

The neural basis of visual body perception

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The human body, like the human face, is a rich source of socially relevant information about other individuals. Evidence from studies of both humans and non-human primates points to focal regions of the higher-level visual cortex that are specialized for the visual perception of the body. These body-selective regions, which can be dissociated from regions involved in face perception, have been implicated in the perception of the self and the 'body schema', the perception of others' emotions and the understanding of actions.

Transcranial magnetic stimulation

(TMS). A technique that delivers brief, strong electric pulses through a coil placed on the scalp. These create a local magnetic field, which in turn induces a current in the surface of the cortex that temporarily disrupts local neural activity.

Humans, like other primates, are highly social — indeed, one of our harshest punishments is solitary confinement. Our lives are intertwined with those of other people, and so we must be able to efficiently determine their identities, actions, emotions and intentions. Much of this information is available from the appearance of the face, and in the field of cognitive neuroscience there has been intense interest in understanding the neural mechanisms that support face perception^{1–3}. By contrast, the perception of the rest of the body has until recently received less attention, even though the body shares many characteristics with the face⁴: it conveys socially relevant information; becomes highly familiar with repeated exposure over the lifespan; is similar in shape across individuals; and is visually salient, as witnessed by its ability to capture attention^{5–7}.

The past few years have brought a remarkable increase in research on the neural basis of visual perception of the human body, which we review here. Our focus is on visual perception of the body and on the occipitotemporal brain systems that are thought to underlie it. We do not review in detail work in related areas that has recently been covered elsewhere, including face perception^{1–3}, fronto-parietal action perception or 'mirror neuron' networks^{8,9}, biological motion perception^{10,11}, disorders of the body schema¹², and emotional body language¹³, although our discussion intersects with all of these topics.

This Review is divided into two main sections. First, we survey evidence for body-selective neural mechanisms in the visual cortex from single-cell recordings in primates, and from event-related potential (ERP), functional MRI (fMRI), transcranial magnetic stimulation (TMS) and neuropsychological studies in humans. Second, we review evidence on how body-selective brain regions relate to perception of the self and the 'body schema',

understanding others' emotions, and action perception and the 'mirror' system. Throughout both sections we consider how the brain systems that are involved in face and body perception might be related. Finally, we discuss some of the many open questions for future research.

Evidence for body-selective neural mechanisms

Non-human primates. Studies on macaque monkeys have revealed that some neurons in the inferior temporal cortex (IT) respond selectively to the shapes of human and monkey bodies and body parts^{14–18} (FIG. 1). For example, hand-selective cells in the IT respond strongly to images of human and monkey hands of different orientation and size, presented at various locations in the visual field, but not to other complex shapes or to faces¹⁵. Other cells in the IT respond selectively to faces but not to hands. Various other object categories were used in this study, but no IT neurons responded selectively to them, indicating that category selectivity in IT neurons is restricted to a small number of categories¹⁵. A recent study measured responses in a large number (>600) of IT neurons to many different images (>1,000) from natural and artificial object categories¹⁴. An analysis on the patterns of activity across cells showed that animate and inanimate images elicited mostly distinct patterns. In the animate category, faces and bodies elicited distinct patterns, with further distinctions between different types of face (animal, monkey or human), and different types of body (human, four-limbed animal or bird). Analyses of single-cell responses revealed many cells that responded selectively to human bodies, hands or faces. Only a few cells selectively responded to a combination of these categories, providing further support for distinct representations of these categories. Other studies have reported cells in the anterior part of the monkey superior temporal sulcus (STS) that respond

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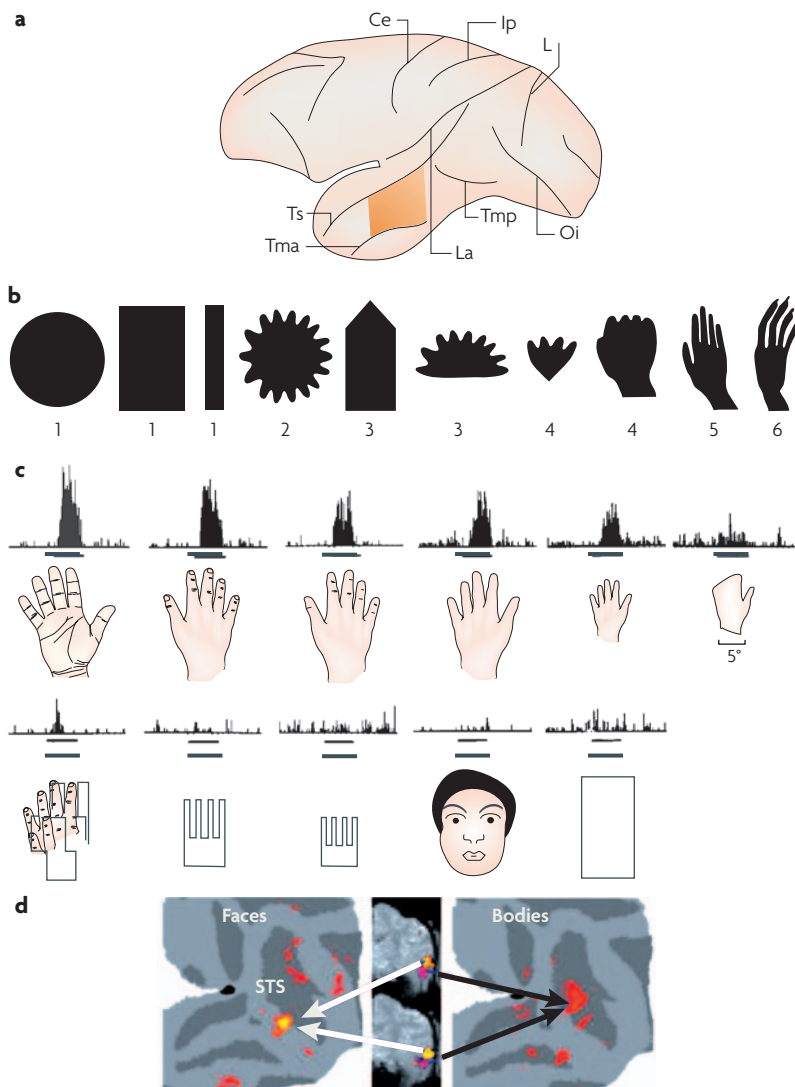


Figure 1 | Key findings from non-human primates. **a** | Orange indicates the region investigated in early single-unit recording studies of macaque inferotemporal cortex^{15–17}. **b** | Increasing responses to progressively more hand-like stimuli in a neuron from macaque inferotemporal cortex. Numbers reflect approximate relative magnitude of responses to different stimuli. **c** | Spike histograms and schematic stimuli from an investigation of a hand-selective neuron¹⁵. This neuron seems to be selectively tuned to the general form of the hand. The response to faces is low, ruling out a general response to all biological stimuli. The response to hand-like geometric stimuli is also low, demonstrating the specificity of the response to realistic hand shapes. **d** | Closely neighbouring regions of the superior temporal sulcus (STS) in the macaque are selectively activated in functional MRI by images of faces (left), as compared with bodies, fruits, artefactual objects and hands. This is also true for images of bodies (right), as compared with faces, fruits, artefactual objects and hands. Ce, central sulcus; Ip, intraparietal sulcus; L, lunate sulcus; La, lateral sulcus; Oi, inferior occipital sulcus; Tma, anterior middle temporal sulcus; Tmp, posterior middle temporal sulcus; Ts, superior temporal sulcus. Panels **a** and **c** modified, with permission, from REF. 15 © (1984) Society for Neuroscience. Panel **b** modified, with permission, from REF. 16 © (1972) The American Psychological Society. Panel **d** modified, with permission, from *Nature Neurosci.* REF. 25 © (2003) Macmillan Publishers Ltd.

to particular body actions and body postures^{19–23}, and to specific body postures as a function of the preceding observed action, such that the cell responds to a particular body posture only when it is preceded by a particular action^{20,21}.

Two recent studies that used fMRI in monkeys provide evidence for two large clusters of body-selective cells in the STS, with those in the right hemisphere being most strongly activated^{24,25} (FIG. 1). Interestingly, in both of these studies the body-selective area was adjacent to, and partly overlapped, a face-selective area. Subsequent recordings from individual neurons in the face-selective area (as identified with fMRI) revealed that almost all of the cells were strongly selective for faces²⁶. This result provides a bridge between single-unit recordings in monkeys and fMRI findings in humans by showing that dense clusters of highly selective individual neurons can underlie selectivity measured at a macroscopic level with fMRI.

Intracranial recordings in humans. Intracranial surface-electrode recordings of electrical activity in human brains, performed on patients being evaluated for surgery to treat epilepsy, benefit from both high spatial and high temporal resolution. Studies using this technique have found body-selective responses in various posterior cortical regions, including the extrastriate visual cortex (FIG. 2). In one study, several electrodes showed hand-selective responses that peaked at about 230 ms after stimulus onset²⁷. These hand-selective electrodes were located in various regions, including the right ventral visual cortex, the left STS and the left inferior parietal cortex. Another study recorded responses in the right lateral occipitotemporal cortex and found that one electrode, at the approximate location of the extrastriate body area²⁸, recorded selective responses to images of whole bodies (without heads), with a body-selective response starting at 190 ms and peaking at 260 ms after stimulus onset²⁹. Interestingly, in these studies, body-selective electrodes did not record significant responses to faces, and face-selective electrodes did not record significant responses to bodies, providing further evidence that the body and its parts activate different neurons to those that are activated by the face.

Evoked potentials in humans. Recordings of electrical and magnetic stimulus-evoked potentials on the scalp show enhanced responses to faces, with peaks at approximately 100 ms (REFS 30–33), 170 ms (REFS 34–37), and 250 ms (REFS 38,39) after stimulus onset. Most attention has been focused on the negative potential that peaks at posterior sites at about 170 ms (the ‘N170’), although the face selectivity of this waveform has been questioned^{33,40}. Recent findings indicate that human bodies, or body parts such as hands, produce a similar evoked response^{41,42}. For both bodies and faces, the response that peaks at around 170 ms is enhanced and delayed by image inversion⁴³ — an index of configural processing^{44–46} — and reduced by image distortion⁴⁷. Another study found a strong response to bodies that peaked at 190 ms, about 20 ms later than the response to faces⁴⁸ (FIG. 3). The body selectivity of this ‘N190’ peak also generalized to stick figures and silhouettes, but not to scrambled versions of these figures⁴⁸. In these studies, the spatial distribution of responses to bodies differed from that of responses to faces, and source localization identified distinct lateral occipitotemporal sources for the face-selective N170 and body-selective N190 peaks.

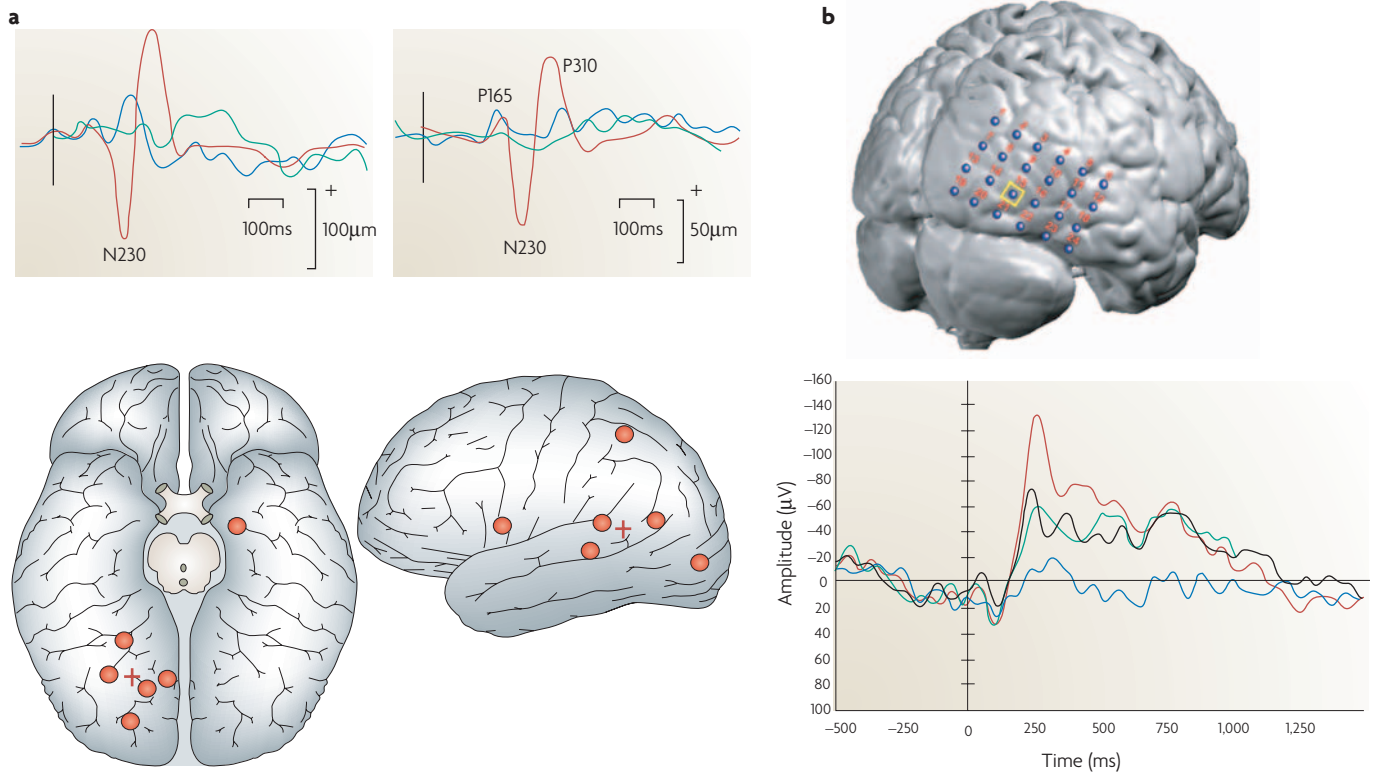


Figure 2 | Key findings from intracranial recordings in humans with epilepsy. **a** | A summary of hand-selective negative potentials (indicated by red lines) peaking at approximately 230 ms post-stimulus. Blue lines indicate the response to images of faces, and green lines the response to images of objects. Red spots indicate body-selective recording sites across different patients. Red crosses indicate the average position of the inserted electrodes. **b** | Pre-surgical intracranial recordings from a patient with epilepsy reveal an electrode at the approximate location of the extrastriate body area²⁸ (electrode 15; indicated by the yellow box) that is body-selective (red line) from 190 ms post-stimulus, relative to faces (blue line), tools (green line) and animals (black line)²⁹. Panel **a** modified, with permission, from REF. 27 © (1999) Oxford University Press. Panel **b** modified, with permission, from REF. 29 © (2007) Elsevier Science.

Stimulus-evoked potential

An electrical or magnetic potential, resulting from coordinated neural activity, that is time-locked to the onset of a stimulus.

Configural processing

The recognition of an object by the specific spatial relationships among (or configuration of) its parts. Sometimes referred to as 'holistic' processing.

Source localization

A technique used in electroencephalogram (EEG) and magnetoencephalogram (MEG) research to estimate the location of the brain areas that give rise to the electrical or magnetic responses that are measured on the scalp.

Structure-from-motion

Even a few dots can create the vivid perception of an object or structure when they move in a way that is typical of that object.

Developmental studies have used event-related potentials (ERPs) to measure the neural response to bodies and to biological motion in infants. Babies as young as 4–6 months old look longer at intact, as opposed to scrambled, human biological motion patterns presented in point-light displays (PLDs), indicating a capacity to perceive the distinction between these stimuli. These displays, which consist of only a few dots, give a vivid perception of the human form through the process of structure-from-motion⁴⁹. This looking preference is restricted to patterns that represent upright bodies^{50,51}. In babies of 8 months of age, differences are apparent between ERPs recorded in response to intact versus scrambled⁵², and to upright versus inverted⁵³, PLDs. These differences emerge in roughly the first 200–400 ms after the stimulus onset and have a right-hemisphere bias. Like adults, infants of just 3 months of age show similar ERPs in response to images of static faces and static bodies. These responses differ from those elicited by distorted face and body images, and the differences in the waveforms emerge at about 450 ms (REF. 47); these effects are similar for both categories. This sensitivity to configuration in very young infants is surprising, given that structural disruption of static body images does not seem to affect looking preferences

until 18 months of age⁵⁴, although this discrepancy may be a result of stimulus differences between studies⁵⁵. Clearly, further developmental experiments are needed that combine behavioural and neuroimaging measures, compare moving and static body, face and object images at a range of ages, and consider the effects of different types of image disruption.

Functional MRI in humans. Perhaps the clearest evidence for body-selective brain regions in humans comes from fMRI studies that compare responses to images of (headless) bodies and body parts with responses to control images (FIG. 4). This approach has revealed that a focal region of the lateral occipitotemporal cortex responds strongly and selectively to static images of human bodies and body parts, but weakly to faces, objects and object parts. The responses of this region generalize to non-photographic depictions of bodies, such as line drawings, stick figures and silhouettes, indicating that this brain area has a body representation that is abstract across specific visual features²⁸. The response of this region to non-human animals is significantly lower than to humans, but higher than to objects, and it is also higher to mammals than to birds and fish,

Voxel

In MRI research, a voxel refers to the smallest measured volume unit, analogous to a three-dimensional pixel. In fMRI studies, these are typically of the order of 30 mm³, although much smaller voxel volumes have been achieved in more recent work.

Human motion-selective area MT

An area in the human extrastriate visual cortex that responds strongly to visual displays containing moving items. It can be functionally localized with fMRI by contrasting activation relating to moving stimuli with that relating to static stimuli.

suggesting that this area is partly activated by objects with a body plan similar to that of humans⁵⁶. On the basis of these and other findings, this region has been labelled the extrastriate body area (EBA)²⁸.

The EBA is found bilaterally in the posterior inferior temporal sulcus/middle temporal gyrus^{57,58}. Depending on the statistical threshold used in imaging studies, body-selective voxels overlap with the human motion-selective area MT (hMT) and with the dorsal focus of the object-form selective area LO^{28,59}. This presents methodological difficulties for the characterization of these regions using group-average fMRI data or even single-subject functional region-of-interest designs. Two recent studies^{59,60} overcame these difficulties by using multi-voxel pattern analyses (MVPA) of fMRI data^{61–65} to disentangle, at a fine-grained level, these regions' patterns of selectivity (BOX 1; FIG. 5a). These considerations indicate that caution is required when interpreting activations — particularly in

spatially-smoothed or group-averaged data — as a reflection of the level of activity in the EBA (or hMT or LO), when this interpretation is simply based on the average peak activation coordinates.

Recent fMRI studies have provided evidence for a second body-selective area that is anatomically distinct from the EBA (FIG. 4). This region, located in the fusiform gyrus and so known as the fusiform body area (FBA), responds selectively to whole bodies and body parts, as well as to schematic depictions of the body^{60,66,67}. The FBA is adjacent to and partly overlaps the face-selective fusiform face area (FFA)⁶⁸. Interestingly, neighbouring face- and body-selective patches have also been found in the monkey STS^{24,25}.

The close proximity of the FBA and FFA also raises the question of whether the apparent body selectivity found in the fusiform gyrus could instead be due to an indirect activation of face-selective neurons, for

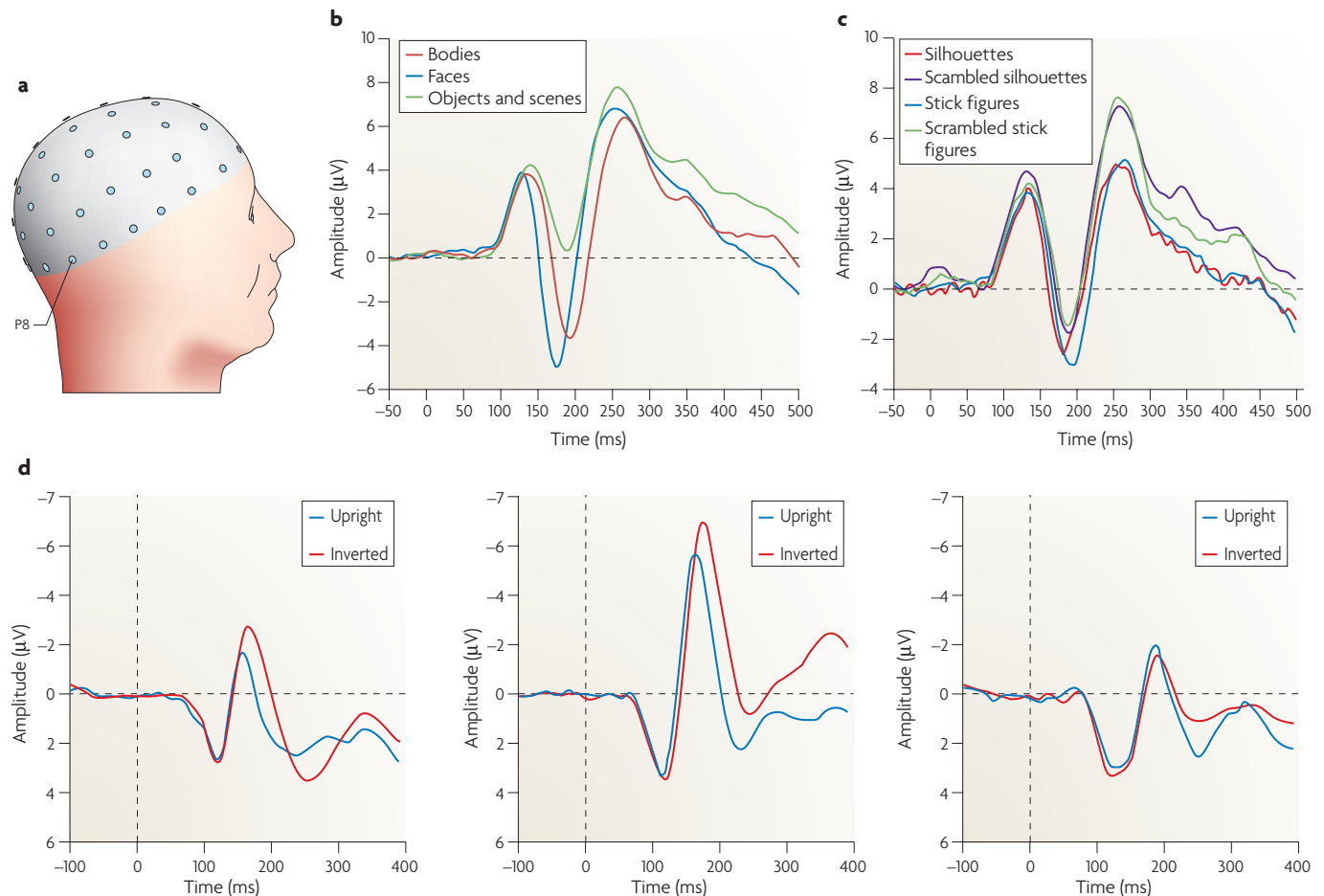


Figure 3 | Event-related potentials reveal similar, but distinct, responses to faces and bodies. **a** | A body-selective event-related potential (ERP) negative (N1) peak is centred approximately at electrode P8, the site from which the data in the remaining panels were acquired. **b** | The body-selective response (red line) peaks at 190 ms post-stimulus, about 20 ms later than the response that is elicited by pictures of faces⁴⁸ (blue line), and roughly the latency at which body selectivity has been observed in intracranial recordings of occipitotemporal sites in human patients with epilepsy (FIG. 2). **c** | This body-selective 'N190' generalizes to abstract depictions of the body, distinguishing between intact and scrambled stick figures, and between intact and scrambled human silhouettes⁴⁸. **d** | For both bodies (left graph) and faces (middle graph), but not objects (right graph), stimulus inversion delays and amplifies the N1 response⁴³. Panels **b** and **c** modified, with permission, from REF. 48 © (2006) Elsevier Science. Panel **d** modified, with permission, from REF. 43 © (2004) Lipincott Williams & Wilkins.

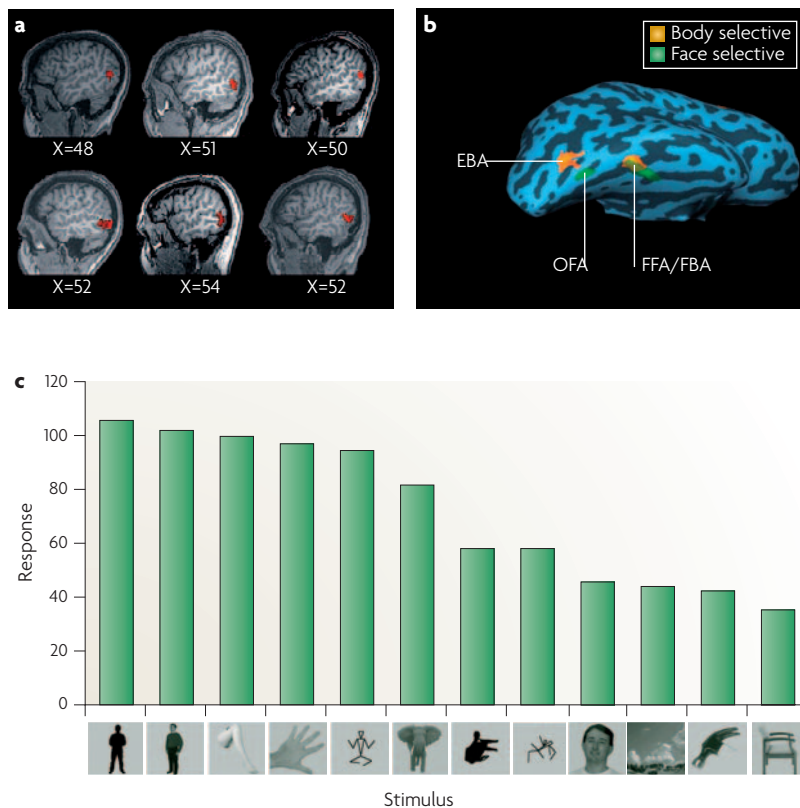


Figure 4 | Body- and face-selective regions of the human occipitotemporal cortex, as revealed by functional MRI. **a** | The extrastriate body area (EBA; shown here in the right hemisphere of six subjects) is found in the posterior inferior temporal sulcus. X values indicate Talairach coordinates for each slice plane. **b** | Body- and face-selective regions of the human visual cortex, in a ventral view of the right hemisphere of one individual, rendered on an inflated anatomical scan from the same individual. Orange indicates body-selective regions (bodies versus tools); green indicates face-selective regions (faces versus tools). Bodies and faces activate similar, but not identical^{66,67}, regions of the fusiform gyrus (the fusiform body area (FBA), and fusiform face area (FFA), respectively). Posterior to this region are nearby but distinct body-selective (EBA) and face-selective (occipital face area (OFA)) regions. **c** | Responses of the functionally defined EBA to various stimuli, indicating the body-selective response of this region. Values are taken from several experiments, each of which included photographs of varied body parts as one condition. Magnitudes reflect the mean response to each stimulus type, averaged across several subjects, with all responses scaled so that the response to body parts is equal to 100. Stimulus conditions, from left to right: body silhouettes; whole bodies; assorted body parts; hands; stick figures of bodies; mammals; scrambled silhouettes; scrambled stick figures; faces; scenes; object parts; and whole objects. Panel **a** modified, with permission, from REF. 119 © (2007) Oxford University Press.

Object-form selective area LO

A region of the human extrastriate visual cortex that responds to object form. It can be functionally localized by contrasting fMRI activation relating to intact objects with activation relating to scrambled objects.

instance through mental imagery or the contextual association of bodies and faces⁶⁹. However, several studies argue against this explanation by showing that the body- and face-selective activations can be anatomically and functionally dissociated. For example, a high-resolution fMRI study found small neighbouring patches of the fusiform gyrus that were either selective for bodies but not faces, or for faces but not bodies⁶⁷. Furthermore, the application of MVPA has shown that the local patterns of selectivity for faces and bodies across fusiform voxels are unrelated⁶⁰. In other words, there was no relationship between face

and body selectivity across voxels — voxels that were relatively strongly face selective were not necessarily also strongly body selective, as would be expected if both categories activated the same underlying neuronal populations (BOX 1; FIG. 5).

The evidence that the body representation in the EBA and FBA is independent of low-level image features is further supported by the finding that these regions are also activated in response to PLDs of human motion^{60,70–75}. The functionally localized EBA and FBA are activated significantly more by such PLDs than by ‘scrambled’ control displays⁶⁰. In standard region-of-interest analyses, the area hMT (which overlaps the EBA) and the FFA (which overlaps the FBA) showed similar responses. However, when MVPA was applied to local patterns of activity in these areas, only body selectivity, and not motion or face selectivity, was related to the voxelwise pattern of selectivity to PLDs⁶⁰. This indicates that PLDs specifically activated body-selective neuronal populations (BOX 1) in both brain areas. Note that the activation of the EBA and the FBA by PLDs is unlikely to reflect processing of biological motion patterns *per se*, as these regions are strongly activated by static body stimuli, even when they do not imply motion²⁸. Instead, the processing of biologically plausible motion has been linked to other areas that are typically activated by PLDs, such as the posterior STS (pSTS)^{76–78}.

Finally, a key question is whether the EBA and FBA can be dissociated on the basis of their functional properties. A recent study of the response to body images of varying completeness (fingers, hands, arms, torsos and whole bodies) found more selectivity for body parts in the EBA than in the FBA, and a relative bias in selectivity for more complete images of the body in the FBA⁷⁹. This finding suggests a possible distinction between these two areas, with the analysis of bodies in the EBA being focused on individual parts, and the function of the FBA being to create a more holistic body representation.

TMS and lesion studies. Are body-selective brain areas necessary for the perception of bodies and body parts? TMS offers the opportunity to test this question in healthy subjects. Because the EBA is located on the lateral surface of the brain, close to the scalp, it is relatively easy to create a ‘virtual lesion’^{80,81} of this region with TMS, whereas the FBA is out of reach of direct TMS effects. The first TMS study to investigate whether the EBA is essential for body processing showed that disrupting activation in this area 150–250 ms after the onset of the stimulus selectively impaired performance on a delayed match-to-sample task involving images of body parts, but not face or motorcycle parts⁸² (FIG. 6). Thus, the EBA is causally involved in creating and/or maintaining an accurate representation of the shape of body parts, but not of object parts. Note that the latency of the TMS pulses in this study, between 150 and 250 ms, generally coincides with the latency of a body-selective peak in ERPs, as measured with electrodes on the scalp (190 ms)⁴⁸ and intracranial recordings (230–260 ms)^{27,29}.

Box 1 | Multi-voxel pattern analysis to interpret overlapping activations

Although functional MRI (fMRI) is hailed for its high spatial resolution compared with other imaging techniques, each measured unit (voxel) reflects the summed activation of thousands of neurons. Therefore, where neuronal populations with different functional characteristics are intertwined at a relatively fine scale, fMRI cannot separate these populations. Recent studies have shown that analysis techniques that take into account patterns of activation across voxels can partly overcome this problem^{59–61,65,97,145,156,157}. The application of multi-voxel pattern analysis (MVPA) is best illustrated by an example from the primary visual cortex (V1), the neural architecture of which is well known from animal work. Single-unit recordings in the monkey brain have shown that neurons in V1 are sensitive to the orientation of bars, with some neurons responding optimally to horizontal bars whereas others prefer bars at other orientations. These differently tuned neurons are intertwined at a sub-voxel scale, and each fMRI voxel therefore contains a mixture of these neurons. Importantly, each voxel will show a slight orientation bias due to differential sampling of orientation-selective neurons. These biases are generally too weak to pick up when each voxel is analysed independently. However, when analysing all V1 voxels simultaneously by looking at the pattern of activation across voxels, these weak (but reliable) biases become informative, because the patterns in response to, for example, horizontal and vertical bars are significantly different. This information can be used with linear classifiers to determine which orientation was viewed by a subject during a block of trials, or even an individual trial^{65,145,158}.

Other studies have used similar logic to dissociate overlapping neuronal populations in the higher-level visual cortex, including the body-selective visual cortex. For example, using MVPA, it has been possible to dissociate body-selective from motion-selective populations in the lateral occipitotemporal cortex^{59,60} (FIG. 5a), and body-selective from face-selective neuronal populations in the fusiform gyrus⁶⁰ (FIG. 5b). More generally, these results show that, when a group of voxels is activated by multiple conditions (for example, bodies and faces, or horizontal and vertical bars), this cannot be assumed to reflect activation of the same underlying neuronal population. MVPA might therefore be a useful tool for interpreting overlapping activations anywhere in the brain^{62–64}.

A related issue is whether permanent lesions to the extrastriate cortex as a result of brain injury can cause body-perception deficits. Focal lesions to the cortex that encompass the EBA are rare (especially bilaterally), as evidenced by the scarcity of patients reported with selective damage to the area hMT (which overlaps closely with the EBA). A case study investigating a patient with bilateral lesions involving the hMT reported significant loss of motion perception, whereas other perceptual functions (including face perception) remained relatively intact^{83,84}. Disordered body perception was not reported but might not have been tested. A more recent study examined deficits of body perception in a large, unselected group of stroke patients with lesions in a single hemisphere⁸⁵. The pattern of deficits in various body-related tasks indicated a three-way dissociation between representations of the body: postural (for example, imagining and performing actions), semantic (such as judging functions of body parts) and structural (for instance, localizing pictured or touched body parts) (see also REF. 54). The semantic and structural representations were associated with lesions of the left temporal lobe, although the anatomical evidence from this study was not precise enough to determine whether this specifically involved the EBA or the FBA.

The recent evidence for a body-selective area in the fusiform gyrus raises the further question of why body-perception deficits are not reported in conjunction with face-perception deficits (prosopagnosia) that arise from occipitotemporal lesions^{1,86}. Given their close

proximity, lesions to the FFA would be expected to significantly affect the FBA as well. However, it is not clear whether the FFA overlaps with the crucial lesion site for acquired prosopagnosia — for example, although some fMRI studies report relatively normal FFA responses in patients with acquired prosopagnosia^{87–89}, others report abnormal^{90,91} face-related activity in this region. It is also possible that people with prosopagnosia might have subtle defects in body perception that are masked by their difficulties with faces and that are not routinely tested for (although this has been ruled out in one comprehensive test of an individual with congenital prosopagnosia⁹²). Finally, it is possible that deficits that result from permanent lesions in the EBA or the FBA are quickly compensated for by the remaining intact body-selective area or by other brain areas that respond to the human form (for example, the pSTS).

Body perception and other processes

In the following sections, we review the implications of the above findings, particularly of the existence of two body-selective regions in the extrastriate cortex, for several related issues in cognitive neuroscience.

Self perception and the body schema. As we act in the world, we maintain a continuous sense of our posture and the positions of our limbs. This sense has been referred to as the ‘body schema’⁹³. Disruption of this schema has been proposed to underlie a number of neurological syndromes, mostly those caused by damage to the parietal cortex¹², although the diversity of these syndromes indicates that there may be a multitude of body schemas rather than a single one. Updating of the schema is thought to depend largely on tactile or somatosensory information (as evidenced, for example, by intact motor functioning in the congenitally blind¹²).

A recent study has indicated that the EBA might receive signals that update the representation of the body after movement; this would indicate a novel coupling between visual and motor representations. Specifically, the EBA responds to the execution of visually guided (but unseen) voluntary movements of a subject’s hands and feet⁹⁴, (see also REF. 95). This finding was interpreted to indicate that the execution of a movement might affect the actor’s body representation through movement-related proprioceptive inputs. Alternatively, or in addition, the EBA could be activated through corollary discharge signals from motor areas. These signals might dynamically update the body representation in the EBA, and adjust for sensory input resulting from the movement (a function that is generally attributed to the inferior parietal cortex). The integration of such internal action signals with external visual input could ultimately serve to distinguish between one’s own and someone else’s body parts⁹⁶. A subsequent study showed that, although body movements activate the EBA, this activation might not be directly related to visual body perception⁹⁷. This study replicated the finding of increased activation in the EBA during execution of motor actions, but reported relatively low spatial overlap

Functional region-of-interest design

A design used in fMRI research in which one or more brain areas are defined on the basis of their functional properties (typically in each subject individually), and their response properties are further investigated in subsequent experiments.

Delayed match-to-sample task

A task in which subjects have to choose which of multiple target stimuli matches a previously presented sample stimulus that is held in memory.

Linear classifier

A statistical procedure in which items are divided into two or more groups on the basis of a weighted linear combination of their features.

Corollary discharge

A copy of the motor signal that can be used to adjust for changes in sensory input that result from the motor action.

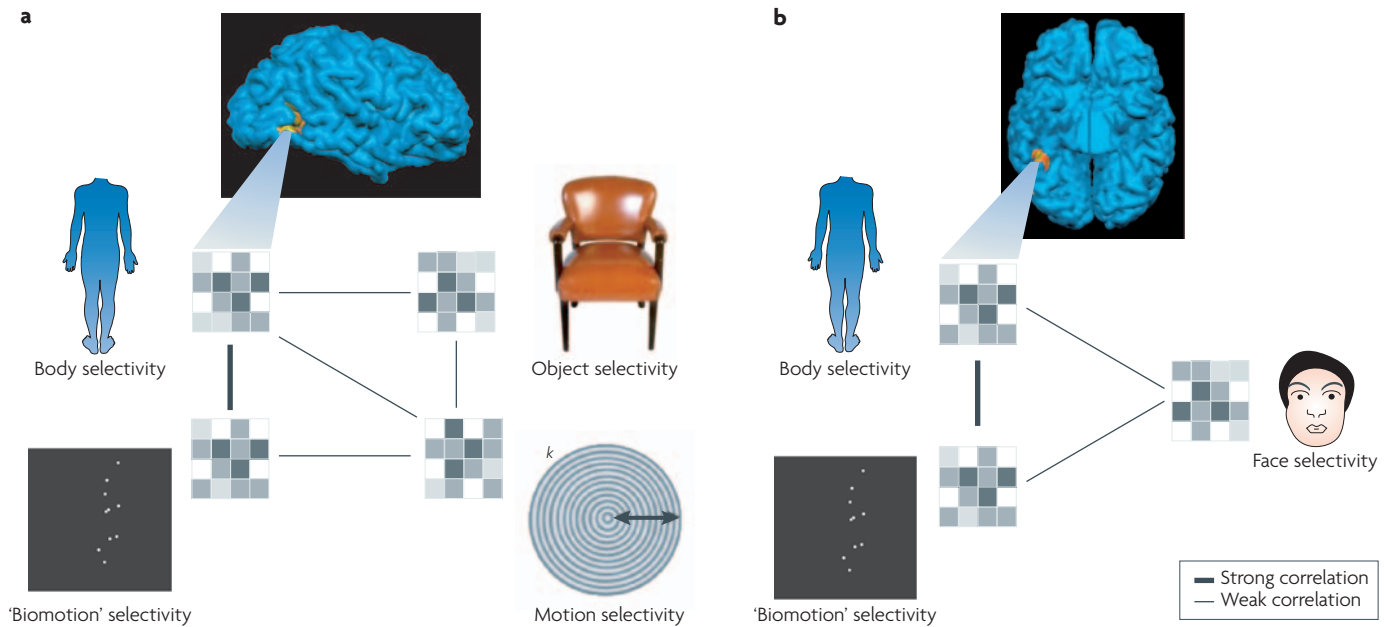


Figure 5 | Disentangling the regions of the occipitotemporal cortex. a | Multi-voxel pattern analyses (MVPA) of functional MRI (fMRI) data disentangle inferior temporal sulcus (ITS) responses to bodies, objects, simple visual motion and biological motion (see also BOX 1). Bodies, objects, ‘point light’ animations of human movements and simple oscillatory motion all activate similar regions of the ITS in human fMRI studies (see rendering at top of figure). These responses can be difficult to disambiguate — for example, even when only the single most object-selective voxel from this region is tested across individuals, significant motion, biological motion and body selectivity is found⁵⁹. Pattern analyses consider the local variations in selectivity across the voxels of the region as a whole. They reveal that body and biological motion selectivity have significant positive correlation, indicating that they engage similar underlying neural populations (that is, the extrastriate body area). By contrast, the variations in motion and object selectivity are uncorrelated with each other and with body selectivity, indicating distinct underlying neural systems^{59,60}. **b** | Similarly, MVPA of fMRI data disentangle posterior fusiform gyrus responses to bodies, faces and biological motion (see also BOX 1). Voxelwise pattern analyses reveal that body and biological motion selectivity show significant positive correlation, indicating that they engage similar underlying neural populations (that is, the fusiform body area). By contrast, these patterns are uncorrelated with the pattern that is elicited by faces, indicating a distinct underlying neural system (that is, the fusiform face area)⁶⁰.

in individual subjects (14–19%) between areas of the brain that were activated by movements and those that were activated by body perception, especially when body movements were contrasted with a stringent control condition⁹⁷. Furthermore, even within this region of overlap, MVPA showed no relationship between perceptual body selectivity and movement-related modulation. That is, variations in body selectivity were uncorrelated, across voxels, with variations in movement-related modulation: voxels that showed strong body selectivity did not necessarily show strong movement-related modulation, and vice versa⁹⁷ (BOX 1). This finding indicates that there may be overlapping but functionally independent mechanisms, similar to the independence of selectivity for the perception of simple visual motion and bodies in this region⁵⁹. Indeed, several studies have linked extrastriate activity in response to body movements to motion perception in the nearby middle temporal area (MT) or medial superior temporal area (MST) rather than in the EBA^{98–100}. Follow-up studies that localize areas that are involved in body perception, motion perception and action responses are needed.

Although schema updating is thought to depend largely on somatosensory input, visual perception of body parts also contributes significantly to our subjective

sense of the position and ‘ownership’ of our own limbs. This can be demonstrated by the visual capture of the sense of limb position that is elicited by the ‘rubber hand illusion’¹⁰¹. A rubber arm is placed in the subject’s view, above and parallel to his or her own arm, which is hidden below a screen. When a brush is stroked over both arms simultaneously, the tactile sensation is often ‘captured’ by the sight of the brush on the rubber arm, and the sense of limb ownership is associated with the rubber arm. Neuroimaging studies have linked cerebellar, parietal, premotor and frontal opercular areas with this illusion, and the premotor and frontal areas in particular with the sense of ownership^{102–104}. These studies did not reveal illusion-related activity in posterior occipitotemporal areas that might coincide with the EBA or the FBA, although no study has specifically tested for this with functionally defined regions of interest. Importantly, any such study would potentially be confounded by differential visual attention or patterns of eye movements to the limb when the illusion occurs.

Finally, vision is also relevant to self perception in that some views of body parts are possible only from an allocentric perspective. Two studies of EBA activity compared views of bodies¹⁰⁵ or hands and feet¹⁰⁶ that would be consistent with egocentric or allocentric

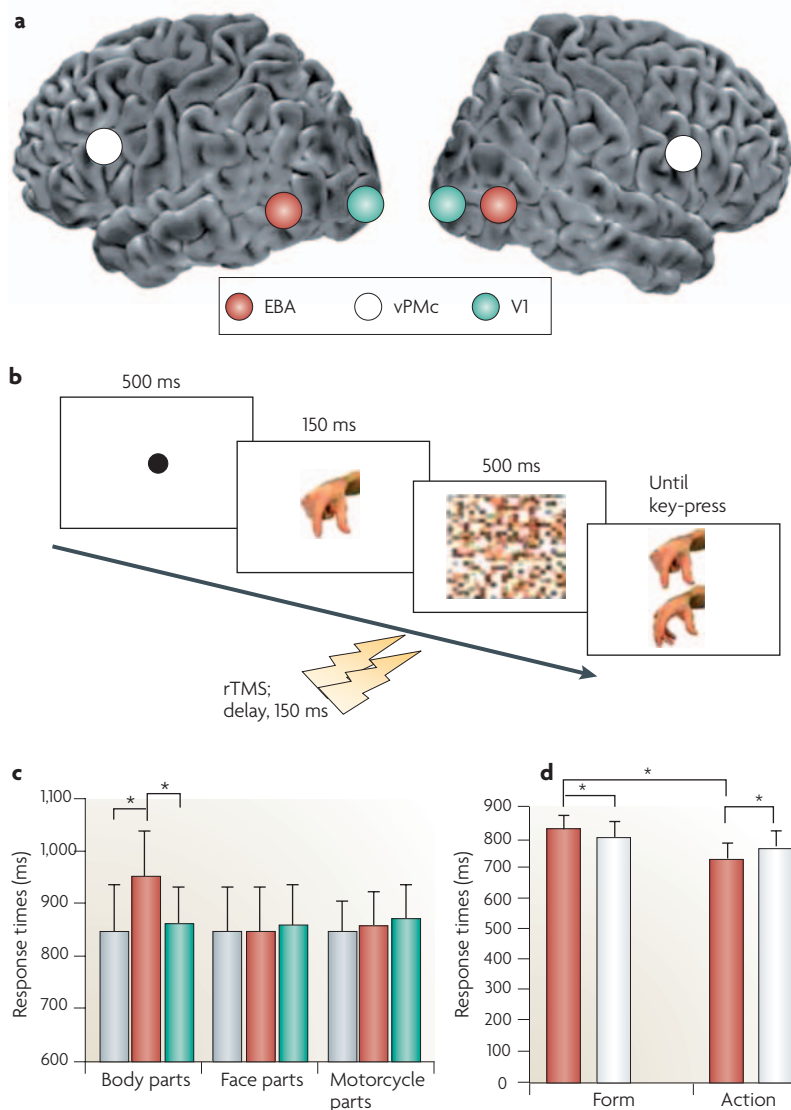


Figure 6 | Transcranial magnetic stimulation studies of the involvement of the extrastriate body area in body-perception tasks. **a** | The cortical sites stimulated in two studies^{82,134} — the extrastriate body area (EBA), the ventral premotor cortex (vPMc) and the primary visual cortex (V1). **b** | Stimulus timing parameters. Two transcranial magnetic stimulation (TMS) pulses were delivered in the interval of a short-term visual memory task in which subjects were asked to compare the initial sample item with two test items, and in which the comparison was based either on identity (form) or on the action implied by the image. **c** | Repetitive TMS (rTMS) over the EBA (red bars) slows response times to judgments on body parts, but not face or object parts, whereas rTMS over the V1 (green bars) and sham stimulation (grey bars) have no effect⁸². **d** | rTMS over the EBA (red bars) and the vPMc (white bars) has differential effects on judgments of body part identity (form) or implied action: form tasks are disrupted by EBA stimulation, and action-judgment tasks are disproportionately slowed by vPMc stimulation¹³⁴. Panels **a** and **d** modified, with permission, from *Nature Neurosci.* REF. 134 © (2007) Macmillan Publishers Ltd. Panels **b** and **c** modified, with permission, from REF. 82 © (2004) Elsevier Science.

views (the FBA was not examined). Both studies found higher activity in the left parietal cortex elicited by egocentric compared with allocentric views, in contrast to a small but reliable enhancement of activity in response to allocentric views in the right (but not the left) EBA. Furthermore, the EBA showed no sensitivity to whether the views were of the subject's own body or the body

of another familiar individual¹⁰⁵. Together, these findings indicate that the body representation in the EBA is relatively blind to higher-level factors such as identity and sense of ownership, although this issue might be revisited with stimuli that include full-motion, live views of subjects' own body parts.

Body perception and emotion. We perceive others' emotional states from multi-modal cues, including postures and movements of the body and face. Although emotional face perception has been studied extensively^{107,108}, emotional body perception has, until recently, been relatively neglected¹³. Recent behavioural and imaging results have shown that emotional body postures can bias attention and modulate activity in the visual cortex, indicating that many previous findings on emotional face processing might extend to emotional body processing. For example, images of emotional body postures presented in the contralesional visual space can reduce the attentional bias towards the ipsilesional space in patients with hemi-spatial neglect⁷, as was shown previously for emotional faces¹⁰⁹. Furthermore, emotional body postures can be perceived implicitly in the absence of the primary visual cortex¹¹⁰, which indicates that emotional signals from the body might be partly encoded by a subcortical visual pathway that involves the pulvinar and amygdala and is known to have a role in processing emotional faces^{111–114}.

Recent fMRI studies have shown that, like emotional faces, images of emotionally expressive bodies and body parts increase activation in the visual cortex when compared with neutral controls^{110,115–119}. In one study, short movie clips of emotional bodies, compared with motion-matched movie clips of neutral bodies, selectively modulated the EBA and the FBA¹¹⁹. Furthermore, this modulation was related, across subjects, to concurrent amygdala activation, indicating that the amygdala is a likely source of this modulation. Although other studies of emotional body perception did not functionally localize the EBA or the FBA^{120–122}, the coordinates of the observed modulations in these studies similarly indicate that emotions expressed by bodies modulate both of these body-selective regions, in the same way that emotional faces modulate the activity of face-selective regions. For example, an fMRI comparison of responses to static fearful body postures and emotionally neutral but semantically meaningful body postures found enhanced activation in the fusiform gyrus¹¹⁵. Other studies have reported similar emotional or motivational modulation at the approximate location of the FBA in the fusiform gyrus^{116,118}, and at the approximate location of the EBA in the lateral occipitotemporal cortex^{110,116,117,123–125}. The function of this emotional modulation could be to increase the speed and accuracy of detection and recognition of emotionally salient bodily actions.

The similarity of the effects of emotion on body and face perception raises the question of how analyses of emotions in these stimuli might interact — after all, bodies and faces are normally seen together. An ERP study on emotion recognition found behavioural and neural

evidence that facial and bodily emotions have congruent effects: subjects recognized emotions from the face more quickly and accurately when the emotion displayed by the body was congruent¹²⁶. Remarkably, ERPs showed a congruency-related modulation as early as 115 ms after stimulus onset. This early congruency effect shows that emotional signals from both the face and body are processed and integrated rapidly.

Action perception and 'mirror' systems. Viewing human body actions activates the pSTS^{73,76–78,127}, the parietal cortex^{78,128} and the ventrolateral premotor cortex (vPMC)^{128–131}, as well as the EBA and the FBA. Whereas the pSTS responds specifically to the observation of biologically plausible motion patterns, the parietal cortex and the vPMC are both involved in the perception and the execution of actions⁸. After the discovery in the macaque of neurons that respond to both the perception and the performance of specific actions¹³² — known as 'mirror' neurons — these areas have been suggested to constitute the human 'mirror' system^{8,133}. Can the EBA and the FBA be functionally dissociated from the 'mirror' system? If so, what role do these areas have in action observation?

Two recent studies have reported functional dissociations between the EBA and the FBA and the frontoparietal mirror areas. TMS was used to investigate what aspect of body processing is impaired after the disruption of activity in the EBA or the vPMC¹³⁴. Subjects had to discriminate either the identity or the (implied) action of a pictured body part. Disruption of the EBA with TMS impaired identity discrimination, whereas disruption of the vPMC impaired action discrimination¹³⁴. A similar dissociation was found in a recent fMRI study¹³⁵. Subjects viewed short movies of whole-body actions, parsed into static frames that were presented slowly, in either the correct or an incorrect sequence. As expected, frontoparietal mirror areas and the pSTS showed increased activity in response to coherent meaningful actions. By contrast, the EBA and the FBA showed a greater response to the incoherent action sequences, which contained more frame-to-frame differences in body posture¹³⁵. Together, these studies indicate that the EBA and the FBA are not involved in the mirroring of actions, but that they instead respond to the form of the body that is present in displays of bodily actions.

One study that brings this proposal into question found that group-average fMRI activity in a region that is similar to the EBA (along with other parts of the visual cortex) was greater when participants observed actions in order to imitate them, rather than simply observe them — a finding that would be consistent with EBA involvement in a mirror system¹³⁶. However, uncertainties in the localization of the EBA in this study, and possible confounding influences of attention (due to increased task demands and stimulus relevance in the imitate condition), leave these results open to alternative interpretations.

Instead, it seems that the EBA is not a core component of the 'mirror neuron' network. A more likely alternative, in our view, is that the EBA creates static, visual

representations of the body — 'snapshots' that, along with form and motion information from other areas, contribute to a full visual representation of human actions¹³⁵. This might, in turn, support the perceptual input to a mirror system, but in this hypothesis the EBA is not a core part of this system, because it does not exhibit mirror-like properties. These suggestions are in line with the results of a detailed computational model of biological motion perception, a key feature of which is a collection of static body-form representations¹³⁷.

Conclusions and future directions

There is now substantial evidence that the perception of bodies, like that of faces, evokes a consistent and selective pattern of neural activity in the extrastriate visual cortex. These findings raise many questions about the functional role of these mechanisms and their interactions with other brain systems. Below we discuss some of the numerous topics that we feel it is important for future research to address.

Body and face perception in the visual cortex. Both bodies and faces provide cues to the identity, emotions, intentions, age and gender of other people. To a large extent, the similarities between bodies and faces are reflected in similarities between the spatial and temporal organization of the neural responses they produce. Bodies and faces elicit globally similar patterns of evoked potentials, similar effects on neural activity when inverted or displaying emotion, adjacent or overlapping selective activity in the monkey STS, and closely overlapping fMRI responses in the posterior fusiform gyrus in humans. Notwithstanding these global similarities, evidence from all of the methods reviewed here points to functional and anatomical distinctions between the neural systems involved in face and body processing. These are sometimes subtle, as in the closely overlapping body- and face-selective fusiform responses. There are also broader differences; perhaps the most striking is the apparent absence of a body-related homologue of prosopagnosia after damage to the extrastriate cortex.

The evidence for similar neural responses to bodies and faces raises the possibility, as yet largely untested, that body and face perception are closely functionally integrated^{18,69,126,138}. A system that is built for fast and accurate recognition of the information present in bodies and faces would benefit from close and rapid interactions between the systems that encode them. The posterior fusiform gyrus, in which body and face representations are in close proximity^{66,67}, would be an ideal place for local interactions between face and body processing. For example, previous fMRI studies have indicated that the FFA might be important for processing face identity^{139–141}. The FBA could similarly be involved in processing body identity. If so, this opens up the possibility that this general region underlies our ability to identify other people on the basis of cues from both the body and the face (BOX 2). The close proximity and interaction of the FFA and FBA would be especially useful when cues from either the face or the body alone are not sufficient for recognition. For example,

Box 2 | Body and face selectivity in the fusiform gyrus, and the expertise debate

A continuing debate in cognitive neuroscience concerns the interpretation of face selectivity in the human fusiform gyrus. According to a domain-general, process-specific account, activation in this region is related to discriminating among structurally similar exemplars of categories for which one has substantial expertise¹⁵⁹. On this account, faces activate this region more than other categories because they are automatically processed at the subordinate level, and because of the greater expertise we have with faces than with most other object categories. By contrast, according to a domain-specific account, face-selective responses in the fusiform gyrus reflect the activation of a 'module' for faces that is not significantly involved in processing other object categories³. What bearing do the recent findings of closely overlapping face- and body-selective responses in the fusiform gyrus^{60,66,67} have on this debate?

Faces and bodies are visually different, yet both are easily processed at the subordinate level, and most people have developed substantial expertise for both. Thus, the finding of overlapping face- and body-selective responses is consistent with the process-specific view, but only at a macroscopic level. At a finer-grained level, the existence of spatially distinct face- and body-selective responses⁶⁷ supports the domain-specific view, in that different categories activate separate regions.

when seeing someone from a distance, facial features alone might not be enough for identification⁶⁹. In this case, cues from the body, processed in the FBA, could inform and perhaps support face-selective processing in the FFA, and vice versa.

Functional role of body-selective regions. We have reviewed evidence for two areas in the human visual cortex that selectively respond to the form of the human body. What is computed by the neurons in these regions? One way to address this question is to test for organizing principles that underlie the activity in a region. For example, do the body representations in the EBA and the FBA correspond to a psychophysical space centred around a 'mean' body shape, as has been argued for faces in the FFA¹⁴⁰? Furthermore, these regions should be tested to determine whether they exhibit retinotopy or somatotopy — that is, are the representations of different body parts organized systematically, or are some body parts overrepresented relative to others, as has been found in the motor and somatosensory cortices? We can also ask whether the activity in these regions is sensitive to, or invariant across, such stimulus variables as retinal size, viewpoint or identity¹⁴². Given their distinct locations in the visual system, there might also be dissociations between the EBA and the FBA on one or more of these aspects^{79,143}. Finally, most studies on the EBA and the FBA have focused on stimulus manipulations. New evidence about their functional properties could be gained by measuring their activity under different task conditions, or by correlating neural activity with behavioural performance on a trial-by-trial basis¹⁴⁴.

Recent advances in MVPA also offer a tool for understanding the neural representations in body-selective brain regions. We have described how these analyses are useful for interpreting overlapping fMRI activations⁶⁴ (BOX 1). MVPA could have further applications for understanding the neural encoding of bodies. Local patterns of activity in the EBA and the FBA might carry information about bodies that is lost when activity is averaged across the voxels of these regions. Methods that have been developed for extracting orientation information from primary visual cortex activity^{65,145}, or motion direction from hMT activity¹⁴⁶, could be adapted

to determine whether and how the EBA and the FBA encode information about features such as gender, identity, posture or action. Also, whole-brain applications of MVPA, which apply an analysis 'searchlight' across the cortex to investigate the information content of different brain regions^{147,148}, could be used to determine whether these features are encoded in brain areas that do not respond significantly more to bodies than to other visual stimuli, a possibility that has not been tested by previous fMRI studies.

Interactions among body- and action-perception regions. What is the interrelationship among the brain regions that respond to static and dynamic bodies? How do these areas coordinate in order to provide a coherent representation of other individuals? We have proposed that the EBA (and possibly the FBA) provides static snapshots of body postures to action perception systems, for example, in the pSTS¹³⁵. More generally, these regions might interact with the frontoparietal mirror areas involved in both the perception and production of actions. Recent studies using TMS have demonstrated the effects of stimulation over some of these regions on performance in various body- and action-perception tasks^{82,149,150}. In light of this, a further useful approach might be to measure the modulation of fMRI activity in the EBA, FBA, pSTS, and frontal and parietal areas that is caused by stimulation of any one of these regions with TMS¹⁵¹. Changes in the functional properties of regions that are distant from the stimulation site could be used as an index of information flow through this network, and of the functional contribution of each node within it.

Timecourse of body-selective neural activity. The visual perception of bodies elicits a selective ERP response (the N190)⁴⁸ early in the timecourse of processing. Although source analyses indicate that this component is generated in the extrastriate cortex, it is not clear whether it is attributable to activity in the EBA, the FBA or some other brain region. Constraining ERP source analysis with fMRI would help to accurately localize the N190 (for an example, see REF. 152). This ERP-fMRI mapping would also benefit from the identification of functional distinctions between the EBA and the FBA; that is, to the extent that these regions respond differentially to a

stimulus or task manipulation, the N190 can be tested with similar manipulations to determine whether its response pattern matches that of one or the other region. This effort may also be useful for developmental studies, for which ERP recordings are the primary source of information on neural substrates. If the N190 can be linked to a specific brain region, it might then be possible to make indirect inferences about the development of specific cortical areas in infants.

If a link between specific brain regions and body-specific potentials can be identified, further ERP studies might help to shed light on how activity in these regions evolves over time, an aspect that fMRI studies cannot measure. For example, the initial sweep of neural activity in the body-selective visual cortex might be largely stimulus-driven, but activity in later stages might reflect

the effects of attention, task relevance, coherence with somatosensory representations, or other top-down influences.

Evolutionary origins. Finally, the problem of identifying and understanding conspecifics is not unique to humans or primates. Any social species must face this problem, although many will not solve it primarily with vision¹⁵³. The evidence for body- and face-selective regions in monkeys and humans raises the question of whether other species exhibit similarly selective visual brain regions. For example, there is now substantial evidence for face-specific neural systems in sheep¹⁵⁴. Further research in other species on the neural basis of the perception of conspecifics would shed light on the evolutionary origins of these cortical systems¹⁵⁵.

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Competing interests statement

The authors declare no competing financial interests.

FURTHER INFORMATION

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