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Review

Why bodies? Twelve reasons for including bodily expressions in affective neuroscience

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Why bodies? It is rather puzzling that given the massive interest in affective neuroscience in the last decade, it still seems to make sense to raise the question 'Why bodies' and to try to provide an answer to it, as is the goal of this article. There are now hundreds of articles on human emotion perception ranging from behavioural studies to brain imaging experiments. These experimental studies complement decades of reports on affective disorders in neurological patients and clinical studies of psychiatric populations. The most cursory glance at the literature on emotion in humans, now referred to by the umbrella term of social and affective neuroscience, shows that over 95 per cent of them have used faces as stimuli. Of the remaining 5 per cent, a few have used scenes or auditory information including human voices, music or environmental sounds. But by far the smallest number has looked into whole-body expressions. As a rough estimate, a search on PubMed today, 1 May 2009, yields 3521 hits for emotion × faces, 1003 hits for emotion × music and 339 hits for emotion × bodies. When looking in more detail, the body × emotion category in fact yields a majority of papers on well-being, nursing, sexual violence or organ donation. But the number of cognitive and affective neuroscience studies of emotional body perception as of today is lower than 20.

Why then have whole bodies and bodily expressions not attracted the attention of researchers so far? The goal of this article is to contribute some elements for an answer to this question. I believe that there is something to learn from the historical neglect of bodies and bodily expressions. I will next address some historical misconceptions about whole-body perception, and in the process I intend not only to provide an impetus for this kind of work but also to contribute to a better understanding of the significance of the affective dimension of behaviour, mind and brain as seen from the vantage point of bodily communication. Subsequent sections discuss available evidence for the neurofunctional basis of facial and bodily expressions as well as neuropsychological and clinical studies of bodily expressions.

1. BODILY EXPRESSIONS ARE RECOGNIZED AS RELIABLY AS FACIAL EXPRESSIONS

Prima facie, there is no historical explanation as to why bodies have not captured much attention. In fact, two of the most illustrious theoreticians of emotion, Darwin and James, discussed whole-body expressions at great length. Darwin famously included postural descriptions in *The expression of the emotions in man and animals* (Darwin 1872/1965), and James (1890) investigated recognition of emotion with photographs of whole-body posture. More recently, theoreticians of emotion like Frijda (1988) and later Tomkins (1995) stressed the intimate link between emotion and action and were thus naturally led to emphasize the importance of the body. The fact that bodily expressions never occupied centre stage in emotion research may have been related to scepticism among observers that has its roots not so much in theory as in empirical results dating from the first generation of investigations of whole-body stimuli. For example, Ekman (1965) performed two studies on recognition of emotion from bodily expressions. But the results seem to have led him to sharing this scepticism. He concentrated on facial expressions to the detriment of bodily ones as chances to find evidence for emotion expression universals loomed larger in the domain of facial expressions.

But in recent decades researchers have taken up the issue of bodily expression recognition, and results from a number of behavioural experiments using independent stimulus sets now allow us to conclude that recognition performance for bodily expressions is very similar for face and body stimuli and this counts for studies with both static and dynamic whole-body stimuli. Available studies, whether focusing on recognition *per se* or preparing a set of validated body stimuli, have indeed found a high degree of agreement

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among observers (de Meijer 1989; Dittrich *et al.* 1996; Wallbott 1998; Hadjikhani & de Gelder 2003; Atkinson *et al.* 2004). A similar high consensus is found for videoclips depicting emotions or emotion expressing instrumental actions (Grèzes *et al.* 2007; Pichon *et al.* 2008, 2009). As is to be expected, performance is lower when point-light stimuli are used instead of full images. Recognition rates are around 10 per cent higher for dynamic images than for their still counterparts and they increase when the face is not blanked out. These are all factors that may be mainly related to the amount of information in the stimulus. In conclusion, when tested with comparable stimuli and under comparable viewing conditions, there is as much consensus for recognition of bodily expressions as there is for recognition of facial expressions.

Two other observations were also made in the earlier and more anecdotal reports on bodily expressions and they have since taken on special importance. These relate to casually observed phenomena that are nowadays referred to respectively as motor and emotional contagion. Indeed, on the occasion of his own experiments, W. James reported that participants sometimes tended to imitate the posture they were looking at. Such emotional motor reaction has since been studied systematically by Dimberg and collaborators. When shown facial expressions and other affective pictures, observers make emotion-specific facial movements. This is seldom visible to the naked eye, and as James commented, observers do not actually take the posture they are observing—at least not in a way that is obvious to the naked eye—but rather experience some kind of kinaesthesia in body parts that are normally involved in the production of the observed posture. Furthermore, James also reported some evidence for what has since been called emotion contagion. He noted that sometimes observers seemed to experience the feelings and emotions typically associated with the posture they saw and indicated that these feelings may follow enacting the posture observed (James 1890, p. 419). Note that James reported these two observations, motor reaction and emotional feeling reaction, as two separate phenomena. Of late there has been a tendency to conflate emotional motor reaction and motor contagion in a single phenomenon, emotional contagion based on mirror neuron activation. But this obscures the fact that facial reactions do not need to mimic the stimulus itself but reflect its affective content irrespective of whether it is a face or a scene, or an emotional voice (Magnée *et al.* 2007) or a bodily expression (Tamietto *et al.* 2008, 2009). It also obscures the fact that there may be significant dissociations between the emotion and the motor perception structures in the brain.

So far researchers have almost exclusively focused on measuring motor and emotional contagion in the facial musculature. This type of work is consistent with the theoretical basis of the facial action coding system developed by Ekman and collaborators (2009). As to spontaneous imitation of bodily postures by observers, we have been developing a bodily action coding system based on whole-body muscle movements (de Gelder & van Boxtel, in preparation), so far observed indirectly.

To conclude this section, the notion that there is more consensus for facial expressions than for bodily expressions has now turned out to be largely unfounded. More importantly, some physiological and autonomic signatures of recognition do occur as well irrespective of whether we view bodily or facial expressions. In the following sections, we will see that bodily expressions are not only well recognized, but they also trigger recognition under conditions of limited attention and awareness in the same way as facial expressions. On the other hand, there are also important differences between facial and bodily expressions. I will review differences between the two types of stimuli and discuss why they are important.

2. UNDERSTANDING THE SOCIOCULTURAL BACKGROUND OF FACE CENTRISM WILL ENRICH HUMAN EMOTION RESEARCH

Out of habit or principle, we tend automatically to fill in 'facial' when talking about emotional expressions. This bias is very clearly reflected in the fact, already mentioned, that studies of emotion recognition have hardly ever ventured away from the face. Yet it is a truism that emotions are conveyed by a whole range of other cues besides the facial expression. The continuity of facial expressions with postural, gestural and auditory signals has tended to remain in the background. Before addressing specific issues, it is worth asking what may possibly be the roots of the face bias in our cultural and ideological heritage.

Emphasis on the face is present in western culture and art but not, for example, in Islamic art. Well before neuropsychologists observed relative selective effects of lesions and neurophysiologists recording from single cells provided evidence for specialized face processes, artists have focused on the face. Traditionally the face is seen as the window of the soul; it is our privileged access route to the thoughts and feelings of the people around us. In their faces we read what others think and feel and we see ourselves reflected, accepted or rejected in their eyes. Faces presumably provide this information rapidly and automatically. But there is also an added moral dimension to the facial communication channel. Indeed, we do not merely learn about what a person thinks by watching his face, but at the same time we evaluate his trustworthiness. And we seem to be able to do so at a glance. This theme has been taken up recently in experiments investigating whether intuitive judgements of the trustworthiness of human faces are accurate. There are now quite a few studies providing evidence of the fact that first impressions are strong and remain so over time (Bar *et al.* 2006). We are very good at telling trustworthiness at a glance (Engell *et al.* 2007). But these two dimensions of facial information reading, emotional expression *per se* and trustworthiness, are traditionally linked. This cultural background is clear not only in the discussions of rapid facial judgements of trustworthiness just mentioned but also in the notion that we can identify lies from the face. Obviously, we can also identify higher order properties from body language, such as deceit (Grèzes *et al.* 2004) or moral violation (Sinke *et al.* submitted).

The philosophical emotion literature from Aristotle to Spinoza, to name just two, discusses emotions in the context of passion, reason and ethics. More fundamentally, this special status of the face is linked to dualism, in recent times typically associated with Descartes and his statement of the mind–body problem. If dualism represents the notion that there is a seemingly unbridgeable gap between our mental life and our material existence, then the face falls on the side of the mind and mental life while the body is relegated to the realm of the machine. The face expresses the mind, but the body, as is typical of machines, does not have a mind of its own and thus does not express anything. Just as the movements of a car do not express the car's feelings or intentions, the movements of the body are equally mechanistic and devoid of meaning.

Besides these, there are many other more directly cultural reasons as to why the body may seem a less reliable source of affective information. Tradition, culture, religion and fashion have a considerable impact on the public presentation of the body. Examples of extreme influence are Greek aesthetics of ideal body proportions, imperatives of the Victorian dress code or, at the other extreme, the burqa (which completely hides from sight all hints of facial and bodily expressions). All these factors together conspire to influence our attitude to the body by underscoring how its visual appearance can be manipulated and end up casting doubt on the body as a natural means of emotional communication.

Finally, consistent with the dualist framework just referred to and with the lingering doubts about whether bodily expressions are easily recognized, one understands that for a universal emotion theory the focus on facial expressions appears to be more promising. And indeed over the last three decades, the case for universal emotional expressions and associated universal emotions has been argued most forcefully by Ekman and collaborators (2009) with the help of analysis of facial expressions.

3. INVESTIGATIONS OF BODIES WILL EXTEND THE SCOPE OF FACE-BASED RESEARCH AND PROVIDE EVIDENCE THAT HUMAN EMOTION THEORIES BASED ON STUDIES OF FACIAL EXPRESSION MAY GENERALIZE TO OTHER AFFECTIVE SIGNALS

It may very well turn out that current models of human emotion perception originally developed for understanding facial expressions perception are just as valid for investigating and understanding bodily expressions. There is very little evidence available at present to support or refute this view.

On the positive side, one may argue that we already know from animal research that the amygdale (AMG), a central structure in affective processes, receives input from visual, auditory and postural cues and is therefore likely to play a role in processing faces, bodily postures and vocalizations. But the AMG is one among other important structures involved in alerting the organism to the presence of affective signals and preparing an adaptive response. For example, the first brain imaging studies led to the impression that the role of the AMG in emotion perception reflects a specialization for fearful facial expressions. Subsequent findings have challenged this picture and pleaded in favour of sensitivity to salience or even to stimulus ambiguity. Furthermore, the AMG is widely connected to a number of other cortical and subcortical brain structures (Amaral & Price 1984). Its embedding in these multiple networks determines to a large extent its specific functional role in relation to the stimulus and the behavioural context. It also determines the subjective emotional experience and the behavioural consequences. For example, the AMG is sensitive to the presence of threat stimuli in the environment irrespective of whether or not the observer is aware of them (Tamietto *et al.* 2009).

On the negative side, new investigations of affective channels other than the face may challenge current face-based models. These issues are now beginning to be addressed and some intriguing similarities and differences between the neural basis of facial and bodily expressions have started emerging already. As direct comparisons become available, significant differences between the neurofunctional basis of facial and bodily expressions are beginning to emerge. An extensive overview of currently available studies that have used behavioural, electrophysiological and brain imaging methods is provided elsewhere (de Gelder *et al.* 2009). Some important tendencies are briefly summarized in what follows.

At the behavioural level, there is clear evidence that both faces and bodies are processed configurally rather than as an assemblage of features. This is assessed by measuring the perceptual processes triggered when the stimuli are presented upside down. The resulting difference in performance is called the inversion effect, which refers to the loss of performance when faces have to be recognized from upside down compared with upright presented stimuli. Contrary to what is often assumed, this is not specific for faces. A similar loss of performance is also observed for other stimuli such as landscapes. Recent findings show that the recognition of faces and bodies presented upside down is relatively more impaired than the recognition of inverted objects (such as houses) when each category is compared with its own inverted counterpart (Reed *et al.* 2003).

Some electrophysiological studies have already been reported and others are underway. The well-known inversion effect measured in the time window of 150–200 ms and labelled N170 is obtained similarly for faces and bodies. We established this in an ERP study that used faces, bodies and shoes, each compared with its inverted counterpart (Stekelenburg & de Gelder 2004). This was confirmed and extended in a study using MRI-constrained magnetoencephalography (MEG), which allows a very good temporal resolution combined with a good spatial one. This study showed very early inversion effects for faces and bodies between 70 and 100 ms post-stimulus with category-specific cortical distributions (Meeren *et al.* 2008). There is also evidence that young infants are already sensitive to the orientation of body stimuli as measured by electroencephalography (EEG) (Gliga & Dehaene-Lambertz 2005).

Investigations of the neurofunctional basis of observing bodily expressions have begun to show that this activates the same brain areas that were hitherto associated with the perception of faces (for reviews, see de Gelder 2006; Peelen & Downing 2007). For example, in the first report of the neural basis of perceiving bodily expressions, we compared neutral and fear expressions and found increased activity for fearful bodily expressions in the AMG and in the fusiform gyrus (FG). The area that showed body responsiveness in the FG was the same as that identified in a separate study using a face localizer. Of course, a more fine-grained analysis of the fMRI signal may in turn show a partial separation as well as an area of overlap with face and body sensitivity, as has indeed been suggested in later studies (Kanwisher *et al.* 1997). There is almost no evidence in the literature to answer this question. For this reason, we designed an fMRI study with the aim of investigating whether the brain shows distinctive activation patterns for perception of faces and bodies.

We presented pictures of faces and bodies with blurred faces that showed a neutral, fearful or happy expression and instructed participants to categorize the stimuli. To untangle brain activation related to faces and bodies, we compared how the brain responds to both categories (irrespective of emotional expression). As expected, given the part–whole relation between bodies and faces, the results showed that the middle part of the FG, which is typically associated with the perception of facial identity, is more activated for bodies than for faces (van de Riet *et al.* 2009). Previous studies have shown that there was partial overlap between the face-selective and body-selective region within the FG (Hadjikhani & de Gelder 2003; Peelen & Downing 2005). In fact, viewing whole-body expressions elicited a wider network of brain areas compared with faces, including other areas previously associated with perception of facial expressions, such as STS. Other brain regions are more active for bodies than for faces, the middle temporal/middle occipital gyrus (the so-called extrastriate body area, EBA (Downing *et al.* 2001)), the superior occipital gyrus and the parieto-occipital sulcus.

When affective information is conveyed by bodies and faces, overall there is comparably more activation for bodily expressions than for facial expressions (Kret *et al.* submitted). Interestingly, emotional bodily expressions activate cortical and subcortical motor areas such as the caudate nucleus, putamen and inferior frontal gyrus (IFG), possibly reflecting the adaptive action component implied in the body expression, which is less pronounced in facial expressions (de Gelder *et al.* 2004). In a follow-up study, we presented video clips of dynamic facial and bodily expressions that conveyed a neutral, fearful or angry expression instead of static picture stimuli. The results were consistent with the previous study while broadening the perspective: bodies, as compared with faces, activated more areas than vice versa, including the FG. Again, motor-related areas were more activated by emotional bodily expressions (Kret *et al.* submitted).

4. STIMULATING A MORE DIRECT UNDERSTANDING OF THE SIGNIFICANCE OF EMOTIONS AS ADAPTIVE ACTIONS

Another benefit to be gained from using bodily expression stimuli is the broader emotion perspective obtained by using affective signals that are in effect operational over longer distances than faces. This also shifts the attention away from personal identity shown by the face, and which may not always matter for rapid decoding of the expression, to action much better conveyed by bodily expressions seen at a considerable distance. A major difference between facial and bodily expressions is that the latter can be recognized from far away while the former require the viewer to be nearby. This is potentially an important difference between how facial and bodily expressions play their communicative roles and it should have consequences for the specific information conveyed.

Focusing on facial expressions tends to make us refer to a person's mental state. But focusing on bodily expressions directs attention to a person's or a group's actions. When we talk about emotions, and ascribe emotions we have in sight or in mind, we implicitly seem to refer to the mental states of the persons whose faces we have in sight (or in mind). But when we refer to emotions we see expressed in the body, it is more frequent to have in mind an action. Therefore, when we are unable to tell the emotional state from reading the face owing to other peripheral visual conditions or impairments, we can still clearly read the action from the sight of the body.

5. CONTRIBUTING TO SOME LONG-STANDING DEBATES ON WHY FACIAL EXPRESSIONS IN ISOLATION ARE OFTEN RECOGNIZED LESS THAN PERFECTLY

Common sense tends to hold that we read facial expressions like we read words on a page, meaning that we directly and unambiguously access the meaning. But as is often the case, the expressly held common sense beliefs and what people routinely do when they behave commonsensically are two different things. In fact, in daily life we only seem to hold to the belief that a facial expression is unambiguous in a few extreme circumstances, such as for example in the case of a really menacing fury or a panic-stricken expression. Most of the time the angry and fearful faces we see do leave some room for interpretation, as is increasingly evidenced by semantic effects and contextual effects on face recognition (Barrett *et al.* in press; for a review, see de Gelder & Van den Stock in press).

Yet as theorists, whether reasoning from common sense principles from available scientific data, we hold on to preferred beliefs in basic emotional expressions universally represented by some facial expressions. The notion that these universal or 'basic emotions' expressions are the bed rock of our mental life thus mirrors our belief that certain emotion category labels correspond to universal mental states with a uniquely associated biological basis and with evolutionary defined triggers. But since researchers began to use the stimulus set provided by Ekman & Friesen (1976), less than perfect recognition rates were reported. For example, recognition rates are rarely above 80 per cent and they often tend to be comparatively lower because of fear, which is otherwise seen as the best candidate for a hardwired mental state expression cum biological substrate. This brings us to the next issue, that some of these basic mental states are most clearly expressed by the face while others are least ambiguous when expressed by the whole body.

6. ADDRESSING SITUATIONS WHERE FACIAL AND BODILY EXPRESSIONS DO NOT PROVIDE THE SAME MEANING AS WHEN FACIAL AND BODILY CUES COMBINE, INTERACT AND CONFLICT; PROVIDING THE MISSING CONTEXT TO THEORIES OF FACE PERCEPTION

For a while, 'Headless body in topless bar' counted as one of the funniest lines to have appeared in US newspapers. But headless bodies and bodiless heads figure only in crime catalogues and police reports and are not part of our daily experience, at the very least not part of the daily experience that constitutes the normal learning environment in which we acquire our face and body expertise. Yet, except for a few isolated studies (de Gelder 2006; Mobbs *et al.* 2006; Righart & de Gelder 2006; for an extended review and discussion, see de Gelder & Van den Stock in press), the literature on face recognition has not yet addressed the issue of context effects in face perception. By 'context', we mean here the whole naturalistic environment that is almost always present when we encounter a face.

Perception of facial expression is influenced by whatever expression the body shows. A popular notion is that our body language gives away our real feelings, for example in situations where we manage to control our facial expressions. A typical example is when one is trying to keep a poker face in situations of social control, dominance and stress. We do not show anger or nervousness, and we smile all the way through the conversation or the interview, however annoying or unenlightening the questions may be. Research on the simultaneous perception of faces and bodies is still sparse. Two behavioural studies directly investigated how our recognition of facial expressions is influenced by accompanying whole-body expressions (Meeren *et al.* 2005; Van den Stock *et al.* 2007). Meeren *et al.* (2005) combined angry and fearful facial expressions with angry and fearful whole-body expressions to create both congruent (a fearful face on a fearful body and an angry face on an angry body) and incongruent (a fearful face on an angry body and an angry face on a fearful body) realistic looking compound stimuli. These were briefly (200 ms) presented one by one while the participants were instructed to categorize the emotion expressed by the face and ignore the body. The results showed that recognition of the facial expression was biased towards the emotion expressed by the body language, as reflected by both the accuracy and the reaction time data. In a follow-up study, facial expressions that were morphed on a continuum between happy and fearful were combined once with a happy and once with a fearful whole-body expression (Van den Stock *et al.* 2007). The resulting compound stimuli were presented one by one for 150 ms, while the participants were instructed to categorize the emotion expressed by the face in a two alternative forced choice paradigm (fear or happiness). Again, the ratings of the facial expressions were influenced towards 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). Evidence from EEG recordings that were collected during the experiment shows that the brain responds to the emotional face–body incongruence as early as 115 ms post-stimulus onset (Meeren *et al.* 2005).

7. UNDERSTANDING EMOTION SPECIFICITY OF AFFECTIVE SIGNALS; THE RELATIVE IMPORTANCE OF FACE VERSUS BODY MAY BE A FUNCTION OF THE SPECIFIC EMOTIONAL SIGNIFICANCE CONVEYED

To repeat a truism, emotions are complex, rich and multilevel phenomena. And in spite of all the research effort devoted to the study of emotions, many researchers have the impression that progress is slow. This has led some authors, for example LeDoux (1996), to argue for a research strategy of concentrating on one emotion, in this case, fear, rather than trying to make progress on all fronts at the same time. But this has not stopped researchers from periodically advancing general theories. For example, a powerful impetus in emotion research over the past few years has tried to capitalize on the potential of mirror neuron activation in the brain. The specific finding that prompted this generalization was a study of disgust and the study used video clips of facial expressions of disgust (Wicker *et al.* 2003). Disgust is clearly an emotion that centres around activity in the mouth region and thus privileges the face as a bearer. The adaptive action component of disgust is unlikely to involve much movement of the lower limbs. But other emotions are more powerfully expressed in the arms and lower limbs of the whole body than in the face. Aggression is a case in point. When viewing aggressive body pictures, observers spend most of the time looking at the hands (Ousov-Fridin *et al.* in preparation). Therefore, a comparison of emotional expressions that is sensitive to the specific emotion is likely to reveal the relative prominence of the face versus the body, depending on the emotion considered and differential contributions form body parts to the specific emotion.

8. UNDERSTANDING GENDER SPECIFICITY OF THE IMPORTANCE OF BODILY VERSUS FACIAL SIGNALS

Notwithstanding widespread stereotypes about gender specificity in emotions and body-related issues, there are so far only a very few studies available on these issues. We designed a study with the goals of comparing neural bases dedicated to processing facial and bodily expressions using video clips of faces and bodies expressing threatening emotions (fear and anger) and of assessing the influence of gender from the viewpoints of both the observer and the actor (Kret *et al.* submitted). Male and female participants recognized all the expressions easily (mean percentage correct: 90% for fear, 95% for anger). There were no significant differences between the accuracy rates for male or female participants, and there was also no difference in the recognition of male or female actors. In contrast to these behavioural results, we did find some striking gender effects in the fMRI results. Activation of classical subcortical emotion areas (AMG, hippocampus, putamen, thalamus and basal ganglia) only showed up when the observers, both male and female, perceived a threat from male actors. In male participants, the dorsal stream was primarily involved in perceiving threat, especially from angry male body language. Strikingly, the superior temporal sulcus, an area often implicated in emotional processing, was not influenced at all by the type of emotion in female participants.

When females perceive *male threatening body language*, they activate the dorsal pathway and a network that involves action preparation and observation. Apart from enhanced activity in the visual areas, there are activations in the precuneus, inferior and superior parietal lobes (action observation), precentral gyrus, SMA and motor cingulate cortex (posterior and anterior), as well as in the caudate nucleus and putamen (action preparation). The activity found in the motor cingulate cortex corresponds to the area known to be involved in arm movements (Pickard & Strick 1996). This may imply that female participants felt the urge to protect themselves (for example covering their faces with their arms when watching male bodily expressions of threat).

9. BODILY EXPRESSIONS ARE PERCEIVED IN A MULTISENSORY ENVIRONMENT, COMBINED WITH AUDIO SIGNALS

An interesting argument in favour of the primacy of the face may be that facial expressions form a more natural pair with voice. Research has shown that recognition of the emotion in the target modality (facial expression) is typically influenced towards the emotion expressed in the task irrelevant modality (affective prosody of the voice) (e.g. de Gelder & Vroomen 2000). In this type of study, two modalities are typically combined to create emotionally congruent and incongruent face–voice pairs in order to provide a window into the integration process (de Gelder & Bertelson 2003).

It is worth noting that the argument concerning the naturalness and ecological validity of considering visual stimuli in a multisensory context applies just as well to the whole body as to the face only. A trainee singer trying to sing only with the upper body will quickly experience the limitations of that approach. Similarly, when trying to shout with the arms folded over the chest one quickly becomes aware of the fact that vocalizations are produced by the body!

In two recent studies, we have taken this issue beyond facial expressions and investigated affective crossmodal influences in whole-body expressions (Van den Stock *et al.* 2007). We investigated naturalistic actions that are part of everyday life and focused on instrumental actions, such as grasping and drinking. Our data showed that affective crossmodal effects occur with body–voice pairs and are thus very similar to previous findings about the combined perception of face–voice pairs (Van den Stock *et al.* 2008).

10. PERCEPTION OR RECOGNITION OF BODILY EXPRESSIONS DOES NOT REQUIRE FULL ATTENTION NOR DOES IT REQUIRE THAT THE VISUAL STIMULUS BE CONSCIOUSLY SEEN

Over past decades, a number of research reports have concluded that emotional information can be processed without observers being aware of it (Kunst-Wilson & Zajonc 1980; Barrett *et al.* 2007). But non-conscious affect perception has almost exclusively been investigated with the use of facial expressions, either on their own or in combination with other visual stimuli. Many studies now provide direct and indirect evidence for visual discriminations of facial expressions in the absence of visual awareness of the stimulus (e.g. Esteves *et al.* 1994; de Gelder *et al.* 1999; Dimberg *et al.* 2000; Jolij & Lamme 2005). Theoretical models have been advanced arguing that separate pathways may sustain conscious and non-conscious emotional perception (LeDoux 1996; Morris *et al.* 1998). The notion of separate pathways has to some extent been accepted by the community at large, although some core findings are still a matter of debate (Pessoa 2005; Duncan & Barrett 2007).

An issue that has so far not received much attention is whether there also exists non-conscious emotional perception for bodily expressions. Data from patients with hemianopia indicate that they may reliably discriminate between bodily expressions that they are unable to see because of striate cortex lesions (de Gelder & Hadjikhani 2006) or because of an attentional disorder following parietal lesions (Tamietto & de Gelder 2008) and, more radically still, in patients with cortical blindness (Tamietto *et al.* 2009).

Other indicators besides behavioural measures also provide evidence for automatic processing. A striking example is represented by the spontaneous tendency to synchronize our facial expressions with those of another person during face-to-face situations. This phenomenon of emotional contagion (Hatfield *et al.* 1994) is now widely observed, but it is still poorly understood. Recent proposals link emotional contagion directly to motor resonance (i.e. stimulus/response motor matching) (Dimberg *et al.* 2000; Carr *et al.* 2003).

A directly related issue concerns the degree of automaticity of emotional contagion and the role of visual awareness of the eliciting stimulus in the unfolding of affective reactions at different levels of emotional experience. Available evidence shows that nonconscious perceptual mechanisms are sufficient for processing emotional signals, most notably so far in facial expressions. The clearest evidence for processing without visual stimulus awareness is obtained in patients with lesions to the primary visual cortex (V1). These patients reliably discriminate the affective valence of facial expressions projected to their clinically blind visual field by guessing (*affective blindsight*), despite having no conscious perception of the stimuli they are responding to (Morris *et al.* 2001; Pegna *et al.* 2005). We recently reported that nonconscious perception of emotions presented in facial as well as in bodily expressions in cortically blind patients may lead to spontaneous facial reactions and to other physiological changes typically associated to emotional responses (Tamietto & de Gelder in press; Tamietto *et al.* in press *a*; Tamietto *et al.* in press *b*).

11. REVEALING THE NEUROFUNCTIONAL CORRELATES OF CATEGORY SPECIFIC CQ. BODY-SPECIFIC PROCESSES AND DEFICITS

A strong impetus for category specificity of neural substrates comes from neuropsychological reports of patients with brain damage acquired in adulthood. There is a well-known neuropsychological deficit related to impaired face recognition, labelled prosopagnosia. These patients are impaired in recognizing faces, and very often have no recognition at all of an individual by just the face. Brain damage occurring in the normally developed brain that affects face perception is often localized in the occipitotemporal cortex and temporal cortex (midfusiform gyrus and inferior occipital gyrus) unilaterally or bilaterally. The developmental counterpart of acquired prosopagnosia is now also often reported. There is substantial similarity between acquired and developmental prosopagnosia at the behavioural level but there are many other differences (see de Gelder & Rouw 2000 for a comparison).

It is important to specify the nature of the disorder though, and this is still a matter of debate. The short definition of prosopagnosia characterizes it as a deficit in face recognition. But this is too broad and also too specific. We are in fact dealing with a deficit that affects recognition of personal identity from the sight of the face. Other dimensions of face information are processed mostly normally, like emotional expression, visual speech or gender. In fact, a good means of defining the typical face deficit of prosopagnosics is by establishing that there exists a dissociation between the different dimensions of face perception, some of which are impaired while others are intact. On the other hand, there are to date only very few cases of pure prosopagnosia, where the perception and recognition deficit is restricted to the face and does not affect in any way the perception and recognition of other object categories. Thus on this axis also, a dissociation must be established requiring that the perception and recognition impairment is not present for non-facial stimuli. To establish the presence of developmental prosopagnosia, the same dimensions of dissociation need to be assessed.

Using body stimuli offers a chance to advance the debate on category specificity. As a matter of fact, there are very few objects other than faces for which strong claims about category-specific representation have been made. An interesting object category not used so far concerns human bodies. Recently, it has been shown in normal subjects that perceiving human bodies or body parts activates an area in the extrastriate cortex, the labelled EBA (Downing *et al.* 2001), and more recently a second body-specific area in the FG (Hadjikhani & de Gelder 2003; Peelen & Downing 2005) overlapping partially with the face-sensitive one, termed the fusiform body area (FBA). These behavioural and neuro-functional similarities between perceiving faces and bodies in neurologically normal observers raise the issue of how bodies are processed in developmental prosopagnosia (DP). Our second main finding concerns the categorical specificity of the face versus the body perception in DPs. We compared the activation of body conditions in the face-selective regions and of the face conditions in the body-selective regions between both groups. On the one hand, our findings indicate that perceiving neutral faces results in a higher activation of EBA in the DP group, compared with the control group. Combined with the lower activation in the fusiform face area (FFA), this increased activation in EBA might indicate an anomalous processing route in the brains of DPs. It may be the case that (neutral) faces are processed in areas more dominantly dedicated to body perception. Combined with the lower activation in FFA, this increased activation in EBA might indicate an anomalous processing route in the brains of DPs. It may be the case that (neutral) faces are processed in areas more dominantly dedicated to body perception. On the other hand, we find a higher activation for perceiving bodies in IOG. These combined findings indicate that the neural correlates of perceiving faces and bodies, as manifested in IOG and EBA, show a lower degree of specificity in DP.

12. INVESTIGATIONS OF BODILY EXPRESSIONS WILL ENRICH BASIC CLINICAL RESEARCH AND LEAD TO THE DEVELOPMENT OF NEW OBSERVATIONAL AND DIAGNOSTIC TOOLS

Many studies of emotional communication disorders have reported deficits in face recognition in clinical populations as well as in psychiatric disorders. These include autism spectrum subjects, schizophrenics, subjects with mood disorders like depression and high-anxiety individuals. Autism spectrum disorder (ASD) is usually behaviourally defined as being characterized by mild to severe impairments in communication and reciprocal social interaction as well as repetitive and stereotyped behaviours. Daily observations document the difficulties that ASD subjects have in recognizing and appropriately reacting to other people's emotions, irrespective of whether they are communicated by facial expressions, vocal tone, gestures or bodily postures. Some of these characteristics have been documented experimentally but much debate remains. Earlier behavioural studies did not consistently find emotion perception deficits

(Hobson *et al.* 1988; Braverman *et al.* 1989; Macdonald *et al.* 1989; Tantam *et al.* 1989; Capps *et al.* 1992; Davies *et al.* 1994), but recent studies (Ozonoff *et al.* 1990; Baron-Cohen *et al.* 1997; Grossman *et al.* 2000; Gepner *et al.* 2001) taking a more fine-grained approach have documented emotion recognition impairments mainly in the perception of negative emotions, especially fear (Baron-Cohen *et al.* 2000; Dawson *et al.* 2004; Welchew *et al.* 2005; Ashwin *et al.* 2006; Corden *et al.* 2006; Gaigg & Bowler 2007; Humphreys *et al.* 2007).

The above illustrates that to date, research on emotion and social communication disorders has focused primarily on impairments in the neurofunctional processes associated with viewing facial expressions. In view of reports that ASD may avoid paying attention to the face, investigations of other channels of communication look particularly promising. We recently performed two studies on bodily expression processing, one using still images (Hadjikhani *et al.* 2009) and another using videoclips (Grèzes *et al.* 2009). The main finding of the first study using still bodies is that brain activation patterns in individuals with ASD do not show evidence of differentiation between bodily expressions of fear and bodies engaged in neutral actions. This finding suggests an abnormality in the network of brain areas that are normally engaged in the perception of bodily expressed emotions in NT individuals, and is consistent with recent behavioural findings of Hubert *et al.* (2007) who reported normal perception of point-light displays of neutral actions in ASD, but abnormal perception of emotions.

In the study using video clips of neutral and fearful actions expressing whole-body actions, normal perception of dynamic actions in ASD was also observed. Yet there were clear anomalies linked to a failure to grasp the emotional dimension of the actions. We measured brain activity using fMRI during perception of fearful or neutral actions and showed that whereas similar activation of brain regions known to play a role in action perception was revealed in both autistics and controls, autistics failed to activate the amygdala, IFG and premotor cortex when viewing gestures expressing fear. Our results support the notion that dysfunctions in this network may contribute significantly to the characteristic communicative impairments present in autism. We observed that ASD subjects fail to engage cerebral regions involved in grasping the emotional meaning of the actions they view. We suggest that this deficit may reflect an important failure of the mechanisms that control normal behavioural responses to emotional signals in the behaviour of others. The ensuing deficiency in the appraisal of emotional cues may lead to the inappropriate behavioural responses and social difficulties that are characteristic of this population. This suggestion takes us well beyond conclusions reached in studies about communication deficits using facial expressions because it allows a specific hypothesis about social interactive impairments that are so clearly present in many ASD individuals and are obviously more far reaching that the unwillingness to pay attention to the face. This traditional stumbling block for measuring emotion recognition in ASD can be overcome by using bodily expressions instead.

13. CONCLUSION

I have reviewed a series of arguments in favour of substantially extending and enriching current human emotion theories by adding investigations of bodily expressions. We have also highlighted the importance of new research on bodily expressions for theories that consider emotions to be closely linked to adaptive action. Finally, we have discussed some recent studies illustrating the potential of bodily expression research for neuropsychological investigations as well as for clinical research.

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