BODY LANGUAGE: EMBODIED PERCEPTION OF EMOTION

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List of abbreviations

AMG = amygdala; almond-shaped nucleus in anterior temporal lobe

EBA = extrastriate body area; brain area lying in temporal-occipital sulcus which is specifically involved in processing bodies

EEG = electroencephalography; a method to measure electrical activity from the scalp related to cortical activity

ERP = event-related potential; EEG waves time locked to specific stimuli

FBA = fusiform body area; brain area in the fusiform gyrus that is specifically involved in processing bodies

FFA = fusiform face area; brain area in the fusiform gyrus that is specifically involved in processing faces

FG = fusiform gyrus; part of the temporal lobe that is involved in visual processing

fMRI = functional magnetic resonance imaging; brain imaging method that measures the hemodynamic response (change in blood flow) related to neural activity in the brain

hMT+/V5 = human motion area; brain area specifically processing movement

IOG = inferior occipital gyrus

IFG = inferior frontal gyrus

MEG = magnetoencephalography; a neuroimaging technique that measures magnetic fields produced by electrical activity in the brain

N170 = ERP component originating from lateral occipitotemporal cortex specifically related to a late stage in the early visual encoding of faces

OFA = occipital face area; brain area in inferior occipital gyrus known to be involved in face processing

P1 = very early ERP component related to very early visual processing

PET = positron emission tomography; brain imaging method whereby radioactive tracers are injected into the blood stream

PM = premotor cortex

STS = superior temporal sulcus; posterior part is involved in processing biological motion

TPJ = temporo-parietal junction

V1 = primary visual cortex

INTRODUCTION

In everyday life, we are continuously confronted with other people. How they behave and move around has a direct influence on us whether we are aware of it or not. In communication, we are generally focused on the face. For this reason, emotion research in the past has focused on faces. Also, facial expressions seem to have universal consistency. However, bodily expressions are just as well recognized as facial expressions, they can be seen from a distance and are from evolutionary perspective much older. Body language therefore has a high communicative role albeit we are less aware of it. Models on facial expression processing might also work for understanding bodily expressions. Similar brain regions seem to get activated for both, but although faces show the mental states of people, body postures in addition show an action intention. Therefore, seeing bodies additionally activates motion areas.

In a naturalistic environment, faces never appear alone: they are mostly always accompanied by a body which influences how the facial expression is perceived. This is also the case for other modalities such as the voice. Which modality is dominant depends on the specific emotion being shown, on the situation and many other factors. For example, aggression seems to be more pronounced in bodily expressions, while shame or disgust can clearly be seen from the face. Also the context, including other people or not, can facilitate recognition of emotions. Moreover, we do not live in a static world; dynamic stimuli give us, just like in the real world, more information. We also would like to put forward that brain responses to emotional expressions are not driven by external features alone but they are determined by the personal significance of expressions in the current social context. For example, individual differences such as personality type and gender play an important role. Moreover, body language of people interacting can tell us much about their relationship.

We argue that the nature of emotion perception cannot be fully understood by focusing separately on social, cultural, contextual, individual or interpersonal factors. The percept of an emotion is embodied, and its bodily-grounded nature provides a foundation for social communication. *"What you see is what you get"* does not apply here. People do not "see" the same, nor do they attend to the same.

Furthermore, perception and recognition of bodily expressions does not require full attention nor does it require that the visual stimulus is consciously seen. This is most evident from patients with hemianopia.

All these topics will be discussed in this chapter. They show us that being able to recognize emotional meaning from others is vital and that body language is of crucial importance in normal communication. This is clearly impaired in disorders such as autism. Therefore, investigations of bodily expressions will enrich basic clinical research and can lead to the development of new observational and diagnostic tools.

SIMILARITIES AND DIFFERENCES IN NEUROFUNCTIONAL BASIS OF FACES AND BODIES

Since a few years the neural correlates of body shape (Downing, Jiang, Shuman, & Kanwisher, 2001) and perception of bodily expressions (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004) are the focus of experimental investigations. Although more or less neglected in the past in favor of faces, it is now increasingly believed that the perception of bodies has a special influence on our behavior. To be able to do this, they must be distinctly processed from other objects.

The major concept used to argue for the specificity of processing is that of configuration. There is clear evidence that both faces and bodies are processed configurally, as a whole, rather than as a collection of features. This has been shown with ‘the inversion effect’: recognition of faces and bodies presented upside-down is relatively more impaired than inverted objects (Reed, Stone, Bozova, & Tanaka, 2003). Besides behaviorally, this effect can also be investigated psychophysically by looking at electrophysiological recordings. With electroencephalography (EEG), electrical activity coming from firing neurons is picked up at the scalp through electrodes. By averaging brain activity to certain events, event-related potentials (ERPs) are formed. One such ERP component is the N1 that is thought to reflect a late stage in the structural encoding of the visual stimulus (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000) and originates from the lateral occipitotemporal cortex which houses the fusiform gyrus (FG). In the case of face processing, the N1 peaks at a different latency (around 170 ms after stimulus onset and hence called the N170) than for objects. The latency of the N170 is delayed when presented faces are inverted, which shows the involvement of FG in processing faces configurally. The N1 peak for body processing also differs from objects; it ranges from 154 to 228 ms after stimulus onset (Gliga & Dehaene-Lambertz, 2005; Meeren, van Heijnsbergen, & de Gelder, 2005; Righart & de Gelder, 2005; Stekelenburg & de Gelder, 2004; Thierry et al., 2006; van Heijnsbergen, Meeren, Grezes, & de Gelder, 2007) and it also shows an inversion effect. Does this mean there is no difference between face and body processing?

No, it does not. Although EEG has a very high temporal resolution and can therefore tell us a lot about the timing of processing, it is hard to link a specific brain area to the found activation. A method better suitable to do this is magnetoencephalography (MEG). This was recently done for investigation of the earliest onset of the electrophysiological inversion effect for different stimulus categories (Meeren, Hadjikhani, Ahlfors, Hamalainen, & de Gelder, 2008). They indeed found that the cortical distribution of this early effect was highly category-specific. Different time courses of activation were observed in the common neural substrate in FG.

Furthermore, faces activated the inferior occipital gyrus (IOG; also named occipital face area (OFA)), whereas for bodies the effect was observed in the posterio-dorsal medial parietal areas (precuneus / posterior cingulate). Hence, whereas face inversion modulates early activity in face-selective areas in the ventral stream, body inversion evokes activity in dorsal areas, suggesting different early cortical pathways for configural face and body perception.

Besides this early processing in perceiving faces and bodies, more general processing on longer time scales can be investigated with functional magnetic resonance imaging (fMRI). With this method, there has actually been found a distinction in the FG between faces and bodies, thereafter called fusiform face area (FFA) and fusiform body area (FBA) (Schwarzlose, Baker, & Kanwisher, 2005). Furthermore, bodies seemed to be processed also in another area: the extrastriate body area (EBA) (Downing et al., 2001). This area lies very close to the human motion area (hMT+/V5), and given that bodies imply action, this finding is not peculiar. Besides, superior temporal sulcus (STS) and premotor cortex (PM) also get activated for bodies (Grèzes, Pichon & de Gelder, 2007), the former is known to be involved in biological motion (Bonda, Petrides, Ostry & Evans, 1996), the latter also being a motor area.

When directly comparing the neural correlates of faces and bodies, the sparse evidence points to a broader network for the perception of bodies, probably due to the action component involved in those. It is remarkable that the literature on isolated face and body perception is more extensive compared to the knowledge of the more ecologically valid combined perception of a face on a body. The few studies available addressing this issue consistently point to a strong mutual influence (Aviezer, Hassin, Ryan, Grady, Susskind & Anderson, 2008; Meeren, van Heijnsbergen & de Gelder, 2005; Van den Stock, Righart, & de Gelder, 2007).

EMOTIONAL MODULATION OF BODY SELECTIVE AREAS

That faces and bodies are processed in a distinct way, being special classes of objects, has probably to do with their ecological value. We are experienced in recognizing many different facial identities and being able to react appropriately to intentions stated in bodies has survival value. Important sources of information about someone's intentions are facial and bodily expressions. Being able to quickly react to these, they must be effectively processed in the brain.

Evidence was found for fast automatic processing of emotional body language. Fear expressed by the body affected the response of the P1 component already at 100-120 ms after stimulus onset and also the N170 component showed a difference (van Heijnsbergen, Meeren, Grèzes & de Gelder, 2007). This means that processing of the emotion goes faster than identifying a body.

This emotional processing partly takes place in the face and body areas, suggesting a better representation of the faces and bodies. Several studies have reported emotional modulation of face selective areas fusiform face area (FFA) and occipital face area (OFA) (Breiter, Etcoff, Whalen, Kennedy, Rauch & Buckner, 1996; van de Riet, Grèzes, & de Gelder, 2009; Vuilleumier, Armony, Driver, & Dolan, 2001). However, this effect may be dependent on age (Guyer, Monk, McClure-Tone, Nelson, Roberson-Nay & Adler, 2008), attachment style (Vrticka, Andersson, Grandjean, Sander, & Vuilleumier, 2008), personality type (Kret, Pichon, Grèzes, & de Gelder, 2008)) and gender of the observer and the observed (Kret, Pichon, Grèzes, & de

Gelder, submitted). So far, only a few studies investigated the effects of emotional information of body expressions on activation of body areas in the brain. The first functional magnetic resonance imaging (fMRI) study addressing this issue observed an increased activation of FG and amygdala (AMG) for fearful body expressions (Hadjikhani & de Gelder, 2003). A follow up experiment showed additionally the involvement of motor areas (de Gelder et al., 2004). Also when directly comparing neutral and emotional faces and bodies (van de Riet et al., 2009), we observed that emotional bodies activate (sub)cortical motor related structures, such as the inferior frontal gyrus (IFG), caudate nucleus and putamen which has probably to do with being able to respond fast to emotional bodies.

Although our findings of emotional modulation of FBA have been replicated (Peelen, Atkinson, Andersson, & Vuilleumier, 2007), emotional modulation of EBA is uncertain. We did not observe a difference between neutral and emotional body images (van de Riet et al., 2009) but our data with dynamic body expressions does show emotional modulation (Grèzes et al., 2007; Kret et al., submitted; Pichon, de Gelder, & Grèzes, 2008; Sinke, Sorger, Goebel, & de Gelder, 2010).

AFFECTIVE GIST OF THE SCENE INFLUENCES THE PERCEPTION OF EMOTIONS

Normally, we do not see isolated people, but we see them in a context. How does this influence our percept of the bodily expression of a single individual?

Emotional context

Because of repetitive co-occurrence of objects or co-occurrence of a given object in a specific context, our brain generates expectations (Bar & Ullman, 1996; Palmer, 1975). A context can facilitate object detection and recognition (Boyce, Pollatsek, & Rayner, 1989; Palmer, 1975), even when glimpsed briefly and even when the background can be ignored (Davenport and Potter, 2004). Joubert and colleagues (2008) also observed that context incongruence induced a drop of correct hits and an increase in reaction times, thus affecting even early behavioral responses. They concluded that object and context must be processed in parallel with continuous interactions possibly through feed-forward co-activation of populations of visual neurons selective to diagnostic features. Facilitation would be induced by the customary co-activation of "congruent" populations of neurons whereas interference would take place when conflictual populations of neurons fire simultaneously. Bar (2004) proposes a model in which interactions between context and objects take place in the inferior temporal cortex.

Just like recognizing objects is not independent from other cues such as context, emotion perception does not proceed on information from one cue (as facial expressions) alone (Hunt, 1941). Knowledge of the social situation (Aviezer et al., 2008; Carroll & Russell, 1996), body posture (Meeren et al., 2005; Van den Stock et al., 2007), other emotional faces (Russel & Fehr, 1987), voice (de Gelder & Vroomen, 2000) or linguistic labels (Barrett, Lindquist, & Gendron, 2007) influence emotion perception and even which emotion is seen in the structural configuration of the participants’ facial muscles. In line with the evolutionary significance of the information, the effects of the emotional gist of a scene may occur at an early level. We previously showed scene context congruency effects on facial expressions in behavioural responses but also in EEG measurements; It could be observed when participants had to explicitly decode the emotional expression of the face (Righart &

de Gelder, 2008) but also when they focussed on its orientation (Righart & de Gelder, 2006). This indicates that it reflects an early and mandatory process and suggests a perceptual basis. Looking at EEG, we see that the presence of a fearful expression in a fearful context enhanced the face-sensitive N170 amplitude as compared to a face in a neutral context. This effect was absent for contexts-only, indicating that it resulted from the combination of a fearful face in a fearful context (Righart & de Gelder, 2006). That scenes are indeed important is also shown in two recent fMRI studies where participants interpreted facial expressions differently and different brain areas were activated depending on the context (Kim, Somerville, Johnstone, Polis, Alexander & Shin, 2004; Mobbs, Weiskopf, Lau, Featherstone, Dolan & Frith, 2006).

Social emotional context

Does it influence our emotional reaction when we watch a single individual fleeing from danger while bystanders are passively standing there? Do we ignore the social scene to focus only on the emotion of the target figure or are we unwittingly influenced by the social scene viewing individual action through the filter it provides us? Studies on crowd behavior (McDougall, 1920) indicate that social scenes provide a context in which individual actions are better understood prompting an adaptive reaction in the observer. Using point-light displays, Thornton & Vuong (2004) have shown that the perceived action of a walker depends upon actions of nearby "to-be-ignored" walkers. Another point-light study by Clarke and colleagues (2005) demonstrates that the recognition of a person’s emotional state depends upon another person’s presence (Clarke, Bradshaw, Field, Hampson, & Rose, 2005). A recent study by (Kret & de Gelder, submitted) report that the social group in which we encounter a person, and especially their bodily expressions, influence how we perceive the body language of this single individual. In this study, images of emotional body postures were briefly presented as part of social scenes showing neutral or emotional group actions. These were more accurately and faster recognized when the actions in the scenes expressed an emotion congruent with the bodily expression of the target figure. These studies show the importance of a social (emotional) scene. However, other processes than the ones measured may contribute to the observed effects, for example the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person and to converge them emotionally (de Gelder et al., 2004; Hatfield, Cacioppo, & Rapson, 1994)). Similar brain areas are involved when subjects experience disgust (Wicker, Keysers, Plailly, Royet, Gallese, & Rizzolatti, 2003) or pain (Jackson, Meltzoff, & Decety, 2005), as when they observe someone else experiencing these emotions. Such a process may contribute to observers' ability to perceive rapidly ambiguity between a person's body language and its social (emotional) context. Such incongruity may create a conflict in emotional contagion processes triggered by the target figure and help to explain the slower and less accurate reaction in the observer.

STATIC VS. DYNAMIC

Research performed with facial and bodily pictures have contributed a lot to our understanding of how our brain processes these stimuli. However, in real life, we are confronted with moving people. Although static body postures already imply motion, dynamic stimuli obviously contain more information, which helps in better understanding someone's intentions and being able to react appropriately to these. Point-light display studies showed that biological motion is quickly detected (Johansson, 1973). A few neuroimaging studies report the importance of movement in processing emotional expressions (see e.g. Decety & Chaminade, 2003; Grosbras &

Paus, 2006; LaBar, Crupain, Voyvodic, & McCarthy, 2003). Adolphs et al. (2003) reported that a patient with a ventral pathway lesion is able to read emotion from dynamic, but not from static facial expressions (Adolphs, Tranel, & Damasio, 2003). In healthy subjects, Sato et al. (2004) found that the AMG, IOG and FG were more activated by dynamic than static fearful facial expressions. Studies of bodily expressions also report better recognition rates for dynamic versus static stimuli (Atkinson, Dittrich, Gemmell, & Young, 2004; de Meijer, 1989). A recent brain imaging study looked at the perception of angry and neutral hand and face movements (Grosbras & Paus, 2006). The authors reported that regions known to be involved in action and emotion generation in oneself also get activated when perceiving action and emotion in faces and hands of others. Furthermore, they reported an interaction between emotion and body part: When hand actions were performed with emotion, a region in the supramarginal gyrus responded mostly to this. Since this region had been implicated before to be involved in getting attention towards a limb (Rushworth, Krams, & Passingham, 2001), it seems here that the emotion in the hand movement increased this attention.

This study, however, was not designed to detect specifically what additional information is contributed by dynamics. Two studies that tried to do this used 3 sec videoclips of someone opening a door in either a neutral or in a fearful (Grèzes et al., 2007) or angry way (Pichon et al., 2008). From each movie, one frame at which the emotion was at its peak was taken and also presented for 3 sec. Not surprisingly, dynamic *vs.* static body expressions (irrespective of the emotional content) caused motor resonance: bilateral activations of PM and parietal cortex, STS and FG. Most interestingly, an interaction was observed between emotion and motion in STS and right PM. In humans, STS, parietal and PM are involved in action observation and probably also in action understanding (Grèzes & Decety, 2001), so since these areas represented the emotional action in this study, they could also be involved in emotion understanding.

INDIVIDUAL DIFFERENCES

Gender

One aspect that has so far not received much attention in the studies of facial and bodily expressions concerns the role of gender in emotional processing. Some isolated findings indicate that there may be gender differences in emotional processes. Females tend to score higher than males on tests of empathy, social sensitivity, and emotion recognition (see (Hall, 1978; McClure, 2000) for reviews). But whereas females show more facial mimicry in response to emotional movie fragments, they did not report experiencing more emotion than males which suggests an expressive, rather than an experiential difference (Kring & Gordon, 1998). Testosterone level is a good predictor of the presence of an anger trait, aggressive behavior and dominance (van Honk & Schutter, 2007) and at the neuronal level, AMG response to fear and anger signals (Derntl, Windischberger, Robinson, Kryspin-Exner, Gur & Moser, 2009). Aleman and Swart (2008) report stronger activation in the IFG and STS in men than women in response to faces denoting interpersonal superiority.

A different issue is whether the gender of the person we observe influences us differently depending on our own gender. When we think of the interpersonal superiority effect in male observers as reported by Aleman and Swart (2008), it probably does. Except for very interesting work on gender stereotypes for different emotions, this question is hardly explored in the field of social neuroscience. Armony and Sergerie (2007) studied memory for fearful, happy and neutral expressions in relation to the gender of the observer. They report that the hemispheric laterality of AMG for memory of facial expressions was a function of the sex of the subjects and the sex of the faces being remembered. The left AMG was more active for successfully remembered female fearful faces in women, whereas in men the right AMG was more involved in memory for male fearful faces. These results demonstrate a subtle relationship between the observer and the stimulus.

A recent study by Kret et al. (submitted) reveals how face and body specific areas are modulated by gender. Two event-related FMRI experiments, using an oddball task, were used to record female and male participants' brain activity while they observed videos showing fear, anger or neutral signals expressed by female and male actors. In the first experiment, short video fragments of the angry and neutral expressions were used, in the second fearful and neutral expressions. The AMG was modulated more by facial than bodily expressions. FG was involved in processing body stimuli, more than in processing faces. Threatening body expressions, whether fearful or angry, modulated activity in hMT+/V5-EBA and the parietal and somatosensory cortex (which may play a role in action understanding). We also found significant influences of the gender of the actors and of the observers. A higher activation of EBA and STS was observed for threatening male versus female actors. Male observers showed more activation for threatening vs. neutral bodies in many visual processing areas, more so than female observers and especially to male body expressions. These results are in line with previous studies that show male observers are more reactive to threatening signals than female observers (Aleman & Swart, 2008).

Human emotion perception depends to an important extent on whether the stimulus is a face or a body and also on the gender of the observer and observed. Therefore these gender effects can also be seen back in the neurofunctional mechanisms of emotion.

Personality differences

‘Embodied cognition’, a concept that has recently been getting a lot of attention in cognitive science, suggests that our mind and thus our perception is shaped as much by our body and how we physically interact with the environment as by 'passive' sensory experience. Increased vigilance and enhanced autonomic activity are part of an adaptive response to threat. In otherwise healthy individuals this can become maladaptive when stress is too great. In various pathological conditions the anxiety response is disproportionate to the stress, either because of a misinterpretation of threat, or because of hyper- or hypo-responsiveness at any of a variety of points in the complex network of neural pathways that serve the stress response. Imaging techniques offer unique opportunities to explore the neurofunctional basis of personality differences and indeed show that perceiving emotions is greatly regulated by top-down processes being different from person to person.

People suffering from social phobia or anxiety generally show increased AMG activity when confronted with threatening faces (for a meta-analysis see (Etkin & Wager, 2007)). However, the role of the AMG in depression is less clear. Whereas some studies report increased AMG response for threatening versus neutral expressions related to depressive symptoms (Canli, Cooney, Goldin, Shah, Sivers & Thomason, 2005; Peluso, Glahn, Matsuo, Monkul, Najt & Zamarripa, 2009), others report a decrease in activity (Thomas, Drevets, Whalen, Eccard, Dahl & Ryan, 2001) or no difference at all (Davidson & Dalton, 2003; Lee, Seok, Lee, Cho, Yoon & Lee, 2008). Several studies report decreased cortico-limbic connectivity in depression in response to emotional stimuli (Anand, Li, Wang, Lowe, & Dzemidzic, 2009; Drevets, 1998; Fossati, Hevenor, Graham, Grady, Keightley & Craik, 2003) but antidepressant treatment shows reciprocal effects (Anand, Li, Wang, Gardner, & Lowe, 2007). Decreased activation in the anterior cingulate cortex has been reported in depression as well (Davidson & Dalton, 2003; Fossati et al., 2003).

Recognition of another's emotion does not suffice for proper communication. The orbitofrontal cortex (OFC) regulates appropriate social responses (Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Rolls, 2000). Socially anxious people are afraid of possible scrutiny and negative evaluation by others. Not surprisingly, many studies find an overactive frontolimbic system (including OFC, insula and AMG) in this group during threat perception (Shah, Klumpp, Angstadt, Nathan, & Phan, 2009; Straube, Mentzel, & Miltner, 2005). Moreover, the OFC has been consistently involved in the pathophysiology of major depressive disorder and bipolar disorder (Davidson & Dalton, 2003; Drevets, 2007).

People with type D ('distressed') personality (21% of the general population) have higher scores on depression and anxiety scales (Denollet, Schiffer, Kwaijtaal, Hooijkaas, Hendriks & Widdershoven, 2009). They suffer from emotional distress ('negative affectivity'), which they consciously suppress ('social inhibition'). This personality type is associated with a negative prognosis in disease and a range of somatic effects. A recent study by van de Riet and colleagues (2009) showed a correlation between the negative affectivity subscale and AMG hypoactivation for fearful facial and bodily versus neutral expressions. So, even small personality differences in the normal population account for a different perception of threat. However, this study focused only on the AMG as region of interest and neglected other possibly interesting effects that could have been detected in a whole brain analysis. Moreover, this study used static stimuli. In a follow-up study, we aimed to reveal neural correlates of Type D personality and perceiving dynamic threatening facial and bodily expressions. We observed a negative correlation in the temporal pole and cingulate cortex on both subscales. Furthermore, a negative correlation was observed between negative affectivity and activation in brain areas commonly involved in emotion: AMG, FG, insula, STS and IFG. The right OFC correlated negatively with social inhibition. Also interesting is the relation between social inhibition and increased activation following threat in the anterior intraparietal sulcus, left TPJ, STS, right IFG, secondary somatosensory cortex, and left OFC. These regions are all involved in the action goal of the observed (see for a recent meta-analysis (Van Overwalle & Baetens, 2009). When observing action, we need to take the others' perspective which we do by activating our mirror and mentalizing system. The mirror system (anterior intraparietal sulcus and PM) is engaged in perceiving and executing motions of body parts and is important for understanding action and emotion (Rizzolatti & Craighero, 2004). TPJ plays an important role in our mentalizing system and computes the orientation or direction of the observed behavior to predict its goal (Van Overwalle & Baetens, 2009). Observing as well as imitating facial expressions activate the IFG (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). People who tend to inhibit socially are likely to over-activate the mirror and mentalizing system.

Taking the others’ perspective is not enough; we need to empathize and reason how to act. The OFC is connected with areas that underlie emotional function and empathy (Hynes, Baird, & Grafton, 2006) and interprets somatic sensations (Bechara, Damasio, Tranel, & Anderson, 1998) mediated by internally generated somatosensory representations that simulate how the other person would feel when displaying an emotion (Adolphs, 2002). Without these representations, appropriate reactive behaviour would be difficult. Rauch et al. (1995) used positron emission tomography (PET) to measure the changes in right cerebral blood flow in phobic patients provoked by exposure to the feared object. They observed significant increases during the symptomatic compared with the control state in OFC and somatosensory cortex. The complex connections between the OFC and areas involved in emotion, suggest implications for its role in anxiety disorders (Fischer, Andersson, Furmark, & Fredrikson, 1998). We hypothesize that people with high scores on social inhibition prefer to avoid social situations because it gives them too much cognitive stress.

PERCEIVING INTERACTIONS

Trying to get additional information going from static to dynamic facial and bodily expressions, including a context and taking into account gender stereotypes, there is another step to take to get to even more naturalistic situations. This is the perception of a person interacting with another person. The interplay between those can inform us about their relationship.

In previous stimuli creation, actors always looked into the camera. Therefore, an emotional expression had an immediate impact on the observing participant. In a direct confrontation, it makes sense that you want to react immediately. But what happens when the threat is not directed towards you? This question has been studied recently by Sinke et al. (2010). In this study, we wanted to investigate how the brain reacts to a situation that is threatening for one of the two persons involved. For this study, we created 3 sec videoclips in which a male actor grabbed the handbag of a female actor. He did this either in a very aggressive way whereby the woman expressed fear, or in a teasing way, as if the two know each other. The actors faced each other and did not attend towards the observer. When you walk on the street you may have your thoughts on an upcoming deadline instead of on the persons on the other side of the street. Will you than still be able to recognize a threat? To investigate this second question, three small dots, presented only for 40 ms, were added to each movie. Participants in the first task had to look explicitly to the bodies and categorize the situation as threatening or teasing. In the other task condition, they had to monitor the randomly appearing dots and categorize their color. Results showed first of all that the AMG showed heightened activation for the threatening interactions as compared to the teasing ones. The AMG seems to act as some kind of warning signal and possibly passes information through to other regions. During unattended threat, also more processing took place in body sensitive visual regions in FG, middle occipitotemporal gyrus and STS than teasing interactions. Furthermore, this heightened activation for unattended threat was paired with better behavioral performance on the dot task during threatening interactions. It seemed as if the threat heightened their attention and because the dots were always placed somewhere on the bodies, they were able to perceive them better. Another finding was that although the threat was clearly not directed towards the observer, regions known to be involved in action observation (IFG, TPJ and inferior parietal lobe) and preparation (PM, putamen) showed increased activation for threat. In conclusion, bodily expressions are easily recognized even though your attention is not explicitly on the situation and the threat is not directed towards you, which has high survival value.

BODIES PROCESSED WITHOUT ATTENTION AND VISUAL AWARENESS

Studies with hemianopia patients already showed that perception or recognition of bodily expressions does not require full attention. Patients with striate cortex lesions or an attentional disorder can react to a visual stimulus even though they have not consciously seen it. Patients with left hemispatial neglect due to a lesion in the right parietal cortex fail to direct attention to stimuli in their left visual field. However, when the stimulus is an expressive in contrast to a neutral face or body or a neutral object, they are better able to perceive it.

The clearest example of being able to process emotional signals has been given by patients with lesions to their primary visual cortex (V1). Under stringent testing conditions, they were able to discriminate between visual properties of stimuli they can not consciously see. This phenomenon is called ‘blindsight’. Later, it was shown that they were also able to guess correctly the emotional valence of facial stimuli presented in their blind visual field, so-called ‘affective blindsight’ (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). In the first behavioral study only moving stimuli but not still images of facial expressions appeared to support affective blindsight. If movement was the critical aspect to support non-conscious discrimination of different emotional expressions, one would expect blindsight also for other attributes that rely on movement. However, blindsight was only observed for emotional facial expressions and not facial speech (de Gelder, Vroomen, Pourtois, & Weiskrantz, 2000). Other facial attributes such as personal identity or gender were also tested with negative results, suggesting that neither movement nor non-emotional facial attributes are per se determinants of the phenomenon. More directly, in later research affective blindsight emerged very clearly also when still images of facial expressions were used, especially when tested with indirect methodologies (Anders, Birbaumer, Sadowski, Erb, Mader & Grodd, 2004; Pegna, Khateb, Lazeyras, & Seghier, 2005). Still unknown is whether affective blindsight is induced by non-conscious processing of overall face configuration or by individual key features. There is evidence that the eye region is most salient in conveying emotion information, and that the most ancient parts of our visual and emotion systems in the brain seem tuned to detect this simple signal rather than the whole face configuration (Kim et al., 2004; Morris, deBonis, & Dolan, 2002).

Aside from facial expressions, other stimulus categories have been used to test whether affective blindsight could be extended to other stimuli. Thus far, the most studied categories are affective scenes and bodily expressions. Generally, negative results have been reported for scenes, suggesting that the appraisal of the emotional content of complex pictures requires cognitive and semantic processing that depends on conscious visual perception (de Gelder, Pourtois & Weiskrantz, 2002). On the other hand, behavioral and neuroimaging results have shown that affective blindsight for bodily expressions may be at least as clearly established as that previously reported for facial expressions, and sustained by a partly overlapping neural pathway (de Gelder & Hadjikhani, 2006). This implies that implicit processing of emotions in blindsight is non-specific for faces but for biologically primitive emotional expressions in general.

CONCLUSION

There are important similarities and differences in the neurofunctional basis of faces and bodies. Both are very strong cues. They grab our attention and can even be processed without attention and visual awareness. Whereas it is widely accepted that the FG plays a role in the perception of emotions, whether from the face or body, emotional modulation of the EBA is still under discussion. The scene in which we perceive emotions can facilitate our recognition and the presence of other people expressing the same emotion naturally helps us perceive another's emotion correctly. Moreover, in a natural social scene, we see people interacting with each other. The perception of emotions is not a pure bottom up process. Several top down processes such as knowledge of the social situation, gender and personality type play a role as well. In real life, people express their emotions in a dynamic way. This movement component adds information, thereby facilitating recognition. To conclude, the perception of emotion is not so straightforward and involves many different kinds of processes.

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