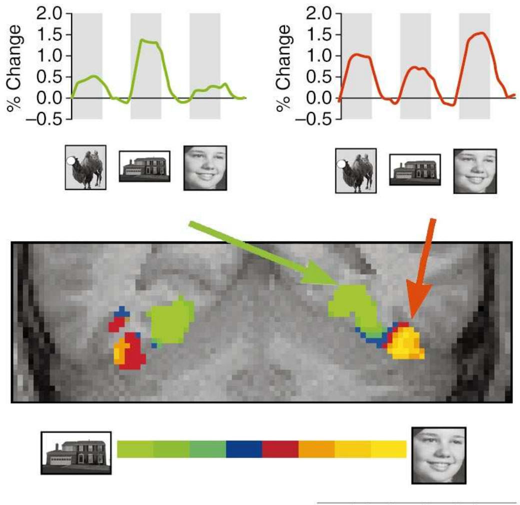

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Fig. I. Responses to animals with faces obscured in lateral fusiform face-selective (red to yellow) and medial fusiform house-selective (green) regions. The strongest response to faceless animals had a center of gravity that was equivalent to that of the response to faces, even though the response to faceless animals was weaker than the response to faces in that region. Note that the response to faceless animals in the medial fusiform region was stronger than the response to faces (Ref. d), indicating that the pattern of response to animals is more widely distributed than the pattern of response to faces.

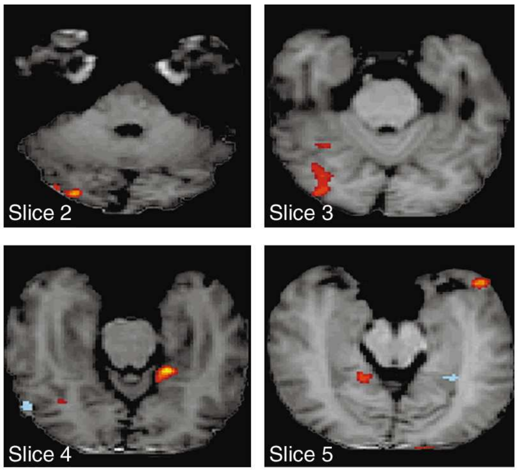

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Fig. II. Regions showing enhanced responses to birds or cars in bird and car experts, respectively (shown in red to yellow). Note the effect of expertise on activation in the right occipital and fusiform face-responsive regions (slices 2–4), as well as in the right and left parahippocampal place areas (slices 4,5). (Reproduced, with permission, from Ref. g.)

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Functional brain imaging evidence in the superior temporal sulcus

The perception of biological movement has consistently been shown to activate a region in the posterior superior temporal sulcus[13,52,53]. This activity has been elicited by movement of the whole human body, the hand, and the eyes and mouth. It is unknown whether the patterns of activity evoked by these different kinds of biological movement can be distinguished from each other because the perception of body and face movement has not been studied in the same individuals.

Box 2. Face inversion

Turning a picture of a face upside-down makes it markedly more difficult to identify the pictured individual (Refs a,b). The detrimental effect of stimulus inversion is much greater for face recognition than for the recognition of other objects, and this discrepancy has often been cited as evidence that face perception is mediated by a specialized system that operates according to rules that differ from those for object perception (e.g. Ref. c). Patients with prosopagnosia, on the other hand, show little or no performance decrement for inverted faces, suggesting that inverted faces may be processed more like other objects in these individuals (Refs d,e).

Given this evidence that the face perception system is not engaged effectively by inverted faces, it would be reasonable to predict that the response to faces in the face-responsive regions of extrastriate cortex would be significantly diminished by stimulus inversion. Furthermore, this effect should be greater than the effect of stimulus inversion on the response to other objects in the regions that respond preferentially to those objects. The results of three fMRI studies of face inversion, however, do not support these predictions (Refs f–h). While face inversion did significantly diminish the response to faces in the fusiform and superior temporal face-responsive regions, the size of this effect was small and face inversion *increased* the response to faces in the inferior occipital face-responsive region (Ref. g). The effect in the fusiform face region is marked only when the face stimuli are so degraded that they are not recognized as faces when inverted (Ref. f). Moreover, these effects are not selective to face inversion (Ref. g). In the inferior occipital and medial temporal regions that respond preferentially to houses and other non-face objects (see Fig. 3), the effects of house inversion (Fig. Ib, left side) are in the same direction and quantitatively equivalent to the effects of face inversion in the adjacent face-responsive regions (Fig. Ia, left side). Face inversion, however, does have a selective effect on the response to faces in the house-responsive regions (Fig. Ia, right side). Whereas house inversion does not have a great effect on the response to houses in face-responsive regions, face inversion dramatically increases the response to faces in house-responsive regions.

These results suggest that inverted faces do engage the neural system for face perception. This is not necessarily inconsistent with the cognitive effect of face inversion. Inverted faces, after all, are readily identified as faces and one has no difficulty identifying the major features of an inverted face, such as the eyes, nose, mouth, chin, cheekbones, etc. The response to faces in the face-responsive cortices, therefore, may reflect the recognition of the generic facial configuration and an attempt to perceive the uniqueness of that individual's face. The effect of selective attention to identity on neural responses to faces indicates that the attempt to perceive the uniqueness of an individual face is mediated more by the fusiform than the superior temporal face-responsive region (Ref. i). The increased response to inverted faces in the house-responsive regions indicates that additional resources are recruited to augment perception when an attempt to perceive uniqueness is unsuccessful. The participation of these regions in inverted face perception may explain why these stimuli appear to be processed more like non-face objects and why prosopagnosic patients show little or no impairment in inverted face perception tasks.

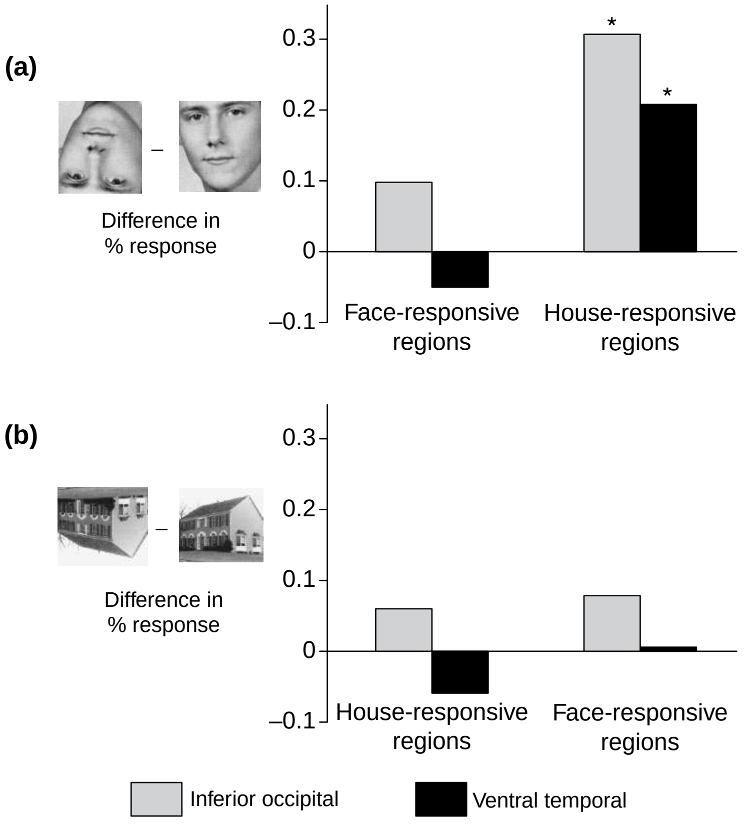

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Fig. I. The effect of stimulus inversion on the response to faces and houses in adjacent inferior occipital and ventral temporal regions that respond preferentially to faces or houses. (a) The effect of face inversion on responses to faces (* indicates a significant difference from the corresponding effects of house inversion in face-responsive regions, $P<0.0001$). **(b)** The effect of house inversion on responses to houses. Note that the effect of inversion on the responses to houses in the house-responsive regions (left hand side of b) shows the same pattern as the effect of inversion on the responses to faces in the face-responsive regions (left hand side of a). The only effect that was specific to face inversion was an increased response to inverted faces in the house-responsive regions (right hand side of a).

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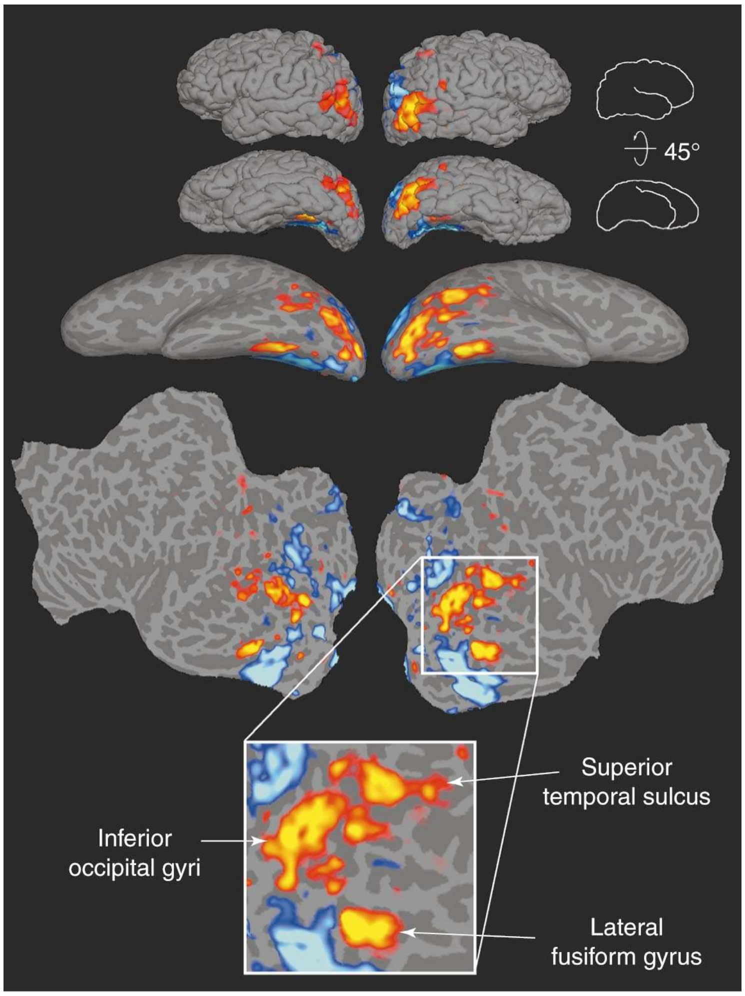

Fig. 3. Cortical regions that comprise the core system for visual analysis of faces from a single subject. The data are from Subject TB in Ref. 5. Regions shown in red to yellow responded more to faces than to houses. Regions shown in blue responded more to houses than to faces. The upper figures are lateral views of the folded cortical surface. The next row of images shows the cortical surfaces of each hemisphere tilted back 45° to show both the lateral and ventral surfaces of the temporal lobe. In the next images, the cortical surfaces are inflated to show the cortex in the sulci, indicated by a darker shade of gray. The lower images show the entire cortical surface of each hemisphere flattened into a two-dimensional sheet. Cortical rendering and flattening was done using C-Surf software (Boston, MA). Note that all three face-responsive regions are bilateral in this subject.

As mentioned earlier, the posterior superior temporal sulcus also is activated during the perception of still pictures of faces[5,6,8,9,35]. This neural activity may reflect the participation of this region in the perception of the changeable aspects of a face that vary with movement, analogous to the differential tuning of neurons in the monkey superior temporal sulcus to the direction of eye gaze, angle of profile, and expression[26–29,48,49]. These changeable aspects are evident in static pictures, but accurate perception of them may involve knowledge about how the face moves to produce different expressions and directions of eye gaze. Some computer vision algorithms for identifying facial expression incorporate models of face movement to make recognition of the static configuration more efficient[54]. Similarly, the face-responsive region in the human posterior superior temporal sulcus may use algorithms that integrate the perception of facial movement and the static configurations produced by such movement.

Functional dissociation of the superior temporal sulcus and lateral fusiform gyrus

We tested the dissociation of the functional contributions of the superior temporal sulcus and lateral fusiform gyrus to face perception in an fMRI experiment by measuring how selective attention to eye gaze direction and identity differentially modulate the responses to faces in these regions[9]. In both conditions, subjects viewed static pictures of faces presented sequentially. To induce attention to eye gaze, subjects were asked to indicate whether the direction of gaze in each picture was the same as in the previous picture, regardless of the identity of the individual pictured. To induce attention to identity, subjects were asked to indicate whether each picture was of the same individual as in the previous picture, regardless of the direction of eye gaze. As predicted, selective attention to eye gaze elicited a stronger response in the superior temporal sulcus than selective attention to identity did. Conversely, selective attention to identity elicited a stronger response in the lateral fusiform gyrus than selective attention to gaze did. These results provide a direct demonstration of a double dissociation between the functional roles played by these two regions in face perception. Interestingly, attentional modulation of activity in the face-responsive inferior occipital region suggested that this region might play a greater role in the perception of identity than in the perception of eye gaze. Further research is needed to determine whether this region also is a major source of input to the face-responsive region in the superior temporal sulcus and, if so, what its role is in the perception of changeable aspects of the face.

An extended neural system for face perception

Processing the significance of the information gleaned from the faces of other individuals involves the participation of additional neural systems. Face perception provides information that is used to access knowledge about another person; to infer his or her mood, level of interest and intentions; to direct ones own attention to objects and events that others are looking at; and to facilitate verbal communication. The results of functional brain imaging studies suggest which brain regions are recruited to process some of these kinds of information. These brain regions are part of neural systems that perform other cognitive functions, such as directing spatial attention and comprehending speech. However, they become part of the face perception system when they act in concert with extrastriate face-responsive regions to extract meaning from faces and, thereby, facilitate recognition of different facial attributes. In other cognitive domains, accurate recognition of stimuli is facilitated or altered by semantic information and by information from other sensory modalities. For example, the perception of speech sounds is influenced by semantic context and perceived lip movements[55]. Similarly, visual recognition of tools depends on access to stored semantic information about how the tools are used and how they typically move[56]. In the case of face perception, information about the emotional tone of an expression appears to facilitate the accurate recognition of expression[57,58]. Similarly, spatial information may sharpen the perception of eye gaze direction.

Face perception and spatial attention

The direction in which the head and eyes of another individual are oriented provides information about what that person is currently attending to. Chimpanzees spontaneously follow gaze direction[59] and recent behavioral evidence has shown that macaque monkeys orient their attention in the direction that another monkey is looking[60]. Human infants as young as six months shift their attention in the direction of perceived gaze[61,62]. As has been demonstrated in adults, these shifts of attention in response to perceived gaze direction may be reflexive and may occur even when the direction of perceived gaze is task-irrelevant[63–66]. An averted gaze that is inconsistent with head orientation is a better stimulus for evoking a shift of attention than a direct gaze that is congruent with head position, even if the eyes and head are directed to the side[65]. Therefore, shifts in attention that are elicited by perceived gaze do not depend on the simple detection of eye position, but rather involve an integrated perception of eye and head position[67].

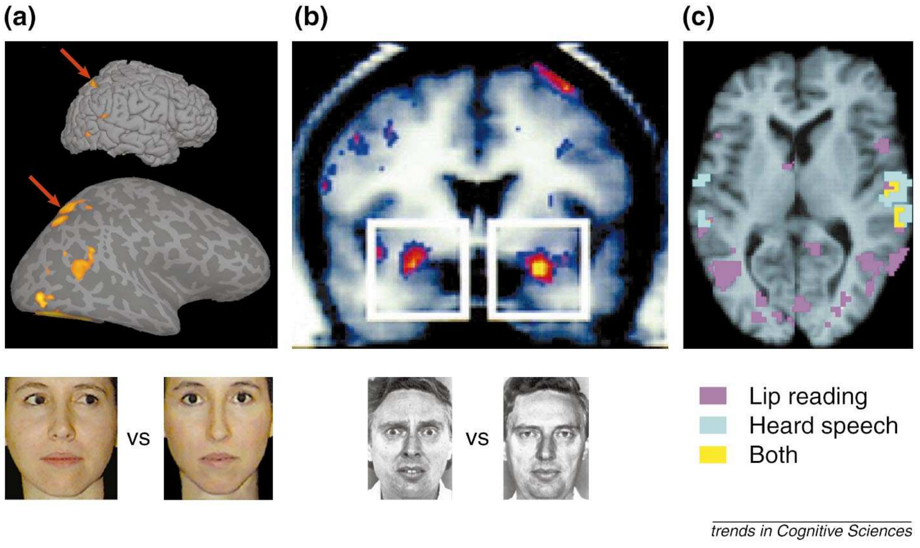

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Fig. 4. Activation of other neural systems to process the meaning of information gleaned from the face. **(a)** The intraparietal sulcus (arrows) is activated by perception of averted gaze[9]. **(b)** The amygdala is activated by perception of fear in the face of another. (Reproduced, with permission, from Ref. 17.) **(c)** Lip-reading activates auditory superior temporal regions that are also activated by hearing speech. (Reproduced, with permission, from Ref. 14.)

Comparisons across species suggest that mechanisms for detecting eye gaze direction, called the 'eye direction detector' or EDD by Baron-Cohen[68], are more primitive and far more ubiquitous than mechanisms for mediating a shared attentional focus [the 'shared attention mechanism' or SAM (Ref. 68)]. The EDD may have evolved to detect threats from potential predators, and evidence of this has been found in non-mammalian species, such as snakes and chickens, as well as in most mammals[68]. Shared attention, on the other hand, appears to be found more exclusively in higher primates and may have evolved to facilitate interactions in complex social groups.

Reciprocal connections exist between cell populations in the superior bank of the superior temporal sulcus and the intraparietal sulcus that could mediate the transfer of information about gaze direction and head orientation to parietal neural systems for spatial attention[69]. In the monkey, parietal cortex plays a central role in spatial perception and attention[70,71]. Neuro-imaging studies have shown that cortex in the human intraparietal sulcus participates in spatial perception, spatial memory and covert shifts of spatial attention[33,72–74].

In our study of selective attention to gaze direction or identity, we found that attention to gaze direction elicited a stronger response in a region in the intraparietal sulcus than attention to identity did, which is similar to the finding in the superior temporal sulcus[9]. We thought that this activity might reflect the recruitment of the spatial attention system to mediate covert shifts of attention. To test this hypothesis, we conducted an experiment in which we examined whether the perception of an averted gaze elicited a stronger response in the intraparietal sulcus than the perception of a direct gaze. As described above, a perceived averted gaze elicits a reflexive shift of spatial attention. We found that passive viewing of faces that have averted gazes, compared to passive viewing of faces with direct gazes, elicited a significantly stronger response in the intraparietal sulcus bilaterally, as well as in the left superior temporal sulcus. This suggests that the intraparietal sulcus is preferentially recruited when perceived eye gaze direction elicits a shift of spatial attention (Fig. 4a). Therefore, activity in the intraparietal sulcus may be specifically associated with the spatial aspects of perceived eye gaze and its role in directing one's own attention. Results from Puce *et al.*'s study of the perception of eye and mouth movement[13] are consistent with this hypothesis. They found that the intraparietal sulcus responded only to eye movement, whereas the superior temporal sulcus responded to both eye and mouth movement.

Face perception and neural systems for processing emotion

Seeing the expression on another's face provides information about the emotion that person is feeling and can evoke that emotion in oneself. The perception of emotional expressions has been found to evoke activity in brain regions that are associated with emotion. In a magnetoencephalography (MEG) study[75], judging emotion from expression elicited a stronger response than simple face detection first in posterior superior temporal cortex (140–170 ms after stimulus onset) and later elicited a response in the right amygdala (with a 220 ms latency), providing a direct demonstration of interaction between these regions in the perception of emotion in faces. Perception of fear in the face of another has been found consistently to evoke a response in the amygdala[15–18] (Fig. 4b). Studies of fear conditioning in rats, non-human primates and humans have shown that the amygdala plays a central role in processing fear[76,77]. Patients with bilateral lesions of the amygdala have a selective impairment of the ability to recognize negative emotions, such as fear and anger, suggesting that this structure contributes to the accurate recognition of facial expression[57,58]. The perception of disgust in the face of another evokes a response in the anterior insula in a region that presumably is also associated with processing smells and visceral sensations[15,16], which may reflect the role played by disgust in rejecting foods that smell bad and are likely unsafe to eat.

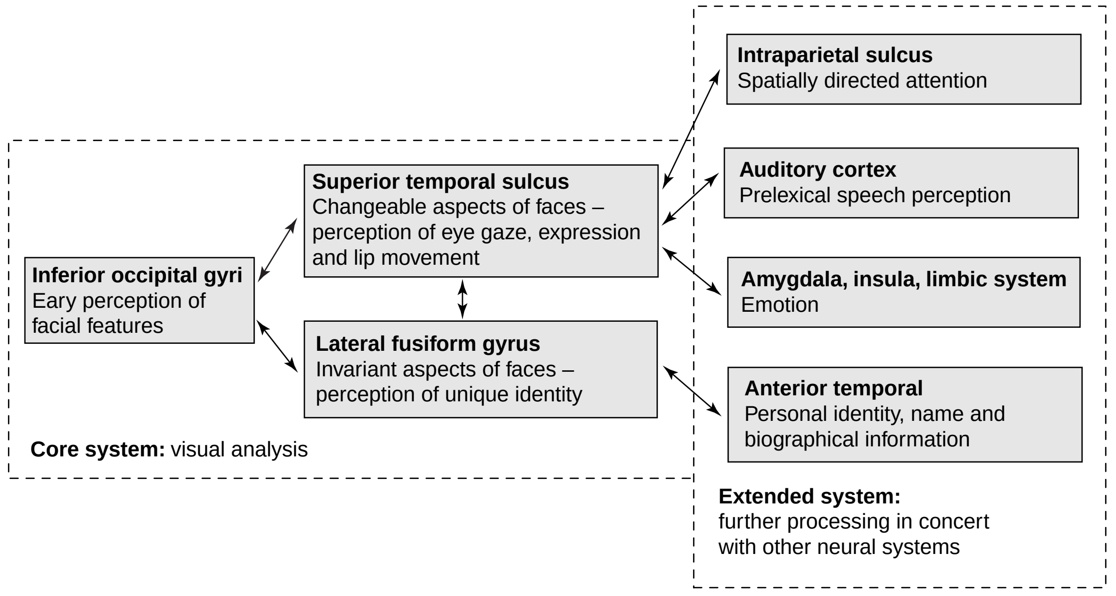

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Fig. 5. A model of the distributed human neural system for face perception. The model is divided into a core system, consisting of three regions of occipitotemporal visual extrastriate cortex, and an extended system, consisting of regions that are also parts of neural systems for other cognitive functions. Changeable and invariant aspects of the visual facial configuration have distinct representations in the core system. Interactions between these representations in the core system and regions in the extended system mediate processing of the spatial focus of another's attention, speech-related mouth movements, facial expression and identity.

The amygdala may also play a role in processing other information gleaned from faces that is critical for social cognition. Brothers[78] and Adolphs[79] have suggested that the amygdala is part of a distributed system that plays an important role in biasing cognition as a function of the emotional and social significance of perceived stimuli. Baron-Cohen *et al.*[80] found that the amygdala was activated by a task that required judgements of state of mind based on perception of the eye region. Interestingly, high-functioning autistic subjects showed less activation of the amygdala and inferior frontal cortex when performing this task, but greater activation of the superior temporal region, suggesting that their impaired social cognition may be associated with abnormal interactions among these structures.

Accurate recognition of complex emotions in facial expressions may also involve the participation of somatosensory cortex, particularly right somatosensory cortex. Adolphs[79] has suggested that complex expressions, which contain blends of emotions, may be interpreted by simulating the perceived expression using somatosensory cortex, either overtly or covertly, and then sensing the emotion produced by that simulation. In addition, a region in the inferior frontal cortex has been implicated in the judgement of the emotional content of facial expressions, although it has not been associated with the evocation of a particular emotion in the viewer[81,82].

Face perception and speech comprehension

Lip-reading plays a large role in speech comprehension, even in people with normal hearing. Lip-reading improves hearing accuracy and lip movements that are inconsistent with auditory speech can cause hearing errors[55].

As discussed above, perception of non-speech mouth movements is associated with activity in the superior temporal sulcus[13] (Fig. 4c). Lip-reading, in the absence of sound, additionally elicits activity in auditory areas in the superior temporal gyrus that are also activated by hearing spoken words[14]. This indicates that the representation of speech-related lip movement involves the coordinated activity of visual regions in the superior temporal sulcus, which are associated with the visual analysis of lip movement, and auditory speech regions in the superior temporal gyrus, which are associated with the analysis of phonemic content.

Face perception and retrieval of semantic knowledge about people

A novel face is perceived as a unique individual even when one has no other knowledge of that person. As discussed above, the perception of the unique identity of a face appears to be associated with activity in the inferior occipital and lateral fusiform gyri[9,11,12]. Cognitive studies suggest that recognizing the identity of a familiar face involves a fixed sequence of events that begins with the activation of the appearance of a familiar individual, followed by activation of semantic information about that person and, finally, retrieval of that person's name[83].

Recognition of the faces of people whom one knows, either because they are famous or personal acquaintances, appears to be associated with activity in anterior temporal regions[12,41,42]. In an early PET–rCBF study, perception of famous faces was associated with activity in the temporal pole and anterior middle temporal gyrus[12]. Subsequent studies with PET and fMRI have consistently found that perception of famous and personally familiar faces is associated with activity in the anterior middle temporal gyrus[41,42]. Activity in this region is also elicited by the perception of the names of famous people and outdoor scenes that are personally familiar[41,42]. The latter findings suggest that these anterior temporal regions may be associated with the representation of biographical and autobiographical knowledge.

Outstanding questions

- What role does the inferior occipital face-responsive region play in the representation of identity and the representation of changeable aspects of faces?
- Do eye gaze, expression and lip movement evoke equivalent patterns of response in the superior temporal sulcus or do they evoke different response patterns, similar to the different patterns evoked by object categories in ventral temporal cortex?
- How do representations of faces change with learning? There are at least three parts to this question: (a) How do representations of individual faces become more integrated across images from different viewing conditions and facial movements? (b) How do representations of faces become more distinctive as they become more familiar? (c) Do representations of familiar faces, as compared to novel faces, have a different distribution across regions that can be dissociated from the representations of biographical and autobiographical information associated with those faces?
- What is the temporal sequence for processing the structural, invariant and changeable aspects of faces, and how is feedback from later regions in the system integrated into the representations that are generated in the earlier regions?

A model of a distributed neural system for face perception

In their model of a cognitive system for face perception, Bruce and Young[2] proposed an organization that was hierarchical and branching. An early stage of processing involved the structural encoding of faces that was view-dependent, by which they meant that the representation of a face at this stage still depended on both the viewing condition (angle of profile, lighting) and facial configuration (expression, eye gaze, mouth position). The representation produced by structural encoding was then processed further by separate systems that perceive personal identity, expression and speech-related mouth movements. Once personal identity was established, further systems retrieved the name and personal information associated with a face.

Based on the human neuro-imaging and evoked potential research reviewed here, we propose a model of the human neural system that mediates face perception (Fig. 5). Our model shares some elements with Bruce and Young's cognitive model[2], but we propose that the perception of expression, eye gaze direction and speech-related movements share a common representation of the changeable aspects of faces that is independent of the representation that underlies the recognition of identity. Our model also amplifies cognitive proposals by suggesting that different face perception processes, such as the recognition of expression, involve the integration of activity in regions that represent the visual configuration of the face and regions that represent the meaning of that configuration, such as its emotional significance. Thus, the model has a branching structure that emphasizes a distinction between the representation of invariant aspects of faces, which underlie recognition of unique identity, and the representation of changeable aspects of faces, which underlie perception of information that facilitates social communication. The model has a hierarchical structure within which a core system for the visual analysis of faces is distinguished from an extended system that processes the meaning of information gleaned from the face. The core system comprises three bilateral regions with an anatomical configuration that suggests a hierarchical organization in which the inferior occipital region may provide input to the lateral fusiform and superior temporal sulcal regions. We suggest that additional neural systems should be considered extensions of the face perception system. The spatial attention system, which includes brain regions in the intraparietal sulcus and, most likely, the frontal eye fields, uses facial cues (primarily gaze direction and head position) to direct attention. Systems for processing emotion, with regions identified thus far in the amygdala and insula, process the emotional content of expression. Systems for auditory verbal comprehension in the superior temporal gyrus participate in processing the phonemic content of speech-related lip movements. Systems for representing biographical semantic knowledge in the anterior temporal lobe participate in retrieving the name and other information associated with a face.

The degree of separation between the functional roles played by the different regions in this system is unclear. The fusiform face-responsive region, for example, may play a supportive role in the perception of expression, perhaps because different individuals can have characteristic expressions, such as a crooked smile or a wry grin, that we associate uniquely with them. The regions in the extended system, such as the amygdala and the intraparietal sulcus, may have some capacity for visual analysis of faces.

At the heart of our model is the proposal that many face perception functions are accomplished by the coordinated participation of multiple regions. For example, lip-reading requires the coordinated participation of regions for the visual analysis of lip movements and for phonemic analysis, and perception of emotional expression involves the coordinated participation of regions for the visual analysis of expression and for the representation and evocation of emotion. Thus, a cognitively defined function, such as lip-reading, does not involve a brain region specialized for that function but, rather, the concerted activity of regions that perform different components of that function. These regions can also participate in other functions by interacting with other systems. For example, intraparietal regions that act in concert with the superior temporal sulcus to mediate shifts of spatial attention in response to perceived gaze are also involved in directing spatial attention in response to other visual cues and, perhaps, to auditory, somatosensory, and endogenous cues, as well. The investigation and modeling of interactions among the regions that comprise the distributed human neural system for face perception, therefore, are essential to develop an understanding of human face perception.

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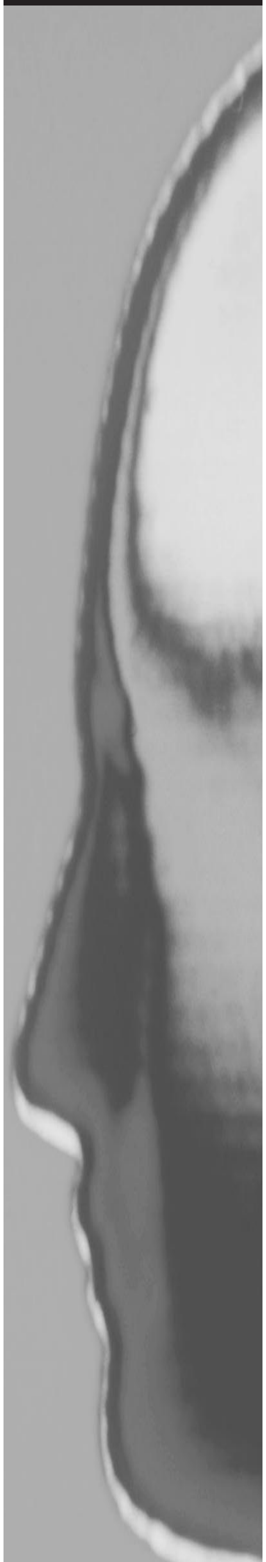

The complementary brain: unifying brain dynamics and modularity

Stephen Grossberg

How are our brains functionally organized to achieve adaptive behavior in a changing world? This article presents one alternative to the computer analogy that suggests brains are organized into independent modules. Evidence is reviewed that brains are in fact organized into parallel processing streams with complementary properties. Hierarchical interactions within each stream and parallel interactions between streams create coherent behavioral representations that overcome the complementary deficiencies of each stream and support unitary conscious experiences. This perspective suggests how brain design reflects the organization of the physical world with which brains interact. Examples from perception, learning, cognition and action are described, and theoretical concepts and mechanisms by which complementarity might be accomplished are presented.

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In one simple view of brain organization, our brains are proposed to possess independent modules, as in a digital computer, and so, for example, we see by processing perceptual qualities such as form, color and motion using these independent modules. The brain's organization into processing streams[1] supports the idea that brain processing is specialized, but it does not, in itself, imply that these streams contain independent modules. Independent modules should be able to compute fully their particular processes on their

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