The perception of emotion in body expressions

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During communication, we perceive and express emotional information through many different channels, including facial expressions, prosody, body motion, and posture. Although historically the human body has been perceived primarily as a tool for actions, there is now increased understanding that the body is also an important medium for emotional expression. Indeed, research on emotional body language is rapidly emerging as a new field in cognitive and affective neuroscience. This article reviews how whole-body signals are processed and understood, at the behavioral and neural levels, with specific reference to their role in emotional communication. The first part of this review outlines brain regions and spectrotemporal dynamics underlying perception of isolated neutral and affective bodies, the second part details the contextual effects on body emotion recognition, and final part discusses body processing on a subconscious level. More specifically, research has shown that body expressions as compared with neutral bodies draw upon a larger network of regions responsible for action observation and preparation, emotion processing, body processing, and integrative processes. Results from neurotypical populations and masking paradigms suggest that subconscious processing of affective bodies relies on a specific subset of these regions. Moreover, recent evidence has shown that emotional information from the face, voice, and body all interact, with body motion and posture often highlighting and intensifying the emotion expressed in the face and voice. © 2014 John Wiley & Sons, Ltd.

INTRODUCTION

While the number of neuroimaging studies on face perception has increased dramatically, studies on body perception still lag behind significantly. This is presumably owing to the longstanding view that faces are a more universal and consistent carrier of (emotional) information than bodies. However, recent behavioral and neuroimaging research shows that recognition performance of bodily expressions is similar to that of facial expressions.[1–5] But as research

progresses, differences between the functions of facial and bodily expressions may emerge more and more. While faces excel at conveying person identity, bodies carry precious information on the actions and, possibly, intentions of others.[6,7]

This review aims to bring together recent literature on body perception with emphasis on affective body processing. First, we discuss brain regions involved in body perception and the underlying neural dynamics. We then move on to explore existing research investigating the perception of affective body expressions, and some recent work showing how such body expressions are perceived in the context of voices or in natural scenes. Finally, we review current studies that discuss subconscious affective body perception. We conclude that current evidence supports the notion that emotional signals from

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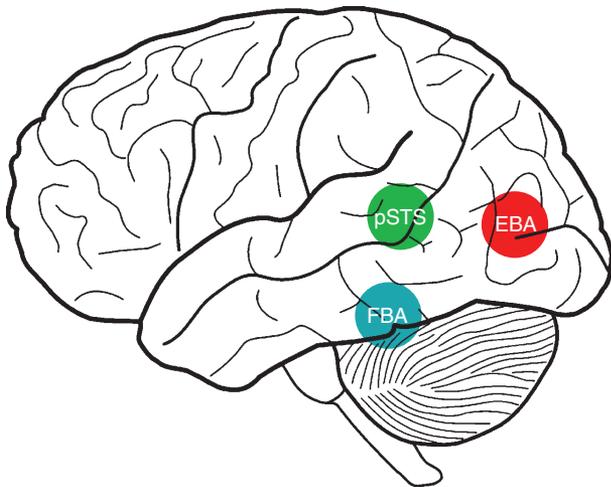
FIGURE 1 | Body perception regions in occipitotemporal cortex (OTC), namely posterior superior temporal sulcus (pSTS), extrastriate body area (EBA), and fusiform body area (FBA).

whole-body expression activate brain systems that underpin reflexive as well as decision-based action preparation.

NEUTRAL BODY PERCEPTION

Body Representation in Inferior Temporal Cortex

In the late 1960s, Gross et al.[8,9] found neurons in the inferior temporal cortex (ITC) that selectively fired to silhouettes of monkey hands. This result was later confirmed for drawings of human hands and faces.[10] More recently, functional MRI (fMRI) studies in monkeys revealed specialized patches for faces and bodies within the object-selective cortex.[11–13] In humans, fMRI investigations into the brain on the basis of body perception have shown that bodies activate brain areas that were associated with the perception of faces (for reviews, see Refs 14, 15). It has been suggested that the mid-FG might contain multiple closely spaced category-selective regions that are partially overlapping.[16] One such region in the mid-fusiform gyrus (FG), the fusiform body area (FBA, see Figure 1), partially overlaps with the fusiform face area (FFA), but was found to respond to whole bodies.[3,16–18] Moreover, earlier research has revealed a distinct area in the occipitotemporal cortex (OTC), the so-called extrastriate body area (EBA, see Figure 1), that activates more to neutral bodies and body parts than to other object categories, including faces.[19] Functional analogies have been proposed between the face-feature-sensitive occipital face area (OFA) and the body-part-sensitive EBA, which are both activated relatively early during cognitive processing, and

between the face sensitive FFA and body-sensitive FBA.[20]

Time Course of Body Perception

Despite the growing number of fMRI studies on body perception, there are many questions on its underlying neural mechanisms that remain unanswered. Electroencephalography (EEG) studies have shown that body processing is associated with a P1 and a prominent N1 (also referred to as N190) component in the event-related potential that is very similar to the components associated with the processing of faces in both timing and scalp topography.[21–27] The N190 for body perception has been localized to the right-dominated middle temporal gyrus (approximately EBA), while the N170 and N190 to face and object perception have been localized in clearly separate regions in, respectively, posterior ITC and posterior middle temporal gyrus.[28] These results were confirmed by another study that compared evoked responses to faces, bodies and control stimuli, and modeled its underlying sources.[29] Activity to face images peaked around 140 milliseconds post-stimulus and recruited a widespread distributed network of cortical areas involving early activation of the lateral occipital cortex (LOC), lateral occipitotemporal cortex (LOTC), and ventral–temporal cortex (VTC, including OFA and FFA), corresponding to the time window of the visual analysis and structural encoding of the stimulus.[30] In contrast, around 150 milliseconds bodies activate a much more restricted area in the LOTC (including EBA), suggesting that the main area for the visual analysis of bodies is the EBA and not the FBA. Extensive body-selective cortical activation occurred at later latencies in dorsal, frontal, and temporal regions, with the orbitofrontal cortex (OFC) showing significant body-selective responses after 200 milliseconds after stimulus onset, and the VTC and lateral-temporal cortex after 500 milliseconds latency. These magnetoencephalography (MEG) results suggest that the hemodynamic activation of the FBA by bodies found in fMRI studies[3,16–18,31] may in fact reflect later stages of visual recognition.

PERCEPTION OF BODY EXPRESSIONS

Bodies carry precious information on emotions, actions, and intentions. Therefore, research has not only focused on how bodies are categorized as objects, but more importantly, how bodies convey information in dynamic expressions.
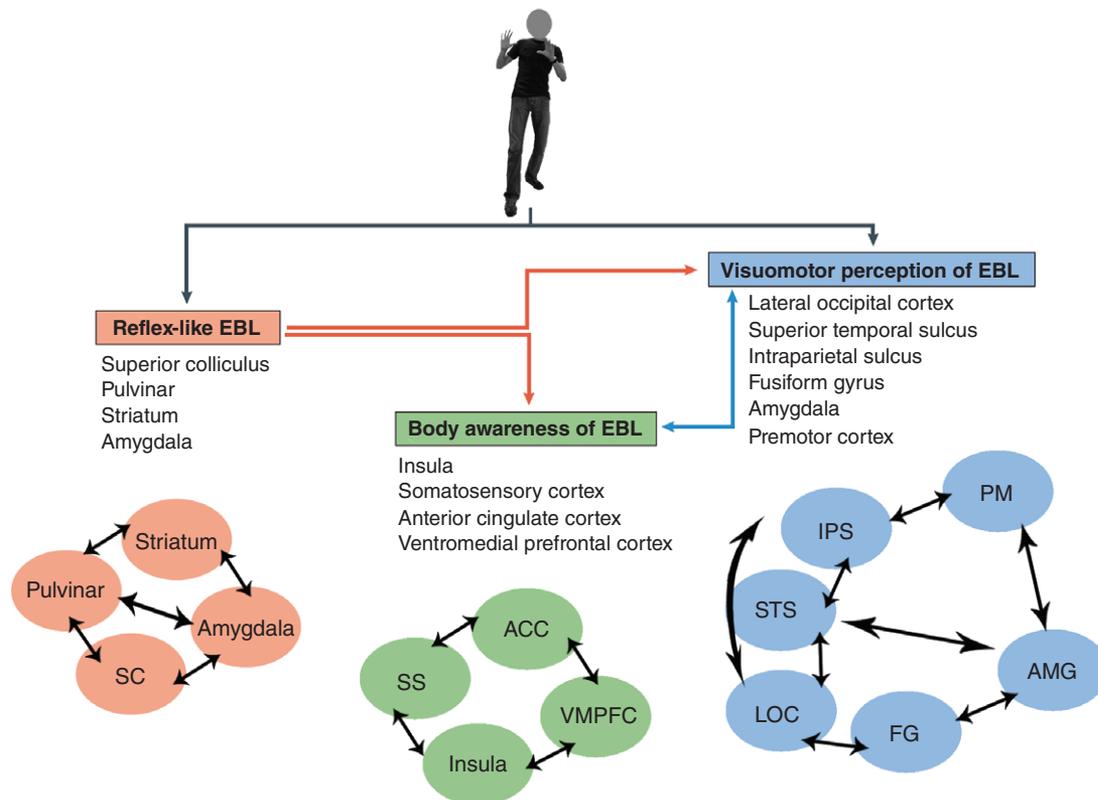
FIGURE 2 | The three interrelated brain networks involved in emotional body language. Left: reflex-like emotional body language (EBL, orange); middle: body awareness of EBL (green); and right: visuomotor perception of EBL (blue). Involved regions: superior colliculus (SC), pulvinar (Pulv), striatum, amygdala (AMG), somatosensory cortex (SS), anterior cingulate cortex (ACC), ventromedial prefrontal cortex (VMPFC), lateral occipital complex (LOC), superior temporal sulcus (STS), intraparietal sulcus (IPS), fusiform gyrus (FG), and premotor cortex (PM).

Body Affect Recognition

Ekman first investigated bodies as affect communicators in 1965.[26,30,32] The consensus at the time was that faces and bodies communicate affect in a different manner, but that faces did so more reliably. More recent behavioral research showed that recognition performance of expressions is relatively similar for face and body stimuli. This applies to studies with static as well as dynamic whole-body stimuli. The available studies have indeed found a high degree of agreement among observers.[1–5] For example, in the validation of the bodily expressive action stimulus test (BEAST), all displayed bodily emotions (happy, sad, anger, fear) were correctly categorized in at least 85% of the cases.[33] A similarly high consensus is found for video clips depicting emotions or instrumental actions performed with a specific emotion.[34] Obviously, there is more information in a video clip than in a still image, and showing the full face rather than blurring it adds more information again. In short, it appears that consensus for recognition of bodily expressions among viewers is as substantial as the consensus for recognition of facial expressions, when tested with comparable stimuli under similar viewing conditions.

Emotional Body Expressions in Human IT Cortex

Similar to studies that reported emotional modulation of face-specific areas, like the FFA and OFA,[31,35,36] other studies have explored the influence of emotional information on body processing in the brain. In the first fMRI study using full bodily expressions, Hadjikhani and de Gelder[3] found increased activation for fearful bodies compared to instrumental bodies in FG and amygdala (AMG). This result corresponds to the most frequently observed result for emotional face processing, and is consistent with previous findings of functional connection between AMG and FG.[37] The AMG seems to be an important link between the visuomotor system underlying emotional body processing and a reflex-like system that is involved in the rapid automatic perception of affective body expressions (see Figure 2). This latter system is described in more detail later in this paper when discussing subconscious processing. In an experiment by

de Gelder et al.,[38] whole brain activations to fearful, happy, and neutral body expressions were compared. A major finding of the study was the involvement of motor areas in the perception of emotional body expressions. Similar results were obtained in a study that directly compared neutral and emotional faces and bodies.[31] Emotional bodies activated cortical and subcortical motor-related structures, such as the inferior frontal gyrus, caudate nucleus, and putamen. These motor areas were not active for emotional faces. Given the importance of action processes in emotion, those activations promise a more in depth understanding of the emotional brain than the focus on object categories (see Figure 2). This is not to say that the two current body-selective areas do not indeed show sensitivity to the emotion the body expresses.

Moreover, emotion modulation in both EBA and FBA has been observed in studies that use dynamic body expressions.[34,39,40] Although no difference was observed between neutral and emotional bodies using static body images,[31,41] several findings suggest that the EBA has additional functions to merely processing body parts. Repetitive transcranial magnetic stimulation (rTMS) over EBA reduced esthetic sensitivity for body stimuli relative to rTMS over ventral premotor (vPM) cortex, while this was absent for non-body stimuli, suggesting that EBA is involved in the esthetic evaluation of body stimuli.[42]

Time Course of Body Expressions

When looking at the time course of body expressions, the N170 shows modulation for emotion, but also effects on other EEG components have been found. A recent study investigated the N170 as a marker of body-sensitive processing.[43] The role of nude over clothed bodies was explored by comparing responses to nude bodies, bodies wearing swimsuits, clothed bodies, faces, and cars. The N170 amplitude increased linearly as the amount of clothing decreased from full clothing via swimsuits to nude bodies. Strikingly, the N170 response to nude bodies was even greater than that to faces, and the N170 amplitude to bodies was independent of whether the face of the bodies was visible or not. In an EEG study, fearful bodies showed an enhanced vertex positive potential and a sustained potential over the midfrontal electrode (Fz) compared with neutral bodies, while an enhanced N170 was only found for fearful faces.[25] This might be an indication that fearful bodies are more ambiguous without the facial information. A follow-up study showed an earlier P1 and VPP latency for fearful bodies compared to neutral bodies and their scrambled counterparts.[27] In an

MEG study, Rudrauf et al.[44] used affective stimuli, including bodies, to study the dynamics of emotion induction in context. They showed enhanced responses for emotional stimuli compared to neutral stimuli in 200–350 milliseconds and 350–500 milliseconds time windows. The early effect is mostly localized to the ventral stream regions (including ITC), while the later effect spreads toward the insula, anterior cingulate cortex, OFC, ventromedial prefrontal cortex, and somatosensory cortex. However, these effects related to the complex emotional scenes as a whole and not bodies specifically. A different picture of the time course of fear expressions emerges in a recently completed MEG study.[45,46] This study shows that the first time window in which there is a significant difference between neutral and fearful body expression images is in the 80–100 milliseconds. This activity is located in the intraparietal sulcus and intraparietal lobule. This finding is consistent with the general idea that whole-body emotion expressions are primarily processed in the dorsal stream. This is in turn an indication that the visual system is triggered on earlier by the information about action that is typically contained in these images.

Dynamic Body Expressions in Superior Temporal Sulcus

Bodies are not solely processed in the ITC. Research on monkey has discovered neurons responding to various types of static body images such as body orientations, body postures that implied motion and body movements in the superior temporal sulcus (STS).[47–52] These cells in STS seem to be responsive to moving stimuli, but also static body images that imply motion, suggesting a role in social perception. This role of STS and specifically posterior STS in body perception has since been confirmed in studies using social signal stimuli, e.g., Refs 53–55. Also in humans, the STS is responsive to biological motion[56] and to different types of body-related stimuli such as mouth movements and eye gaze,[57,58] hand movements,[59–61] and implied body motion.[62]

The role of the STS is important to consider, because when we encounter bodily expressions of emotion in the real world, these are almost always dynamic. Body motion thus forms an important and integrated part of body expressions. When comparing dynamic with static bodily expressions of fear, the STS, superior temporal gyrus and premotor cortex show enhanced activation.[34,40] While dynamic bodily expressions of fear and anger compared with neutral stimuli show partially overlapping activity in regions such as AMG, temporal cortices, and prefrontal cortex,[63] the expression of anger activates

the ventromedial prefrontal cortex and STS more strongly and additionally activates the hypothalamus, temporal pole, and middle occipital gyrus.[40,63] Many of these similar regions are also activated during the perception of threat.[64,65] A TMS study,[66] targeting EBA, ventral premotor (vPM) cortex and posterior STS, revealed that only posterior superior temporal sulcus (pSTS) shows an effect on distinguishing two threatening human body postures compared with that on neutral body postures. No such effects were found in EBA and vPM or for animal stimuli.

It has been suggested that the STS could play a role in the convergence of representations of body form in the ventral stream and body motion in the dorsal stream.[67,68] Giese and Poggio[67] proposed a hierarchical neural model that consists of a form pathway and a motion pathway. The form pathway goes from visual cortex to ITC, the faces areas (FA), and STS, in which 'snapshot' neurons enable biological motion analysis. The motion pathway follows from visual cortex to MT and subsequently to STS and FA, but relies on optical flow pattern neurons. In the model, 'snapshot' neurons as well as optical flow neurons are connected through lateral connections and merge onto motion pattern neurons in STS, F5, and FA, which could integrate information from both streams. This model lays a foundation for how motion can be inferred from still images. However, also other regions, such as EBA and FBA have been shown to integrate information from ventral and dorsal streams, and suggest an earlier and automatic integration in OTC with subsequent processing of human form in ITC and complex human motion in pSTS.[69]

BODILY EXPRESSIONS IN CONTEXT

Body/Scene Contextual Effects

Studies of scene recognition and context effects have demonstrated the rapidity with which scenes can be processed and scene gist recognized.[70–72] To date, however, there have been very few studies investigating the influence of emotional scenes on the perception of faces and bodies. One of the first studies on this field highlighted a facilitating effect of context congruence on perception of affective faces.[73] A more recent fMRI study[74] demonstrated the associative link between natural scenes and bodies. Participants were shown images of natural scenes, which were either neutral or designed to evoke feelings of fear (e.g., a fire and a car crash). These scenes served as both independent stimuli, and a background on top of which a neutral or fearful face was presented. Thus, compound stimuli had either a congruent emotional valence for the face and the background or an incongruent one.

Interestingly, although this design did not focus on bodily expressions and there were no prior predictions about body processing areas, a striking finding was high and selective activation in the EBA. The observed EBA activation was specifically related to threatening scenes, but interestingly was not dependent on the presence of fearful faces as it was also activated in the conditions where there was no face or body present in the threatening scene. One explanation is that this activation reflects a mental imagery of a stimulus completion process, as observed in a study by Ref 75, which identified activity in the FFA for body stimuli that were presented without a face visible. However, the authors argue that the observed activation was not simply due to imagination of the body as FFA reacted significantly less to the no-face stimuli. Another possible explanation for the EBA activation is that it is also involved in integrating sensory-motor signals related to the representation of one's own body, including when no real motion is present (as during motor imagery).[76] This may potentially be owing to the overlap of EBA and MT.

Body/Face Contextual Effects

In the real world, bodies and faces are almost never perceived in isolation, but rather as an integrated whole. Two behavioral studies investigated how recognition of facial expressions is influenced by the accompanying whole-body expressions. In the first, participants were presented with congruent (fearful face on fearful body, angry face on angry body) or incongruent (fearful face on angry body, angry face on fearful body) compound stimuli, while they had to categorize the facial expression and ignore the bodily expression. The results showed that recognition of the facial expression was biased toward the emotion expressed by the body language, as reflected by both the accuracy and reaction time data.[22] In a follow-up study, facial expressions that were morphed on a continuum between happy and fearful were then combined with a happy or fearful whole-body expression.[77] Again, the ratings of the facial expressions were influenced toward the emotion expressed by the body, and this influence was highest for facial expressions that were most ambiguous (expressions that occupied an intermediate position on the morph continuum).

Body/Voice Contextual Effects

Research investigating audiovisual affect integration has mostly explored face–voice combinations. Behaviorally, these studies have highlighted a facilitated or impaired categorization judgment for congruent

and incongruent information, respectively, or simply that the percept of emotion is somehow altered when different types of affective information are presented in an audiovisual situation.[78,79] More recently, these multisensory effects have been generalized to a broader domain by investigating affective crossmodal influences in whole-body expressions. Participants were presented video clips of happy or fearful body language showing persons engaged in an everyday activity and in a realistic context.[80] These were simultaneously presented with either congruent or incongruent non-verbal human or animal vocalizations, or without auditory information. The results indicated that recognition of body language was indeed biased toward the emotion expressed by the simultaneously presented auditory information, whether it consisted of human or of animal sounds, showing that a crossmodal influence from auditory to visual emotional information can be obtained also for whole-body video images. Recently, a work from our laboratory has paralleled the set-up of de Vroomen and de Gelder,[81] who used morphed facial expressions, by using morphed body stimuli. Initial results suggest that the baseline categorization curve for bodies if shifted toward the emotion conveyed in a simultaneously presented voice, implying that the body and voice are perceptually combined into an audiovisual percept (manuscript in preparation).

More recent studies have used both electrophysiological and neuroimaging techniques to uncover the cerebral correlates of body–voice affect integration. One electrophysiological study demonstrated an amplitude reduction of the early auditory N1 component, followed by an enlarged P2 potential in audiovisual compared with unimodal conditions.[82] Furthermore, they also showed an emotion effect on the auditory N1, expressed by a shorter latency for fearful than for neutral audiovisual sets. Fearful displays also induced larger late positive components than all other emotional conditions. These results indicate some preference for the neural representation of emotionally relevant stimuli during early auditory processing stages.

One related fMRI study explored whether there exist brain regions that represent emotional mental states regardless of the particular sensory input that is perceived—that is, their aim was to isolate modality-independent representations of emotion.[55] Participants evaluated the intensity of emotions expressed by body movements, facial movements, or vocal intonations. The authors then used multi-voxel pattern analysis to search for brain regions in which emotion-specific patterns in one modality (e.g., bodies) could predict emotion-specific patterns in

another modality (e.g., voices). Such modality-independent activity patterns were found in the medial prefrontal cortex (MPFC) and left STS. Distinct patterns were found for each emotion (i.e., disgust, anger, fear, sadness, and happiness) across all different modality comparisons (i.e., face–body, face–voice, and body–voice). Thus, the authors suggest that MPFC and STS represent perceived emotions at a supramodal, modality-independent level.

SUBCONSCIOUS PERCEPTION OF BODY EXPRESSION

In view of the phylogenetic continuity in body expression of some central emotions and the underlying evolutionary basis of these is ability, a reasonable hypothesis is that perception can proceed without full attention and without visual awareness of the stimuli. We have accumulated some evidence in support of this, but a lot needs to be done still, especially in neurotypical populations.

Non-conscious perception of bodily expressions has been investigated using several different methods and patient groups. For example, Stienen and de Gelder[83] used backward masking to investigate the role of visual awareness in the perception of bodily expressions. Participants had to detect fearful, angry, or happy bodily expressions with different stimulus-onset asynchronies among neutral body distractors using a button press. After each trial, they had to indicate whether they were sure or guessed. Accuracy was high for all emotions, but fearful bodily expressions showed a lower covariance between objective and subjective experience. This suggests that fearful expressions automatically activate fear responses and capture the attention. Recently, masking techniques were also employed in order to show that multisensory integration of body–voice effect may also occur independently of visual attention.[84] These authors investigated via two related experiments whether whole-body expressions and voices can influence each other, even when the observer is not consciously aware of seeing the bodily expression. In the first experiment, the authors employed masking in order to hide the visibility of angry and bodily expressions. Participants then categorized these expressions while ignoring congruent or incongruent emotional voices. Results showed that the congruency between the emotion in the voice and the bodily expressions influenced the categorization of body expressions, regardless of their visibility—when emotional expression was congruent, categorization was aided. Interestingly, there was also a dissociation between objective and subjective measures: objective

categorization performance was still facilitated by the congruent emotional voice while this facilitation effect was absent in the subjective confidence ratings. In the second experiment, participants categorized the emotional voices combined with masked bodily expressions as fearful or happy. When the bodily expression was fearful, participants categorized the voice as being more fearful when the voice was a 50/50 morph between fearful and happy. Surprisingly, masked neutral bodily actions triggered more fear responses to the voice than when the voice was already slightly more fearful. Overall, these findings are consistent with earlier studies showing the cross-modal influence of human emotional sounds on the recognition of emotional body postures and the influence of emotional body postures on the interpretation of voice prosody.

Using a binocular rivalry paradigm, another technique for exploring subconscious processing[83] showed that differences in predominance ratio in favor of either faces or bodies were found for the fearful emotion compared with angry and neutral emotion, and that this effect was stronger for fearful faces. Fearful bodily expressions are such a salient signal that they can even overcome attentional biases in patients with hemispatial neglect. Tamietto et al.[85] tested in three such patients' visual awareness for fearful, happy, and neutral bodily expressions. When fearful bodies were presented in the contralesional visual field together with neutral bodies in the ipsilesional visual field, they were detected more frequently than happy or neutral bodies in the contralesional visual field. These results provide more evidence for automatic processing of emotion- and action-related information.

Moreover, studies involving patients with cortical blindness have provided strong evidence supporting the subconscious nature of body affect perception. For example, de Gelder and Hadjikhani[86] presented emotional (happy) and neutral body images (with the faces blurred) in the blind field of a patient with unilateral striate cortex damage. Behavioral results indicated that the patient could discriminate above chance happy from neutral body expressions, while neuroimaging results showed that unseen happy body images (as compared with neutral action images) selectively activated area MT, STS and the pulvinar nucleus of the thalamus, while the unseen instrumental neutral body images activated the premotor cortex. This suggests that in the absence of the striate cortex perception of implicit bodily emotion may be possible (see Figure 2).

Following from this, Van den Stock et al.[87] investigated the neural correlates of residual visual perception for dynamic whole-body emotional (angry) and non-emotional (neutral) actions in a patient with unilateral destruction of the striate cortex. Body stimuli were presented both in the intact and in the blind visual hemifields of the patient, and then comparison between angry and neutral bodies was performed separately for each hemifield. Results showed that in both hemifields, the comparison between emotional and non-emotion expressions resulted in increased activation in the primary somatosensory, premotor, and motor cortices. Furthermore, direct comparison of emotional modulation in the blind with intact visual hemifield highlighted selective activity in the right superior colliculus and bilateral pulvinar, which the authors suggests indicate a selective involvement of these subcortical structures in non-conscious visual emotion body perception (see Figure 2).

Finally, Tamietto et al.[88] used a complementary technique, diffusion tensor imaging (DTI), to study the connections between the AMG—a subcortical structure implicated in the perception of emotion—and subcortical visual structures (i.e., superior colliculus and visual pulvinar) in age-matched controls and in one patient with early unilateral destruction of the visual cortex. Specifically, the authors were investigating whether destruction of the visual cortex (a major input to the AMG) induced modifications in anatomical connections along this subcortical pathway, particularly the reduction of strength in the superior colliculus–pulvinar pathway, and strengthening of the pulvinar–amygdala and direct superior colliculus–pulvinar–amygdala pathways. This evidence strongly suggests that there is considerable neural plasticity in the anatomical connections between subcortical visual structures that are involved in the processing of emotional stimuli.

CONCLUSIONS

A decade of research has now established that emotional body expressions are stimuli that are reliably perceived and have a solid neural basis. Future research starting from these findings need to address questions on the specificity. In the course of investigating this neural basis, our research increasingly provides evidence for the active component at the core of body expression perception. In the original sense in which Darwin used the notion, perceiving body expression triggers adaptive action. Further research is needed to understand how our original notion that 'fear fosters flight'[38] leads to adaptive action preparation at different levels in the brain. Reflex-like

actions and intentional actions are fundamentally different and are presumably subserved by different brain systems. The challenge is to show that already at the reflex stage, without dependence on conscious action intention, we are in the presence of meaningful behavior.

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