Opinion

A computational neuroethology perspective on body and expression perception

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Survival prompts organisms to prepare adaptive behavior in response to environmental and social threat. However, what are the specific features of the appearance of a conspecific that trigger such adaptive behaviors? For social species, the prime candidates for triggering defense systems are the visual features of the face and the body. We propose a novel approach for studying the ability of the brain to gather survival-relevant information from seeing conspecific body features. Specifically, we propose that behaviorally relevant information from bodies and body expressions is coded at the levels of midlevel features in the brain. These levels are relatively independent from higher-order cognitive and conscious perception of bodies and emotions. Instead, our approach is embedded in an ethological framework and mobilizes computational models for feature discovery.

From body areas to behavioral features

Human and nonhuman primates are experts at gathering crucial survival information from body posture and movement perception. Social threat situations and reactions to them are among the most studied [1,2]. However, what is it specifically about the body posture or movement of a conspecific that triggers adaptive behavior? In our intuitive thinking about that question, we typically retrieve one or another salient characteristic such as head orientation, the position of the arms, or the overall movement velocity [3]. So far, very few studies have objectively measured which visual features are crucial for understanding expressive body postures and movements, and even fewer have looked at their possible brain correlates. To understand why this novel approach is needed, we must frame it in the context of current research on the brain basis of body perception. Most studies on body perception have followed in the tracks of face research by adopting a theoretical framework of object **category** (see Glossary)-selective areas [4] as the top level of a hierarchical model [5,6]. In this framework, emotion expression processes are dependent on successful high-order visual category perception.

We sketch here a different approach centered not on the notion of high-level body **representation** as the gateway to subsequent expression decoding, but on **midlevel body feature** computations (Figure 1). Midlevel features are different from classical low-level visual features (e.g., edges, spatial frequency, motion direction) [7] as well as from subjective semantic features that we intuitively notice and believe to be the features we act upon (i.e., high-level semantic categories of emotions, actions, and intentions) [8]. Some examples of midlevel feature candidates derived from computational analysis of body posture and movements are limb contraction [3,9], head orientation, and hand to head distance [10]. Recent studies identified brain correlates of semantic features such as agentic action [11], animacy [12], and sociality [13]. These high-level concepts are used and validated in subjective perception, but they may turn out to reduce to, or emerge from, midlevel feature computations. The goal of midlevel feature models is to provide a functional and adaptive characterization of whole-body expressions in naturalistic contexts. Notions such as ethological action maps [14] and functional

Highlights

Body and expression perception may be sustained by midlevel feature computations rather than by body category-selective processes.

Body expression coding in the brain may be organized by feature statistics of body posture and movements rather than by natural language semantic categories.

Midlevel features at stake in biological computations of body posture and movements exploit ethological characteristics of organism–environment interactions.

Midlevel feature processing may on its own sustain rapid expression perception and action preparation, and may not require or depend on computations of the high-order category.

Feelings can be associated with midlevel processing and may be precursors to conscious emotional states because they are an intermediate layer between unconscious processes and fully formed conscious emotional states.

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domains [15] have already proved to be useful in characterizing an intermediate level of organization in the motor domain, and an intermediate processing level has been proposed between low- and high-level action representations [16]. Systematic discovery of midlevel features of naturalistic behavior needs ethological observation of behavior combined with computational methods to counter, on the one hand, the naïve observer bias and, on the other, the dimensionality explosion of unconstrained neural networks.

Body and body expression processing in the brain

Studies on body perception have consistently described areas in the human brain [17,18] and body patches in the monkey brain [19] that are selective for body images. In humans, originally one and later two areas were reported: the extrastriate body area (EBA) in the middle occipital gyrus/middle temporal gyrus [17,20], and the fusiform body area (FBA) in the fusiform cortex [18,20,21]. The respective roles of the EBA and FBA are still not well understood. It has been suggested that the EBA may be more selective for body parts whereas the FBA may be biased towards whole-body images [22]. More recent evidence indicates that the EBA may also encode details pertaining to the shape, posture, and position of the body [23]. The current lack of clarity concerning the functions of the two body areas may in part be related to their anatomical complexity. For example, there is substantial overlap between the EBA and the human motion complex (hMT+), which makes it difficult to determine the actual involvement of the former in body motion processing [24,25]. In addition, the EBA is not a single area, as illustrated by evidence from anatomical landmarks, visual field maps, and functional stimulus comparisons [26].

Although current evidence clearly supports the involvement of the FBA and EBA in body expression perception [21,27,28], it is not clear whether the EBA or the FBA is more important for expression recognition, or whether they may have different roles depending on the specific emotion. For example, it has been shown that fear modulates the activity of the EBA but not of the FBA, although no difference has been found for other emotions [29]. Emotion-specific differences may also be related to their different **connectivity** patterns (Figure 2C). Interestingly, and along these lines, the fact that the EBA seems to be more sensitive to fearful body expressions than the FBA makes more sense from a survival point of view because the EBA has been suggested to be the interface between perceptual and motor processes [30].

In addition to body-selective areas, the first **functional magnetic resonance imaging (fMRI)** studies on body expressions showed that other areas are also involved in their processing (Figure 2) [27,31,32]. For example, the action observation network shows increased activity for threatening body expressions than for neutral expressions [27,32,33]. The motor system, that is responsible for action preparation, also plays an important role, especially in the case of fear [31,34–37], as do subcortical areas [9,38] and cerebellum [39]. A subcortical pathway between the pulvinar, superior colliculus, and amygdala interacts with other areas to support defensive reflexes (e.g., withdrawal, freezing, startle) [40,41], and specifically does so for threatening body expressions [28]. In particular, there is substantial evidence supporting a pivotal role of the amygdala in the assignment of affective value to incoming stimuli, and in the preparation for adaptive behaviors, by modulating attentional, perceptual, and motor processes [42].

Beyond category-based models of expression perception

For over a decade, studies on body perception have implicitly assumed that body category areas constitute the gateway for processing various body attributes, in the same way as face category areas are involved in face perception [4,43–46]. With the gradual shift from category-based to network models, the notion of encapsulated category computations is loosened. Certainly, the available evidence shows that body expression perception is associated with activity in ventral

Glossary

Autism spectrum disorder (ASD): a neurological and developmental disorder that impairs normal social interaction and verbal and nonverbal communication, and is also characterized by repetitive behaviors.
Blindsight: the ability of patients with lesions in the visual cortex to identify visual stimuli in the absence of conscious visual experience.
Category: a class of entities identified by everyday concepts and language that share some visual and functional characteristics, and that are often defined at several hierarchical levels of perception (e.g., animals, mammals, dogs).
Connectivity: the relation between two or more brain regions in terms of their pattern of anatomical connections ('anatomical connectivity'), causal relations ('effective connectivity'), or statistical dependencies ('functional connectivity').
Electroencephalography (EEG): a non-invasive technique with excellent temporal resolution that measures electrical activity of the brain at the scalp.
Event-related potential: changes in electrical brain activity triggered by a specific sensory, cognitive, or motor event that are measured using EEG.
Functional magnetic resonance imaging (fMRI): a non-invasive technique with excellent spatial resolution that localizes brain activity by detecting changes in blood oxygenation and flow.
Hemispatial neglect: a neuropsychological condition characterized by a deficit in attention to, and awareness of, one side of the field of vision after damage to one hemisphere of the brain.
Magnetoencephalography (MEG): a non-invasive technique with excellent temporal resolution that can localize brain activity.
Midlevel body feature: properties of posture and movement of body expressions at processing stages between low-level and semantic features.
N170: an event-related potential component characteristic of the initial neural processing of stimulus categories such as faces, bodies, familiar objects, or words that occurs in the time-window ~170 ms after stimulus presentation.

body areas, but is associated equally well with activity in areas outside the body-selective areas [32,40]. However, whether the computations attributed to category-selective areas are needed at all for expression and action perception is an open question.

Functional category models assume that category areas represent the category [47,48] in a way that is relatively stable, and is also independent from the actual task (e.g., detection, object and/or attribute identification, passive viewing, explicit recognition) and from specific stimulus attributes (e.g., emotion, gender) [29,49]. However, there is growing evidence showing that all these factors significantly impact on the activity in object category areas, including body-selective areas (Box 1). For example, selective attention-related increases have been found in category representation areas for the preferred category during visual search tasks [50,51].

The gateway role of category areas for extended attribute processing has also been challenged by **transcranial magnetic stimulation (TMS)** and **magnetoencephalography (MEG)** studies showing category-nonspecific modulations in these areas before categorical encoding [28,52]. Furthermore, MEG measurements have shown differences between fearful and neutral bodies as early as 80 ms in a complex of areas in the right parietal cortex [36] before the time-window that is typically associated with category processing in body-selective areas. In addition, there are interesting findings about activity modulations in body category areas not as a function of the presence of a body but of faces and scenes. The presence of a body also influences how faces are processed [53], a scene without a body present in it triggers FBA activity [54], and a body without a face activates face neurons [55]. These findings suggest that body representation is dynamic and relative rather than absolute [56], in the sense that it depends on the context, particular stimulus attributes, the task, and attention (Box 1).

Admittedly, the notion of a functional hierarchy where a category area is regarded as the gateway for attribute perception is more explicit in face models [57] than in body models [58,59] or in models of expression perception [40], but it is still sufficiently present in the background to trigger an appeal for an alternative non-hierarchical model [60]. In the framework we propose, the mechanisms of information exchange between, the action or emotion networks and body-selective areas may be based on coding a specific body part or a particular feature rather than on category coding. There is no functional hierarchy between category-selective and attribute coding,
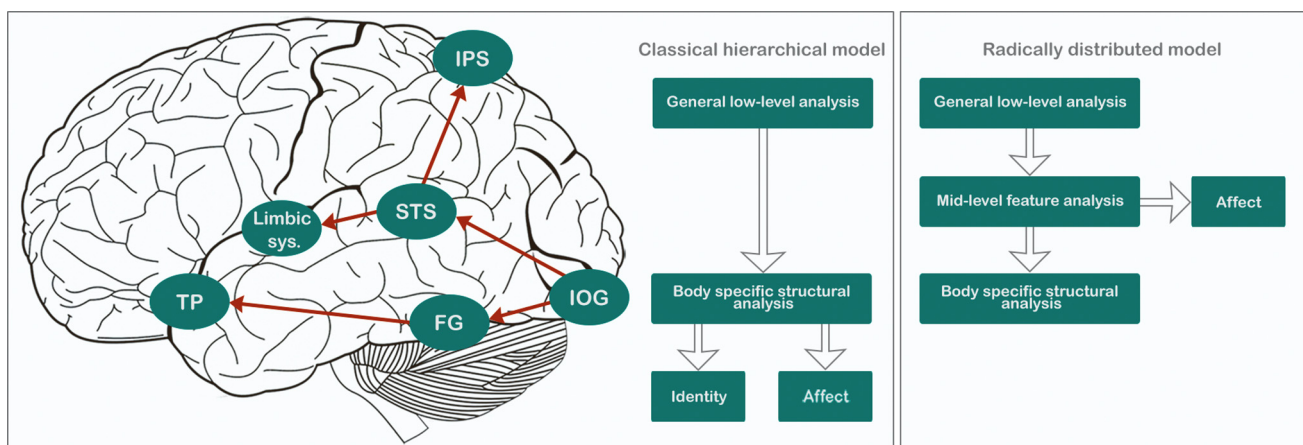
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Figure 1. Body expression perception. The classical hierarchical model (left) and the radically distributed model (right) proposed here for body expression perception. Abbreviations: FG, fusiform gyrus; IOG, inferior occipital gyrus; IPS, intraparietal sulcus; STS, superior temporal sulcus; TP, temporal pole.
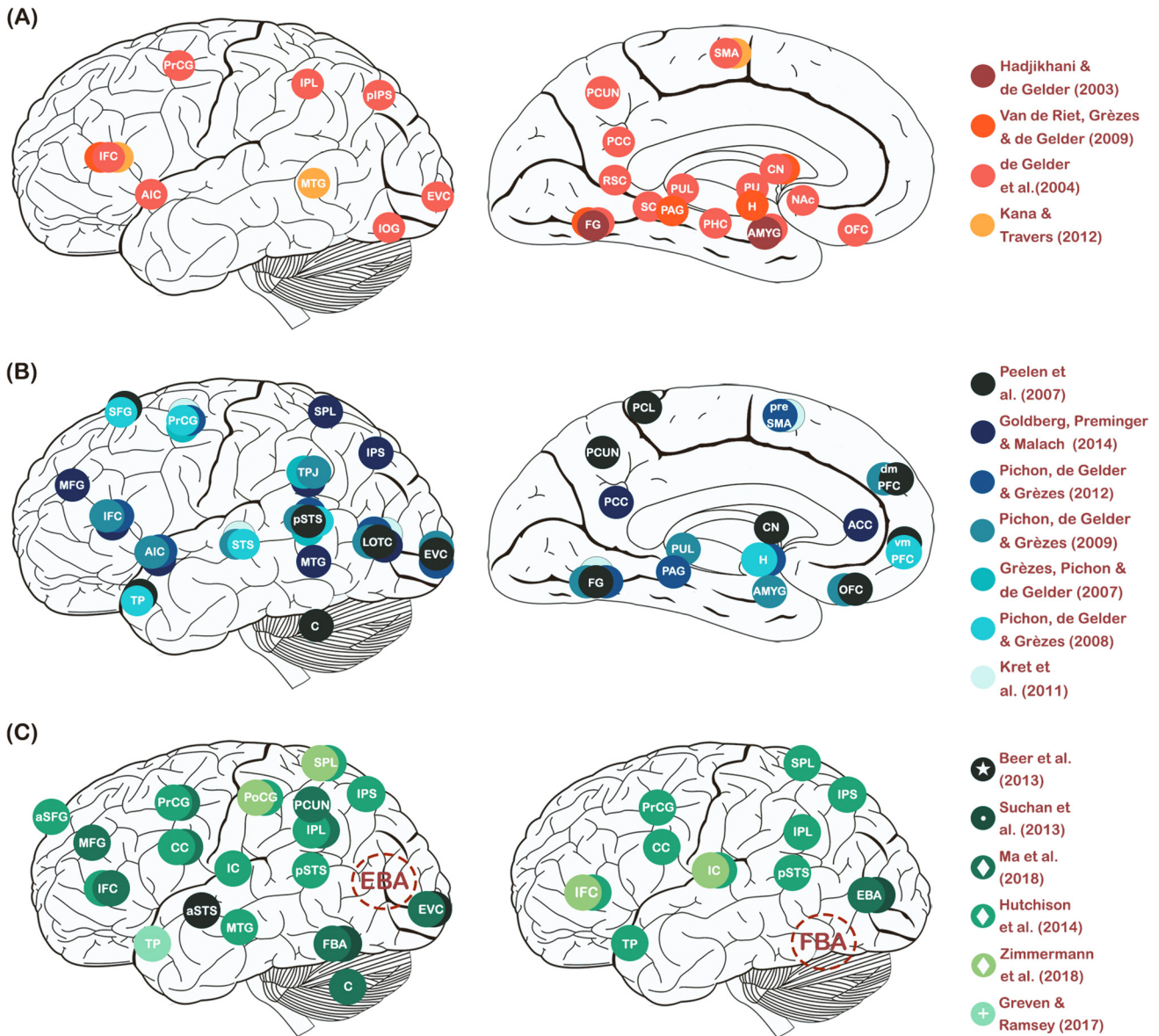
Figure 2. Body concept representation. Activation reported for (A) still and (B) dynamic body expressions in fMRI studies that contrasted naturalistic emotional body expressions with emotionally neutral expressions. (C) Areas presenting connectivity to the EBA (left) and FBA (right), respectively, in terms of anatomical connectivity (★), functional connectivity (♦), effective connectivity (●), or psychophysiological interactions (+). Data from [20,21,27–33,134–141]. Abbreviations: ACC, anterior cingulate cortex; aSFG, superior frontal gyrus, anterior part; AIC, anterior insular cortex; AMYG, amygdala; aSTS, superior temporal sulcus, anterior part; C, cerebellum; CC, cingulate cortex; CN, caudate nucleus; dmPFC, dorsomedial prefrontal cortex; EBA, extrastriate body area; EVC, early visual cortex; FBA, fusiform body area; FG, fusiform gyrus; H, hippocampus; IC, insular cortex; IFC, inferior frontal cortex; IOG, inferior occipital gyrus; IPL, inferior parietal lobule; IPS, intraparietal sulcus; Limbic sys., limbic system; LOTC, lateral occipito-temporal cortex; MFG, middle frontal gyrus; MTG, middle temporal gyrus; NAc, nucleus accumbens; OFC, orbitofrontal cortex; PAG, periaqueductal gray; PCC, posterior cingulate cortex; PCL, paracentral lobule; PCUN, precuneus; PHC, parahippocampal cortex; pIPS, intraparietal sulcus, posterior segment; PoCG, postcentral gyrus; PrCG, precentral gyrus; pre-SMA, pre-supplementary motor area; pSTS, posterior superior temporal sulcus; PU, putamen; PUL, pulvinar; RSC, retrosplenial cortex; SC, superior colliculus; SFG, superior frontal gyrus; SMA, supplementary motor area; SPL, superior parietal lobule; STS, superior temporal sulcus; TP, temporal pole; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex.

Box 1. A more dynamic view on body areas

Hierarchical models assume that each area elaborates on the stimulus representation of previous areas [48] in a way that is relatively stable, independently from various task-related processes and the different stimuli attributes involved (e.g., detection, identification, emotion, gender). However, some studies have reported substantial variability in how stimuli are represented in their specific category areas, indicating that their role may not be as abstract, static, high-level, and conceptual as often assumed. From research on facial expressions it is well known that, for identical stimuli, the type of task clearly influences activity in face areas (e.g., active vs passive observation, emotion recognition vs an orthogonal task) [116–119]. There are similar findings about task effects on brain activity in the body perception literature. For example, increased activity in the FBA and EBA has been reported for emotion-naming compared to a color-naming task [28]. Using multivariate pattern analysis we found that the difference between explicit and implicit body expression processing can be decoded with high accuracy specifically in the EBA but not in FBA [120]. Similar strong task-driven variability in body representation has been reported with **electroencephalography (EEG)** [121].

Substantial variations in body processing are also linked to attention and stimulus awareness. Along these lines, affective body information has been shown to modulate attention processes, as observed for example with the differential effects that fearful body expressions have on saccades compared to neutral bodies [122]. In **hemispatial neglect** patients, contralesional presentation of fearful body expressions overcomes attentional deficits [123]. In the intact brain, consciously, as opposed to non-consciously, viewed images are associated with major differences in brain responses in ventral body category areas and in frontoparietal regions [61,124,125]. There is also evidence for body processing without awareness in EBA, but not in FBA, in patients with full bilateral visual cortex lesion [126]. This EBA activation indicates that category-specific areas in the ventral stream can still receive visual input through a V1-independent pathway (Box 2). Some features of the body shape or movement may be sufficient to drive these responses, but we do not know which partial and feature-based computations of the body image sustain the non-conscious percept.

meaning that the computations that characterize category areas are not or are only weakly needed for attribute coding. This may explain why ventral body areas are active for consciously seen but not for unseen bodies [61]. Along the same lines, one may try to explain **blindsight** or residual vision in patients with primary visual cortex lesions (Box 1).

Midlevel ethological features: a unifying framework

We propose that the information exchange between body-selective areas and action and emotion networks for body expression perception crucially involves midlevel body-feature information. Midlevel features refer to posture and movement properties of body expressions that drive perception at processing stages between low-level and high-order semantic representations. They are not high-order concepts, semantic features, or attributes [e.g., emotion, (in)animate], nor are they parts of a stimulus (e.g., hands of the body). Midlevel features are also different from low-level features (e.g., spatial frequency, luminance). This functional definition of body representation builds on findings in nonhuman species showing that many behaviors cluster in some basic functional domains [15,62]. Currently, a major obstacle for understanding midlevel feature processing is the lack of an analytical and quantitative model of body posture and movement perception. The development of such a model is best guided by biological/ethological considerations of brain and behavior.

Ethology as the heuristic basis of midlevel features

The notion that the visual system evolved in particular environments and for specific functions is a cornerstone of ethology [63,64]. An ethological framework, as opposed to a traditional mentalist one, is the logical point of departure for emotion theories because concepts such as fear or anger are about survival behaviors triggered in a variety of concrete situations. Without an ethological framework, we are confined to the traditional psychological perspective of mapping intentions and emotions onto brain structures in a holistic fashion. An ethological framework can provide a theoretical and systematic background for identifying the crucial variables at stake in the organism–environment interaction [65,66]. More specifically, midlevel ethological features are those that code for the recognition of conspecifics and for relations between agents in social contexts. Many relevant facets of individual action and social interaction have already been tackled (e.g., personal distance, direction of movement, face to face interaction, dominance, gender,

context, etc.), and there are already interesting findings about possible midlevel features in the literature. For example, 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]. An ethological framework is also essential for capturing the real diversity of situations an organism is engaged in. For example, a fear episode is variously described as an instance of being alarmed, scared, frightened, or panicking. These are not merely some psychological nuances that one tries to catch in questionnaires and reduce entirely to the fear center of the brain [69]. These episodes correspond to different behaviors in different contexts, and are presumably associated with specific posture and movement patterns. Each also triggers a different behavior in the observer. Therefore, the search for abstract emotion categories in mental or neural processes must take a back position in favor of investigations of actual behavior [66].

Computational approaches to midlevel ethological features

The intuitions of observers about the most striking characteristics of the behavior of conspecifics are not the best guide to discovering the features that play a crucial role in brain processes. Undoubtedly, intuitions, conventions, and culture do bias us to pay attention to some features at the detriment of others. For example, people privilege the face as the mirror of the feelings and intentions of an individual [70], while the facial impression is strongly influenced by the body expression [53]. Naturalistic observations outside an ethological framework traditionally suffer from two major problems: massive dimensionality and observer subjectivism [71]. Traditional ethology circumvented the first by focusing on functional animal–environment interactions and the second by studying a different species than one's own. Computational ethology holds the promise of circumventing both in a similar way, thus reducing the number of dimensions and picking out the relevant space from the myriads of features and feature spaces.

Models are already being developed in the field of computer vision, interested in the automatic recognition of body expressions [72–75]. These models share the aim of mapping the spatiotemporal information of body movements into abstract emotion labels. Different methodologies are already being used for detecting and tracking body movements, and different approaches can be followed for modeling emotion [76]. For example, the estimation of body poses across frames can be achieved by tracking different body parts (head, hands, torso, etc.) or by mapping a kinematic model (i.e., skeleton) to the image or frame (e.g., OpenPose [77] or DeepLabCut [78]). Emotion labeling can be categorical (classifying affect into distinct classes), dimensional (using dimensions such as valence), or componential (complex emotions are hierarchically built on emotions of previous layers) [76].

Although these models have already provided critical body features such as motion cues and orientation or shape descriptors, the crucial question is whether the resulting midlevel features correspond to processes in the human visual system (*cf* [79]). A biologically plausible model is presumably a model that is consistent with the neurophysiological properties of the visual cortex [7,80] as well as with those of other relevant brain areas for body expression perception. However, such model is not yet available [81]. Adopting a neuroethological framework will guide the discovery of biologically plausible midlevel features. In turn, this will allow us to formulate specific and testable hypotheses about critical features [82].

Quantitative analysis of body perception and body expressions in neuroscience

Studies of movement kinematics are among the first to have opened a quantitative analysis perspective on the brain representation of bodies and related this to brain processes. For

example, body-part speed and the distance between body parts are related to brain activity in the extrastriate and posterior superior temporal cortex [83]. Another study found sensitivity to human actions complying or not with kinematic laws in left dorsal premotor, dorsolateral prefrontal, and medial frontal cortex, areas that play an important role in action perception [84]. Another recent study investigated the relation between an index of whole-body movement and brain activation [85]. This motion index was related to brain activity in a single cluster in the right inferior temporal gyrus, an area frequently reported in studies of body movement perception as seen in a recent meta-analysis [86]. Studies of action intention also illustrate how a kinematics-based quantification of behavior allows decoding of action intentions [87,88]. With a different approach, models of visual processing of actions have been developed that are closely inspired by neurophysiological properties, such as shape **selectivity**, at different stages in the visual processing stream [7].

In affective neuroscience, a few studies have investigated how objectively defined and subjectively reported emotions are related to quantitative descriptions of movement (e.g., velocity) and postural (e.g., symmetry, limb contraction) configurations [3,75,89]. For example, a machine-learning algorithm was used to extract emotion-specific postural and movement features from motion capture (mocap) recordings of expressive gait [89]. Interestingly, these automatically defined emotion-specific features strongly correlated with the emotional judgments of observers [89]. In another study it was shown that quantitative descriptions of several gait properties, such as the intersegmental plane or the angular rotation of the leg segments, can distinguish between different emotions [90].

A different source of input for midlevel feature-based hypotheses is provided by measuring muscle activity related to body expression perception [91] and production [92]. A feature such as muscle contraction can be measured with electromyography, and this information could, in turn, provide insights into feature organization. For example, clear activation was found in the trapezius, deltoid, and triceps muscles during fear perception, whereas the biceps showed inhibition. Based on these electromyography measurements, a body action coding system (BACS) was developed [91,92] that is comparable to the facial action coding system (FACS) [93]. Further developments along these lines may help to clarify and validate computational features and to understand how observing body expressions triggers adaptive action [94].

Brain representation of quantitative descriptions of body expressions

The previous sections reviewed some work aimed at finding crucial stimulus properties of body movements and postures that carry expression information. What is crucially needed next is to understand if and how these properties are processed in the brain and how they can explain body expression perception. We recently undertook computational analyses and behavioral tests of naturalistic videos to define critical body features. We then asked whether these body features are encoded in the brain. We found that computationally defined features are systematically related to brain activity in several specialized brain areas. For example, one study focused on several features taken from a computational model of dance perception [95]. Low-level computational body features (e.g., acceleration), as defined in that model, were represented in areas related to early visual and motion processing, whereas mid-level body features related to postural body dynamics (e.g., symmetry, lightness) were encoded in occipital-temporal cortex, pSTS, and superior parietal lobe [95].

In another study, we showed that the midlevel features 'limb contraction' and 'limb angles' play a central role in fearful body expression perception and are specifically represented in action observation,

motor preparation, and affect coding regions, including the amygdala (Figure 3) [9]. Importantly, with this new feature-based approach we can now clarify in detail the functions of areas that have so far only been associated with general body selectivity at the visual category level. For example, we observed that the EBA and FBA present a similar encoding of body features, with a greater sensitivity to postural rather than kinematic features. Although the feature-encoding activity was similar in these areas, the feature representation of the body-movement stimuli was dissimilar, suggesting that they play different roles in body expression processing. This functional difference may be related to the different anatomical connections of these areas and their role in adaptive reaction to specific emotions (Figure 2C) [30]. Another surprising result was that we did not find a representation of kinematic body features in pSTS, despite previous studies implicating this area in the processing of biological motion [96–98]. This is consistent with a recent study concerning its role in biological motion processing, showing that pSTS is involved in parallel networks rather than being the gatekeeper in a hierarchical system [99]. A recent 7T fMRI study correlated brain activity with several features of body expressions that covered stages from low- to high-level processing. High-level attributes, such as actor identity, were represented in the left middle temporal sulcus. Among the defined midlevel visual features, only head orientation and the shortest hand-to-head distance were positively correlated with brain activity, indicating that these features might be biologically relevant [10].

Taken together, these results suggest that movement and emotion encoding in the brain are organized by feature statistics of body movements rather than by semantic categories [95]. Indeed, many of these areas have been reported previously, but so far remained without a clear functional description other than that a correlation was observed with qualitatively and holistically described emotion categories. To understand the specific role of the brain areas involved in body expressions, midlevel features are of the essence. There are currently very few examples of analytical and quantitative approaches to body posture and movement perception that could serve as inputs for brain models that sidestep abstract categories. Furthermore,
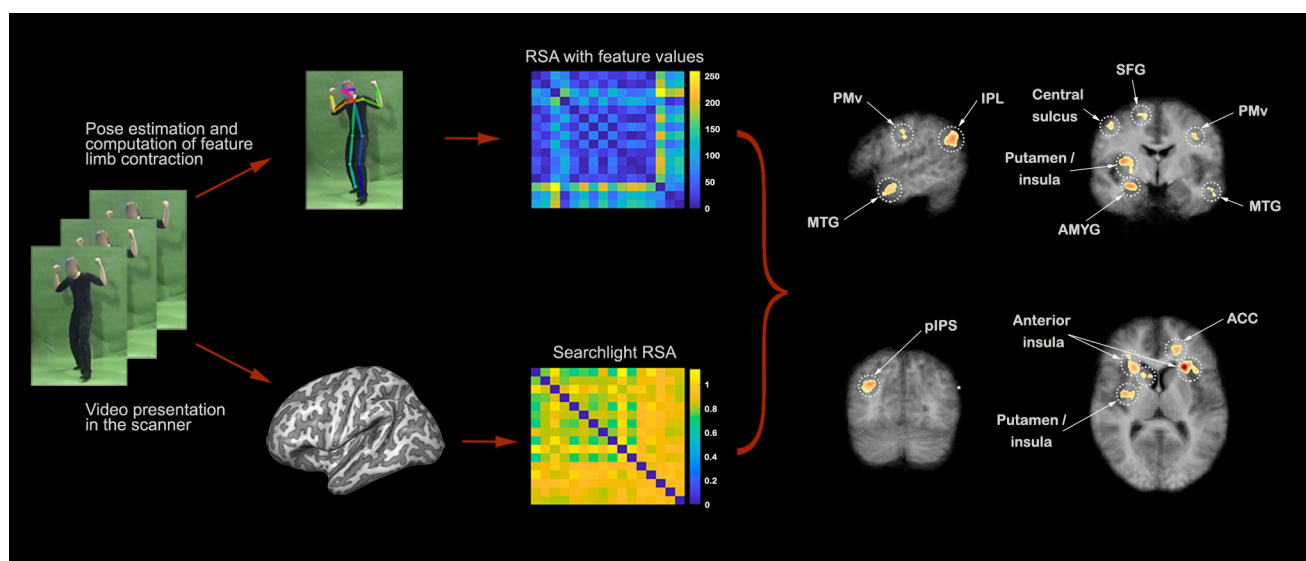
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Figure 3. Feature-based approach to body expression perception. Poyo Solanas *et al.* [9] investigated the subcategorical representation of emotional body movements by relating computed features of body movement to multivariate patterns of fMRI data using representational similarity analysis. This figure shows the results for the feature limb contraction (average of the distances between the wrists and ankles to the head). Abbreviations: ACC, anterior cingulate cortex; AMYG, amygdala; IPL, inferior parietal lobule; MTG, middle temporal gyrus; pIPS, intraparietal sulcus, posterior segment; PMv, premotor cortex, ventral part; RSA, representational similarity analysis; SFG, superior frontal gyrus. Figure modified, with permission, from [9].

there is a need for methods that describe and quantify the natural behavior of freely moving humans under various natural circumstances [65,66]. Data obtained with such methods should provide a fertile terrain for hypotheses about midlevel feature computations. With the advent of novel technologies and computational tools, the time may be ripe for a systematic analysis of human affective behavior [100–102].

Concluding remarks and future perspectives

Social adaptive behavior capitalizes on specific features of the body manifestations of conspecifics. The discovery of ethological and computationally driven midlevel features promises a novel understanding of the processing stages between low-level perception and high-order concept representation. It also promises to cast new light on four important issues that remain outside the scope of this review. One is a better understanding of the visual basis of social interaction. Although studies of category, action, and emotion representation have provided evidence that the brain prioritizes social stimuli, most explanations of body expression perception have remained mentalistic and used high-level qualitative concepts. A midlevel feature approach might provide insights into the specific visual processes driving social perception. Notions such as ethological action maps [14] and functional domains [15] have proved to be useful in characterizing an intermediate level of organization in the motor domain. Nevertheless, on the side of perception we do not currently know how best to characterize the input into those areas from visual areas. The notion of ethological midlevel features provides a framework for studying the visual characteristics of basic natural actions such as defensive reactions or dominance postures [103].

Second, research on midlevel features offers novel opportunities for clarifying the temporal dynamics. One hitherto puzzling finding concerns the timecourse of processing the emotional expression. For example, some studies did not find emotional modulation of the **N170** by body expressions [104]. This is in line with the classical hierarchical view that the ventral body-selective areas are the gateway to subsequent processing of various body attributes such as emotion expressions. Others showed an increase in N190 amplitude for fearful than for neutral or happy body postures [105,106]. A study using stimuli matched for the action category displayed (opening a door in a neutral vs a fearful fashion; i.e., matching action features) found faster processing of fearful body expression compared to neutral body expression for two early **event-related potential** components: the P1 component at ~110 ms and the vertex positive potential component at ~175 ms [107]. Similarly, MEG measurements have shown differences between fearful and neutral bodies as early as 80 ms after stimulus onset and in a complex of areas in the right parietal cortex [36]. These early activities are consistent with feature-based recognition that is relatively independent of later ventral area processing. A much more complex issue concerns the time-window in which body expressions unfold. Although only a very short time is sufficient to perceive movement, the perception of whole body behaviors may require a minimal duration. One hypothesis is that some critical feature information is already available at intermediate stages and allows perceptual predictions [108] while the full action sequence is still unfolding. An interesting question for future research is whether perception uses a temporal chunking procedure to build minimal syntactic structure-like sequences using midlevel features rather than high-level semantic categories. Given its long evolutionary history and its survival importance, it seems unlikely that our ability for visual recognition of conspecifics is only based on a loose collection of movement templates [40].

Third, understanding development may gain considerably from a focus on midlevel features, and this will in turn provide constraints on modeling adult body expression perception. For example, it has been suggested that the FFA and FBA might develop along different trajectories, with the FBA being on average 70% larger than the FFA in children [109]. When specifically looking at

Outstanding questions

How do brain structure and function embody the range of survival actions of the organism in its environment? Recent findings suggest that sensorimotor circuits include both perceptual and sensorimotor neuronal activity. This presumably reflects the fact that brain architecture evolved for active behavior in the natural and social environment.

How can we connect survival-based behavior networks with the facts about phenomenal experience that high-order theories exploit? So far, differences in methods for studying emotions in human and non-human species have only reinforced the species gap and lead to the notion that higher-order theories are necessary to render the specificity of human emotions. A focus on midlevel features offers a novel research program for bridging this gap and for a better integration of findings across different methods in human and nonhuman species.

How to discover midlevel features? In contrast to computational theories of object recognition, computational neuroethology is guided by the discovery of visual features with a focus on the ethological action repertoire of the species. Midlevel visual features are presumably closely linked with, and provide input to, processes in premotor and motor cortex.

How does learnability constrain computational models? Within some genetics-based boundaries to be discovered, species-specific learning takes place based on fine-tuning of feature selectivity rooted in relevant environment–organism categories.

Is affective information decoded before high-order concept driven categorization? To date only isolated findings support this contention. Is this early expression signature based on the underlying features of body movement/posture? How does a new processing model then address current puzzles of implicit, minimally conscious or unconscious perception of affective signals?

expression representation in adults, adolescents, and children, we observed that right hemispheric activity in EBA, FBA, and STS increased across age. However, no difference in these areas and in the amygdalae was seen between age groups when contrasting angry or happy versus neutral body movements [24,110]. A difference in the developmental course of body-selective areas awaits elucidation from a developmental feature approach. In return, this promises a more specific understanding of nonverbal emotion deficits and a better way to connect with epidemiological and epigenetic studies.

Finally, and in this regard, midlevel features may also represent plausible candidates for characterizing the basis of clinical deficits such as nonverbal communication in **autism spectrum disorder (ASD)**. Several explanations of ASD have been put forward, with at one end, high-level cognitive theories such as theory of mind (ToM) [111] and, at the other, hypotheses about impaired biological movement perception [112], possibly with a genetic basis. Integrating these findings into a single picture has so far been very difficult. A feature-based approach may help to pinpoint some core midlevel social perception problems and in turn advance treatment options by building bridges between features, genetics, emotion, and social communication disorders [113].

In conclusion, postural and kinematic feature information appears to predict brain activity in cortical and subcortical areas, and ultimately may predict a range of behaviors. If so, the brain activity associated with these midlevel feature processes may be sufficient to sustain expression perception and thereby social communication and therefore may not require high-level, category-driven perception and semantic representation of the full stimulus. This new approach to body perception promises to throw light on rapid expression perception and action preparation (Box 2 and see Outstanding questions). However, the few studies that are so far available do not yet propose a theoretical framework of midlevel vision processes that could serve as feature-level heuristics [114]. In addition, the relation between ethological analysis and computer-vision models has yet to be pursued systematically. What could be a midlevel feature defined from ethological, functional domains may, however, correspond to other processing levels of the architecture of computer-vision models. Therefore, what is urgently needed is a biologically plausible feature-based computational model of naturalistic body expressions that reflects the relevant principles and structures of

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Box 2. The missing link in emotion and consciousness research: feelings and midlevel features

Imagine walking in the woods at dusk. A shifting shape begins to appear at a distance and immediately frightens you. The acute feeling of fear and the rapid defensive actions it prompts are already triggered at intermediate stages of perception. The experience will intensify or fade as its cause becomes clearer and assigned to one or another label. This labeling process is typically called 'emotion construction' in high-order theories [69], meaning that a fear experience results from high-order cognitive constructions. In this account, any fear experience is a conscious experience of having fear [69]. By contrast, subjective states associated with midlevel feature processing may be akin to feelings. Feelings are the intermediate layer between unconscious processes and fully formed conscious and cognitively constructed emotional states [127]. Instead of considering (emotional) consciousness as an all-or-nothing concept, it may be useful to distinguish between the state of feeling fearful (driven by emotion-perception-action feature loops) versus being conscious of a fearful object (driven by object recognition, consciousness of the object, and memory). In contrast to consciousness of one's fear (consciousness of oneself as having fear), fearful feelings may be akin to an anoetic state of consciousness [128,129]. The distinction between these two notions of fear/consciousness parallels findings about two separate fear circuits, one reactive and the other cognitive [31,130].

The focus on the midlevel features may throw light on some paradoxical phenomena such as vision without awareness – blindsight. We found that limb contraction is distinctly associated with fear expressions. Thus, it may be perceived as signaling fear and prompting action, and this may take place without conscious thought and independently of processing the whole-body posture or movement. As such, this may be an explanation for the findings that fear can be triggered in the absence of conscious perception of body object awareness, as seen in binocular rivalry [131], continuous flash suppression [132], and blindsight patient studies [133].

organism–environment interaction. Similar to how ethologists proceed, we need to discover what features and feature configurations of a range of emotional behaviors (e.g., defensive movements, freezing, dominance displays) a conspecific picks up and reacts to. The case of body expressions is a particularly important area in which to try out this approach. Body expressions are not so much representations of emotions as behaviors whereby the organism adapts to real-life conditions. Perception of such behaviors is driven by the ability of the brain to pick up specific features relatively independently of the conceptual processes that operate in high-level vision [115].

Declaration of interests

The authors declare no conflicts of interest.

References

1. Roelofs, K. (2017) Freeze for action: neurobiological mechanisms in animal and human freezing. *Philos. Trans. R. Soc. B* 372, 20160206
2. Terburg, D. *et al.* (2018) The basolateral amygdala is essential for rapid escape: a human and rodent study. *Cell* 175, 723–735
3. Poyo Solanas, M. *et al.* (2020) The role of computational and subjective features in emotional body expressions. *Sci. Rep.* 10, 6202
4. Kanwisher, N. (2000) Domain specificity in face perception. *Nat. Neurosci.* 3, 759–763
5. Bruce, V. and Young, A. (1986) Understanding face recognition. *Br. J. Psychol.* 77, 305–327
6. Haxby, J.V. *et al.* (2000) The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233
7. Giese, M.A. and Poggio, T. (2003) Neural mechanisms for the recognition of biological movements. *Nat. Rev. Neurosci.* 4, 179–192
8. Grill-Spector, K. and Weiner, K.S. (2014) The functional architecture of the ventral temporal cortex and its role in categorization. *Nat. Rev. Neurosci.* 15, 536–548
9. Poyo Solanas, M. *et al.* (2020) Computation-based feature representation of body expressions in the human brain. *Cereb. Cortex* 30, 6376–6390
10. Zhan, M. *et al.* (2021) Subjective understanding of actions and emotions involves the interplay of the semantic and action observation networks in the brain. *BioRxiv* Published online April 15, 2021. http://dx.doi.org/10.1101/2021.04.15.439961
11. Haxby, J.V. *et al.* (2020) Naturalistic stimuli reveal a dominant role for agentic action in visual representation. *NeuroImage* 216, 116561
12. Thorat, S. *et al.* (2019) The nature of the animacy organization in human ventral temporal cortex. *eLife* 8, e47142
13. Tarhan, L. and Konkle, T. (2020) Sociality and interaction envelope organize visual action representations. *Nat. Commun.* 11, 3002
14. Graziano, M.S. (2016) Ethological action maps: a paradigm shift for the motor cortex. *Trends Cogn. Sci.* 20, 121–132
15. Kaas, J.H. *et al.* (2013) Cortical networks for ethologically relevant behaviors in primates. *Am. J. Primatol.* 75, 407–414
16. Wurm, M.F. and Lingnau, A. (2015) Decoding actions at different levels of abstraction. *J. Neurosci.* 35, 7727–7735
17. Downing, P.E. *et al.* (2001) A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473
18. Peelen, M.V. and Downing, P.E. (2005) Selectivity for the human body in the fusiform gyrus. *J. Neurophysiol.* 93, 603–608
19. Pinsk, M.A. *et al.* (2005) Representations of faces and body parts in macaque temporal cortex: a functional MRI study. *PNAS* 102, 6996–7001
20. van de Riet, W.A. *et al.* (2009) Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Soc. Neurosci.* 4, 101–120
21. Hadjikhani, N. and de Gelder, B. (2003) Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr. Biol.* 13, 2201–2205
22. Taylor, J.C. *et al.* (2007) Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *J. Neurophysiol.* 98, 1626–1633
23. Downing, P.E. and Peelen, M.V. (2011) The role of occipitotemporal body-selective regions in person perception. *Cogn. Neurosci.* 2, 186–203
24. Ross, P.D. (2014) Body form and body motion processing are dissociable in the visual pathways. *Front. Psychol.* 5, 767
25. Vangeneugden, J. *et al.* (2014) Distinct neural mechanisms for body form and body motion discriminations. *J. Neurosci.* 34, 574–585
26. Weiner, K.S. and Grill-Spector, K. (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, 2183–2199
27. Grèzes, J. *et al.* (2007) Perceiving fear in dynamic body expressions. *NeuroImage* 35, 959–967
28. Pichon, S. *et al.* (2012) Threat prompts defensive brain responses independently of attentional control. *Cereb. Cortex* 22, 274–285
29. Peelen, M.V. *et al.* (2007) Emotional modulation of body-selective visual areas. *Soc. Cogn. Affect. Neurosci.* 2, 274–283
30. Zimmermann, M. *et al.* (2018) Is the extrastriate body area part of the dorsal visuomotor stream? *Brain Struct. Funct.* 223, 31–46
31. de Gelder, B. *et al.* (2004) Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *PNAS* 101, 16701–16706
32. Goldberg, H. *et al.* (2014) The emotion–action link? Naturalistic emotional stimuli preferentially activate the human dorsal visual stream. *NeuroImage* 84, 254–264
33. 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, 1873–1883
34. Borgomaneri, S. *et al.* (2015) Early changes in corticospinal excitability when seeing fearful body expressions. *Sci. Rep.* 5, 14122

35. Hortensius, R. *et al.* (2016) When anger dominates the mind: increased motor corticospinal excitability in the face of threat. *Psychophysiology* 53, 1307–1316

36. Meeren, H.K.M. *et al.* (2016) Early preferential responses to fear stimuli in human right dorsal visual stream – a MEG study. *Sci. Rep.* 6, 24831

37. Borgomaneri, S. *et al.* (2017) Behavioral inhibition system sensitivity enhances motor cortex suppression when watching fearful body expressions. *Brain Struct. Funct.* 222, 3267–3282

38. Utter, A.A. and Basso, M.A. (2008) The basal ganglia: an overview of circuits and function. *Neurosci. Biobehav. Rev.* 32, 333–342

39. Sokolov, A.A. *et al.* (2020) Brain circuits signaling the absence of emotion in body language. *PNAS* 117, 20868–20873

40. de Gelder, B. (2006) Towards the neurobiology of emotional body language. *Nat. Rev. Neurosci.* 7, 242–249

41. Dean, P. *et al.* (1989) Event or emergency? Two response systems in the mammalian superior colliculus. *Trends Neurosci.* 12, 137–147

42. Emery, N.J. and Amaral, D.G. (2000) The role of the amygdala in primate social cognition. In *Cognitive Neurocience of Emotion* (Lane, R.D. and Nadel, L., eds), pp. 156–191, Oxford University Press

43. Shallice, T. (1988) *From Neuropsychology to Mental Structure*, Cambridge University Press

44. Kanwisher, N. and Yovel, G. (2006) The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. B* 361, 2109–2128

45. Kanwisher, N. *et al.* (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311

46. Peelen, M.V. and Downing, P.E. (2007) The neural basis of visual body perception. *Nat. Rev. Neurosci.* 8, 636–648

47. Van Essen, D.C. and Maunsell, J.H. (1983) Hierarchical organization and functional streams in the visual cortex. *Trends Neurosci.* 6, 370–375

48. Josephs, E.L. and Konkle, T. (2020) Large-scale dissociations between views of objects, scenes, and reachable-scale environments in visual cortex. *PNAS* 117, 29354–29362

49. Kanwisher, N. (2017) The quest for the FFA and where it led. *J. Neurosci.* 37, 1056–1061

50. Çukur, T. *et al.* (2013) Attention during natural vision warps semantic representation across the human brain. *Nat. Neurosci.* 16, 763–770

51. Peelen, M.V. *et al.* (2009) Neural mechanisms of rapid natural scene categorization in human visual cortex. *Nature* 460, 94–97

52. Meeren, H.K. *et al.* (2008) Early category-specific cortical activation revealed by visual stimulus inversion. *PLoS One* 3, e3503

53. Meeren, H.K. *et al.* (2005) Rapid perceptual integration of facial expression and emotional body language. *PNAS* 102, 16518–16523

54. Sinke, C.B. *et al.* (2012) The constructive nature of affective vision: seeing fearful scenes activates extrastriate body area. *PLoS One* 7, e38118

55. Arcaro, M.J. *et al.* (2020) The neurons that mistook a hat for a face. *eLife* 9, e53798

56. de Beeck, H.P.O. and Baker, C.I. (2010) The neural basis of visual object learning. *Trends Cogn. Sci.* 14, 22–30

57. Grill-Spector, K. *et al.* (2017) The functional neuroanatomy of human face perception. *Annu. Rev. Vis. Sci.* 3, 167–196

58. Urgesi, C. *et al.* (2007) Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *J. Neurosci.* 27, 8023–8030

59. Hodzic, A. *et al.* (2009) Distinct cortical networks for the detection and identification of human body. *NeuroImage* 45, 1264–1271

60. Peelen, M.V. and Downing, P.E. (2017) Category selectivity in human visual cortex: Beyond visual object recognition. *Neuropsychologia* 105, 177–183

61. Zhan, M. (2018) Ventral and dorsal pathways relate differently to visual awareness of body postures under continuous flash suppression. *eNeuro* 5 ENEURO.0285-17.2017

62. Orban, G. *et al.* (2021) From observed action identity to social affordances. *Trends Cogn. Sci.* 25, 493–505

63. Lorenz, K. (2013) *The Foundations of Ethology*, Springer Science & Business Media

64. Tinbergen, N. (1963) On aims and methods of ethology. *Z. Tierpsychol.* 20, 410–433

65. Anderson, D.J. and Adolphs, R. (2014) A framework for studying emotions across species. *Cell* 157, 187–200

66. Anderson, D.J. and Perona, P. (2014) Toward a science of computational ethology. *Neuron* 84, 18–31

67. Salva, O.R. *et al.* (2015) Roots of a social brain: developmental models of emerging animacy-detection mechanisms. *Neurosci. Biobehav. Rev.* 50, 150–168

68. Di Giorgio, E. *et al.* (2017) Visual cues of motion that trigger animacy perception at birth: the case of self-propulsion. *Dev. Sci.* 20, e12394

69. LeDoux, J.E. and Brown, R. (2017) A higher-order theory of emotional consciousness. *PNAS* 114, E2016–E2025

70. 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. *Neurosci. Biobehav. Rev.* 34, 513–527

71. Gomez-Marin, A. *et al.* (2014) Big behavioral data: psychology, ethology and the foundations of neuroscience. *Nat. Neurosci.* 17, 1455–1462

72. Piana, S. *et al.* (2016) Adaptive body gesture representation for automatic emotion recognition. *ACM Trans. Interact. Intell. Syst. (TiiS)* 6, 1–31

73. Glowinski, D. *et al.* (2008) Technique for automatic emotion recognition by body gesture analysis. In *2008 IEEE Computer Society Conference on Computer Vision and Pattern Recognition Workshops*, pp. 1–6

74. Zacharatos, H. *et al.* (2014) Automatic emotion recognition based on body movement analysis: a survey. *IEEE Comput. Graph. Appl.* 34, 35–45

75. Kleinsmith, A. and Bianchi-Berthouze, N. (2012) Affective body expression perception and recognition: A survey. *IEEE Trans. Affect. Comput.* 4, 15–33

76. Noroozi, F. *et al.* (2018) Survey on emotional body gesture recognition. *IEEE Trans. Affect. Comput.*

77. Cao, Z. *et al.* (2017) Realtime multi-person 2D pose estimation using part affinity fields. In *Proceedings of the IEEE Computer Society Conference on Computer Vision and Pattern Recognition*, pp. 7291–7299, IEEE

78. Mathis, A. *et al.* (2018) DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* 21, 1281–1289

79. Zhuang, C. *et al.* (2021) Unsupervised neural network models of the ventral visual stream. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2014196118

80. Hasson, U. *et al.* (2020) Direct fit to nature: an evolutionary perspective on biological and artificial neural networks. *Neuron* 105, 416–434

81. Serre, T. (2014) Hierarchical models of the visual system In *Encyclopedia of Computational Neuroscience* (Vol. 6) (Jaeger, D. and Jung, R., eds), pp. 1–2, Springer

82. Hesse, J.K. and Tsao, D.Y. (2020) The macaque face patch system: a turtle's underbelly for the brain. *Nat. Rev. Neurosci.* 21, 695–716

83. McAleer, P. *et al.* (2014) The role of kinematics in cortical regions for continuous human motion perception. *Cogn. Affect. Behav. Neurosci.* 14, 307–318

84. Casile, A. *et al.* (2010) Neuronal encoding of human kinematic invariants during action observation. *Cereb. Cortex* 20, 1647–1655

85. Noble, K. *et al.* (2014) Event segmentation and biological motion perception in watching dance. *Art Percept.* 2, 59–74

86. Grosbras, M.H. *et al.* (2012) Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. *Hum. Brain Mapp.* 33, 431–454

87. Soriano, M. *et al.* (2018) Movement kinematics drive chain selection toward intention detection. *PNAS* 115, 10452–10457

88. Koul, A. *et al.* (2018) Action observation areas represent intentions from subtle kinematic features. *Cereb. Cortex* 28, 2647–2654

89. Roether, C.L. *et al.* (2009) Critical features for the perception of emotion from gait. *J. Vis.* 9, 15

90. Barliya, A. *et al.* (2013) Expression of emotion in the kinematics of locomotion. *Exp. Brain Res.* 225, 159–176

91. Huis in 't Veld, E.M. *et al.* (2014) The body action coding system I: muscle activations during the perception and expression of emotion. *Soc. Neurosci.* 9, 249–264

92. Huis in 't Veld, E.M. *et al.* (2014) The body action coding system II: muscle activations during the perception and expression of emotion. *Front. Behav. Neurosci.* 8, 330

93. Ekman, P. and Friesen, E. (1978) *Facial Action Coding System: A Technique for the Measurement of Facial Movement*, Consulting Psychologists Press

94. Sussillo, D. *et al.* (2015) A neural network that finds a naturalistic solution for the production of muscle activity. *Nat. Neurosci.* 18, 1025–1033

95. Vaessen, M.J. *et al.* (2019) Computational feature analysis of body movements reveals hierarchical brain organization. *Cereb. Cortex* 29, 3551–3560

96. Allison, T. *et al.* (2000) Social perception from visual cues: role of the STS region. *Trends Cogn. Sci.* 4, 267–278

97. Grossman, E.D. *et al.* (2005) Repetitive TMS over posterior STS disrupts perception of biological motion. *Vis. Res.* 45, 2847–2853

98. Grossman, E.D. *et al.* (2010) fMR-adaptation reveals invariant coding of biological motion on human STS. *Front. Hum. Neurosci.* 4, 15

99. Sokolov, A.A. *et al.* (2018) Structural and effective brain connectivity underlying biological motion detection. *PNAS* 115, E12034–E12042

100. Krakauer, J.W. *et al.* (2017) Neuroscience needs behavior: correcting a reductionist bias. *Neuron* 93, 480–490

101. Mobbs, D. *et al.* (2015) The ecology of human fear: survival optimization and the nervous system. *Front. Neurosci.* 9, 55

102. Cisek, P. (2007) Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos. Trans. R. Soc B* 362, 1585–1599

103. Tucciarelli, R. *et al.* (2019) The representational space of observed actions. *Elife* 8, e47686

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

105. Borhani, K. *et al.* (2016) The effect of alexithymia on early visual processing of emotional body postures. *Biol. Psychol.* 115, 1–8

106. Borhani, K. *et al.* (2015) Emotional and movement-related body postures modulate visual processing. *Soc. Cogn. Affect. Neurosci.* 10, 1092–1101

107. Van Heijnsbergen, C. *et al.* (2007) Rapid detection of fear in body expressions, an ERP study. *Brain Res.* 1186, 233–241

108. Aglioti, S.M. *et al.* (2008) Action anticipation and motor resonance in elite basketball players. *Nat. Neurosci.* 11, 1109

109. Peelen, M.V. *et al.* (2009) Differential development of selectivity for faces and bodies in the fusiform gyrus. *Dev. Sci.* 12, F16–F25

110. Ross, P. *et al.* (2019) Emotion modulation of the body-selective areas in the developing brain. *Dev. Cogn. Neurosci.* 38, 100660

111. Tager-Flusberg, H. (2007) Evaluating the theory-of-mind hypothesis of autism. *Curr. Dir. Psychol. Sci.* 16, 311–315

112. Blake, R. *et al.* (2003) Visual recognition of biological motion is impaired in children with autism. *Psychol. Sci.* 14, 151–157

113. Taschereau-Dumouchel, V. *et al.* (2015) Measuring how genetic and epigenetic variants can filter emotion perception. *Psychiatr. Genet.* 25, 216–222

114. Long, B. *et al.* (2018) Mid-level visual features underlie the high-level categorical organization of the ventral stream. *PNAS* 115, E9015–E9024

115. Millikan, R.G. (2017) *Beyond Concepts: Unicepts, Language, and Natural Information*, Oxford University Press

116. Gur, R.C. *et al.* (2002) Brain activation during facial emotion processing. *NeuroImage* 16, 651–662

117. Habel, U. *et al.* (2007) Amygdala activation and facial expressions: explicit emotion discrimination versus implicit emotion processing. *Neuropsychologia* 45, 2369–2377

118. Hariri, A.R. *et al.* (2003) Neocortical modulation of the amygdala response to fearful stimuli. *Biol. Psychiatry* 53, 494–501

119. Winston, J. *et al.* (2003) Common and distinct neural responses during direct and incidental processing of multiple facial emotions. *NeuroImage* 20, 84–97

120. Marrazzo, G. *et al.* (2020) The dynamics of body category and emotion processing in high-level visual, prefrontal and parietal cortex. *BioRxiv* Published online July 15, 2020. https://doi.org/10.1101/2020.07.14.202515

121. Jessen, S. and Kotz, S.A. (2011) The temporal dynamics of processing emotions from vocal, facial, and bodily expressions. *NeuroImage* 58, 665–674

122. Milders, M. *et al.* (2011) Detection of emotional faces is modulated by the direction of eye gaze. *Emotion* 11, 1456

123. Tamietto, M. *et al.* (2015) Once you feel it, you see it: insula and sensory-motor contribution to visual awareness for fearful bodies in parietal neglect. *Cortex* 62, 56–72

124. de Gelder, B. *et al.* (2012) Attention and awareness each influence amygdala activity for dynamic bodily expressions – a short review. *Front. Integr. Neurosci.* 6, 54

125. Zhan, M. *et al.* (2015) The body as a tool for anger awareness – differential effects of angry facial and bodily expressions on suppression from awareness. *PLoS One* 10, e0139768

126. Van den Stock, J. *et al.* (2015) Body recognition in a patient with bilateral primary visual cortex lesions. *Biol. Psychiatry* 77, e31–e33

127. Carvalho, G.B. and Damasio, A. (2021) Interoception and the origin of feelings: a new synthesis. *Bioessays* 43, 2000261

128. Damasio, A. and Dolan, R.J. (1999) The feeling of what happens. *Nature* 401, 847

129. Vandekerckhove, M. and Panksepp, J. (2011) A neurocognitive theory of higher mental emergence: from anoetic affective experiences to noetic knowledge and autonoetic awareness. *Neurosci. Biobehav. Rev.* 35, 2017–2025

130. Qi, S. *et al.* (2018) How cognitive and reactive fear circuits optimize escape decisions in humans. *PNAS* 115, 3186–3191

131. Stienen, B. and de Gelder, B. (2011) Fear modulates visual awareness similarly for facial and bodily expressions. *Front. Hum. Neurosci.* 5, 132

132. Zhan, M. and de Gelder, B. (2019) Unconscious fearful body perception enhances discrimination of conscious anger expressions under continuous flash suppression. *Neuropsychologia* 128, 325–331

133. Van den Stock, J. *et al.* (2014) Neural correlates of body and face perception following bilateral destruction of the primary visual cortices. *Front. Behav. Neurosci.* 8, 30

134. Suchan, B. *et al.* (2013) Reduced connectivity between the left fusiform body area and the extrastriate body area in anorexia nervosa is associated with body image distortion. *Behav. Brain Res.* 241, 80–85

135. Kret, M. *et al.* (2011) Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *NeuroImage* 54, 1755–1762

136. Ma, F. *et al.* (2018) Investigating the neural basis of basic human movement perception using multi-voxel pattern analysis. *Exp. Brain Res.* 236, 907–918

137. Beer, A.L. *et al.* (2013) Combined diffusion-weighted and functional magnetic resonance imaging reveals a temporal-occipital network involved in auditory-visual object processing. *Front. Integr. Neurosci.* 7, 5

138. Hutchison, R.M. *et al.* (2014) Distinct and distributed functional connectivity patterns across cortex reflect the domain-specific constraints of object, face, scene, body, and tool category-selective modules in the ventral visual pathway. *Neuroimage* 96, 216–236

139. Greven, I.M. and Ramsey, R. (2017) Person perception involves functional integration between the extrastriate body area and temporal pole. *Neuropsychologia* 96, 52–60

140. Pichon, S. *et al.* (2008) Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Soc. Neurosci.* 3, 199–212

141. Kana, R.K. and Travers, B.G. (2012) Neural substrates of interpreting actions and emotions from body postures. *Soc. Cogn. Affect. Neurosci.* 7, 446–456