More than the face: representations of bodies in the inferior temporal cortex.

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Acknowledgments. Supported by the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement No. 856495). I thank Y. Zafirova and A. Bognar for critical reading of an earlier version of this paper.

This is an uncorrected version of the paper.

Abstract.

Visual representations of bodies, in addition to those of faces, contribute to the recognition of con- and heterospecifics, to action recognition and nonverbal communication. Despite its importance, the neural basis of the visual analysis of bodies has been less studied than that of faces. Here, I review what is known about the neural processing of bodies, focusing on the macaque temporal visual cortex. Early single-unit recording work suggested that the temporal visual cortex contains representations of body parts and bodies, with the dorsal bank of the superior temporal sulcus representing bodily actions. Subsequent fMRI studies in both humans and monkeys showed several temporal cortical regions that are strongly activated by bodies. Single-unit recordings in the macaque body patches suggest that these represent mainly body shape features. More anterior patches show a greater viewpoint-tolerant selectivity for body features, which may reflect a processing principle shared with other object categories, including faces.

Keywords: body patches; superior temporal sulcus; inferior temporal cortex; body representations; body shape; body perception.

Summary points:

1. The temporal visual cortex contains representations of static and dynamic, acting bodies.
2. The temporal cortex of humans and monkeys has multiple category-selective regions that are activated more by bodies than by objects and faces.
3. Body patches are close to face patches in the macaque visual temporal cortex.
4. Macaque body patches contain a large number of single units that respond, on average, more to bodies compared to other stimulus categories.
5. Body patch neurons are not semantic body detectors but respond to features that are prevalent in bodies. Single body patch neurons can respond also to images of non-body objects that contain those features.
6. Body patch neurons represent mainly shape features, showing a similar selectivity for images of bodies and their silhouettes.
7. Moving from posterior to anterior, body patch neurons increase their viewpointtolerant selectivity for body identity and posture, while decrease in

viewpoint selectivity. A similar posterior-anterior gradient is observed for identity and viewpoint

in the face patch network, reflecting a processing principle shared between body and face patch networks.

8. The temporal cortical body patches can provide body descriptions to systems involved in actions and socio-affective processing.

Future Issues:

1. High spatial resolution fMRI in monkeys may refine our understanding of the body patch organization in visual temporal cortex.
2. More studies are required to address the homology of monkey and human body category-selective areas. High-resolution fMRI in both species, especially in humans, may be needed to clarify the homology since in humans some areas might be a lowresolution, smoothed depiction of distinct regions.
3. fMRI mapping using dynamic (acting) bodies is needed and may show additional body patches, in particular in the dorsal bank of the macaque STS. Related to this, the contribution of motion cues to body patch neuron responses is still unexplored at the single-unit level.
4. We do not have a full understanding of the feature selectivity of single neurons in the different body patches. Recordings using parametric stimulus manipulations, combined with modeling, are expected to provide deeper insights into the stimulus selectivity of the neurons and how this differs amongst patches.
5. The information flow within the temporal cortical body patch network, which is unlikely to be only feedforward, and how it is affected by the task of the subject needs to be elucidated.
6. Little is known about the encoding of (social) interactions between agents, especially in body patches and visual temporal cortex in general. This is an important avenue for future research.
7. Studies of the connections of body patches to other areas are needed to clarify how they are integrated into social, affective, and action networks.
8. Causal studies, manipulating the activity of the different body patches, together with behavioral read-outs are needed to assess the contribution of the body patches to perception and recognition.

A large body of work exists on the perception of faces (Oruc et al 2019) and its neural basis (Grill-Spector et al 2017, Hesse & Tsao 2020). This is not surprising given the uttermost importance of faces as social and affective stimuli in primates. However, the body is also a highly relevant stimulus for humans and nonhuman primates. Indeed, visual processing of bodies of conspecifics and other animals is instrumental for many social, affective, and cognitive functions. Obviously, body shape is an important cue to discriminate different species. The body also contributes to the detection of persons in complex scenes (Bindemann et al 2010). Faces are important for the identification of conspecifics, but also bodies, especially when faces are poorly visible, are employed by humans to recognize the identity of a person (Hahn et al 2016, Hu et al 2020, Rice et al 2013, Robbins & Coltheart 2012). Also, macaques can recognize familiar conspecifics (Dasser 1987) and categorize gender (Koba & Izumi 2006) using body parts. Body posture is also an important component of emotional expressive displays in humans (de Gelder et al 2010, Tracy & Matsumoto 2008). Macaques use not only their face but also their body to signal submission, dominance, affiliative behavior, and social play (Altmann 1962, Sade 1973, Yanagi & Berman 2014). Such body displays are used by monkeys to learn the dominance relationship amongst other monkeys (Paxton et al 2010).

Despite the importance of bodies for social cognition, reproduction, and survival in primates, the processing of visual images of bodies has been less studied than faces, and correspondingly less is known about the neural basis of body representations. In this review, I will discuss what is currently known about the neural basis of the visual analysis of bodies and bodily actions, concentrating on the macaque temporal visual cortex. Early single-unit recordings suggested that the inferior temporal (IT) cortex and the fundus/dorsal bank of the Superior Temporal Sulcus (STS) represent bodies and visual actions. Later, fMRI, first in humans and then in monkeys, showed regions in the occipito-temporal cortex/STS that are selectively activated by bodies in both species. This opened up the possibility to examine the representation of bodies at the single-unit level in the macaque body patches, which we view as a cortical network engaged in the visual analysis of bodies. In addition to reviewing monkey single unit and fMRI studies on body processing in the temporal visual cortex, I will also discuss the human fMRI work and relate that to the monkey studies. Indeed, the macaque brain is used as a model for the human brain, and the macaque studies aim to increase our understanding of the neural basis of body processing in both species.

Macaque IT : a very brief primer.

Macaque IT consists of the ventral bank of the rostral STS and the lateral convexity ventral to the STS, bordered ventromedially by the occipitotemporal sulcus and the perirhinal cortex. Posteriorly, it extends to area V4, but recently other areas have been defined with retinotopic mapping between posterior IT and V4 (Zhu & Vanduffel 2019). Cytoarchitectonics and tracttracing studies suggest an intrinsically connected network of distinct areas, without a clear functional correspondence so far (**Figure 1a**; (Kravitz et al 2013)). fMRI studies show a patchy organization of clusters of neurons that process preferentially particular shape features, color, and disparity (Bao et al 2020, Conway 2018). These patches are organized in a parallel fashion from posterior to anterior IT, forming parallel networks with a different preference for particular object properties. The body patch network is one of those. More locally, smaller clusters of neurons, like columns, prefer similar features (Fujita et al 1992, Tanaka 2003, Verhoef et al 2012).

The dorsal bank of the rostral STS, the superior temporal polysensory area, is multimodal (Baylis et al 1987, Bruce et al 1981), unlike IT, and shows motion-selective responses (Anderson & Siegel 2005). Its connections differ from those of IT, including the ventral STS. For instance, unlike IT, the dorsal bank of the STS shows strong connectivity with the cingulate cortex (Vogt & Pandya 1987). Many dorsal bank STS neurons still respond after V1 lesions and require additional superior colliculus ablation to become silenced (Bruce et al 1986). Dorsal bank STS neurons have larger receptive fields than IT neurons (Anderson & Siegel 1999, Bruce et al 1981). Thus, the dorsal bank of the STS and IT, including the ventral bank of the STS, are functionally quite different temporal visual cortical regions.

Early single-unit studies of body representations in temporal visual cortex.

Before the advent of monkey fMRI, single-unit studies targeted IT at random. Pioneering studies by the late Charles Gross and colleagues found that IT neurons show a variety of stimulus selectivities, including selectivity for shape, texture, and color (Bruce et al 1981, Desimone et al 1984, Gross et al 1969, Gross et al 1972, Gross et al 1967, Schwartz et al 1983). One of the first single-unit studies of IT already reported a neuron for which the most effective (tested) stimulus was the silhouette of a body part, a monkey hand (Gross et al 1969). Interestingly, this neuron was recorded ventrally to the STS, thus outside the STS body patches (see below).

In the same lab, pioneering recordings from the dorsal bank of the rostral STS provided the first demonstration of single neurons that responded to a walking person, some of which showed selectivity for walking direction (Bruce et al 1981). Recordings in the dorsal bank and fundus of the rostral STS in David Perrett's lab showed that some of these neurons were selective for both walking direction (e.g. forward versus backward) and walker orientation (**Figure 1b**), thus integrating motion and form cues (Barraclough et al 2006, Oram & Perrett 1996, Perrett et al 1985). When the full body was reduced to a "biological motion" point-light display (JOHANSSON 1973), only a small minority of these neurons preserved their selectivity (Oram & Perrett 1994), suggesting that the large majority of the neurons require shape features for a selective response. More anteriorly, STS neurons respond to a particular walking direction, irrespective of the orientation of the walker (Jellema & Perrett 2006), thus showing encoding of walking direction in an agent-centered reference frame.

In these studies, the human agent walked from one side to the other and this translationary and spatial component may have contributed to the direction selectivity for walking (Jellema et al 2004). As a compromise between difficult to control real-life stimuli and the highly reduced point-light displays, Vangeneugden et al (2011) employed agents with body parts replaced by shaded cylinders. The position and kinetics of the limbs were preserved, based on motion-capture data of human walkers. Using these computer-generated stimuli, walker orientation and locomotion direction (forward-backward walking) were manipulated without translation of the agent, i.e. treadmill walking. Recordings from both banks of the rostral STS showed a strong encoding of orientation and a weaker encoding of forward-backward walking. The majority of the neurons responded to static presentations of the frames of the walking sequence at least a strongly as to the walking displays. These neurons typically responded only during a particular segment of the walking display, which could be predicted by the static frame they responded to. Other neurons responded weakly to static presentations, requiring motion. The latter neurons were mainly found in the dorsal bank of the STS, in keeping with previous observations of motion-related responses in the dorsal bank of the STS (Anderson & Siegel 1999, Baylis et al 1987, Bruce et al 1981, Vangeneugden et al 2009). As a population, these neurons, and those responding to static posture, were sensitive to posture sequence, which can contribute to the encoding of bodily actions (Vangeneugden et al 2011).

The Perrett group observed also selective responses of dorsal bank STS neurons to human body movements other than walking. Some cells responded to the movement of body parts, e.g. of the upper body, hip, arm, leg, hand, or fingers (Jellema & Perrett 2006, Perrett et al 1985). Anterior dorsal bank STS neurons responded selectively to bending or rotation of the upper body, relative to the lower body, irrespectively of the orientation of the agent (Jellema & Perrett 2006). It is unclear which spatiotemporal features were driving the responses of these remarkable neurons. Ascertaining this is difficult, if not impossible, with real-life displays and will require well-controlled computer-animated actions. Singer & Sheinberg (2010) recorded STS neurons (mainly ventral bank) while the monkeys were engaged in recognizing actions made by different computer-generated humanoid avatars. Their population of neurons signaled both actor identity and action during free-viewing. Classification of action based on the full actor motion displays generalized poorly to displays in which the action was depicted by formless random dot motion, suggesting a strong contribution of form features.

Perrett and colleagues documented also responses of STS neurons to manipulative hand actions (Barraclough et al 2009, Perrett et al 1989). These neurons were sensitive to body part – object interactions. Miming the action (i.e. without object) and presentation of the object alone reduced their response. Interestingly, the response was also reduced when there was a gap between hand and object or the act was not targeting the object. However, it was unclear which features of the hand were needed to elicit the responses. These hand action cells were recorded predominantly in the ventral bank of the STS, suggesting a patch of hand-object interaction cells. A later monkey fMRI study showed activations to hand grasping actions in the ventral bank of the STS at what appears to be similar locations (Nelissen et al 2011). Interestingly, that same study showed that this ventral bank STS region is connected to areas outside the temporal cortex also activated by observed hand actions.

In sum, these studies suggest that the monkey rostral STS has neurons that respond selectively to bodies and body parts. Dorsal bank STS neurons tend to respond less to a static presentation of a body than to an acting, moving body. Ventral bank STS neurons respond as well to static and moving bodies but also show some sensitivity to the sequence of postures during bodily actions, implying a selectivity for body posture. The motion and shape features that these neurons respond to, however, remain unclear.

Body-category selective areas in humans.

Perrett et al (1985) noted that STS neurons that responded to the same body action type were grouped in small clusters estimated to be 1mm in size. Later human fMRI studies showed an organization at a much coarser level: cms wide regions, “body areas”, that were more activated by bodies compared to objects (Downing et al 2001, Peelen & Downing 2005). The first discovered body area, the “Extrastriate Body Area” (EBA) is located in the lateral occipitotemporal cortex (**Figure 2a**) and is activated by static and dynamic images of bodies of humans, with or without a head, and human body parts, compared to human-made objects (Downing et al 2001). We will only summarize the large body of work on the EBA here (for reviews see (de Gelder et al 2010, Downing & Peelen 2011, Downing & Peelen 2016, Peelen & Downing 2007). Line drawings of bodies, stick figures, and silhouettes are sufficient to produce the body-selective activations in the EBA. EBA is even activated by dynamic pointlight displays of human bodies compared to faces (Atkinson et al 2012). Activations to mammals, birds, fish, and even invertebrates (e.g. insects and crabs) are in-between those to human bodies and objects (Downing et al 2001, Ritchie et al 2021), though not much stronger than to articulated objects. Representational Similarity Analysis (RSA), in which activation patterns for different image categories are correlated (Kriegeskorte et al 2008), showed that EBA separates faces, objects, and bodies (Caspari et al 2014). EBA is near a face-selective area (Caspari et al 2014, Downing & Peelen 2011, Weiner & Grill-Spector 2013) and partially overlaps with the motion complex hMT (Downing & Peelen 2011, Ferri et al 2013). The classic EBA may consist of distinct areas that differ in their visual field maps (Ferri et al 2013, Weiner & Grill-Spector 2011). Transcranial Magnetic Stimulation studies suggest that the right EBA, which is typically activated more strongly than the left EBA, is causally involved in the perceptual matching of the shapes of bodies and body parts (for review see Downing & Peelen (2016)).

A second body-selective area, labeled the Fusiform Body Area (FBA; **Figure 2a**), was identified close to the face-selective Fusiform Face Area (FFA) in the fusiform gyrus (Peelen & Downing 2005, Schwarzlose et al 2005). Standard localizers such as bodies-objects and faces-objects show considerable overlap between the FBA and FFA, but both can be dissociated. The FBA is activated by both full (headless) bodies and body parts (Schwarzlose et al 2005). It has been reported to respond equally strongly to single fingers, hands, and arms, but much less than to the full body (Taylor et al 2007). The same study reported a more gradual increase in activation from finger to full body in EBA. This much-cited finding has been taken to suggest that EBA represents body parts while FBA represents the configuration of body parts as a whole body (Taylor & Downing 2011, Taylor et al 2007), which agrees with the more anterior location of FBA. However, as noted before (Op de Beeck et al 2010), in that study each body part (e.g. torso) did not occur in the body part and body conditions. Thus, the difference between single body parts and whole bodies might have been due to selectivity for particular body parts. Furthermore, another study did not find a difference between a larger collection of single body parts and headless bodies in the FBA (Schwarzlose et al 2005). RSA of 7T fMRI activation patterns in the lateral ventral temporal cortex, where FBA and FFA are located, showed a tight clustering of headless bodies and limbs (Margalit et al 2020), which would not be expected if FBA contained predominantly whole-body representations. Interestingly, this clustering was similar for supra- and infragranular layers, suggesting body-category selectivity at different cortical depths in FBA. In sum, the evidence for a more configural body representation in FBA compared to EBA is weak at present.

One notable difference between EBA and FBA is their visual field biases. EBA shows a lower visual field bias (Schwarzlose et al 2008, Weiner & Grill-Spector 2011). However, FBA has, as does the neighboring face area FFA, a central visual field bias without a difference between upper and lower field responses (Schwarzlose et al 2008).

Another difference between EBA and FBA was suggested by RSA using human bodies, monkey bodies, birds, and four-legged mammals, which showed more similar activation patterns in EBA compared to FBA (Caspari et al 2014). This finding suggests a greater ordinate-level selectivity in FBA compared to EBA. Indeed, EBA clustered monkey and human bodies, while FBA did not. However, caution should be applied in interpreting differences between areas in RSA or multi-voxel pattern analysis (MVPA) of fMRI activations since differences in stimulus selectivity of the single units can be confounded with differences in the spatial clustering of stimulus preferences due to the low spatial resolution of fMRI compared to single units (Dubois et al 2015).

What is represented in EBA and FBA? A recent study suggests that the activity to an image of an animal in both these areas depends on its similarity, as judged by human subjects, to a human body (Ritchie et al 2021). As discussed above, so far there is little evidence to support whole-body representations in these areas. These areas do not appear to represent bodies as a semantic category, since the ventral occipito-temporal cortex represents objects not by category but feature similarity (e.g. a cow mug evokes a more similar activity pattern to a cow than to a mug (Bracci et al 2019)). What are these features? Some studies reported that lowlevel visual features such as spatial frequency and orientation differences can explain stimulus selectivity in the occipito-temporal cortex (e.g. (Rice et al 2014)), but this is not a general finding (Long et al 2018, Ritchie et al 2021). More likely candidates are mid-level visual features, falling in between high-level semantic concepts and low-level features. Indeed, midlevel visual features that represent texture and form (“texforms”) but are insufficient for basiclevel object recognition can mimic to some extent category selectivity in the ventral stream (Long et al 2018), but still do not capture the full activation pattern. A model of a linear combination of units of a layer of a deep convolutional neural network, fitted to the activation of EBA to images of various categories, showed the strongest response to images that included body parts (Ratan Murty et al 2021). Further analysis of the EBA model showed that its activation was driven by hand and torso features. More work is required to reveal the visual features that drive responses in different body-category areas (for a perspective, see de Gelder & Poyo Solanas 2021).

It has been suggested that EBA and FBA are part of a larger map of body parts in the occipitotemporal cortex, with representations of body parts extending beyond EBA and FBA (Orlov et al 2010). In that study, EBA was found to prefer mainly the upper limbs. However, the upper limb region was also activated well by lower limbs, suggesting activations by both extremities in the EBA. FBA was found to prefer mainly face parts, perhaps due to the expected overlap with the FFA when using a bodies-objects contrast. It was close to a representation of the torso which also was activated well by the lower limbs. A later study found overlapping activations to different body parts largely contained within regions that were activated by whole bodies, including the face, compared to chairs (Bracci et al 2015). MVPA of both posterior (including EBA) and anterior (including FBA) regions tended to show a cluster of body extremities and a cluster of parts of the torso. These studies suggest that there is some clustering according to body parts, or visual features that are related to different body parts (e.g. extremities present in upper and lower limbs) in both EBA and FBA.

Interestingly, MVPA showed that discrimination of body parts is greater for those of the left compared to the right side of the body in the right compared to the left visual field in EBA (Chan et al 2010). Since humans typically fixate on the face during encounters, these biases in discrimination may reflect the influence of visual experience on the representations of body parts in the EBA. Qualitatively the same interaction between the body part side and visual field was present at the behavioral level. Note that similar results were obtained for half-face stimuli in the FFA (Chan et al 2010), suggesting a role of visual experience in body and face representations.

EBA, but not FBA, is activated while subjects haptically explore body parts during scanning (Costantini et al 2011, Kitada et al 2009), suggesting that visual stimulation is not necessary for activation of the EBA but visual imagery of body parts is sufficient. More intriguing studies show body-category selective activations to bodies and body parts that are signaled by haptic or auditory input in congenitally blind (Kitada et al 2014, Striem-Amit & Amedi 2014) and anophthalmic subjects (van den Hurk et al 2017). However, the category-selective activations in the seeing and blind subjects to the non-visual stimuli are stronger in seeing subjects and only partially overlap (Kitada et al 2014, Mattioni et al 2020, Striem-Amit & Amedi 2014). Furthermore, the correspondence between overall category organization for auditory and visual stimuli is weak for the animal category (Mattioni et al 2020). Nonetheless, these results highlight the ill-understood interplay of visual experience and other factors such as connectivity, for the development of category-selective areas (Arcaro & Livingstone 2021, Op de Beeck et al 2019).

Selective activations to bodies and/or body parts also occur in other visual cortical areas than the EBA and FBA. An area selectively activated by hands (compared to other body parts and chairs) was found just anterior to the left EBA (Bracci et al 2010) which overlaps with an area that responded stronger to tools relative to animals and chairs (Bracci et al 2012). Furthermore, the activation patterns to objects in the hand area correlated with the rated usability of the object as an effector, i.e. extension of the hand (Bracci & Peelen 2013), suggesting a role of body part-object interactions in shaping the stimulus selectivity in that area.

Greater activations to bodies compared to objects have been reported also in the human STS **(Figure 2a)** for static (Caspari et al 2014, Pinsk et al 2009) and dynamic stimuli (Grosbras et al 2012, Ross et al 2014). The posterior STS has been implicated in biological motion (Allison et al 2000, Blake & Shiffrar 2007, Yovel & O'Toole 2016), being activated by point-light displays of human bodies (Blake & Shiffrar 2007, Grosbras et al 2012, Grossman & Blake 2002, Jastorff & Orban 2009). This posterior STS (pSTS) region appears to respond equally well to static faces and headless bodies or body parts (Grossman & Blake 2002, Pinsk et al 2009). However, pSTS activations to dynamic faces are somewhat more anterior than those to biological motion displays of human actions (Deen et al 2015). Activations were stronger for whole-body stick figures, even when these were partially occluded, compared to randomly reconfigured sticks, which was taken to show that the pSTS is sensitive to the human body configuration (Thompson et al 2005). The STS is activated stronger by moving than static presentations of human bodies and moving articulated than translating or rotating bodies (Beauchamp et al 2002, Peuskens et al 2005). The former is in line with greater responses to moving compared to static faces in face-selective STS areas (Pitcher et al 2011). The pSTS is activated marginally stronger by coherent uninterrupted sequences of 630 ms long frames of whole-body human actions than by a random succession of frames of different actions, while the EBA and FBA show the opposite effect (Downing et al 2006). This demonstrates different processing of action sequences in the human STS versus the EBA/FBA areas. It agrees with the idea that the pSTS encodes the temporal sequence of an action, while the EBA and FBA encode individual (static) snapshots of a sequence. Also, unlike for EBA and FBA, selective activation to human actions in point-light displays is seen in the pSTS when subjects discriminate the stimuli but is much weaker during passive fixation, which may reflect the deeper processing of action kinetics during the task compared to passive fixation (Jastorff & Orban 2009). However, at least parts of EBA, e.g. representing the arm, may also process kinetics (Orlov et al 2014). Another dissociation between the pSTS and EBA/FBA concerns the role of motor actions during action viewing. In both EBA and FBA, there is no effect of concurrent action execution on the activation to the same or a different hand action, but pSTS is activated less when executed and observed actions are compatible compared to different (Kontaris et al 2009). Note that the human STS is activated also by other social stimuli and tasks, including other modalities (for review, see Pitcher & Ungerleider (2021)), and some of these activations partially overlap with those by bodies (e.g. Deen et al (2015)).

Body patches in monkeys

Body-category selective regions, body patches, have also been identified in monkeys with fMRI. Tsao et al (2003) were the first to map body patches in the monkey. They employed human bodies, contrasting these with faces, hands, objects, and scrambled patterns, and found one body patch in the ventral bank of the STS, posterior-medial to (likely) the Middle Lateral (ML) face patch. Later monkey fMRI studies employed a variety of body image classes to map body patches: monkey body parts (Bell et al 2009, Bell et al 2011, Pinsk et al 2009, Pinsk et al 2005), headless monkey bodies (Fisher & Freiwald 2015, Popivanov et al 2012, Sliwa & Freiwald 2017), headless human bodies (Premereur et al 2016), a combination of monkey bodies, four-legged mammals and birds (Bao et al 2020), scenes of multiple images of headless monkey bodies (Arcaro et al 2017) and a combination of headless monkey and human bodies and body parts (Lafer-Sousa & Conway 2013). Also, control image classes differed between studies, ranging from man-made objects (Fisher & Freiwald 2015, Pinsk et al 2009, Pinsk et al 2005, Popivanov et al 2012) to combinations of objects, vegetables, fruits, scenes, etc. In the latter case, either the contrast bodies-control classes (Bao et al 2020, Lafer-Sousa & Conway 2013, Premereur et al 2016) or a conjunction analysis of bodies minus each of the other classes (Bell et al 2009, Bell et al 2011, Sliwa & Freiwald 2017) was employed.

It appears that across the different stimulus sets and contrasts used in these studies, the most consistently observed body patches are two in the ventral bank of the STS (**Figure 2b-d**). One, which we labeled the middle STS body (MSB) patch (**Figure 2b,c**; Kumar et al 2017, Popivanov et al 2014), is located anterior and lateral to the Fundus of the Superior Temporal (FST) area, close and medial to face patch ML (**Figure S1**). This body patch appears to be present in many monkey fMRI studies (Bao et al 2020, Bell et al 2009, Bell et al 2011, Fisher & Freiwald 2015, Lafer-Sousa & Conway 2013, Pinsk et al 2005, Popivanov et al 2012, Premereur et al 2016, Sliwa & Freiwald 2017, Tsao et al 2003). The second one is located more anteriorly in the lateral part of the ventral bank of the STS, close and medial to the Anterior Lateral (AL) face patch (**Figure 2b,d; Figure S1**), and can be discerned in several fMRI studies (Bao et al 2020, Bell et al 2009, Bell et al 2011, Fisher & Freiwald 2015, Lafer-Sousa & Conway 2013, Pinsk et al 2009, Pinsk et al 2005, Popivanov et al 2012, Premereur et al 2016, Sliwa & Freiwald 2017). We labeled this patch the anterior STS body (ASB) patch (Kumar et al 2017). Recent studies (Bao et al 2020, Premereur et al 2016, Sliwa & Freiwald 2017) have also observed a smaller body patch in anterior IT, ventral to the STS, dorsolateral to the Anterior Medial (AM) face patch (**Figure 2e; Figure S1)**. We will label this anterior patch the Anterior Ventral Body (AVB) patch.

Dorsal bank activations to bodies are more variable amongst monkeys and studies. For instance, Popivanov et al (2012) reported that 3 of their 4 monkeys showed a body patch in the dorsal bank of the STS, dorsal to MSB. More anteriorly, close to ASB, a dorsal STS body patch was observed in some monkeys also. These dorsal bank patches, defined with the contrast monkey bodies-manmade objects, were however equally activated by bodies and faces (Jastorff et al 2012). The inconsistent activations in the dorsal bank might be due to the use of static instead of dynamic stimuli in the fMRI mapping studies.

Noteworthy, in all studies the body patches were observed close to face patches **(Figure S1),** and, depending on the contrast being used (bodies-objects versus contrasts that include faces as control category), overlapped with the face patches. This is similar to what has been observed in humans (e.g. overlap of FFA and FBA). The extent of body patches depends (trivially) on the threshold being used in the fMRI analysis. Improvement of monkey fMRI technology and the use of implanted coils (Zhu & Vanduffel 2019), which increases the spatial resolution, promises to reveal further the precise organization of the body patches in IT, which is expected to be more complex than envisaged now.

Both MSB and ASB were activated in the studies that employed body parts instead of headless bodies. Thus, also ASB is well activated by body parts and does not require a whole (headless) body. The body patches, defined with monkey bodies, are also activated by four-legged mammals and birds (Popivanov et al 2012). MSB and ASB are connected, as revealed by electrical microstimulation combined with fMRI, and constitute a network that only weakly overlaps with the face patch network (Premereur et al 2016).

Two studies examined responses to dynamic bodies in body patches defined by static stimuli. Biological motion point-light displays of monkeys showed stronger activation in both MSB and ASB compared to scrambled and translation controls (Jastorff et al 2012), which agrees with similar activations to human point-light displays in human EBA and FBA (Jastorff & Orban 2009). Free viewing of videos of social interactions between monkeys activated both face and body patches (Sliwa & Freiwald 2017), which is not surprising since the monkeys have a body and a face. During free-viewing, videos of monkeys interacting with an object activated body but not face patches (Sliwa & Freiwald 2017). This might be because the monkeys fixated less on the face and more on the body during the free-viewing of monkey-object interaction videos (see Figure S2 in Sliwa & Freiwald (2017)).

How do the body patches of monkeys relate to the body category-selective areas of humans? Answering this difficult question requires at least that the same stimulus conditions are employed in the two species (Bell et al 2009, Caspari et al 2014, Pinsk et al 2009). Based on a comparison of face- and body-selective areas, Pinsk et al (2009) suggested that FBA corresponds to their macaque anterior body patch which likely was ASB. Also, a comparison of the relative locations of face and body-selective regions between both species (Caspari et al 2014, Popivanov et al 2012) suggested that MSB corresponds to EBA and ASB to FBA. Based on this putative homology, one predicts a more anterior body-category selective area in humans, close to the human anterior face area (Rajimehr et al 2009, Tsao et al 2008), which would be the homologue of the monkey AVB. However, MR signal drop-out and distortion caused by susceptibility artifacts in this anterior region of the human brain complicates seeing this anterior area. The STS of the human brain likely corresponds to the rostral dorsal bank but not ventral bank STS of the monkey: both human STS (Pitcher & Ungerleider 2021) and monkey dorsal bank STS favor moving stimuli (Anderson & Siegel 1999, Baylis et al 1987, Bruce et al 1981, Pitcher & Ungerleider 2021, Vangeneugden et al 2011, Vangeneugden et al 2009).

Like for the face patches (Hesse & Tsao 2020, Yovel & Freiwald 2013), these homologies of human and monkey body patches are tentative, requiring further work in both species.

Stimulus selectivity of body patch single neurons.

The finding of fMRI body patches in monkeys allows the investigation of the body representations at the level of single units in the fMRI-defined monkey patch network. Such strategy, examining and comparing stimulus selectivity of single units in different fMRIdefined category-selective patches, has been successful in advancing our understanding of face processing (Hesse & Tsao 2020) and I believe the same will hold for body processing.

Most fMRI-guided single-unit recordings have targeted MSB and/or ASB. As expected from the fMRI mapping, the response, normalized per single unit and then averaged across units, is greater for bodies compared to other categories in both patches (Bao et al 2020, Bao & Tsao 2018, Kumar et al 2017, Popivanov et al 2014). Also, body patches contain a higher proportion of neurons preferring body parts (compared to faces, objects, and scenes) than other regions in the ventral bank of the STS (Bell et al 2011). Average responses to headless human bodies, monkey bodies, four-legged mammals, and birds tend to be similar in both MSB and ASB, and are greater than the response to manmade objects, fruits, vegetables, and faces (Kumar et al 2017, Popivanov et al 2014). However, these mean responses, averaged across units and images of the same category, hide considerable variability in image selectivity amongst single units (**Figure 3a**). Indeed, single MSB and ASB neurons respond to some but not all body images and can respond to non-body images too (Bao et al 2020, Kumar et al 2017, Popivanov et al 2014). In fact, some ASB and MSB neurons can respond quite well to faces in addition to bodies (Bao et al 2020, Popivanov et al 2014). In other words, the body category selectivity that is observed at the population response level results from averaging a population of single units that has quite a heterogeneous image selectivity. This heterogeneity of the image selectivity at the single-unit level endows the body patches with a rich potential to signal various stimulus categories and properties. Thus, one can decode not only body versus nonbody images (Kumar & Vogels 2019, Popivanov et al 2014) but also human versus monkey bodies and to some extent monkey versus human faces from the activity of a small population of MSB or ASB neurons (Kumar & Vogels 2019). Even manmade objects that differ in their aspect ratio are classified reliably by a population of MSB neurons (Popivanov et al 2014). This is because the body patch neurons do not exclusively respond to bodies. Note that individual non-face images can also be decoded from the activity of face patches (Meyers et al 2015), suggesting that responses to non-preferred object categories are not unique to the body patch network. Importantly, it is not because one can decode stimuli or categories from the activity pattern of a patch that this information is being used downstream. It is well possible that only information about preferred categories, e.g. about bodies in body patches and faces in face patches, is employed by downstream areas. Causal studies, using a manipulation of activity together with behavioral read-outs, which are required to answer this important question, appear to suggest that the latter is the case, at least for a face patch (Sadagopan et al 2017, Schalk et al 2017).

MSB neurons show selective responses to body parts (Popivanov et al 2014, Popivanov et al 2016), and responses to an effective body part can equal the response to the whole body (Popivanov et al 2016). Bubbles, a technique in which an image is presented through randomly positioned Gaussian apertures, and reverse correlating the responses with the apertures, suggested that MSB neurons respond to fragments of bodies such as extremities (limbs), curved boundaries, and parts of the torso, but rarely whole bodies (Popivanov et al 2016). Some of the effective features are also present in non-body images, e.g. the “leg” of a plier, explaining responses to such nonbody images. In other words, these neurons are not “semantic body detectors” but respond to features that are prevalent in images of bodies but also occur in images of other objects. Thus far, there is no evidence that single MSB neurons are sensitive to the configuration of the body parts, but it cannot be ruled out either.

Using a parametric object space, defined with Principal Component Analysis (PCA) on the activations in a deep layer of a convolutional neural network (Alexnet; Krizhevsky et al (2017)) to a large set of objects (including animal bodies, faces, objects, and houses), it was found that body patch neurons of MSB, ASB and AVB show ramp-shaped tuning along an axis in the 50 dimensional PCA space and no tuning along orthogonal axes (Bao et al 2020). Ramp-shaped tuning for axes in this object space was present also for IT neurons in neighboring patches that were defined by non-body stimuli and was suggested to be a general coding principle in IT (Bao et al 2020, Chang & Tsao 2017). The same study showed that MSB neurons responded strongly to images of four-legged mammals (with a head) in which the legs were well visible. These images were selected by their projection onto the same quadrant of the first two PCs of the object space. Images of human body fragments, e.g. torso, hand, feet, and a knee, which projected weakly onto that PC quadrant, produced a smaller response averaged across the images (Bao et al 2020). However, this difference in average responses could be due to the larger variability in shape features amongst the human body parts compared to the mammals, which all had extremities and similar profile postures. As predicted by their projection onto the 2D object space, responses to a set of object images, e.g. a plier, wine glass, drum set, and chair, produced average responses that were similar to those for the human body parts, with even a shorter response latency. The object space defined by Bao et al (2020) provides an advance in understanding the global organization of feature maps in IT, but it is as yet unclear how far it can explain the selectivity of single neurons to the wide variety of body images.

MSB neurons typically respond well to silhouettes of bodies and the selectivity for silhouettes corresponds to that for the original textured and shaded images (**Figure 3b**), suggesting that shape is a strong determinant in driving body patch neurons (Bao et al 2020, Popivanov et al 2015). This shape selectivity may underlie the discrimination of body shape and posture. The silhouette shape selectivity of single MSB neurons can be modeled to some extent by deeper layers of convolutional neural networks (Kalfas et al 2017), as can IT responses for other objects (Yamins et al 2014), but this work did not provide an insight about which features underlie the selectivity.

The contribution of 3D shape and motion cues to body patch neuron responses is still unexplored at the single-unit level. Temporal integration of moving shape features under partial occlusion, like when watching an animal moving behind a static narrow slit, is rather limited in ASB: ASB neurons appear to respond to instantaneous, visible body fragments when these are presented through a narrow slit (Bognar & Vogels 2021).

As is typical for IT, the response of body patch neurons depends on the position and size of the image, but their feature preference is largely invariant to its size and position within the receptive field (Kumar et al 2017, Popivanov et al 2015, Popivanov et al 2016). Receptive fields in MSB and ASB have typical sizes for IT (Kumar et al 2017, Popivanov et al 2015). Their receptive fields are usually to some extent bilateral with stronger responses in the contralateral hemifield. The population of MSB and ASB neurons showed the peak response at the foveal location, but in addition, MSB, but not ASB, has a lower visual field bias (Kumar et al 2017, Popivanov et al 2015). The latter agrees with the visual field biases observed with fMRI in (human) EBA and FBA (Schwarzlose et al 2008, Weiner & Grill-Spector 2011).

MSB neurons are well-tuned to the 2D rotation of the body while ASB neurons show greater tolerance to 2D orientation (Kumar et al 2017, Popivanov et al 2015). Likewise, selectivity for 3D viewpoint decreases from posterior to anterior body patches (Bao et al 2020, Kumar et al 2017). The increased view tolerance for anterior patches appears to be a general coding principle in IT since it has been observed also for face (Freiwald & Tsao 2010) and other object patches (Bao et al 2020). MSB and ASB neurons are selective for natural postures (threatening, submissive, neutral) of monkey avatars and their identity (as defined by their body mass (Kumar et al 2017)). Body posture and identity can be decoded better, irrespective of their viewpoint, from a sample of ASB neurons than from MSB (Kumar et al 2017); **Figure3c**). This aligns well with the better decoding of face identity, irrespective of their viewpoint, from anterior compared to posterior face patch neuron populations (Meyers et al 2015). This suggests a general principle of object coding in IT: a greater tolerance to image transformations that preserve identity (Bao et al 2020) and, in the case of bodies, posture, for more anterior patches. The monkey data fits human fMRI work that found viewpoint-invariant decoding of body identity in the FBA but not the EBA (Foster et al 2021), but as noted above, between-area differences in fMRI MVPA outcomes are difficult to interpret (Dubois et al 2015).

The population activity pattern of MSB neurons shows a clustering of images of bodies versus non-bodies, which is less the case in ASB, where different clusters of body images appear. This suggests that ASB neurons might be more involved in discriminating between different bodies than MSB (Kumar et al 2017), in line with the better decoding of view-tolerant posture and identity in ASB. This aligns with observations suggesting lesser category but stronger individuation signals more anterior in the human occipito-temporal cortex (Clarke & Tyler 2015). Significant decoding of bodies versus non-bodies has a later onset in ASB compared to MSB, which agrees with ASB being at a hierarchically higher stage than MSB (Kumar & Vogels 2019).

Agents consist of a body and a face and thus the question arises whether and how faces and bodies interact in body patches. There is evidence from human fMRI studies that activations in the FBA to a body interact with the face (reviewed by Hu et al (2020)). A superadditive interaction between bodies and faces (i.e. response to a whole monkey larger than the sum of body and face activations) has been reported for anterior face patches but appears to be absent for monkey body patches (Fisher & Freiwald 2015). The response of single MSB neurons to the simultaneous presentation of a body and a face is similar to that of the body alone when the two stimuli are in the upper and lower visual field (Bao & Tsao 2018). Highly similar effects were observed when pairing a body and an object, suggesting no specific interactions for bodies and faces in that body patch. However, in that study, human faces were paired with monkey bodies, which may have prevented integration. Also, faces and bodies might interact in patches anterior to MSB, as suggested by some human fMRI studies (Hu et al 2020). Agent-selective cells, i.e. responding to a whole body but not a face or headless body, have been reported in the rostral STS (Wachsmuth et al 1994), but it is unknown how these relate to the body or face patches. Definitely, how faces and bodies interact at the single-cell level requires further study in face (Arcaro et al 2020) and body patches. Other important gaps in our knowledge include the encoding of social interaction between agents and the processing of dynamic, acting bodies at the single-unit level in body patches.

Body patches: providing body descriptions to action and socio-affective networks.

The body patches are embedded in larger networks. However, electrical microstimulation of body patches has so far not yielded activations outside IT (Premereur et al 2016), but this could be because the monkeys in that study were anesthetized. MSB and ASB are located in the ventral bank of the STS and thus one could make an informed guess about the connectivity of body patches by taking the results of tract-tracing studies of the ventral bank of the STS. Ventral prefrontal (Borra et al 2011, Gerbella et al 2010) and parietal cortex, including the intra-parietal sulcus (for review, see Borra & Luppino (2019)) connect to the ventral bank of the STS. The ventral bank of the STS is also connected to the basal ganglia and its rostral part with the ventral striatum, amygdala, orbitofrontal cortex, and perirhinal cortex (Kravitz et al 2013). Connections to the insula have also been reported (Seltzer & Pandya 1991). Interestingly, the cingulate cortex is connected strongly to the dorsal bank but only weakly to the ventral bank of the STS (Vogt & Pandya 1987). *The above connections are typically patchy* *in the STS and to what extent these involve body patches is still unclear. Also, it is not known* to what extent the body patch connections differ from those of the neighboring face patches (Grimaldi et al 2016, Moeller et al 2008).

In humans, resting-state fMRI studies suggest that EBA is connected to the parietal cortex, auditory cortex, somatosensory cortex, motor and premotor cortex, cingulate cortex, insula, medial temporal lobe structures, and basal ganglia (Hutchison et al 2014, Zimmermann et al 2018). FBA shows connections to most of these structures, although the two studies differed concerning its connectivity to the frontal cortex. Some of these connections were also demonstrated with diffusion-weighted MRI (Zimmermann et al 2018). These studies would imply that the body category-selective regions are connected with parts of the brain involved in sensory processing of different modalities, high-level cognition, and sensory-motor control. However, these noninvasive methods suffer from limitations, not always reflecting monosynaptic connectivity.

The current evidence suggests that body patch neurons provide information about body parts, body shape/identity, body posture, and body (part) orientation. Different body patches differ in their representation of these body properties. For instance, in the monkey MSB shows a stronger body orientation selectivity than ASB. These body descriptions will be useful for neural networks that require such descriptions. For example, visual body descriptions computed in body patches can inform other areas like the parietal cortex (for a recent review, Orban et al (2021)), that contribute to planning actions when viewing or interacting with other agents. Other examples of neural networks that employ body descriptions include those for emotion (de Gelder et al 2015), social cognition (Tremblay et al 2017, Wittmann et al 2018), and observational learning (Meunier et al 2007). Thus, one can view the body patch system as an entry point for other systems that require body descriptions for their function. It is tempting to speculate that the kind of body information needed by an area, e.g. the orientation of a limb versus an orientation-invariant representation of body posture, will determine the effective connectivity between the body patch, e.g. MSB versus an anterior patch, and that area, but this remains to be examined. Other important questions concern the information flow within the temporal cortical body patch network, which is very unlikely to be only feedforward, how this flow evolves during the perception of the body stimulus and is affected by the task of the subject.

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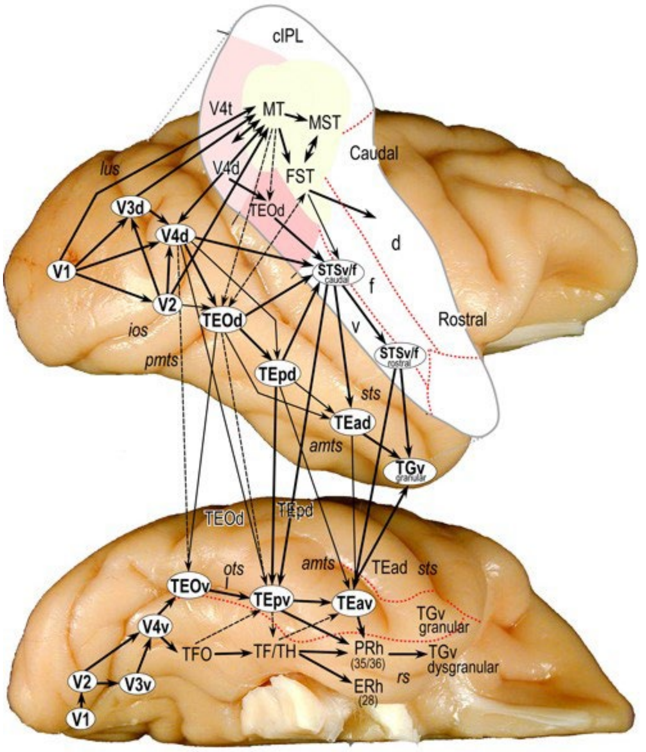
Figure Legends.

Figure 1. Anatomy and connectivity of macaque IT and single-unit selectivity for a walking human in the STS. a. Connectivity of IT subregions, illustrating reciprocal connections on a lateral (top) and ventral view (bottom) of the macaque brain. The STS is opened to show its subregions. Subregions of the dorsal bank (d) of the STS anterior to FST are not shown. The primary visual cortex (V1) provides input through subregions of the preoccipital (V2; V3d/v), prelunate (V4d/v), posterior IT (TEOd/v) and posterior ventral bank and fundus of the STS (STSv/f caudal), into area TE (TEpd, TEpv, TEad, and TEav) and the temporal pole (area TGv) as well as the rostral STSv/f. Also shown is a connection between V4v and the medial temporal lobe (parahippocampal (TF/TH/TFO), perirhinal (PRh), and entorhinal (ERh) cortices). Abbreviations: 28, ERh; 35/36, areas 35 and 36 of the PRh; amts, anterior middle temporal sulcus; cIPL, caudal inferior parietal lobule; FST, floor of superior temporal sulcus; ios, inferior occipital sulcus; lus, lunate sulcus; ots, occipitotemporal sulcus; pmts, posterior middle temporal sulcus; rs, rhinal sulcus; sts, superior temporal sulcus; STSf, fundus of superior temporal sulcus; STSv, ventral bank of superior temporal sulcus; TEad, dorsal subregion of anterior TE; TEav, ventral subregion of anterior TE; TEOd, area TEO, dorsal part; TEOv, area TEO, ventral part; TEpd, dorsal subregion of posterior TE; TEpv, ventral subregion of posterior TE; TF/TH, areas TF and TH of parahippocampal cortex; TFO, area TFO of parahippocampal cortex; TGv, ventral temporal pole; V1, primary visual cortex; V2, visual area 2; V3d, visual area 3, dorsal part; V3v, visual area 3, ventral part; V4d, visual area 4, dorsal part; V4t, V4 transitional area; V4v, visual area 4, ventral part. Panel adapted from Kravitz et al (2013). **b.** Responses of a single unit recorded in the dorsal bank of the STS to walking bodies and controls (indicated by the square and the vertical arrows) moving in 4 directions. The neuron showed a greater response to the back view of the body walking away from the monkey than to either controls or the front view of the body moving away from the monkey. The neuron did not respond to other body views moving in other directions or to static images (not shown). Panel adapted from Oram & Perrett (1996).

Figure 2. Human body-category selective areas and body patches in macaque IT. **a.** Illustration of the location of the EBA, FBA, and STS body area on an inflated cortical surface. The fMRI activations are from a single human subject contrasting static images of human bodies without heads to human faces, small artifacts, houses, outdoor scenes, and phase scrambled images. Unpublished data provided by M. Fang, A. Anglinskas, Y. Li, and S. Anzellotti and used here by permission. **b.** Saggital section of the monkey brain illustrating, from posterior (left) to anterior, the body patches MSB, ASB, and AVB. The body patches were obtained by contrasting 20 images of monkey bodies without heads to 20 monkey faces and 60 manmade objects. The fMRI activations in the fixating monkey were performed using the contrast agent Monocrystalline Iron Oxide Nanoparticle and analyzed following the procedures for a block design (Popivanov et al 2012). Based on unpublished data from our lab by Y. Zafirova and R. Vogels. **c.** Coronal section illustrating the location of MSB in the STS. **d.** Coronal section illustrating the location of ASB. **e.** Coronal section illustrating the location of AVB. The data of c-e were from the same experiment and animal as b. Note that the locations of body patches can vary amongst monkeys.

Figure 3. Stimulus selectivity of macaque body patches. a. Stimulus selectivity of single MSB neurons. Top: Responses of single neurons (rows) recorded from MSB of a single monkey to 100 images (columns). Stimuli from left to right: 10 monkey faces, 10 human faces, 10 headless monkey bodies, 10 headless human bodies, 10 mammals, 10 birds, 10 Mooney sculptures, 10 fruits/vegetables, 20 manmade objects. The net response, normalized per neuron, is indicated for each image (columns) and neuron (rows) with a color code (warm colors correspond to higher responses). The lower bar shows the normalized response averaged across neurons. Individual neurons vary markedly in their selectivity, but the population of MSB neurons responds on average stronger to bodies compared to other categories. Panel adapted from Popivanov et al (2014). **b.** Mean ranked responses of MSB neurons to original and silhouette versions of images of various categories, including bodies. Before averaging the net responses across the single neurons, stimuli were ranked from best to worst by their response to the original versions. Error bars denote the standard error of the mean and *N*

corresponds to the number of neurons. Panel adapted from Popivanov et al (2015). **c.** left panel: classification accuracy (Support Vector Machines; 6-fold cross-validation; see Kumar et al (2017) for details) of the decoding of 3 monkey body avatar identities, irrespective of their posture and viewpoint from a population of MSB (red) and ASB neurons (blue); middle panel: the same for decoding of 5 postures, irrespective of identity and viewpoint; right panel: decoding of 8 viewpoints, irrespective of posture and identity. Panel adapted from Kumar et al (2017).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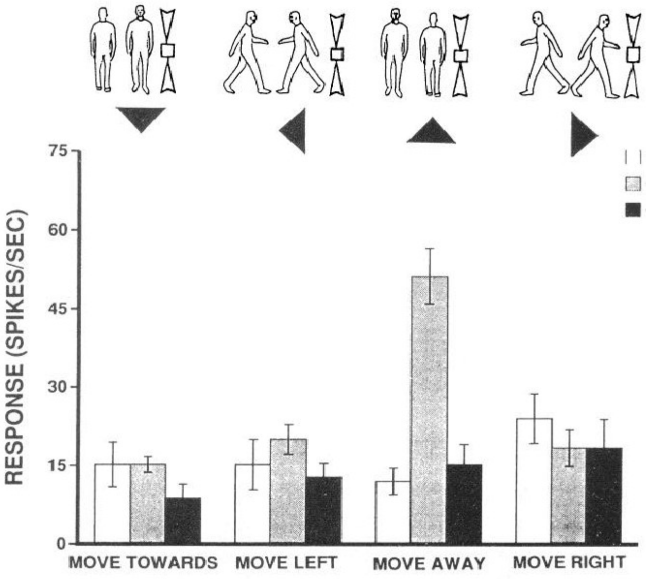
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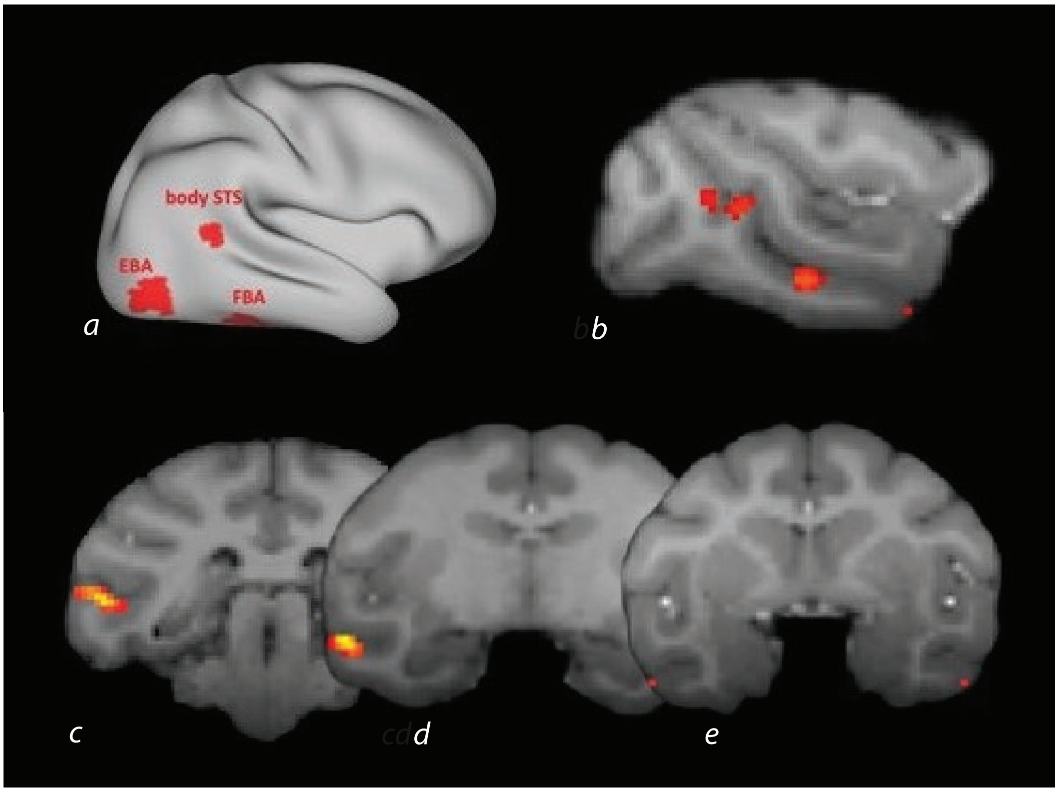
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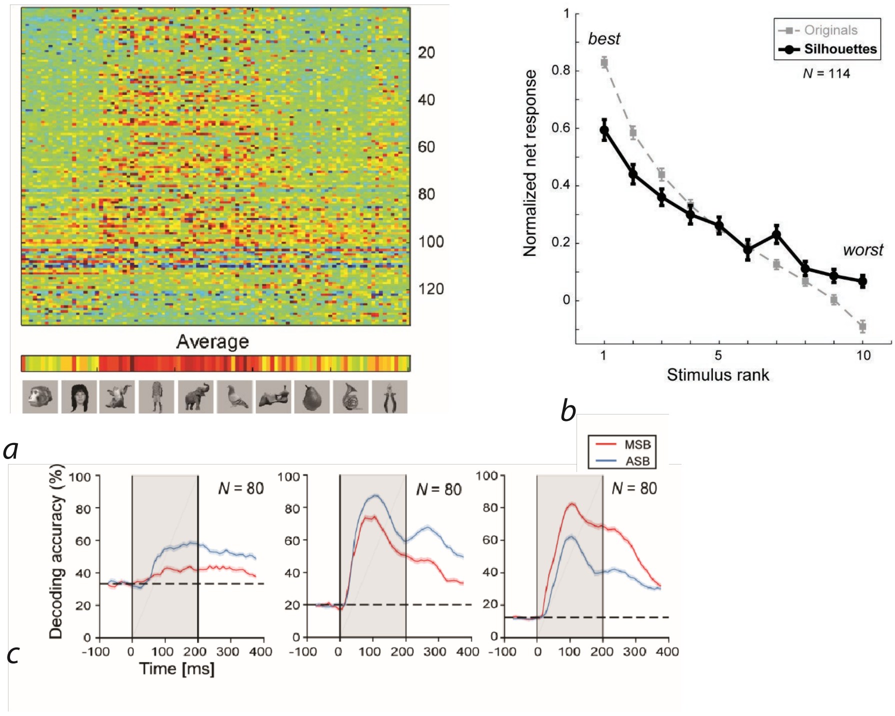
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