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OPINION

Towards the neurobiology of emotional body language

Beatrice de Gelder

Abstract | People's faces show fear in many different circumstances. However, when people are terrified, as well as showing emotion, they run for cover. When we see a bodily expression of emotion, we immediately know what specific action is associated with a particular emotion, leaving little need for interpretation of the signal, as is the case for facial expressions. 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 automatically perceived and understood, and their role in emotional communication and decision-making.

What do body positions and movement reveal about emotions? From everyday experience we know that an angry face is more menacing when accompanied by a fist, and a fearful face more worrisome when the person is in flight (that is, running away). When a frightening event occurs, there might not be time to look for the fearful contortions in an individual's face, but a quick glance at the body may tell us all we need to know. This article reviews what has been discovered so far and provides a framework for the interpretation of and further investigation of emotional body language (EBL).

Many valuable insights into human emotion and its neurobiological bases have been obtained from the study of facial expressions. By comparison, the neurobiological bases of EBL are relatively unexplored[1–5]. Human and non-human primates are especially sensitive to the gestural signals made by other primates, and use these signals as guides for their own behaviour. Fearful faces signal a threat, but do not provide information about either the source of the threat or the best way to deal with it. By contrast, fearful body positions signal a threat and at the same time specify the action undertaken by the individuals fearing for their safety. Unravelling these behavioural aspects brings emotion researchers closer to the evolutionary link between emotion and behaviour and the phylogenetic continuity of emotion–action circuitry across species. It also sheds light on disorders that combine emotional and motor components, such as autism, schizophrenia and Huntington's disease.

Studying the neurobiology of EBL is particularly timely because the topic introduces a new and biologically realistic context to what has already been learned about human emotion from isolated facial expressions during the past two decades. EBL consists of an emotion expressed in the whole body, comprising coordinated movements and often a meaningful action, and so prompts research to go beyond facial expressions and to consider issues of perception of movement and action, which have so far been researched in isolation and not specifically related to perception of EBL.

After discussing why the role of the body is important in understanding emotion and communication, I describe research on perceptual similarities in the neuroanatomy and temporal dynamics between face and body perception, and conclude that recognition of facial expressions is strongly influenced by EBL. First, I ask why seeing emotional bodies automatically transmits the emotion and I relate this question to the combined presence of emotions, movement and actions. Next, I review dissociations between these different aspects in some clinical populations, including the role of deliberate processes and consciousness. Finally, I suggest an integrated framework for research on EBL perception and discuss key outstanding questions.

History of emotional body language

There is considerable history associated with the link between emotion and behaviour[6], and the relationship between emotion and whole-body action was at the centre of the pioneering work of Bulwer[7], Bell[8], Gratiolet[9] and Duchène de Boulogne[10], culminating in Darwin's evolutionary approach to emotions and their bodily expressions[11]. In a radical departure from the Cartesian view of emotions as private mental episodes, Darwin argued that emotions are adaptive in the sense that they prompt an action that is beneficial to the organism, given its environmental circumstances. Darwin described the body expressions (for example, EBL, vocalizations and facial expressions) associated with emotions in animals and humans, with a particular emphasis on the link between emotion and action[6,12], and highlighted the roots of facial expressions in adaptive actions[13]. So, a species' ability to produce and perceive some basic categories of EBL is an integral part of its phylogenetic history.

Box 1 | **Emotions and the amygdala**

The involvement of the amygdala in emotional behaviour has been known for some time[87], and the amygdala figures prominently in both human and non-human emotion research[16,23]. The amygdala has a complex structure consisting of twelve different subnuclei, many of which are bilaterally connected to different basal ganglia and cortical structures[18,78,88]. In the macaque, the amygdala receives inputs from the superior temporal sulcus and the ventrolateral orbitofrontal cortex (OFC)[89], as well as from their reciprocal connections, which gives the amygdala, to some extent, control over the ventrolateral OFC[90]. The amygdala seems to be particularly involved in the assignment of signal relevance[17,75,91–93] and, as a consequence, in the modulation of brain structures that control behaviour. Of particular interest is the modulation of structures that relate to fear behaviour, elicited by fear signals, whether these signals consist of sound[16], sight, smell or touch[25]. Lesions of the amygdala cause a lack of social inhibition in the adult primate[93] and abolish characteristic fear behaviour[94,95], and, in humans, lead to excessive trust of others[96]. Congenital anomalies and acquired lesions, as well as deficits in functional connections, cause changes in the social behaviour of the young macaque[97–99].

As proposed here, the amygdala has one role in a network of predominantly subcortical structures and another in a network of cortical structures. The first circuit is the basis of automatic reflex-like emotional behaviour and the second sustains recognition of emotional body language (EBL), deliberation and action (see also BOX 2). The amygdala exerts a crucial modulatory effect on other (sub)cortical structures that process sensory input and on motor structures without in depth processing by higher cognitive and cortical systems. So, emotional behaviour can be initiated even if visual stimuli such as EBL, facial expressions, sounds or smells are processed without conscious recognition[100–102]. This 'blindfeeling' might occur when unseen EBL automatically activates facial mimicry and triggers peripheral physiological changes, which William James considered the essence of emotion. These feedforward effects of EMG (electromyography) occur in parallel with feedback effects on the amygdala from detailed stimulus processing in the ventral cortex, as has been shown for fusiform cortex to amygdala modulations[33,34,102].

Emotion and the amygdala. Emotion is a multidimensional phenomenon, and theories of the human emotional brain range from highly cognitive processes preceeding deliberate action to perception, and to reflex-like behaviour[6,14–16]. However, I focus only on the perception of EBL. Current models of human emotion[17–23] place the amygdala at the core of a network of emotional brain structures, involving the orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), premotor cortex and somatosensory cortex. In animal models it is thought that there is a wider network of amygdala connections, as animal species investigated by researchers show a broader range of behaviours, including posture, movement, vocalizations, odour and touch. The amygdala decodes the affective relevance of sensory inputs and initiates adaptive behaviours via its connections to the motor systems[24] (BOX 1). Similar processes are triggered in situations in which the body is directly attacked, for example, when external stimuli invade personal space and defensive EBL is evoked by direct stimulation of the areas listed above[25].

Faces belong to bodies

From our encounters with others, we are just as familiar with EBL as with facial expressions. EBL is perceived as a means of influencing others, for which social psychologists have provided detailed descriptions (for examples, see REF. 26). During the past few decades, some isolated psychological studies have appeared[5,27], but neuroscientific experiments on how humans perceive bodies have been reported only recently. A challenging question in the wake of the long-standing debate about whether the brain is functionally specialized to process faces is whether there is also an area in the brain that is specifically activated by seeing body movement or posture. Are we as expert at interpreting body language as we are faces? There are areas in the brain that respond to facial stimuli, but is there a corresponding area in the brain that is dedicated to bodies? Are the same areas involved in perceiving facial expressions and EBL? Are consciousness and attentional resources needed for processing bodies and recognizing body movement and posture? Some of these questions can already be answered.

How do we perceive bodies? Research on visual recognition of bodies started by addressing the classic questions in the face recognition literature: whether the perceptual system is tuned to the overall structure and whether there is a dedicated functional neural system. It is already clear that faces and bodies both have configurational properties. In the first stages of face, as well as body, perception the brain is tuned to extracting the overall configuration rather than the details[28,29].

Besides behavioural evidence, there are findings from single-cell recordings that also show a degree of specialization for either face or neutral body images in the superior temporal sulcus (STS)[30,31]. Functional MRI studies in humans[32] indicate that a region near the middle occipital gyrus (known as the extrastriate body area, EBA) responds selectively to bodies but shows little response to isolated faces[33–35]. Interestingly, precursors of adult body recognition are already apparent in early development, as has been noted for facial recognition[36]. In 3-month-old infants, distorted bodies have a significant effect on the brain potential that is typically evoked by the sight of faces and bodies[37].

Does the convergence across these results indicate a degree of body specificity even more strongly, or does it imply that there is a module for body perception, as is sometimes argued for faces? Or, alternatively, as is clearly the case for face perception, is body perception implemented in several different areas (mainly concentrated in the occipital gyrus and fusiform gyrus) that have different functions and are active at different moments in time[21,38]? An answer on the specific neural basis of body representation depends on which body attribute is being considered (for example, posture, movement, instrumental action or emotional expression). Adopting this network perspective, I concentrate on how the brain deals with the emotional expression imparted by whole bodies.

Neural basis and temporal dynamics. The first brain imaging study of EBL with realistic body stimuli used fearful and happy EBL images, each of which was compared with images of neutral whole-body actions (for example, getting dressed or opening a door). Fearful bodies activate the two main areas associated with the processing of facial expressions of fear — the amygdala and the right middle fusiform gyrus. When we see neutral, fearful or happy whole-body expressions with the facial expression blurred, fear images activate these areas[34] (FIG. 1).

The similarity between perception of facial expressions and EBL extends to temporal dynamics. Recent studies show that we process bodies as rapidly as faces[29,37,39], and perceive the same properties of both facial and body stimuli. This is shown by the finding that body images produce the N170 (a waveform in the electroencephalogram (EEG) with negative amplitude that peaks about 170 ms after stimulus presentation), which was originally viewed as the first temporal marker of face-specific processing. It seems that the initial facial and body image processing stages are probably similar[37,39,40], as these stimuli elicit comparable amplitude, latency and scalp distribution of the N170. Evidence suggests that objects are not processed in the same way, as control objects did not generate an N170 (REF. 29; FIG. 2).

EBL overshadows facial expressions. If bodies are recognized rapidly, it would be expected that EBL might influence face processing in the earliest stages of facial recognition, and even when attention is focused on the facial expression. To investigate this possibility, facial expressions were combined with congruent or incongruent bodily expressions (FIG. 3). EEG responses to these face–body combinations[39] showed that the brain is sensitive (within 100 ms) to any incongruence between facial expression and EBL.

So, compared with a range of control objects, both bodies and faces trigger specialized visual recognition skills. However, why they do this is not clear. Is it because of our visual expertise, or because bodies are salient and grab our attention more than inanimate or even animate objects in the environment? Or is it because the sensory, emotional and motor attributes we are capable of generating in our own mind and body influence our visual perception of bodies and faces? New research indicates that our own emotional and behavioural competences do affect our visual perception, and so the issue of body perception moves out of the strictly visual domain to include those brain areas that are involved with emotion and behaviour.

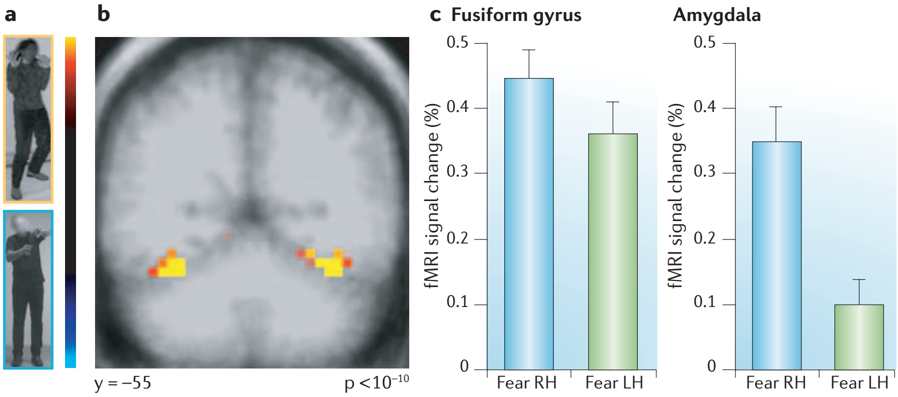

Figure 1 | **The fusiform gyrus and the amygdala show increased activation in response to bodily expressions of fear. a** | Example of the stimuli used: top, body expression of fear; bottom, emotionally neutral body posture (pouring liquid into a container). **b** | Functional MRI (fMRI) activation associated with fearful compared with neutral bodies, averaged across seven participants, in Talairach space. Activation shown is in response to the fearful bodies (yellow) in the fusiform face area (FFA). No activation is seen for the neutral bodies (blue). **c** | Average percentage signal change in functionally defined regions of interest in the FFA and amygdala in fearful compared with neutral body postures. The right hemisphere (RH) shows significantly more activation than the left (LH) in the amygdala only (p <0.001). Adapted, with permission, from REF. 34 © (2003) Cell Press.

Why emotional bodies are contagious

Fear is contagious, as are joy and sadness, but what is the underlying mechanism for this? Is it the emotion expressed? Perhaps it is the movement represented or implied? Or the action represented? Or is it a combination of all these factors? If so, does one trigger the others? Functional brain imaging in participants passively viewing images of whole bodies shows activity in a complex of areas that are known for processing not only emotions and biological movement but also goal-directed actions. By comparison, viewing fearful whole-body expressions increases activity in areas that are known to specifically process emotional information (that is, the amygdala, OFC, ACC, anterior insula and nucleus accumbens)[2] as well as in subcortical structures (mainly the superior colliculus, pulvinar and caudate nucleus) (BOX 2).

Furthermore, the use of body images might boost the activity in structures that have a role in our own body experience, such as the somatosensory cortex and insula, more than images of faces or affective pictures do. The OFC controls regulation of emotion and bodily feelings as well as the brain's representation of the body[15], and acts in concert with the amygdala and somatosensory cortex and insula, which are activated in the fear body condition. This is consistent with neural activity in cortical areas that provide internal representations of one's bodily state[41], such as the anterior insula, which is important in connecting the medial prefrontal cortex and the limbic system, and, in turn, has a role in interoception[42].

The data so far indicate that emotional contagion — the automatic spread of emotion and body movement to another person

Box 2 | **Emotions and motor programs**

Emotion has traditionally been connected with motor activity, but the direction of the connection has long been a matter of speculation. One extreme view is the James–Lange theory, which argues that the subjective experience of emotion is a byproduct of the motor activity elicited by the stimulus. The discovery of mirror neurons again draws attention to motor structures. 'Mirror neurons' in the ventral premotor cortex area F5 and in the parietal area 7b fire when an animal performs a given action, as well as when the same action is observed (for a review, see REF. 103). Functional neuroimaging provides evidence that humans have similar mirror neurons. Based on these findings, it has been proposed that mirror neurons are the basis of social cognition[58]. However, direct support for the role of mirror neurons in perceiving emotion is still scarce. A strong defence of the role of mirror neurons in emotion comes from research into autism. People with autism show less activity in the mirror neuron system when either passively observing or actively imitating facial expressions[104], consistent with reduced cortical thickness in mirror neuron brain areas in autism[71,105]. However, alternative explanations can be envisaged. One is that a deficit in action representation and mirror neurons is itself due to a deficit in the amygdala[99] that causes poor connectivity to superior temporal sulcus and premotor cortex structures[62]. This makes the clinical pattern of emotion deficits observed so far in autism quite similar to that of patients with amygdala lesions, who also show normal mimicry[49]. In neither case does the (in)ability to show automatic facial mimicry prove that mirror neurons are the basis of social cognition.

However, there is a more general explanation — in line with the two-systems theory proposed here — for the apparent similarity between fear observed and that displayed in response to it by the observer. Perception of a fear stimulus (whether this is a sound, face or body) triggers a fear reaction in the observer (either in the face or body, or both) based on direct activation of a fear motor program that is encoded in subcortical circuitry and not on imitation. Fear reactions and fear contagion following the observation of fear reactions need not involve the cortical action circuit in which mirror neurons have a role, at least not at the basic level. Of course, detailed studies of emotional body language other than fear are needed in order to understand the interactions between the two systems.

when an individual is viewing EBL — is based on perception of the emotion, and it is therefore not surprising to find an overlap with the activations observed in studies using facial expressions. However, significant fear-related activation in response to EBL was also observed in areas that have a role in action representation and in other motor areas. An important issue to resolve is whether the fear-related activation observed in the motor area follows from fear perception, or the other way around, as when perception of a movement leads to recognition of its emotion.

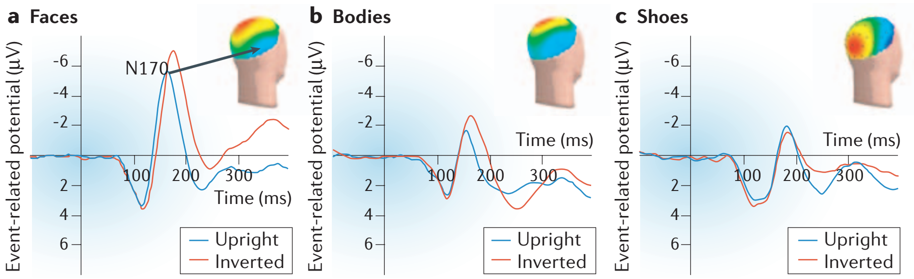

Figure 2 | **Recordings of the amplitude of the N170 waveform triggered by various stimuli.** Faces and bodies generate similar amplitude patterns, and the same increase is observed when the faces and bodies are inverted. However, this effect is not obtained for control objects. Traces show averaged event-related potentials (ERPs) at the P8 scalp site for upright and inverted faces (**a**), bodies (**b**) and control objects (**c**). Insets show scalp distributions of peak amplitude of the N170 electroencephalogram produced by upright stimulus presentations. ERPs and topographies of faces and bodies were pooled across neutral and fearful faces and bodies[29]. Adapted, with permission, from REF. 29 © (2004) Lippincott, Williams & Wilkins.

Bodies in movement. As movement is a key feature of EBL in the natural world, it probably contributes to the recognition of EBL, and may induce emotion with minimal input from the other aspects of EBL. How much of EBL recognition/perception is perception of movement? And which comes first — perception of movement or perception of emotion? Passive viewing of still body images activates motor areas of the brain. This might be a consequence of the brain filling in the missing dynamic information[43,44], but it is noteworthy that activity in the fear-related brain areas is much higher than for neutral bodies representing actions, which suggests another source beyond implicit movement perception. Indeed, during the centuries before the advent of media that enabled dynamic image production, powerful emotional effects were generated in the visual arts with still images (for an example, see BOX 3).

Biological movement provides important information about the nature of the object that is moving, the direction of movement or the meaning of the action, and this is observed even in the early stages of development. Three-month-old infants can discriminate point-light displays of human movement from random patterns[45]. Neurons selectively activated by biological motion have been found in the monkey STS[46]. Animal study results indicate that sensitivity to biological movement appears early in development. For example, newly hatched chicks preferentially approached point-light sequences that suggest biological motion[47], which might be a prerequisite for 'filial imprinting'. Early sensitivity to movements of members of the same species might sustain body recognition in infants. It might be an important trigger in neonatal development, as is indicated by deficits in perceiving biological movement that are associated with autism[37] (BOX 2).

There is already some evidence of the power of movement alone in the induction of emotion. The movement of an area of dots as a collective that is perceived as pleasant triggers amygdala and fusiform cortex activity[33], as well as activity in premotor cortex and sensorimotor areas[48]. Consistent with these findings, damage to the amygdala[48] impairs our ability to recognize emotions from simple geometrical figures, and, as a consequence, affected patients report the movement but do not perceive this movement as an interaction between agents. Of course, these are cognitively challenging stimuli requiring the observer to 'anthropomorphise'[48], and these may appeal more to the so called 'theory of mind' skills, whereby the brain is challenged to come up with more theory-based interpretations than that it is engaged in perception.

Bodies in action. The previous question concerning the role of movement in EBL perception can also be raised about EBL and action. Both the fusiform body area[49] and the EBA are sensitive to actions shown by the body[50]. In real life, biological movements frequently consist of goal-directed actions. For example, on seeing someone fleeing, observers describe the action rather than the movement — that is, the person is trying to reach the exit rather than is running away. Consistent with single-cell recordings in the macaque brain, the results of brain imaging studies in humans[51–53] show that the STS, parietal cortex and premotor cortex are activated during the perception of biological movements (for a review, see REF. 54) and of object-directed actions[55]. The dorsolateral prefrontal cortex, precentral gyrus, supplementary motor area (SMA) and inferior parietal lobule (IPL)[55] all have central roles in organizing and realizing our motor behaviours, as well as in the perception of the behaviours of others (for a review, see REF. 53).

More recently, the discovery of neurons that encode complex movements and actions (mirror neurons)[52,56,57] has added a new dimension to the role that motor areas might have in perception of body movement and EBL. It has been proposed that mirror neurons provide the neurobiological basis for all emotional and social cognition skills[58,59] (BOX 2). This means that, in contrast to animal models, in which the amygdala emotionally tunes the motor system, in humans it could be motor neuron activity that spreads to the amygdala. This hypothesis was tested in a study that compared brain activations during passive viewing of still facial expressions and viewing of the same stimuli but with the instruction to imitate[60]. Higher amygdala activity was obtained in the imitation condition, and was taken as direct support for the hypothesis that motor system activation triggers the amygdala. However, this higher activity was obtained after instructions to imitate the expressions were given, so it could be argued that the imitation instruction led to more active encoding of the faces.

More recent studies used video clips of angry and neutral hand actions[61], and either fearful or neutral whole-body gestures[62]. Comparing passive observation of neutral body gestures with angry hand movements and angry face movements revealed substantial overlap between the face and hand conditions, with other areas involved besides the face area in the fusiform cortex. When the observed hand action was performed with emotion, additional regions were recruited, including the right dorsal premotor area, the right medial prefrontal cortex, the left anterior insula and a region in the rostral part of the supramarginal gyrus. Interestingly, only the supramarginal gyrus was specific for angry faces[61]. The results of this study suggest that watching an action that is performed

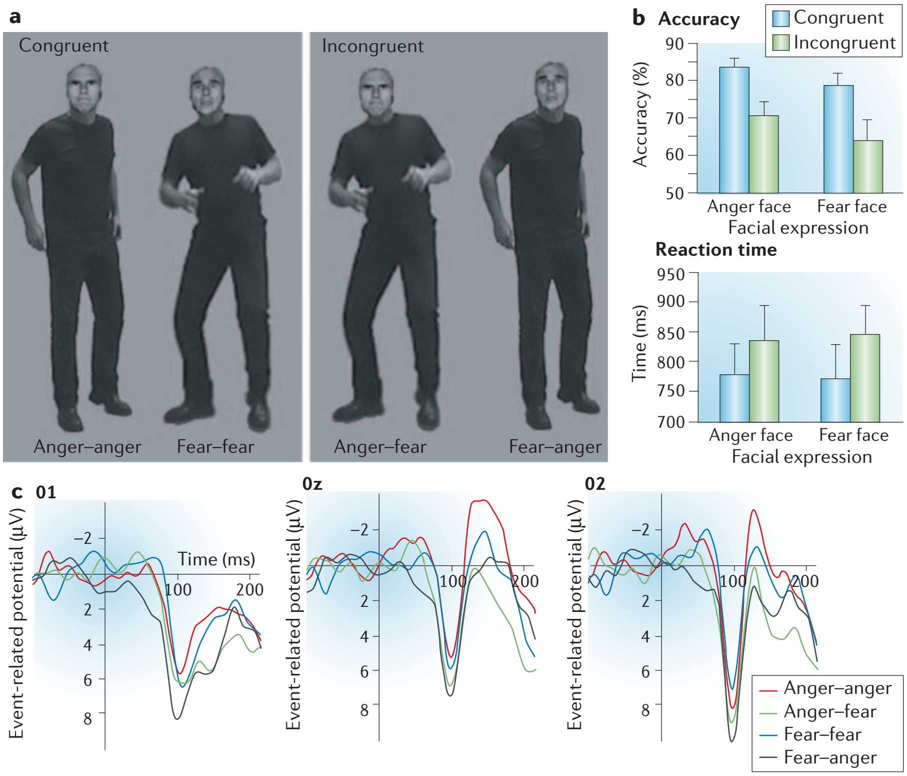

Figure 3 | **Time course of face–body incongruence sensitivity. a** | Examples of the four different categories of face–body compound stimuli used. Congruent and incongruent stimuli consisted of the same material in different combinations. The bodies of the two congruent stimulus conditions were swapped to create a mismatch between the emotion expressed by the face and that expressed by the body. **b** | Behavioural results of the facial expression task for the compound stimuli. Participants had to judge the expression of faces that were accompanied by either a congruent or incongruent bodily expression. Categorization of facial expressions in the presence of an incongruent body emotion significantly reduces accuracy and increases observers' reaction times. **c** | Event-related potentials at occipital electrodes at scalp sites O1, Oz and O2 for the face–body compound stimuli, showing a sharp positive deflection peaking at ~100 ms. This so-called P1 scalp site component is sensitive for the mismatch between the facial expression and the emotional body language. Adapted, with permission, from REF. 39 © (2005) National Academy of Sciences USA.

with emotion induces affective modulation of the motor program.

This particular issue was addressed in a study using video clips of whole bodies showing either a neutral or a fear expression[62]. Amygdala activity was found to be enhanced during the perception of both static and dynamic fear bodies, with increased activity in the STS and premotor cortex. Augmented responses in the STS and premotor cortex are related to increased connectivity between these regions and the amygdala. These results support the idea that the amygdala has a crucial role in tuning the motor system to the affective meaning of sensory inputs. Moreover, they support a relative independence between fear processing and action representation systems, rather than substantiate the alternative proposal that perception of the emotion expressed in actions is primarily based on the representation of that action.

Neuropsychological dissociations

Sensory, emotional and behavioural systems are closely interlinked in the normal perception of EBL and, together with emotional awareness required for decision making and carrying out actions, they define normal adult emotional cognition. But the study of clinical populations with selective deficits in one of the components sheds light on the integration that normally occurs between these areas.

Nonconscious recognition of EBL. The extensive literature on the role of attention and consciousness in the recognition of facial expressions convincingly establishes that some facial expressions are processed without full awareness, either because they are processed with minimal attention or because they are simply not consciously seen. The fact that unattended EBL influences face recognition already suggests that EBL need not be explicitly noticed to have an effect[39]. Patients with hemispatial neglect ignore stimuli in the space contralateral to their right parietal lesion, but this neglect is strongly reduced when a fear body is presented in the normally neglected visual field[63]. This suggests that intact frontolimbic and visual areas might continue to mediate representation of emotional and action-related information conveyed by fearful EBL despite damage to the right parietal lobe.

Patients with complete loss of vision in one hemifield present a radical test of unconscious perception of EBL, because under appropriate testing conditions they are not aware that a stimulus is being presented in their lesioned visual field. Following up on earlier findings of nonconscious recognition of facial expressions[64–67], we observed that two such patients had affective blindsight[68] for EBL that was at least as strong as their previously reported blindsight for facial expressions[63]. This is consistent with the possibility[68] that, in the absence of cortical input sustaining visual awareness, accurate blind guessing of the emotional stimulus category might, in part, be based on information from sensorimotor structures and the anterior parietal cortex that has a role in bodily experience and emotional feelings[41]. The subcortical pathway mediating affective blindsight might exert an influence on the cortical areas representing bodily states and emotional feelings, possibly involving the right somatosensory cortex[69]. Both the amygdala and somatosensory cortex, as well as the OFC, have connections with visceral, autonomic and muscular centres of the body[15,23,70].

Studies of visual deficits have already provided evidence that perceptions of emotion and movement can be dissociated from each other. Patients with amygdala deficits perceive the movements of animated shapes but do not describe them as social emotional interactions[48]. They can imitate the facial expression[49], as can patients with autism who have severe difficulty processing the emotions of others[71]. In other cases (for example, patients with Huntington's disease), impairments in perceiving the movement, as well as the emotion, have been observed, and this population offers us the possibility of understanding the combined role of subcortical and cortical emotion networks[72,73].

A two-systems theory of EBL

Reviewing how emotion from EBL is processed in the brain leads us to a 'two-systems' model of emotion–behaviour connectivity. The amygdala is a key piece in the orchestration of two separate emotional circuits, an automated reflex-like circuit that predominantly resides in subcortical structures and a cortically controlled circuit in the service of recognition and deliberation. In higher organisms, both systems cooperate in decoding EBL signals and monitoring behaviour following an emotional signal provided by EBL. The two-systems model regroups the structures that have been reported in the relevant literature so far, but viewed from the perspective of EBL, which could direct future research and help to define outstanding questions. Both systems are closely connected with a set of structures that support bodily sensations and bodily awareness. This model is added for the sake of completeness, but it is not the focus of this review.

The primary network sustains the rapid automatic perception of EBL and preparation of adaptive reflexes. Subcortical structures are thought to have roles in this rapid, non-conscious route that have some similarities with what has been proposed for non-conscious recognition of faces[74,75], but with stronger and more direct connections with motor structures. This route involves the superior colliculus, pulvinar, striatum (putamen and caudate) and basolateral amygdala. Interactions in the pulvinar–superior colliculus–amygdala circuit might sustain preparation for adaptive behaviour, such as automatic fear behaviour following observation of a fear expression in EBL, and autonomic responses (increases in heart rate and blood pressure). Single-cell recordings in the superior colliculus have shown that this area responds to the appearance and movement of stimuli, and that this detection of events is not dependent on detailed stimulus analysis[76]. Most importantly, subregions of the superior colliculus support defensive reflexes (for example, freezing, withdrawal, flinching and exaggerated startle)[77]. The basolateral amygdala complex assigns affective value to incoming stimuli either directly or through its connections with other sensory systems[75,78–80]. It either stores associations directly, or modulates other areas[78]. The striatum is part of a neural circuit that guides behaviour, based on reward function (FIG. 4).

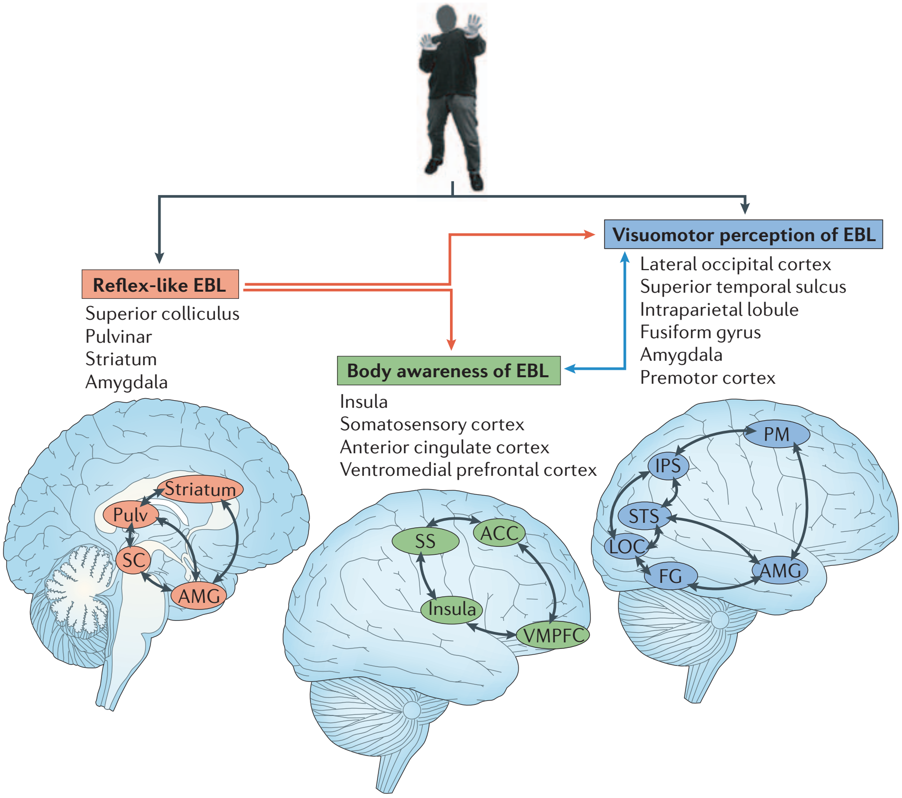

Figure 4 | **The three interrelated brain networks involved in emotional body language.** **a** | Reflex-like emotional body language (EBL) (orange) involves the superior colliculus (SC), pulvinar (Pulv), striatum and amygdala (AMG). **b** | Body awareness of EBL (green) involves the insula, somatosensory cortex (SS), anterior cingulate cortex (ACC) and ventromedial prefrontal cortex (VMPFC). **c** | Visuomotor perception of EBL (blue) involves the lateral occipital complex (LOC), superior temporal sulcus (STS), intraparietal sulcus (IPS), fusiform gyrus (FG), amygdala (AMG) and premotor cortex (PM). Visual information from EBL enters in parallel via a subcortical (red) and a cortical (blue) input system. Feedforward connections from the subcortical to the cortical system and body awareness system are shown in red, reciprocal interactions between cortical system and body awareness system are shown in blue. Anatomical image adapted, with permission, from REF. 106 © (1996) Appleton & Lange.

The second system consists of a cortical network with reciprocal connections to the primary circuit. This system includes the frontoparietal motor system, and connectivity between the amygdala and the prefrontal and ventromedial prefrontal cortex has a major role in the processing carried out by this system. In this system, affective stimulus input is decoded in combination with past experience and memory. The main role of the second system is to perceive EBL in detail and to compute the behavioural consequences of an emotion and to decide on a course of action in response to the stimulus; typically, the action is determined by the stimulus eliciting the bodily reaction (for example, fear expressed in running).

Both systems have connections with brain structures that have a role in connecting awareness of bodily states to decision making[41,69]. The two input systems also have numerous interconnections, as well as connections with the body awareness system, but can function relatively autonomously, and this relative autonomy guarantees that an alerting event signalled in the subcortical pathway elicits a rapid reflex-like reaction in the absence of detailed stimulus processing and is not systematically overruled by

BOX 3 | **Feeling the fall of the angels**

Still images can evoke strong emotional responses on first sight, and this ability to resonate with the emotional movement expressed in these images has been explored by visual artists since the beginning of painting and sculpture. For example, picture yourself in front of Rubens' painting 'The Fall of the Damned' (see Further information). The first impression is one of turbulence and movement, and the cascade of falling bodies gives one an immediate feeling of vertigo. Only after that initial sensation does the story of the fallen angels come to mind and does the eye start to analyse the cascade of human bodies and speculate on the meaning of the visual scene. Initial reactions are based on our capacity to effortlessly read body language. It is only at a later, more deliberate stage of recognition that we elaborate on the context of the body language depicted in an image and explore it consciously.

concurrently available positive information[65]. Similarly, fearful EBL can be triggered through electrical stimulation of the ventral premotor cortex[25] without there being a connection with the primary system to provide the emotional dimension of the EBL. The relative autonomy of the two systems has also been underscored in relation to other aspects of behaviour. For example, the primary system can gain dominance when pleasure-seeking behaviour becomes habitual, as in drug addiction. The change from voluntary to more habitual and compulsive drug use represents a transition at the neural level from prefrontal cortical to striatal control over drug-seeking and drug-taking behaviour[81,82]. The interactions between the two systems might also be modulated by contextual knowledge that can diminish reliance on feedback mechanisms in the neural circuitry of trial-and-error reward learning[83].

Outlook

The available literature suggests that the brain processes EBL rapidly by a mechanism that involves neural resources known to have a role in perceiving emotional signals, such as facial expressions and structures involved in triggering behaviour and perceiving action. I suggest a two-systems model of EBL that encompasses, in dynamic equilibrium, EBL manifestations that are based on reflexes, which are automatically evoked by the emotional signal, and those that consist of deliberate emotional actions and are underwritten by a cortically controlled system of reflection and decision-making. How specific is the two-systems model for EBL? To the extent that this model represents how the brain reacts to emotional signals, there are similarities with existing models of how facial expressions are recognized[20,23], most directly with models based on two separate, relatively independent systems of cortically and subcortically based face processing[21,36,74]. However, there are significant differences when compared with face models of emotion, and future research will need to investigate this further. Indeed, the sight of a fearful face can mean many different things to the observer, including a signal to look for sources of danger or an invitation to empathize. However, the sight of a fearful body is a more direct cue to act. Moreover, the major structures in EBL described here also have a central role in pleasure-seeking behaviour, and the present model has important similarities with the model of a dynamic interaction between an impulsive (reflex-like), and deliberate reflective (cortically controlled) behaviour that is related to both affective experience and decision-making[81]. The distinction between a reflex-like and a deliberate emotion–action system will allow us to integrate types of EBL other than that that is closely linked to the basic emotions covered here, for example, the more deliberate and controllable EBL that occurs in sophisticated social interactions. Like primates, humans use their fine sensitivity to the gestural signals of others in assessing status and manipulating outcome (for example, in negotiations in microeconomic situations), and in situations in which it is beneficial to hide our intentions (for example, when gambling).

Is EBL akin to language? At present, the expression 'EBL' is a convenient shortcut. It might be a useful heuristic approach to view EBL as a language consisting of a core emotional motor system with genuine primitives and a combinatorial syntax. So far, this hypothesis seems consistent with results from motor control studies showing that the control of multi-joint movements is based on synergies between simpler components that encompass only a limited number of joints[84,85]. Synergies between the building blocks of EBL might define meaningful components for modelling kinematics[84] and for explaining the perception of biological motion[86].

Finally, the relationship between emotion and behaviour might depend on the specific emotion. For example, food-induced disgust is rigidly linked with specific motor activity, but this link is much more complex in the case of fear, in which the range of adaptive actions varies from running away from the sound of gunfire to freezing on the spot on seeing a snake. Furthermore, EBL might not have the typical one-to-one relationship with specific emotions that has been assumed for basic facial expressions since the work of Ekman in the 1970s. As exemplified by the results of basic facial expression studies, the context largely determines which behaviour is adaptive. Because, in contrast to an isolated facial expression, EBL provides the emotion as well as the associated action. EBL is a less ambiguous signal and a more direct call for attention and action in the observer.

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Competing interests statement

The author declares no competing financial interests.

FURTHER INFORMATION

Fall of the Damned: http://www.pinakothek.de/alte-pinakothek/sammlung/rundgang/rundgang_inc_en.php?inc=bild&which=6368

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