The body inside out

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Background.

The body outside. From the earliest known cave paintings to contemporary performance art representations of the human body occupy a central place in (western) art. Why bodies?

The body inside. There is a long tradition of analyzing artistic experience by reference to the impact of art on the viewer. Some of this is in terms of emotions expressed in the work and of subjective body states (heartbeat, breathing, shivers etc.) Some of this language is metaphorical, other expressions describe physical sensations in the body (falling, climbing, altitude etc). Psychology and neuroscience inspired researchers have begun to measure corporeal sensations and physiological processes associated with artistic experience (more for music than for visual arts or architecture). In turn, artists create work partly steered by the viewers' physiology or incorporating subjective experience data in the work, even have the audience as the composer (eg. Muntendorf).

The discovery of mirror neurons three decades ago has given a whole new impetus to these subjective experience theories. Mirror neurons sustain simulation or (re) enacting of the artwork and this activity triggered in the brain by the sensory processes (vision, audition) of the brain processes sustaining postures, movements and sounds constitute access to the meaning of the artwork (Freedberg & Gallese 2007). In simulating, embodying or mimicking what they see, the postures and gestures, observers enact the emotions expressed and access the artistic meaning.

This paper briefly reviews research addressing a basic question underlying some of the above literature: Is there a privileged representation of the human body in the brain and what are its characteristics?

Social species make extensive use of collaborative and competitive signals from conspecifics, allowing them to navigate successfully in the natural and social world. In the visual domain, social signals from faces and bodies are the central sources of information about conspecific presence, intentions, emotions, and actions. An extensive literature on face perception has already illustrated the importance of face perception for regulating interactions between nearby conspecifics (Panksepp, 1989). Like the face, the body is a rich and powerful means of social communication allowing quick and easy inferences about identity, gender, sex, physical health, attractiveness, emotional state, and social status. Body perception already operates at a much longer distance than face perception and provides information about emotions, intentions, and actions relevant for social interaction (de Gelder et al., 2010). The social brain hypothesis launched by Brothers during research on nonhuman primates has triggered extensive research on social perception. In view of the relevance of bodily communication across many social species, one may expect that there exist preferential processing routes for bodies (Downing and Kanwisher, 2001) and body expressions (de Gelder et al., 2010) in the brain. Recent theories about social perception and social brain networks remain focused on face perception and do not yet integrate findings from body perception studies (Patel et al., 2019; Pitcher and Ungerleider, 2021; Orban et al., 2021).

1. State of the art and beyond

1.1 Traditional perspective on cortical visual representation

Mainstream studies on body perception endorsed the framework of object and face perception research. Object vision is commonly thought to involve a hierarchy of brain regions processing increasingly complex image features, starting with processing low level physical stimulus properties to high-level visual cortex supporting object categorization and recognition. A similar approach dominated the research on bodies. Early investigations into the neural correlates of human body perception were motivated by localizing body category-selective areas, typically by contrasting bodies with other categories such as faces and objects. These studies identified the extrastriate body area (EBA) in the middle occipital/temporal gyrus (Downing et al., 2001), and later the fusiform body area (FBA) in fusiform cortex (Peelen and Downing, 2005; Schwarzlose et al., 2005), as well as a body-selective region of the posterior superior temporal sulcus (pSTS; Figure 2) (Pinsk et al., 2009).

The classical cortical category representation perspective on body perception is confronting some central issues. First, concerning the division of labor between EBA and FBA, it is still unclear whether EBA is primarily involved in processing body parts and FBA may then have a relative bias for holistic or configuration-based processing of whole-body images (Taylor et al., 2007; Downing and Peelen, 2011). It is un clear what specific computations take place in each body-selective area and what their functional connectivity is. Thirdly, activity category selective areas is significantly affected by the participants' task (Marrazzo 2022). Fourthly, other brain regions beyond these two body-category selective areas are also shown to contribute to body perception when more naturalistic stimuli are used (de Gelder et al., 2010; de Gelder and Poyo Solanas, 2021) and how the two classical body-selective areas contribute to processing whole body information for real life tasks like emotional expression or identity recognition (de Gelder and Poyo Solanas, 2021).

Studies focusing on body perception as part of research on action and emotion recognition revealed other areas in addition to those known from category- based studies. A comparison of expressive with neutral whole body still images (de Gelder et al., 2004, 2010) and studies using video images and controlling for action category (Grezes et al., 2007) reported the posterior superior temporal sulcus (pSTS), temporoparietal junction (TPJ), frontal cortex and parietal motor regions (Pichon et al., 2009; Peelen et al., 2007; Gr`ezes et al., 2007), as well as the amygdala (AMG) (de Gelder and Poyo Solanas, 2021; Poyo Solanas et al., 2020b; Pichon et al., 2012). Notably, most of the clusters found in body expression studies were also reported in studies of the action observation network (Grezes et al., 2007; Goldberg et al., 2014; Pichon et al., 2009), emotion (de Gelder et al., 2004; Borgomaneri et al., 2015) and included subcortical areas (Poyo Solanas et al., 2020b; Utter and Basso, 2008). The relation between category-selective areas and areas that seem to be involved in perceiving various functional roles of the body is still poorly understood.

This matter is particularly relevant since, like the non-human primate studies above, most human studies establishing category selectivity used static images neglecting the contribution of movement to body selectivity. For example, the pSTS is not viewed as a body sensitive area but has a key role in biological movement processing (Allison et al., 2000; Grossman et al., 2005). The few studies dealing with movement used point-light displays (PLD)16. While this allows for the control of possible confounds in movement vs. shape, permitting systematic variations of kinematic and postural features, point-light displays are far from representing natural stimuli. Integrating movement and thus using more naturalistic dynamic stimuli are needed to gain insight on how visual body attributes contribute to the perception of specific affective states.

While research in human and non-human primates addressing the above issues (Vogels 2022), a different perspective can be adopted. Body category selective areas do not consist of abstract body detectors that are the gate keepers for perception of emotional expression, gender etc. Rather, their activity may be driven by visual features that are statistically more prevalent in bodies yet shared by some objects. *Figure 1 about here.*

1.2 An integrative perspective

A very different approach is to consider the brain as a fine-tuned network for adaptive action. Just like facial expressions (Bagnis et al. 2019), body language conveys emotions through specific postural configurations, but it also simultaneously suggests the adaptive actions that these emotions typically trigger (de Gelder et al. 2004; de Gelder 2006). For instance, a fearful face signals a threat without indicating a clear coping strategy, whereas a fearful body posture openly indicates a flight response (Kret et al. 2011; Kret et al. 2013; Liang et al. 2019). Passive observation of fearful bodily expressions activates brain regions implicated in both emotional processing and social perception (e.g., the AMG , OFC, and fusiform gyrus), alongside motor-related areas (e.g., premotor and supplementary motor areas) (Hadjikhani and de Gelder 2003; de Gelder et al. 2004; Van Den Stock et al. 2011). This integrated network is thought to underlie mechanisms of fear contagion and action preparation in response to observing fear in others (de Gelder et al. 2004; Tamietto and de Gelder 2008; Schiano Lomoriello et al. 2024).

An integrated model is based on the notion of a single processing stream for body and affective information processing rather than models where subsequent processing of action and emotional expression depend on prior abstract body category processing. Recent fMRI research corroborates this integrative perspective, as body-selective processes have been shown to overlap with the neural processing of biological movement (Jastorff & Orban, 2009), postural features (Marrazzo et al., 2023; Marrazzo et al., 2021; Poyo Solanas et al., 2020), action recognition (Goldberg et al., 2014; Shmuelof & Zohary, 2005), and social perception (Kret et al., 2011; Moreau et al., 2023). Most notably, emerging evidence points to a large-scale neural network specifically selective for naturalistic body motion in the human brain (Li et al., 2023) as well as the non-human primate brain (Kumar et al., 2023) (see section 3). (Note recent findings eg Livingstone (2024) about what is contributed by non-face sensitivity of face neurons; Johnson & Fusi (2024) on emergence of modularity). To summarize, distributed network models connect with older connectionism ideas about neural representation as subsymbolic, with new insights from DNN, and with increasing understanding of neural coding.

2. Subsymbolic representation, midlevel features.

The older literature contains several detailed descriptions of how specific emotions and actions are conveyed through body posture or movement and (James, 1890; Frijda, 1986; Wallbott, 1998). For example, among important features discriminating between affective expressions head inclination (typical for sadness) and limb flexion, associated with the expression of anger are often reported is (4,5). Other candidate features are the degree of lateral opening of the body (e.g. the body is more extended for happy than for sad), the vertical extension of the body (e.g. hands are often raised for happy but remain low for sad), symmetry (e.g. joy is often depicted by symmetric up and down hand movement) or the directionality of the movement (e.g. forward whole-body movement depicts anger) (for a review see ref. 6).

Most studies have so far investigated how bodies convey emotion by relating such verbal descriptions of features of body posture and movement to qualitative descriptions and emotion labels (3,4). In contrast to the use of, computer scientists are increasingly interested in modelling the properties of body postures and movements (6–11). This requires a detailed analysis of the complex information conveyed by body movements: kinematic (e.g. velocity), dynamics (e.g. mass and force) and posture/form information and its changes over time (12). For example, regarding kinematics, it has been found that velocity, acceleration, and jerkiness strongly influence the perception of emotion in expressive arm (13–15) and in whole-body movements (10) been used (11,17) but, although more naturalistic, they are often exaggerated and do not represent day-to-day emotional movements, actions or social interactions.

Recent methodological and technical advances for tracking and quantifying naturalistic body movements and postures e.g., OpenPose (Cao et al., 2017) or DeepLabCut (Mathis et al., 2018), along with novel computational analysis methods using Deep Neural Networks (Cichy and Kaiser, 2019), promise to make the field more systematic and objective. Turning away from commonsense and language dependent qualitative descriptors may be a condition for understanding the underlying perceptual and neural basis body perception. This was the goal of recent studies. Kinematic and postural features of whole-body movements were computed and the results related to the emotional category of the stimuli as well as to subjective ratings of similar feature descriptors (Poyo Solanas et al., 2020b). An example of the results obtained was that two key postural features, limb angles and symmetry, allowed to distinguish fearful movements from other emotional expressions. *Figure 2 here.*

An important question is how computationally defined features relate to subjective perception. While the former are designed to have explanatory value for understanding how the images are computed, the latter remain relevant for understanding phenomenal experience.

For example, in the case of the behavioral rating of "contraction", three different computed counterparts were defined: shoulder ratio, surface and limb contraction. However, the behavioral rating of this attribute was closer to the representation of limb contraction and limb angles than to surface or shoulder ratio. How well phenomenal features and computational features map onto each other seems to vary with the feature considered. As the above example shows, a specific body movement attribute can be computed in multiple ways. It also depends on the methods and algorithms used to compute the features (see next section).

2.1.2 Features in the brain.

A central question for using computational models in neuroscience (of human body movement) is how features from computational models may be related to brain processes. Older literature using macrolevel distinctions distinguished between brain pathways for form and movement information (Vaina et al. 1990; Giese and Poggio 2003; Milner and Goodale 2006, 2008) or even ventral and dorsal stream and a more recent proposal about a third stream for social information (Pitcher & Ungerleider 2022) but none of this use detailed or computational analyses or (mathematical, geometrical, computational) models of the stimuli. Body expression feature analysis described above presents an opportunity chance for a much more detailed approach. Using fMRI we measured the mapping between computational analyses of the body expression features and the BOLD signal. Our results reveal six major findings. First, computationally defined features are systematically related to distributed brain areas. Second, postural rather than kinematic features reflect the affective category structure of the body movements. Limb angles and symmetry were important for differentiating neutral from emotional body movements. Limb angles and especially limb contraction were particularly relevant for distinguishing fear from other body expressions. These two features were represented in several regions including affective, action observation and motor preparation networks. Third, the pSTS differentiated fearful from other affective categories using limb contraction rather than kinematics, despite this area being known for its involvement in biological motion processing. Fourth, EBA and FBA also showed greater tuning to postural features. Although the pattern of feature representation in these areas was similar, the stimuli representation in EBA was very dissimilar to that of FBA, possibly reflecting their different roles in body processing. Fifth, kinematic and postural feature processing was not segregated into dorsal and ventral streams, except for the feature velocity. Finally, the brain representation of emotional categories showed a distributed pattern and illustrate the involvement of classically as well as other body sensitive areas.

2.2 Computational features

Taking a more methodological and systematic approach, other authors have used data-reduction methods such as PCA factor analysis or blind-source separation algorithms (Smelak in preparation). One way of constraining the possible set of computational models for brain is to adopt an ethological framework and compute features from online behavioral analysis using DNN.

2.2 Ethological features

Ethological questions focus on how natural behavior is formatted by the responses of the organism to environmental conditions that are relevant for the organism (Tinbergen, 1951). From this perspective behavioral features are characteristics of body-environment interactions that are stamped into them. This is certainly the case for body movements. Using data-driven clustering of ethological recordings may reveal additional, possibly different action classes and different motor primitives and hierarchies than those provided by naïve observations.

Some examples in the literature. Visually naïve chicks are more attracted to objects that move with changing speed than to objects that move linearly. This suggests that it is not movement or speed per se (a low-level feature) but the perception of dynamic changes in speed that leads neonates to seeing animacy, viewed here as indicative of a midlevel feature [67,68], and that differs from how the semantic feature animacy is defined by Thorat et al. [12]. Some exemplary work has already been done for other species showing how nervous systems evolve in relation to their embodiment (Hochner 2012 on the octopus). See examples from studies on humans behave in different built/architectural environment and cities.

3. Body representation networks

Investigations at the feature level revealed that body representation is distributed over multiple brain areas none of which uniquely codes for one or another defining feature or for one or another an emotion category. (Note that the former is new while concerning the latter it is now well accepted that basic emotion concepts do not have an identifying brain basis).

3.1 A brainwide whole body network

Using dynamic multispecies stimuli, 7 T fMRI scanning and data- driven methods we investigated body sensitivity at the whole brain level and investigated possible species specificity by including animal body videos. We discovered two large-scale networks specifically modulated by human body videos, the LOC network and the rSTS network. Our ICA analysis discovered two networks with significant selectivity for bodies and very different response profiles for other categories. The connectivity of these networks is significantly influenced by bodies and shows human body specificity, especially the rSTS network. The LOC network mainly consisted of a large cluster in the lateral occipital cortex and the fusiform cortex, covering most of the previously defined category-selective areas (Grill-Spector and Sayres, 2008). The rSTS network showed a right hemisphere-dominant coverage including EBA, FBA, STS, PMd/PMv and IFG. Its other nodes such as the premotor cortex, medial prefrontal cortex, TPJ, and amygdala, have also been related to social cognition (Schurz et al., 2014; Van Overwalle, 2009; Young et al., 2010; Patel et al., 2019; Alcala-Lopez et al., 2018). Most notably, this network showed the highest response for human faces and human bodies, followed by monkey faces, and lastly monkey bodies (Fig. 2c). While the contrast was not significant between human bodies and faces, significantly higher responses were found for human videos than for the monkey ones. Thus, the rSTS network may involve the processing of human-specific social information. We were also interested in identifying the nodes within each network that were involved in body processing compared to the other stimulus conditions. Using condition-omitted ICA, we first found body modulations of node connectivity only in the bilateral posterior EBA in the LOC network. *Figure 3*.

To consolidate the evidence of human body specificity of the nodes detected above, we further searched for the voxels with distinct or shared dependence for human bodies compared to the human face and monkey body. The result showed that among the rSTS body nodes, voxels within the EBA, TPJ, PMv, SMA, SFG and IFG nodes showed significantly larger connectivity decreases for the human-body-regressed network than for the human-face- or monkey-body-regressed ones. This result suggested a subnetwork for human-specific body processing.

3.2 ***Body network based coding of emotional expressions***

Li et al. (2024) investigated how different affective whole-body movements impact that network activity. Note also that this network approach throws light on the important anatomical and functional complexity of EBA itself (Weiner and Grill-Spector, 2011) as Li et al. (2024) showed four different EBA nodes. Depending on the specific action considered (aggressive, defensive etc.) different EBA nodes were involved in separate networks as a function of the specific action mapped. *Figure 4.*

Four different body selective network nodes. We identified four body-selective nodes within the TOC body network (Li et al., 2023). The largest node was the bilateral LOCi located in the inferior division of LOC and the lateral occipital sulcus (LOS). Another node, the bilateral LOCs, was defined in the superior division of LOC. Anterior to the LOCi and LOCs, two unilateral nodes were found in the posterior middle temporal gyrus (MTG), one on the left hemisphere and one on the right (lpMTG and rpMTG). Overall, our findings provide evidence for a distributed network of body representation consistent with an early proposal by Weiner and Grill-Spector (2010). Furthermore, other areas were also involved in limb representation including ITG and MTG. Our results confirm their findings on the anterior-posterior separation of body areas (Weiner & Grill-Spector, 2011). Yet importantly, we extend these findings by demonstrating a distinction between the dorsal and ventral LOC in terms of body processing, challenging the conventional definition of EBA as a homogeneous cluster.

5. Biomechanics coding

Having shown that perceiving body expressions takes the whole brain (…) we now turn to the question of the specific computations in the entry stages of the networks. Here we can use model based fMRI (as opposed for example to the classic ROI definition). Marrazzo (2023; 2024) compared the predictive performance of encoding models based on 3D keypoints, similarity distances, and categorical differences (kp3d, simdist, categorical). At the group level, we observed that a combination of the three models significantly predicted fMRI BOLD responses in the ventral visual cortex after applying permutation testing and correcting for multiple comparisons. The variance partitioning in EBA across cortical layers revealed hemispheric differences between models. In the left hemisphere, the kp3d model explained a larger portion of the variance (40%) compared to the simdist and categorical models (both around 30%) consistently across cortical depths (see Fig. 4). In contrast, in the right hemisphere, while the kp3d model explained approximately one-third of the variance, the simdist and categorical models exhibited an opposite trend within inner and superficial layers. Specifically, the simdist model explained more variance in the inner layers, whereas the categorical model accounted for more variance in the superficial layers, although these differences were not statistically significant. *Figure 5*

Low-level and high-level features in the Occipitotemporal Cortex

Our findings reveal a combination of low and high-level features within the occipitotemporal cortex. In early visual cortical areas, the kp3d and simdist models alone, or in combination, best predicted neural responses (red, blue, magenta-purple color patches in Fig. 4b) indicating that postural and biomechanical features play a significant role in these regions. These results align with the understanding that early visual areas process low-level features such as orientation, spatial frequency, and basic shape attributes (Carandini et al., 2005; Kay et al., 2008; Naselaris et al., 2011; Nishimoto & Gallant, 2011; Nishimoto et al., 2011).

Our results show that as processing advances to higher visual areas, the categorical model (ie. possible vs impossible biomechanics, not body vs. object) becomes increasingly dominant. This shift suggests that higher-order areas integrate lower-level features into more abstract representations, reflecting a progression toward semantic processing (Grill-Spector & Weiner, 2014; Haxby et al., 2001; Huth et al., 2012; Kriegeskorte, Mur, & Bandettini, 2008).

Encoding of Body Stimuli in EBA

A combination of the three encoding models—kp3d, simdist, and categorical—significantly predicted neural responses in EBA, accounting for approximately 10% of the variance in the BOLD signal (see Fig. 4). This joint representation suggests that EBA integrates various levels of information, including postural and biomechanical features as well as categorical distinctions. Specifically, in the superior part of EBA — covering middle occipital gyrus (MOG) and superior occipital gyrus (SOG)— (see Fig. 3b and 4), the kp3d and simdist models exhibited dominance, explaining a greater proportion of the variance compared to the categorical model (purple-magenta patches).

In contrast, the anterior inferior —spanning areas like the anterior part of the inferior temporal gyrus (aITG) and anterior lateral occipital sulcus (aLOS)— part of EBA's tendency towards categorical encoding (cyan-orange-green patches) suggests an integration of postural information with more abstract representations. This may involve linking specific body configurations to semantic concepts such as the type of action being performed or the emotional state conveyed by the body movement (Foster et al., 2021; Foster et al., 2019) This functional heterogeneity within EBA aligns with anatomical findings that identify distinct body-selective areas within the occipitotemporal cortex (Weiner & Grill-Spector, 2011). Recent findings by Li et al. (Li, Poyo Solanas, Marrazzo, & de Gelder, 2024) further support this notion by identifying four adjacent body-selective nodes within the temporo-occipital cortex using data-driven methods. Specifically, the superior subregions' emphasis on kp3d and simdist models may explain their role in detailed sensory processing, as they show stronger connectivity with regions involved in processing fine-grained visual details (Li et al., 2024). In contrast, the anterior inferior subregions' reliance on categorical encoding supports their involvement in higher-order interpretation and integration of body-related information, consistent with the broader connectivity profiles observed there (Li et al., 2024). These findings reinforce the functional heterogeneity within the EBA, highlighting specialized subregions dedicated to different aspects of body and action perception. (Li et al., 2024). (Zimmermann, Mars, de Lange, Toni, & Verhagen, 2018) provided further insights into EBA's connectivity, showing that EBA is more functionally and structurally connected to dorsal-stream regions compared to other body-related areas, such as FBA and the lateral occipital complex (LOC). This connectivity supports the EBA's role in bridging perceptual and motor functions, particularly in specifying goal-directed postural configurations for motor planning. Notably, the study suggests that EBA's connectivity with parietal regions, such as the superior parietal lobule and postcentral gyrus, may enable it to access somatosensory information, which is essential for planning and executing actions based on body posture. Figure 6.

6. Biomechanics vs. body schema, embodiment and mirror neurons.

The studies described so far present a journey from traditional object-focused theories of body representation going onward to investigating body perception in the neural code of the observer. Next, we contrast the resulting picture with comparable proposals in the literature.

To summarize so far, across different studies we find evidence that the brain sustains a human body specific representation. We developed an integrated approach to body category sensitivity and action representation by identifying a body-sensitive network and discovering that different action categories correspond to distinct activity patterns across network nodes. During this network analysis, we expanded on previous findings that EBA encompasses multiple subclusters. Here, we found four different nodes involved in body representation within the TOC, each with clear anatomical and functional distinctions. By relating these nodes to variations in action representation, we gained deeper insights into their functional significance. Furthermore, each node exhibited a unique connectivity profile corresponding to different affective whole-body action videos. Our approach replaces a modular view of body sensitivity with a distributed network perspective, helping explain earlier findings on multiple body-selective clusters, showing that their involvement varies with the demands of action representation. Furthermore, using model driven fMRI we found that, beyond simply recognizing posture, body parts and movement, the brain may encode biomechanical constraints on posture and movement of human bodies. The ability to differentiate between possible and impossible movements likely involves detecting deviations from typical joint configurations and movement patterns. This is compatible with the hypothesis of an internal model of human biomechanics. What does this mean and how is it different from explanations have been offered previously?

Body schema, body image. This contrast has been a tool in behavioral neurology and neuropsychology since Head and Holmes (1912) 1) the " Body Schema " as " A combined standard against which all subsequent changes of posture are measured ... before the changes of posture enter consciousness" , " as a central mapping of somatotopic information derived from the tactile information and 3) the " Body Image " as an internal representation in the conscious experience of visual, tactile and motor information of corporal origin. In contemporary discussions (in neuropsychology, cognitive neuroscience and philosophy (e.g., de Vignemont, 2010, Dijkerman and de Haan, 2007, Di Vita et al., 2016, Gallagher, 1986, Paillard, 1999), the body schema is at stake in action planning and performance whereas the body image corresponds to how we (consciously) perceive our body. This distinction is in line with the general notion that perception and action mobilize different processes along the sensory pathways and involve different cortical and subcortical pathways. It echoes that between ventral and dorsal pathways. However, the distinction between body schema and body image, one for perception and one for action, is getting blurred as it does not seem to fit very the various patterns of association and dissociations observed in the clinic (eg. the Pinocchio illusion, the Alice in Wonderland illusion; distortions of the body schema in anorexia). The focus seem to have shifted away from a clear contrast between body schema and body image to the notion of ‘internal model’ Internal models of the body play a crucial role in motor control, spatial awareness, self-perception, and the ability to interact with the environment. They help the brain predict the consequences of motor actions, maintain posture and balance, and coordinate movements based on sensory feedback. How these models also contribute to body awareness, self-consciousness, and the sense of ownership and agency over one's body is an open question.

Embodiment theories. In past decades various approaches have been proposed as alternatives for higher cognitive abilities with and abstract cognitive semantics that turn the spotlight to the role of the body. Various embodiment theories have in common to assign a critical role to sensorimotor as opposed to conceptual processes and to processes of simulation as opposed to abstract understanding. Notions of embodiment have significantly motivated work in AI and robotics but also inspired artists and architects. The notion of embodiment came to the foreground in neuroscience with the discovery of the RHI followed by research on whole body illusions (O. Blanke). Embodiment as methodology has proven useful in many fields, applied and clinical research. One of the first to investigate embodied VR with fMRI de Borst et al (2020) showed how embodiment as 1 vs 3th person activates different brain processes underscoring that for the same stimulus, brain activity differs as a function of the embodiment condition. Overall, embodiment is widely used in clinical settings and its success is linked to creating multisensory presence (ultimately based on sensorimotor contingencies) but its neural basis is still poorly understood.

Mirror neuron theory (MN). One could look at mirror neuron theories as a type of embodiment theories. Like embodiment theories, MN argues that semantic information is presumably carried by and conveyed by movements of the body. As is well known, the original MN findings in monkey suggested that the same neurons fired whether an action was observed or performed. This was taken as evidence that perception could be viewed as an enactment of production and through enactment of the observed action the semantics become accessible to the observer. The discovery of mirror neurons (MNs) in rhesus macaques demonstrated that motor sequences can be viewed as actions (grasping) because they are organized by high-level goals (e.g., eating food) rather than by the physics of the effectors. For a critical assessment see Giese & Rizzolatti 2015. The core inspiration for many more speculative interpretations of MNs was that sensorimotor processes implement social perception by sustaining direct other-to-self mappings.

Empirical research on MN in nonhuman and human species has progressed and the original MN position has evolved. Bonini et al 2022 review the recent literature and highlight two pivotal changes. One is that the mirror function of neurons is implemented not at the single neuron level but in a "complex neural machinery constituted by a variety of cell types that are distributed among multiple brain areas and play an evolutionary conserved and fundamental role in social learning and behavior. " The other is that in this evolved landscape the function of MN is best described as 'other' neurons, or neurons specifically tuned to the actions of others. The old as well as the new MN assume that action semantics is direct, in the sense that understanding postures or movements does not depend on higher order conceptual representation

How does the brain perceive conspecifics, and do MNs play a core role? Bonini et al. propose that there is ‘neural selectivity for information related to others’ ([1], see p. 3). But MN does not dwell on the visual processes on input side, taking for granted that perception is tuned to selecting actions of conspecifics. Our results so far suggest that conspecific perception is not sustained primarily by MNs picking out conspecific actions but by a brain network engaged in the visual analysis of bodies including ventral and dorsal areas as well as subcortical structures. Do we want to relate all this not to motor primitives but to priors in the visual system? Does the interoceptive system lay a role in linking visual and motor systems eg.

during development? Possibly ‘grounding’ interoception/feelings in establishing visual-motor connectivity?

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FIGURES

Figure 1

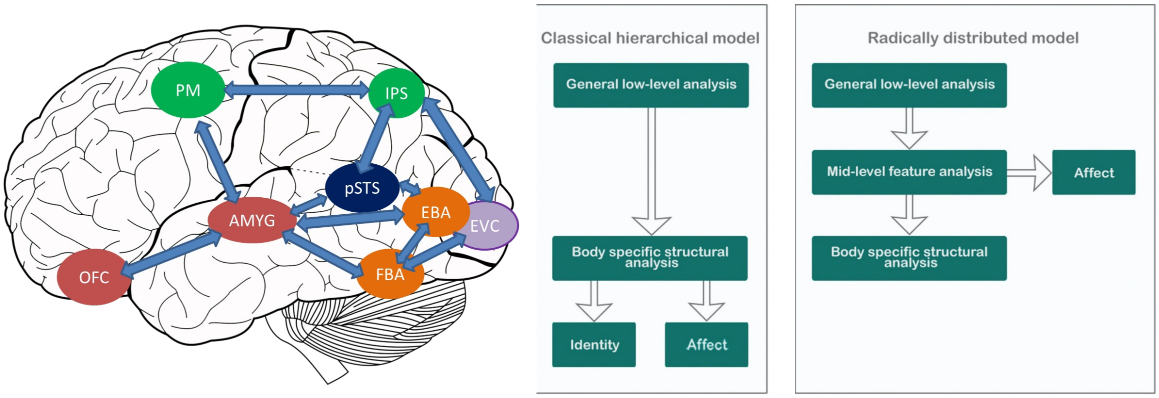
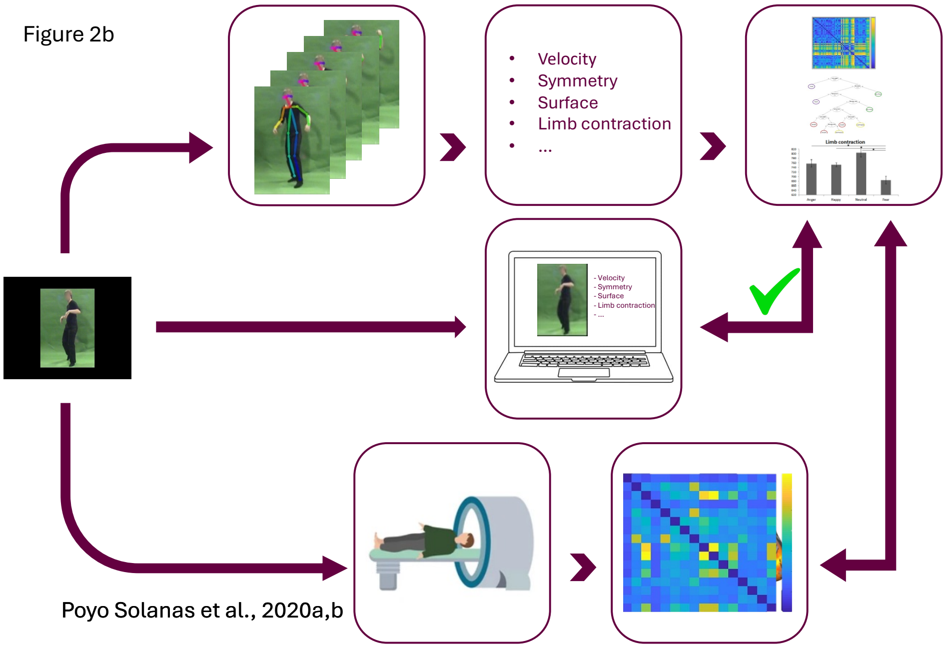


Figure 2b

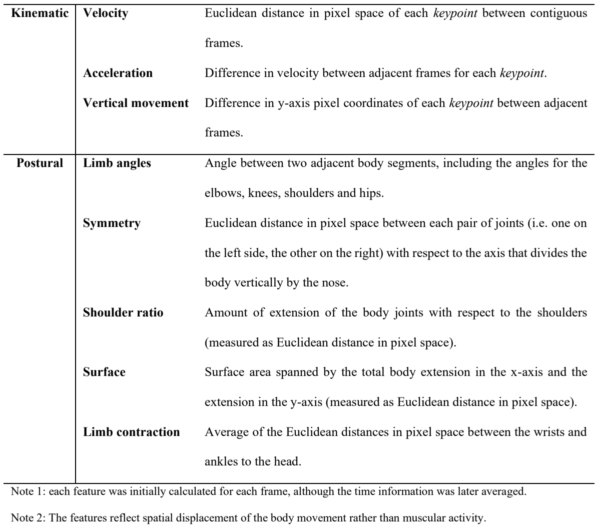


- Velocity
- Symmetry
- Surface
- Limb contraction
- ...

Poyo Solanas et al., 2020a,b

Figure 2a

Table 1. Feature definition



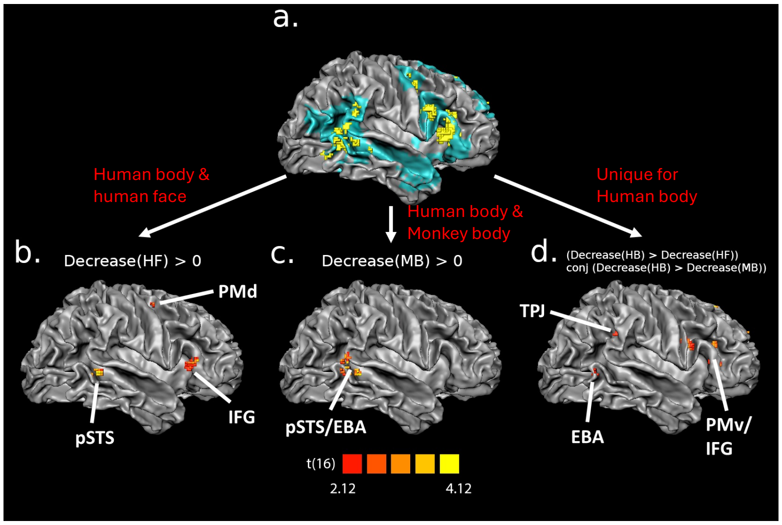
Kinematic	**Velocity**	Euclidean distance in pixel space of each *keypoint* between contiguous frames.
	Acceleration	Difference in velocity between adjacent frames for each *keypoint*.
	Vertical movement	Difference in y-axis pixel coordinates of each *keypoint* between adjacent frames.
Postural	**Limb angles**	Angle between two adjacent body segments, including the angles for the elbows, knees, shoulders and hips.
	Symmetry	Euclidean distance in pixel space between each pair of joints (i.e. one on the left side, the other on the right) with respect to the axis that divides the body vertically by the nose.
	Shoulder ratio	Amount of extension of the body joints with respect to the shoulders (measured as Euclidean distance in pixel space).
	Surface	Surface area spanned by the total body extension in the x-axis and the extension in the y-axis (measured as Euclidean distance in pixel space).
	Limb contraction	Average of the Euclidean distances in pixel space between the wrists and ankles to the head.

Note 1: each feature was initially calculated for each frame, although the time information was later averaged.

Note 2: The features reflect spatial displacement of the body movement rather than muscular activity.

Poyo Solanas et al., 2020

Figure 3. Network nodes showing shared human body specific connectivity



Detecting the condition-dependent network nodes (blue= overall network coverage)

- Regress out one condition from the time courses and reconstruct the networks
- Expecting decreased network weights on condition-dependent nodes
- Different dependence properties revealed by the weight decreases when regressing out human body, human face, and monkey
    - Human-specific body nodes were found in TPJ, EBA, PMv/IFG (Fig d)

Figure 4

Selective network activity for different body expression/action types

LOCi subsystem

- V2

LOCi subsystem

- Posterior cingulate, SFG (nodes c DMN, cognitive control & dorsal attention)

lpMTG & rpMTG subsystems

- SMG, Insula, MFG & SFG (ventral attention & salience)

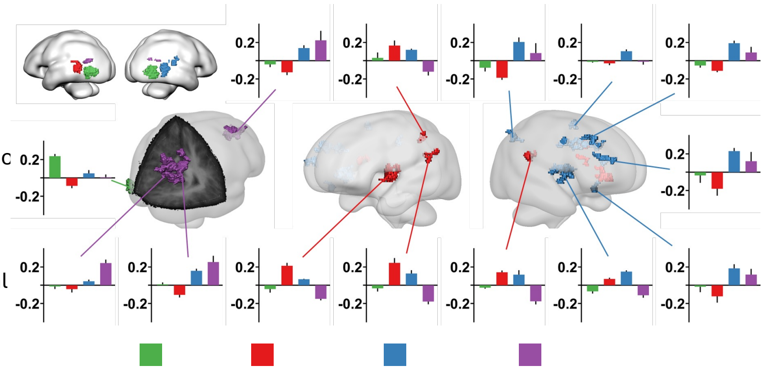
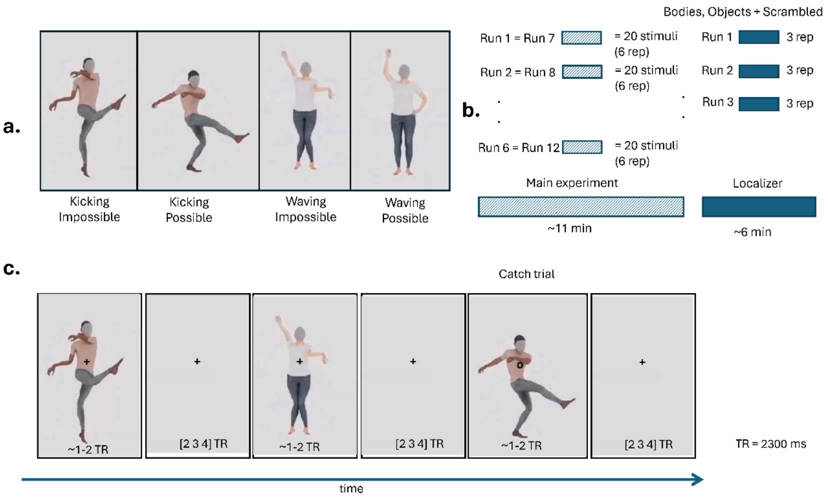
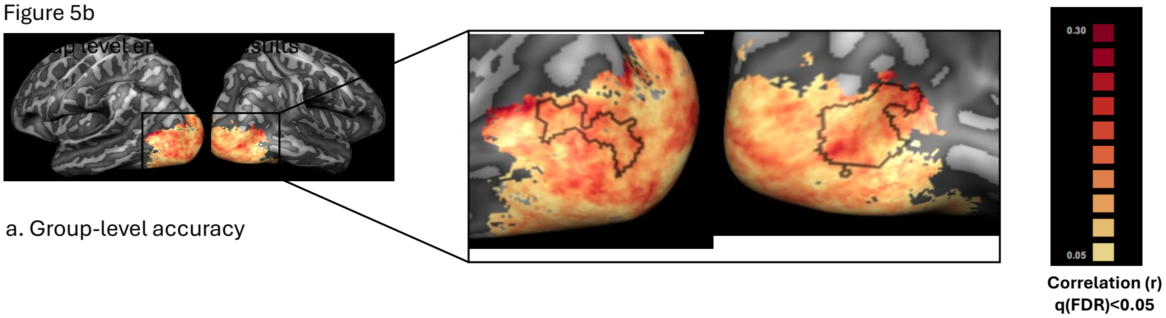


Figure 5a

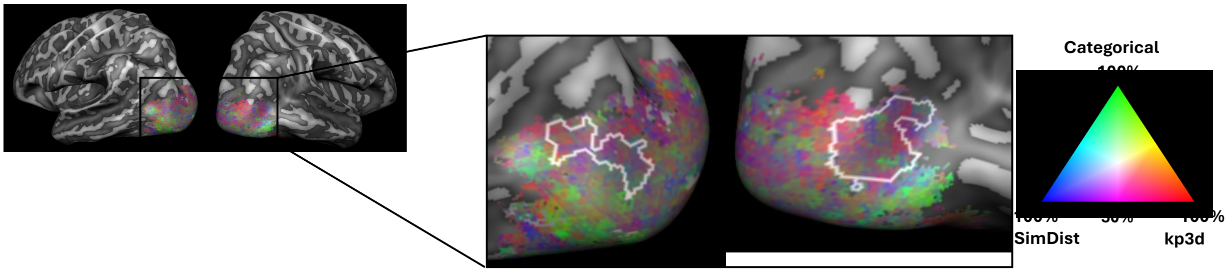


(a) The videos were generated by animating mocap data. Sixty possible videos were created from 17 actors performing 4 actions: kicking, jumping, pointing, waving. Additionally, we modified the joint angles of the elbows and knees to create 60 biomechanically impossible videos. In panel (a) snapshots of possible videos and their equivalent impossible. (b) For each run 1/6 of the stimuli (20) where presented in a pseudo-randomized order following a fast event-related design. Each stimulus was repeated three times per run. Each run was repeated two times across sessions resulting in a total of 120 stimuli repeated six times. To identify body sensitive region, the localizer stimuli included videos of humans performing natural body movement, objects, and their scrambled version. We presented stimuli following a block-design with each block repeated three times per run. (c) During the main experiment participants fixated on the cross and were presented with the stimuli depicting possible and impossible body movement for 1-2 TRs (depending on the length of each video) followed by a blank screen which appeared for 2, 3 or 4 TRs. When the fixation cross turned to a circle, they had to press a button whether with the right index finger. TR= 2300ms. (Ghorbani et al., 2021, MoVi dataset

Figure 5b



a. Group-level accuracy



b. RGB map with each vertex color coded for relative contribution to each model

REFERENCES.

Alcalá-López, D., et al. (2018). "Computing the social brain connectome across systems and states." Cerebral Cortex 28(7): 2207-2232.

Allison, T., et al. (2000). "Social perception from visual cues: role of the STS region." Trends in Cognitive Sciences 4(7): 267-278.

Bagnis, A., et al. (2019). "Toward an integrative science of social vision in intergroup bias." Neuroscience & Biobehavioral Reviews 102: 318-326.

Balconi, M. and A. Bortolotti (2013). "Conscious and unconscious face recognition is improved by high-frequency rTMS on pre-motor cortex." Consciousness and Cognition 22(3): 771-778.

Basil, R. A., et al. (2017). "A causal role of the right superior temporal sulcus in emotion recognition from biological motion." Open Mind 2(1): 26-36.

Bastos, A. M., et al. (2012). "Canonical microcircuits for predictive coding." Neuron 76(4): 695-711.

Berlucchi, G. and S. M. Aglioti (2010). "The body in the brain revisited." Experimental Brain Research 200: 25-35.

Blake, R. and M. Shiffrar (2007). "Perception of human motion." Annual Review of Psychology 58(1): 47-73.

Bonini, L., et al. (2022). "Mirror neurons 30 years later: implications and applications." Trends in Cognitive Sciences 26(9): 767-781.

Borgomaneri, S., et al. (2015). "Transcranial magnetic stimulation reveals two functionally distinct stages of motor cortex involvement during perception of emotional body language." Brain Structure and Function 220: 2765-2781.

Bracci, S., et al. (2012). "Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex." Journal of Neurophysiology 107(5): 1443-1456.

Brunet, E., et al. (2000). "A PET investigation of the attribution of intentions with a nonverbal task." Neuroimage 11(2): 157-166.

Bubb, E. J., et al. (2017). "Hippocampal–diencephalic–cingulate networks for memory and emotion: An anatomical guide." Brain and neuroscience advances 1: 2398212817723443.

Calbi, M., et al. (2017). "“Embodied Body Language”: an electrical neuroimaging study with emotional faces and bodies." Scientific Reports 7(1): 6875.

Candidi, M., et al. (2011). "Event-related repetitive transcranial magnetic stimulation of posterior superior temporal sulcus improves the detection of threatening postural changes in human bodies." Journal of Neuroscience 31(48): 17547-17554.

Candidi, M., et al. (2008). "Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions." Social Neuroscience 3(3-4): 388-400.

Cao, Z., et al. (2017). Realtime multi-person 2d pose estimation using part affinity fields. Proceedings of the IEEE conference on computer vision and pattern recognition.

Carandini, M., et al. (2005). "Do we know what the early visual system does?" Journal of Neuroscience 25(46): 10577-10597.

Caspari, N., et al. (2014). "Fine-grained stimulus representations in body selective areas of human occipito-temporal cortex." Neuroimage 102: 484-497.

Cichy, R. M. and D. Kaiser (2019). "Deep neural networks as scientific models." Trends in Cognitive Sciences 23(4): 305-317.

Costantini, M., et al. (2005). "Neural systems underlying observation of humanly impossible movements: an fMRI study." Cerebral Cortex 15(11): 1761-1767.

Costantini, M., et al. (2005). "Neural systems underlying observation of humanly impossible movements: an fMRI study." Cerebral Cortex 15(11): 1761-1767.

Dary, Z., et al. (2023). "Neural bases of the bodily self as revealed by electrical brain stimulation: A systematic review." Human Brain Mapping 44(7): 2936-2959.

de Borst, A. W., et al. (2020). "First-person virtual embodiment modulates the cortical network that encodes the bodily self and its surrounding space during the experience of domestic violence." Eneuro 7(3).

de Gelder, B. (2006). "Towards the neurobiology of emotional body language." Nature Reviews Neuroscience 7(3): 242-249.

de Gelder, B. and M. Poyo Solanas (2021). "A computational neuroethology perspective on body and expression perception." Trends in Cognitive Sciences 25(9): 744-756.

de Gelder, B., et al. (2010). "Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions." Neuroscience & Biobehavioral Reviews 34(4): 513-527.

De Vignemont, F. (2010). "Body schema and body image—Pros and cons." Neuropsychologia 48(3): 669-680.

Di Vita, A., et al. (2016). "To move or not to move, that is the question! Body schema and non-action oriented body representations: An fMRI meta-analytic study." Neuroscience & Biobehavioral Reviews 68: 37-46.

Dijkerman, H. C. and E. H. De Haan (2007). "Somatosensory processing subserving perception and action: Dissociations, interactions, and integration." Behavioral and Brain Sciences 30(2): 224-230.

Downing, P. E., et al. (2001). "A cortical area selective for visual processing of the human body." Science 293(5539): 2470-2473.

Downing, P. E. and M. V. Peelen (2011). "The role of occipitotemporal body-selective regions in person perception." Cognitive Neuroscience 2(3-4): 186-203.

Downing, P. E. and M. V. Peelen (2016). "Body selectivity in occipitotemporal cortex: Causal evidence." Neuropsychologia 83: 138-148.

Engelen, T., et al. (2018). "Dynamic interactions between emotion perception and action preparation for reacting to social threat: a combined cTBS-fMRI study." Eneuro 5(3).

Felleman, D. J. and D. C. Van Essen (1991). "Distributed hierarchical processing in the primate cerebral cortex." Cerebral cortex (New York, NY: 1991) 1(1): 1-47.

Foster, C., et al. (2021). "Separated and overlapping neural coding of face and body identity." Human Brain Mapping 42(13): 4242-4260.

Foster, C., et al. (2019). "Decoding subcategories of human bodies from both body-and face-responsive cortical regions." Neuroimage 202: 116085.

Freedberg, D. and V. Gallese (2007). "Motion, emotion and empathy in esthetic experience." Trends in Cognitive Sciences 11(5): 197-203.

Freedberg, D. and V. Gallese (2007). "Motion, emotion and empathy in esthetic experience." Trends in Cognitive Sciences 11(5): 197-203.

Frijda, N. H. (1986). The emotions, Cambridge University Press.

Gallagher, S. (1986). "Body image and body schema: A conceptual clarification." The Journal of Mind and Behavior: 541-554.

Giese, M. A. and T. Poggio (2003). "Neural mechanisms for the recognition of biological movements." Nat. Rev. Neurosci 4(3): 179-192.

Giese, M. A. and G. Rizzolatti (2015). "Neural and computational mechanisms of action processing: interaction between visual and motor representations." Neuron 88(1): 167-180.

Glasser, M. F., et al. (2016). "A multi-modal parcellation of human cerebral cortex." Nature 536(7615): 171-178.

Goldberg, H., et al. (2014). "The emotion–action link? Naturalistic emotional stimuli preferentially activate the human dorsal visual stream." Neuroimage 84: 254-264.

Grezes, J., et al. (2007). "Perceiving fear in dynamic body expressions." Neuroimage 35(2): 959-967.

Grezes, J., et al. (2014). "A direct amygdala-motor pathway for emotional displays to influence action: A diffusion tensor imaging study." Human Brain Mapping 35(12): 5974-5983.

Grill-Spector, K. and R. Malach (2004). "The human visual cortex." Annual Review of Neuroscience 27(1): 649-677.

Grill-Spector, K. and R. Sayres (2008). "Object recognition: Insights from advances in fMRI methods." Current Directions in Psychological Science 17(2): 73-79.

Grill-Spector, K. and K. S. Weiner (2014). "The functional architecture of the ventral temporal cortex and its role in categorization." Nature Reviews Neuroscience 15(8): 536-548.

Grossman, E., et al. (2000). "Brain areas involved in perception of biological motion." Journal of cognitive neuroscience 12(5): 711-720.

Grossman, E. D., et al. (2005). "Repetitive TMS over posterior STS disrupts perception of biological motion." Vision Research 45(22): 2847-2853.

Grossman, E. D., et al. (2010). "fMR-adaptation reveals invariant coding of biological motion on human STS." Frontiers in Human Neuroscience 4: 954.

Hadjikhani, N. and B. de Gelder (2003). "Seeing fearful body expressions activates the fusiform cortex and amygdala." Current Biology 13(24): 2201-2205.

Han, Q., et al. (2024). "Prior knowledge biases the visual memory of body postures." iScience 27(4).

Haxby, J. V., et al. (2001). "Distributed and overlapping representations of faces and objects in ventral temporal cortex." Science 293(5539): 2425-2430.

Head, H. and G. Holmes (1912). "Researches INTO SENSORY DISTURBANCES FROM CEREBRAL LESIONS." The Lancet 179(4612): 144-152.

Hochner, B. (2012). "An embodied view of octopus neurobiology." Current Biology 22(20): R887-R892.

Hoshi, E. and J. Tanji (2007). "Distinctions between dorsal and ventral premotor areas: anatomical connectivity and functional properties." Current Opinion in Neurobiology 17(2): 234-242.

Huth, A. G., et al. (2012). "A continuous semantic space describes the representation of thousands of object and action categories across the human brain." Neuron 76(6): 1210-1224.

Isoda, M. (2005). "Context-dependent stimulation effects on saccade initiation in the presupplementary motor area of the monkey." Journal of Neurophysiology 93(5): 3016-3022.

James, W. (1890). The principles of psychology, Henry Holt and Company.

Jastorff, J. and G. A. Orban (2009). "Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing." Journal of Neuroscience 29(22): 7315-7329.

Johnson & Fusi (2024)

Kay, K. N., et al. (2008). "Identifying natural images from human brain activity." Nature 452(7185): 352-355.

Kilner, J. M., et al. (2007). "Predictive coding: an account of the mirror neuron system." Cognitive Processing 8: 159-166.

Kolster, H., et al. (2010). "The retinotopic organization of the human middle temporal area MT/V5 and its cortical neighbors." Journal of Neuroscience 30(29): 9801-9820.

Krajbich, I., et al. (2021). "A causal role for the right frontal eye fields in value comparison." Elife 10: e67477.

Kret, M. E., et al. (2011). "Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study." Neuroimage 54(2): 1755-1762.

Kret, M. E., et al. (2013). "Emotional signals from faces, bodies and scenes influence observers' face expressions, fixations and pupil-size." Frontiers in Human Neuroscience 7: 810.

Kriegeskorte, N., et al. (2008). "Representational similarity analysis-connecting the branches of systems neuroscience." Frontiers in Systems Neuroscience 2: 249.

Kumar, S., et al. (2019). "Transformation of visual representations across ventral stream body-selective patches." Cerebral Cortex 29(1): 215-229.

Kumar et al., 2023

Larkum, M. (2013). "A cellular mechanism for cortical associations: an organizing principle for the cerebral cortex." Trends in Neurosciences 36(3): 141-151.

Larsson, J. and D. J. Heeger (2006). "Two retinotopic visual areas in human lateral occipital cortex." Journal of Neuroscience 26(51): 13128-13142.

Leech, R. and D. J. Sharp (2014). "The role of the posterior cingulate cortex in cognition and disease." Brain 137(1): 12-32.

Li, B., et al. (2024). "Connectivity and functional diversity of different temporo-occipital nodes for action perception." bioRxiv: 2024.2001.2012.574860.

Li, B., et al. (2023). "A large-scale brain network of species-specific dynamic human body perception." Progress in Neurobiology 221: 102398.

Liang et al. 2019
Livingstone 2024

Longhi, E., et al. (2015). "Discrimination of biomechanically possible and impossible hand movements at birth." Child development 86(2): 632-641.

Longo, M. R., et al. (2008). "Automatic imitation of biomechanically possible and impossible actions: effects of priming movements versus goals." Journal of Experimental Psychology: Human Perception and Performance 34(2): 489.

Luppino, G., et al. (1991). "Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: an intracortical microstimulation study in the macaque monkey." Journal of Comparative Neurology 311(4): 463-482.

Lyu, D., et al. (2023). "Causal evidence for the processing of bodily self in the anterior precuneus." Neuron 111(16): 2502-2512. e2504.

Marrazzo, G., et al. (2023). "Voxelwise encoding models of body stimuli reveal a representational gradient from low-level visual features to postural features in occipitotemporal cortex." Neuroimage 277: 120240.

Marrazzo, G., et al. (2021). "Decoding the difference between explicit and implicit body expression representation in high level visual, prefrontal and inferior parietal cortex." Neuroimage 243: 118545.

Mathis, A., et al. (2018). "DeepLabCut: markerless pose estimation of user-defined body parts with deep learning." Nature Neuroscience 21(9): 1281-1289.

Milner, A. D. and M. A. Goodale (2008). "Two visual systems re-viewed." Neuropsychologia 46(3): 774-785.

Milner, D. and M. Goodale (2006). The visual brain in action, OUP Oxford.

Moreau, Q., et al. (2023). "Early categorization of social affordances during the visual encoding of bodily stimuli." Neuroimage 274: 120151.

Morita, T., et al. (2012). "Infant and adult perceptions of possible and impossible body movements: An eye-tracking study." Journal of Experimental Child Psychology 113(3): 401-414.

Nachev, P., et al. (2008). "Functional role of the supplementary and pre-supplementary motor areas." Nature Reviews Neuroscience 9(11): 856-869.

Naselaris, T., et al. (2011). "Encoding and decoding in fMRI." Neuroimage 56(2): 400-410.

Nishimoto, S. and J. L. Gallant (2011). "A three-dimensional spatiotemporal receptive field model explains responses of area MT neurons to naturalistic movies." Journal of Neuroscience 31(41): 14551-14564.

Nishimoto, S., et al. (2011). "Reconstructing visual experiences from brain activity evoked by natural movies." Current Biology 21(19): 1641-1646.

Oliveri, M., et al. (2003). "Influence of the supplementary motor area on primary motor cortex excitability during movements triggered by neutral or emotionally unpleasant visual cues." Experimental Brain Research 149: 214-221.

Orban, G., et al. (2021). "From observed action identity to social affordances." Trends in Cognitive Sciences 25(6): 493-505.

Paillard, J. (1999). "Body Schema and body image-a double dissociation." Motor control, today and tomorrow 197: 214.

Panksepp, J. (1989). "The neurobiology of emotions: Of animal brains and human feelings."

Patel, G. H., et al. (2019). "The evolution of the temporoparietal junction and posterior superior temporal sulcus." Cortex 118: 38-50.

Peelen, M. V. and P. E. Downing (2005). "Selectivity for the human body in the fusiform gyrus." Journal of Neurophysiology 93(1): 603-608.

Peelen, M. V. and P. E. Downing (2007). "The neural basis of visual body perception." Nature Reviews Neuroscience 8(8): 636-648.

Picard, N. and P. L. Strick (2001). "Imaging the premotor areas." Current Opinion in Neurobiology 11(6): 663-672.

Pichon, S., et al. (2008). "Emotional modulation of visual and motor areas by dynamic body expressions of anger." Social Neuroscience 3(3-4): 199-212.

Pichon, S., et al. (2009). "Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions." Neuroimage 47(4): 1873-1883.

Pinsk, M. A., et al. (2009). "Neural representations of faces and body parts in macaque and human cortex: a comparative FMRI study." Journal of Neurophysiology 101(5): 2581-2600.

Pitcher, D. and L. G. Ungerleider (2021). "Evidence for a third visual pathway specialized for social perception." Trends in Cognitive Sciences 25(2): 100-110.

Pitcher, D. and L. G. Ungerleider (2021). "Evidence for a third visual pathway specialized for social perception." Trends in Cognitive Sciences 25(2): 100-110.

Poyo Solanas, M., et al. (2020). "Computation-based feature representation of body expressions in the human brain." Cerebral Cortex 30(12): 6376-6390.

Poyo Solanas, M., et al. (2020). "The role of computational and subjective features in emotional body expressions." Scientific Reports 10(1): 6202.

Ratan Murty, N. A., et al. (2021). "Computational models of category-selective brain regions enable high-throughput tests of selectivity." Nature Communications 12(1): 5540.

Reed, C. L., et al. (2003). "The body-inversion effect." Psychological Science 14(4): 302-308.

Rizzolatti, G., et al. (1996). "Premotor cortex and the recognition of motor actions." Cognitive brain research 3(2): 131-141.

Robert, S., et al. (2023). "Disentangling object category representations driven by dynamic and static visual input." Journal of Neuroscience 43(4): 621-634.

Rockland, K. S. and D. N. Pandya (1979). "Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey." Brain Research 179(1): 3-20.

Rodigari, A. and M. Oliveri (2014). "Disrupting SMA activity modulates explicit and implicit emotional responses: an rTMS study." Neuroscience Letters 579: 30-34.

Sayres, R. and K. Grill-Spector (2008). "Relating retinotopic and object-selective responses in human lateral occipital cortex." Journal of Neurophysiology 100(1): 249-267.

Schiano Lomoriello, A., et al. (2024). "Sensitivity to basic emotional expressions and the emotion perception space in the absence of facial mimicry: The case of individuals with congenital facial palsy." Emotion 24(3): 602.

Schubotz, R. I. (2007). "Prediction of external events with our motor system: towards a new framework." Trends in Cognitive Sciences 11(5): 211-218.

Schurz, M., et al. (2014). "Fractionating theory of mind: a meta-analysis of functional brain imaging studies." Neuroscience & Biobehavioral Reviews 42: 9-34.

Schwarzlose, R. F., et al. (2005). "Separate face and body selectivity on the fusiform gyrus." Journal of Neuroscience 25(47): 11055-11059.

Shmuelof, L. and E. Zohary (2005). "Dissociation between ventral and dorsal fMRI activation during object and action recognition." Neuron 47(3): 457-470.

Spratling, M. W. (2017). "A hierarchical predictive coding model of object recognition in natural images." Cognitive Computation 9(2): 151-167.

Stekelenburg, J. J. and B. de Gelder (2004). "The neural correlates of perceiving human bodies: an ERP study on the body-inversion effect." Neuroreport 15(5): 777-780.

Tamietto, M. and B. de Gelder (2008). "Affective blindsight in the intact brain: Neural interhemispheric summation for unseen fearful expressions." Neuropsychologia 46(3): 820-828.

Taubert, J., et al. (2022). "A broadly tuned network for affective body language in the macaque brain." Science Advances 8(47): eadd6865.

Taubert, J., et al. (2022). "One object, two networks? Assessing the relationship between the face and body-selective regions in the primate visual system." Brain Struct Funct 227(4): 1423-1438.

Taylor, J. C., et al. (2007). "Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas." Journal of Neurophysiology 98(3): 1626-1633.

Tinbergen, N. (1952). "" Derived" activities; their causation, biological significance, origin, and emancipation during evolution." The Quarterly review of biology 27(1): 1-32.

Urgesi, C., et al. (2007). "Transcranial magnetic stimulation reveals two cortical pathways for visual body processing." Journal of Neuroscience 27(30): 8023-8030.

Urgesi, C., et al. (2007). "Representation of body identity and body actions in extrastriate body area and ventral premotor cortex." Nature Neuroscience 10(1): 30-31.

Utter, A. A. and M. A. Basso (2008). "The basal ganglia: an overview of circuits and function." Neuroscience & Biobehavioral Reviews 32(3): 333-342.

Vaina, L. M., et al. (1990). "Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study." Visual Neuroscience 5(4): 353-369.

Van den Stock, J., et al. (2011). "Cortico-subcortical visual, somatosensory, and motor activations for perceiving dynamic whole-body emotional expressions with and without striate cortex (V1)." Proceedings of the National Academy of Sciences 108(39): 16188-16193.

Van Overwalle, F. (2009). "Social cognition and the brain: a meta-analysis." Human Brain Mapping 30(3): 829-858.

Veniero, D., et al. (2021). "Top-down control of visual cortex by the frontal eye fields through oscillatory realignment." Nature Communications 12(1): 1757.

Vossel, S., et al. (2014). "Dorsal and ventral attention systems: distinct neural circuits but collaborative roles." The Neuroscientist 20(2): 150-159.

Wallbott, H. G. (1998). "Bodily expression of emotion." European Journal of Social Psychology 28(6): 879-896.

Wegrzyn, M., et al. (2015). "Investigating the brain basis of facial expression perception using multi-voxel pattern analysis." Cortex 69: 131-140.

Weiner, K. S. and K. Grill-Spector (2010). "Sparsely-distributed organization of face and limb activations in human ventral temporal cortex." Neuroimage 52(4): 1559-1573.

Weiner, K. S. and K. Grill-Spector (2011). "Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex." Neuroimage 56(4): 2183-2199.

Young, L., et al. (2010). "What gets the attention of the temporo-parietal junction? An fMRI investigation of attention and theory of mind." Neuropsychologia 48(9): 2658-2664.

Zhang, H., et al. (2016). "Face-selective regions differ in their ability to classify facial expressions." Neuroimage 130: 77-90.

Zimmermann, M., et al. (2018). "Is the extrastriate body area part of the dorsal visuomotor stream?" Brain Structure and Function 223(1): 31-46.

Zimmermann, M., et al. (2018). "Is the extrastriate body area part of the dorsal visuomotor stream?" Brain Structure and Function 223(1): 31-46.