The Many Faces of the Emotional Body

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Abstract The perception of emotional signals is at the core of the study of the social brain. In this chapter, we discuss research in the field of affective and social neuroscience that specifically uses bodily expressions. Starting with the initial studies mapping the neural substrate of perception of simple bodily expressions, several steps have been taken to grasp the full extent of genuine interactions, from the use of multiple emotional cues, to dynamic social interactions, and recently the use of virtual reality. With increasing complexity of the emotional signals used in neuroscientific research, we can approximate the natural richness of the social and emotional reality.

Introduction

During the past few decades psychologists, and more recently neuroscientist, have tried to capture the reality of emotions. A notion that has repeatedly cropped up in the affective and social neuroscience literature is that of the "social brain." The concept is most often used as an umbrella term covering many of the social skills observed in animals. In a more narrow sense, the concept refers to the neurobiological basis of the ability to engage with conspecifics. A social species is one that spends the better part of its time interacting with others and for whom interaction provides essential benefits. While researchers have tried multiple routes to study the

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neurobiological basis of emotion, almost all the studies in the literature, including most of our own, take the viewpoint of the passive observer. This has already led to a detailed picture of how the brain of the observer reacts to the sight of a social affective stimulus like a conspecific face, body part, whole body, smell or vocalization and how these neural processes underlie adaptive behavior. This chapter will discuss research that uses bodily expressions from both single and multiple bodies, in a range from prototypical to complex social interactions.

What steps have been taken in the past to gain an understanding of human emotion processing? From the beginning of research on emotion perception, a variety of emotional signals have been used (see Fig. 1). Facial expressions dominated the field for years, the only alternatives being emotional pictures (e.g., International Affective Picture System; Lang et al. 1999) and emotional sounds (e.g., voice or music). In the last decade the field of affective and social neuroscience has started to investigate bodily expressions as an emotional signal (Hadjikhani and de Gelder 2003). We will start this chapter by providing several arguments for why bodies have their place in the study of the social brain. Next, we briefly discuss research that maps the neural substrate of bodily expression perception. In the last few years, the combinations between faces and bodies and between those and contextual information have been used to gain a more accurate picture of emotion perception. As we will discuss, the use of multiple emotional cues provides a valuable starting point to understand the richness of the emotional world. We will end the overview of past research by discussing a new and interesting step that uses social interactions to measure the dynamics of emotion perception. In the remainder of this chapter, we describe a prospect for the future of affective and social neuroscience by providing new ways of investigating the human emotional brain (e.g., the use of virtual reality). Ideally, neuroscientists will leave the comfort of the lab and step into the real world to study real humans having real emotion responses in real interactions. The end result will be a true social and affective neuroscience. While in this chapter we illustrate the evolution of the study of emotion perception in affective and social neuroscience from the perspective of the perception of bodily expressions, we do not mean that research using other methods or emotional signals is not of value. We do not wish to provide an all-encompassing review; we will merely illustrate the flow of research over the last two decades.

Why Bodies?

It is surprising that although Darwin (1872/2002) and James and Lange (1922), forefathers of modern emotion science, wrote on this topic, whole body expression have since largely been ignored. In recent times, the importance of these expressions has been stressed by Frijda (1986) and Tomkins (1995) in their discussion of the interplay between emotion and action. But until recently, these theoretical ideas and early studies by Ekman and colleagues (1965; 1967) and Dittmann et al. (1965) on face and body affect communication did not prompt empirical investigations and

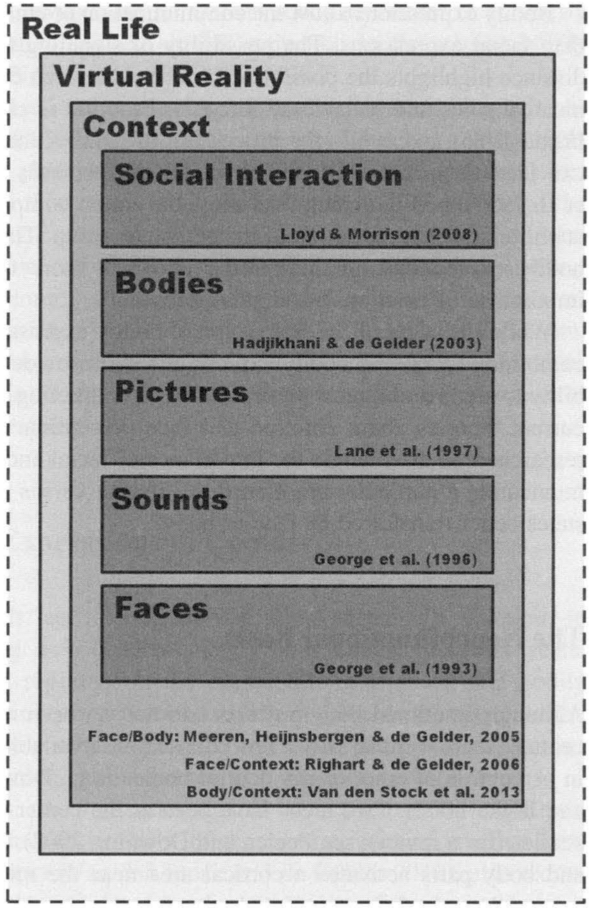

Fig. 1 The use of emotional signals as building blocks of the natural richness of the social and emotional reality Note, only the first published article per emotional signal in the study of emotion perception using imaging techniques (e.g., PET, fMRI) are listed since the emergence of modern social and affective neuroscience

emotion research has used facial expressions as the primary emotional signal to study. Previously, we gave a number of reasons why the field of affective and social neuroscience should integrate bodily expressions in the study of social behavior (de Gelder 2009). Here, we briefly summarize several relevant ones.

In everyday interaction, people not only rely on both facial and bodily communication. Similar to facial expressions, bodily expressions are easily recognized (e.g., Atkinson et al. 2004; de Gelder and Van den Stock 2011) and, as one might observe in an elevator or during a conversation, people imitate each other's posture. Indeed, emotional mimicry can also be observed when bodies are used as stimuli rather than just faces (Magnée et al. 2007). Furthermore, similar to the face action coding system developed by Ekman and collaborators (FACS; Ekman and Friesen 1978), it is possible to build a body action coding system (BACS; Huis in 't Veld et al., submitted for publication) that allows measurement of the muscle groups involved in whole body expressions.

Bodily expressions allow the communication of emotions over a wider spectrum than facial expressions. The possibility of signaling to an observer over a larger distance highlights the possible differences between emotional signals in communicative roles and behavioral outcome. Emotion is closely linked to action (e.g., Frijda 1986) and, while the processing of another individual's facial expressions can lead to an automatic inference of the person's mental state (Baron-Cohen et al. 1997), bodily expressions show the action component of emotion by biasing attention towards the action of the person or group. Thus, an understanding of how bodily expressions are interpreted allows a more direct understanding of the importance of emotions as adaptive actions.

While the study of the perception of bodily expressions in isolation is valuable, combining facial and bodily expressions will provide researchers a unique possibility to study ambiguous perception (e.g., conflicting affective signals) and to test current theories about emotion and face perception. Furthermore, it will permit researchers to disentangle the importance of facial and bodily expressions in communicating a particular emotion (e.g., disgust versus anger). Are some emotional states better transferred by face or body?

The Neurofunctional Basis

Although emotional body postures had not yet been used at the beginning of this century, there were already a few publications available on the brain areas involved in perception of emotionally neutral bodies (e.g., Downing et al. 2001; Grossman and Blake 2002). Two areas have been at the center of research in human fMRI studies (for a review, see Peelen and Downing 2007). Seeing whole human bodies and body parts activates a cortical area near the middle occipital gyrus/middle temporal gyrus, the extrastriate body area. A second area, the fusiform body area, which partially overlaps with the fusiform face area, is also body-selective. While emotion-specific modulation of these areas has been reported (for a review, see de Gelder et al. 2010), the goal of these studies is to identify the brain areas that are specifically dedicated to the representation of bodies as one specific category of visual objects.

From an evolutionary perspective, as noted before, emotions are closely linked to actions. When confronted with an emotional signal in the environment, affect programs will be activated in the individual that produce neurophysiological changes that trigger adaptive behavioral responses (e.g., Darwin 1872/2002; Frijda 1986; Panksepp 1998). Indeed, this is also reflected in the neural substrate. The first fMRI study on the perception of emotional bodily expressions reported the activation of the amygdala and fusiform cortex when subjects observed a fearful whole body expression (Hadjikhani and de Gelder 2003). A follow-up study reported not only activation in areas important for visual and emotional processes but also action representation and motor responses (de Gelder et al. 2004), and this action component was later found to be systematically associated with passive observation of bodily expressions (for a review, see de Gelder 2006; de Gelder et al. 2010). Studies using dynamic images reported similar activation to threatening bodily signals (Grèzes et al. 2007; Pichon et al. 2008, 2009, 2012).

To allow adaptive responses, the processing of threatening bodily expressions needs to be rapid and relatively independent of attention. Indeed, a non-striate, subcortical-based route may play an important role here (Tamietto and de Gelder 2010; Tamietto et al. 2012). First, there is fast detection of and orientation to the bodily expression (superior colliculus and pulvinar). Next, subcortical and cortical connections underlie integration of affective content (superior colliculus, pulvinar, amygdala, and orbitofrontal cortex), followed by adaptive responses (periaqueductal grey, putamen, caudate nucleus, and premotor cortex) (de Gelder et al. 2012). In sum, studies on the neural mechanisms of perception of emotional bodily expressions emphasize more the automatic consequence rather than the cognitive interpretation of the communicated emotion expression.

Perception of Bodily Expressions in Context

While most of the research has focused on emotional signals in isolation, in everyday life no such thing as a headless happy body exists. In recent years, multiple studies have been reported on the combinations of facial and bodily expressions and context. Not only has this approach been valuable to study emotion perception in a more realistic context but also to investigate individual differences in, and the influence of neurological impairments on, emotion perception.

During social interaction, one's attention has to be focused on different cues (e.g., facial or bodily cues). Indeed, not only influences emotional information from bodily expression face memory (Van den Stock and de Gelder 2012), also recognition of facial expressions is modulated by the expression of the body (Aviezer et al. 2008; Kret et al. 2013; Meeren et al. 2005; van den Stock et al. 2007). The perceptual integration of facial and bodily cues, even when not attended to, is rapid (Aviezer et al. 2011; Meeren et al. 2005). Interestingly, subjects with basolateral amygdala damage have a deficit in ignoring task-irrelevant bodily threat signals when recognizing facial expressions (de Gelder et al., submitted for publication) and decreased recognition of happy facial expressions when paired with aggressive bodily expressions was observed in imprisoned aggressive male offenders (Kret and de Gelder 2013).

We have outlined several possible mechanisms underlying this body context effect elsewhere (Van den Stock and de Gelder 2012). First, the overlap between facial expressions of surprise and fear illustrate the notion that facial expressions in isolation are ambiguous (de Gelder et al. 2006). Without context, surprise faces can be interpreted as negative or positive in valence, which is reflected in physiological responses (Neta et al. 2009). Bodily expressions provide this context (Aviezer et al. 2012). Second, bodies and faces overlap in terms of the underlying neural network, which might induce competition for neural resources (e.g., Stienen et al., submitted for publication). Lastly, action and information relevant to a behavioral response is better transferred by bodily expressions and, therefore, biases emotion perception.

Similar to previous studies using facial expressions (e.g., de Gelder et al. 2006; Righart and de Gelder 2006; Wieser and Brosch 2012), multiple studies have investigated the effect of emotional context (e.g., a threatening scene) on the recognition and processing of bodily expression (Kret and de Gelder 2010, 2013; Kret et al. 2013; van den Stock et al. 2013). Explicit recognition is influenced by the emotion of the scene (Kret & de Gelder 2010), and the influence of the context is increased in imprisoned aggressive male offenders (Kret and de Gelder 2013). Happy bodily expressions were interpreted by this group as being angry when depicted in an aggressive context. At the neural level, activity in the EBA was increased when an emotionally neutral body was shown in a threatening scene (Van den Stock et al. 2013). The emerging picture is that the effect of context is an early perceptual process, in which the threatening scene biases the perception of bodily expressions and hijacks neural resources (c.f., Sinke et al. 2012).

Social Interactions

In animals, evidence for social abilities is traditionally derived from behavioral observations. In a highly social species, individuals rarely isolate themselves but are constantly involved with each other. Naturalistic observations rarely focus on a single individual but on multiple individuals actively engaged with each other. What we see is small groups or dyads continuously organizing and changing their composition, individuals constantly leaving or joining others, group movements in various directions, and so on. A few recent studies using point-light displays, animations, realistic videos of social interactions or crowds have already put interactions on the agenda and, even if they still involve participants that passively observe others interacting, quite a bit can already be learned from them.

One way to study the neural basis of information transferred in social interaction is the use of whole body point-light displays (Johansson 1973). Using only biological motion, one can distinguish known individuals (Cutting and Kozlowski 1977), gender (Kozlowski and Cutting 1977), action (Dittrich et al. 1996), and emotion (Atkinson et al. 2004; Pollick et al. 2002). Moreover, using only information derived from biological motion, people can easily recognize emotions in a social interaction (Clarke et al. 2005). Minimalistic whole-body point-light displays lead to differential activity for social interactions in brain regions underlying perception of emotion and action (Centelles et al. 2011). While the use of point-light displays in the field of affective and social neuroscience remains infrequent, the possibility of studying the perception-action link with manipulation of motion, spatial and temporal coherence of the used stimuli (e.g., Christensen et al. 2011) provides a unique and intriguing next step.

Another line of research tapping into the dynamics of emotionally interacting people uses fully realistic dynamic stimuli. A study by Lloyd and Morrison (2008) found that the brain codes subtle differences in social interactions (see also, Iacoboni et al. 2004). We have complemented these previous studies by focusing on the effect of attention in the processing of social interaction. Participants implicitly or explicitly observed a social interaction that was threatening or teasing (Sinke et al. 2010). Results showed less deactivation of the amygdala for the threatening compared with the teasing social interaction for both tasks. Moreover, action-related areas, the putamen and premotor area, were activated in both tasks. These results show that, also during complex social interactions, threat can be processed automatically and trigger defensive behavior (cf., Pichon et al. 2012).

Recently, we have started to investigate the neural mechanisms of the perception of a social emotional situation in the context of a group (Hortensius and de Gelder, submitted for publication). Borrowing a phenomenon well studied in social psychology, the bystander effect, we investigated the influence of the group on neural responses to an emergency. The bystander effect refers to the decrease in helping behavior that occurs when one is confronted with an emergency in the presence of other onlookers. It was expected that group influences would already be reflected in neural responses underlying preparation for action (c.f., motor regions). While participants performed an unrelated color-naming task in an fMRI scanner, they observed an emergency with either no, one, two or four bystanders. The results indeed showed a decrease in activity with the increase in group size in the regions that are relevant for action preparation and adaptive behavioral responses (pre- and postcentral gyrus, medial frontal gyrus). This study illustrates how one can investigate the perception of complex everyday situations that lead to emotional reactions in the observer inside the laboratory.

Extending the research perspective from a single individual to that of dyads or small groups is an important next step. Going even further, studies have been performed that investigated crowd perception (Gilbert et al. 2011; McHugh et al. 2010). While this is a first step, it will hopefully provide answers about the neural basis of how emotional reactions (e.g., panic, aggression) are spread within groups and how they guide individual behavior.

Outlook

In the previous sections, we have discussed research on the neural mechanisms of perception of bodily expressions. This research is part of the broad field of social and affective neuroscience. The field is currently thriving and embracing issues as diverse as empathy, decision-making and cultural stereotypes. It is worth noting that research in human social neuroscience is still very much pitched at the individual level. Almost all studies address the social abilities as a set of skills the individual has and that allows him/her to live in a social context with others. But these skills are analyzed as individual attributes. Our current research on bodily perception obviously presents rather a partial view of social perception because it has as its focus the behavior of an observer that is passive and static. The person observed is not influenced by the way his/her actions are perceived by others. On the other hand, the observer does not get any feedback or insight from his/her correct perception; neither does he/she suffers the consequences of misperception. Emotions are relational; they are primarily defined for at least two people interacting rather than for a single subject. Studies focussing on a single individual tend inevitably to look at emotion as an internal process. This passive perspective on social interactions seems one-sided and therefore incomplete.

In contrast, animal studies have traditionally taken the social dimension more literally and have traditionally studied the individual as part of the group and focused on group characteristics. Fortunately, this approach has recently been adopted in human social neuroscience (Konvalinka and Roepstorff 2012; Schilbach et al. 2013). Indeed, two-people neuroscience allows a new vista on the emotional social brain. However, this approach has so far mainly been restricted to action observation and joint action (Sebanz et al. 2006).

Interactions create affective loops, and being involved in these interactions with our bodies is the source of strong affective experiences. Virtual reality provides the field of affective and social neuroscience with a powerful tool to study just that. From body perception (Giannopoulos et al. 2011) to social situations (Pan et al. 2012; Slater et al. 2013), virtual reality allows the study of affective loops under well-controlled conditions and in settings where real life manipulation is not possible, too expensive or unethical. It has successfully been used to study the behavioral and physiological effects of social anxiety on a social interaction (Pan et al. 2012) and it allows the embodiment in an out-group member (Peck et al. 2013), child (Banakou et al. 2013), or even a rat (Normand et al. 2012). Furthermore, virtual reality is well suitable for the study of complex social situations and phenomena. For example, Slater and colleagues (2013) confronted participants with a violent incident involving another individual to investigate the likelihood of helping the victim. Combining virtual reality with new techniques such as motion capture not only gives researchers the possibility of using point-light stimuli in body perception and social interaction research but also provides a tool to systematically vary certain components of a body or social interaction and makes it possible to analyze how kinematics differentiate between emotional scenarios (Barliya et al. 2013; Roether et al. 2008). In sum, the use of new techniques will give the field of affective and social neuroscience valuable and important tools to grasp the full extent of the social world in a well-controlled manner.

Conclusion

Social perception may be an area where the notion of direct perception of intentionality may be studied most successfully. Presently there is still a striking contrast between the view based on available scientific research, which is that of an isolated individual sitting in front of a computer screen and still mostly having his/her reactions measured to still pictures of disembodied faces, and the relentless social communication we are engaged in daily life. In the past, we have used more naturalistic stimuli, e.g., bodily expression, combining facial and bodily expressions, adding contextual information, and social interactions, as a first step to fill this gap. However, the adequate, successful study of social perception predicts, modifies and changes the perceived interacting agent as well as the perceiver. How can we approach the study of genuine interactions? Investigations of this transformative nature of social perception require that we create new concepts and develop the necessary methodological tools. Our perspective is that social interaction abilities are part and parcel of the evolutionary endowment of the species. The consequence of this is that the neuroscience community needs to confront the fact that the brain's natural task is thus not labeling prototypical emotions but registering and responding to the interactive emotional coloring that is part of daily communication. Although this chapter has little to report that is directly related to interactive affective perception in the strictest and most realistic sense, we hope to have made clear that our focus on the body represents a next step towards a novel understanding of active social interaction.

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