Context, gender and personality factors influencing the perception of facial and bodily expressions of emotion

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Context, gender and personality factors influencing the perception of facial and bodily expressions of emotion

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Chapter 1

Introduction

Perceiving emotions from facial and bodily expressions

Social communication includes intuitively grasping signals of hostility and reacting with empathy to signals of distress. Over decades, a large body of evidence has been published showing that emotion perception is not just based on facial information alone (Hunt, 1941). Humans are especially sensitive to the gestural signals and facial expressions made by other people, and use these signals as guides for their own behavior. However, social and affective neuroscience has largely focused on the perception of emotions from static facial expressions (Adolphs, 2002; Haxby, Hoffman, & Gobbini, 2000). From evolutionary perspective, bodily expressions of emotion are much older than facial expressions as Darwin (1872) described in his famous book 'The expression of the emotions in man and animals' (Darwin, 1872). Also William James (1890) discussed body expressions at great length (James, 1890). Moreover, in our natural world, a face is usually encountered not as an isolated object but as an integrated part of a whole body, situated in a scene.

Emotion perception is influenced by numerous factors, including body postures (Aviezer et al., 2009; Meeren, van Heijnsbergen, & de Gelder, 2005; Van den Stock, Righart, & de Gelder, 2007), prosody (de Gelder & Vroomen, 2000; de Gelder & Vroomen, 2000; Van den Stock et al., 2007), emotional scenes (Righart & de Gelder, 2006, 2008a, 2008b), the presence of other emotional people (Russel & Fehr, 1987) and dynamic cues (Grèzes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grèzes, 2008; Sato, Fujimura, & Suzuki, 2008; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). Besides these bottom-up factors, emotion perception is regulated via an unlimited range of top-down mechanisms including, to name a few, knowledge of the social situation (Carroll & Russell, 1996), gender-stereotypical thinking (Barrett & Bliss-Moreau, 2009), attitudes towards and exposure to minority groups (Elfenbein & Ambady, 2002; 2003) which are framed by ones personality.

In this thesis I discuss the neurological processes underlying the perception of emotion which I studied by the use of several techniques. Whereas most studies focused on static facial expressions, I took a broader perspective and included bodily expressions, the influence of a social scene in which we naturally encounter one another, as well as dynamic information (videos). Moreover, when we observe someone, the emotion is not all that we see; we see a female versus a male and we notice it when this person is from a certain out-group at which point stereotypes come into play. In my research I focused on individual differences in the normal student population (different personality traits such as social anxiety, but also gender differences and negative attitudes towards an out-group) and beyond (violent incarcerated offenders).

A variety of methods is available for measuring specific aspects of emotion. Some behavioral tasks focus on manual responses (for example accuracy rates or reaction times) while others relate to fixation behavior or physiological measures. Neuroimaging includes the use of various techniques to either directly or indirectly image the structure, function/pharmacology of the brain. I will here briefly introduce several techniques that I applied in the experiments that are discussed in this thesis.

Methods

Functional magnetic resonance imaging (fMRI)

fMRI provides a "snapshot" of the active, dynamic, functioning brain that allows one to pinpoint the region where brain activity is taking place. fMRI uses magnets to measure small changes in the brain's blood oxygenation level that occur while a task is performed. The first fMRI study was performed in the early '90s (Belliveau et al., 1991), but since then the technology has evolved, with much more powerful, high-field magnets, such as 7 Tesla or 9 Tesla, now available. The hemoglobin has different magnetic properties depending on if it is oxygenated or not. These differences can be seen in the whole brain imaged by fMRI technology. This process relates to the energy expended by the brain's neurons within a specific area of the brain. The powerful magnets stimulate the atoms and molecules within the blood flowing to the brain's cells. An advantage of fMRI is the high spatial resolution, a disadvantage, however, is that fMRI has poor temporal resolution. The Blood Oxygenation Level Dependent (BOLD) response peaks approximately 5 seconds after neuronal firing begins in an area. This means that it is hard to distinguish BOLD responses to different events which occur within a short time window.

Facial electromyography (EMG)

We spontaneously synchronize our facial expressions with the emotion of another person during interactions, a phenomenon termed emotional contagion (Hatfield, Cacioppo, & Rapson, 1994). Facial EMG has been used for measuring these emotional reactions (Dimberg, 1990). Studies have found that activity of the corrugator muscle, which lowers the eyebrow and is involved in producing frowns, varies inversely with the emotional valence of presented stimuli and reports of mood state. Activity of the zygomatic muscle, which controls smiling, is associated with positive emotional stimuli and positive mood state.

Eye tracking

Eye tracking is the process of measuring either the point of gaze or the motion of an eye relative to the head. In the 1800s, studies of eye movement were made using direct observations. Early studies of eye tracking have noted that human gaze control is highly regular; viewers tend to concentrate their fixations on semantically informative regions when shown pictures of scenes or faces (Buswell, 1935; Yarbus, 1967). In the 1970s, eye tracking research expanded rapidly and new technologies were developed. Today, the most popular method uses video images from which the eye position is extracted. Head mounted systems are designed to accurately track pupil size, eye movement and eye point-of-regard data from subjects while allowing freedom of head movement. The adoption of eye tracking technology provides a direct and continuous measure of attention.

Observing people

Looking at faces

Humans are experts at processing faces. They can recognize thousands of individual faces and can quickly decode a variety of emotional expressions and direction of gaze. There is a large consensus in the literature that like the face itself, facial expressions are processed configurally, a processing style that presumably enables speed and efficiency (Tanaka & Farah, 1993). The hallmark of this processing routine is the inversion effect (Yin, 1969; for a review, see Maurer, Grand, & Mondloch, 2002) or the impaired recognition performance when the face is shown upside down. The N170 is a negative brain potential peaking at 170 ms after stimulus onset at the lateral occipito-temporal sites. The N170 to inverted faces is larger and more delayed than to upright faces, but there is no such difference when observing objects (Watanabe, Kakigi, & Puce, 2003).

The inversion effect is also observed with facial expressions of emotion (de Gelder, Teunisse, & Benson, 1997). However, face inversion did not hinder identification of a smiling expression but reduced accuracy for fearful, sad, and angry expressions (McKelvie, 1995). But interestingly, identification of emotions was easier when only the upper part of the face carried the affective message and the lower part was neutral than when the full face was shown. This effect was obtained for fearful, sad and angry but not happy faces (de Gelder, Vroomen, & Bertelson, 1998). It has been proposed that both the parts and the overall configuration play a role in emotion identification (White, 2000).

The eyes are richly informative and important in understanding emotion and communicative intention of other individuals (Emery, 2000). Emotion-driven complex musculature changes such as the raising and lowering of eyelids and eyebrows enables perceivers to decode emotions from just the eye region (Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997). The eyes capture more attention than other areas of the face in adults (Adolphs et al., 2005; Janik, Wellens, Goldberg, & Dell'Osso, 1978) as well as in infants (Haith, Bergman, & Moore, 1977) and this bias may reflect an innate predisposition (Argyle & Cook, 1976). It has been observed that whereas people express fear mainly with the eyes, they express happiness with the mouth (Morris, deBonis, & Dolan, 2002; Vuilleumier, 2005).

In view of the importance of the eye region, one may expect that information from the eyes is robust such as to resist influence from the surrounding context and from other non-visual accidental factors. Yet we often only see the eyes because caps, hats, helmets, medical masks or headdresses hide the rest of the face. Whether the expression of the eyes is sensitive to such visual context factors (beard or a hat etc.) is still unknown. There is some evidence that emotion categorization from the eye region is a process that is triggered automatically in a bottom-up fashion on the basis of the information available from the position of the eyebrows (Sadrô, Jarudi, Sinha, 2003; Leppänen , Hietanen & Koskinen, 2008) and the eye white (Whalen et al., 2004). On the other hand, recent evidence suggests that as far as the whole face is concerned, the perception of expressions is influenced by context more than had previously been assumed. In fact, a task-irrelevant context can dramatically shift the emotional category recognized in basic facial expressions and bias the valence judgment of facial expressions toward this information (e.g., Meeren et al., 2005; Righart and de Gelder, 2006; Van den Stock et al., 2007; Aviezer et al., 2008; Koji & Fernandes, 2010). Therefore, it seems premature to rule out that context does play a role in eye perception expression. I investigated this question and the results are described in chapter 11.

Looking at bodies

Prior research has shown that visual recognition of human bodies is more difficult for upside down than upright presentations (Reed, 2006). This body inversion effect is similar to the face inversion effect (Yin, 1969) and suggests that bodies are processed configurally (Stekelenburg & de Gelder, 2004). Using magneto encephalography, this effect was visible already at 70–100 ms post-stimulus onset (Meeren, Hadjikhani, Ahlfors, Hamalainen, & de Gelder, 2008). For faces, it was observed in well-known face-selective areas: inferior occipital gyrus (including occipital face area) and fusiform gyrus (including fusiform face area), whereas for bodies, in the precuneus and posterior cingulate cortex. Hence, whereas face inversion modulates activity in face-selective areas in the ventral stream, body inversion evokes activity in dorsal areas, suggesting different early cortical pathways for face and body perception.

Distinct expressions of emotions are readily recognized even in the absence of facial and vocal cues, when emotions are portrayed by body language (for an overview, see de Gelder et al., 2010). Even biological-motion cues are sufficient for the perception of emotion (Dittrich, Troscianko, Lea, & Morgan, 1996; Johansson, 1973; Pollick, Paterson, Bruderlin, & Sanford, 2001). Whereas there exists a broad literature on how people look at faces and on which face parts are important for emotion perception, there is hardly any literature on how we look at bodily expressions of emotion. This question has been investigated in a study by Ousov-Fridin et al (2009). When perceiving pictures associated with joy, people fixated on the head, whereas for anger and fear, most attention was devoted to the hands and arms. For sad pictures, people fixated on the whole body. The legs almost never drew participants' attention. So far, it is not known whether the bodily expression modifies fixation behavior on the face and the inverse. I elaborate on this question in chapter 3.

Faces and bodies in the brain

The most studied brain area in affective neuroscience is the amygdala. This area responds to salient signals and is the key area in the social brain network (Adolphs, 2009). In the early stages of processing emotions, bodily resonance is automatic and reflex-like, while in the later, more cognitive and conscious processing stages, it is under strategic control and influenced by higher order knowledge.

The first route involves a subcortical pathway to the amygdala via the superior colliculus and pulvinar, and is concerned with fast, subconscious processing following salient, threatening stimuli (de Gelder, Pourtois, van Raamsdonk, Vroomen, & Weiskrantz, 2001; de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Morris, de Gelder, Weiskrantz, & Dolan, 2001; Morris, Ohman, & Dolan, 1998; Morris, Öhman, & Dolan, 1999; Pegna, Khateb, Lazeyras, & Seghier, 2005) The second route, via the lateral geniculate nucleus and striate cortex to cortical regions including the superior temporal sulcus, occipital face area and fusiform face area, is concerned with detailed and fine-grained processing in case stimuli are ambiguous and full blown awareness of the perceived stimulus is necessary (de Gelder, 2006; de Gelder et al., 2009). These parallel routes interact and modulate each other with feed-forward and feed-back projections in order to establish a fine-grained percept composed of identity and emotional aspects of the observed, which can be accessible to consciousness (Pessoa, 2010). Especially the amygdala has strong functional and structural connections with cortical regions like the fusiform face area, superior temporal sulcus and occipital face area (functional connectivity: Morris et al., 1998; Iidaka et al., 2001; Vuilleumier et al., 2004; structural connectivity: Carmichael & Price, 1995); or with striate cortex (structural connectivity: (Amaral & Price, 1984; Catani, Jones, Donato, & Ffytche, 2003).

The neural network underlying face perception is well known and includes the fusiform face area (Kanwisher, McDermott, & Chun, 1997), the occipital face area (Gauthier, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996), the superior temporal sulcus and the amygdala (Haxby et al., 2000). Two areas in the body perception network have been the targets of categorical selectivity research. The one reported first is an area at the junction of the middle temporal and middle occipital gyrus, labeled the extrastriate body area (Downing, Jiang, Shuman, & Kanwisher, 2001). Another one is in the fusiform gyrus and termed the fusiform body area (Peelen & Downing, 2005). Recent evidence suggests that these areas are particularly responsive to emotional body language (Grèzes et al., 2007; Peelen, Atkinson, Andersson & Vuilleumier, 2007; Pichon et al., 2008).

An important consideration when examining brain responses to emotional expressions is that in real life, these are dynamic. Observers are highly sensitive to biological movement, and can use abstract temporal cues alone to discriminate between self- and other-produced actions (Flach, Knoblich, & Prinz, 2004). Several lines of psychological studies have investigated the effect of dynamic presentations of facial stimuli and reported a facilitative effect on facial processing. For example, the dynamic presentation of facial expressions has been shown to improve recognition (Frijda, 1953; Harwood, Hall, & Shinkfield, 1999; Wehrle, Kaiser, Schmidt, & Scherer, 2000) and to enhance EMG and fMRI responses (Sato et al., 2008; Sato et al., 2004).

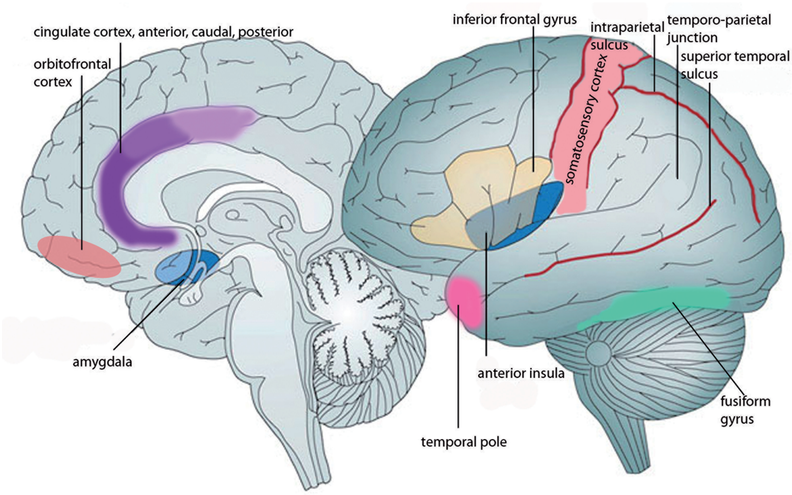
A study by Grosbras and Paus (2006) showed that video clips of angry hands trigger activations that overlap with those reported for facial expressions in the fusiform gyrus. Increased responses in the superior temporal sulcus and the temporo-parietal junction have been reported for dynamic threatening body expressions (Grèzes et al., 2007; Pichon et al., 2008; Pichon, de Gelder, & Grèzes, 2009). Different studies have demonstrated a role for the temporo-parietal junction in "theory of mind", the ability to represent and reason about mental states (Saxe & Kanwisher, 2003; Samson et al., 2004). Other functions of this area involve reorienting attention to salient stimuli, sense of agency and multisensory body-related information processing, as well as in the processing of phenomenological and cognitive aspects of the self (Blanke & Arzy, 2005). Whereas the temporo-parietal junction is implicated in higher level social cognitive processing (Decety & Lamm, 2007), the superior temporal sulcus has been frequently highlighted in biological motion studies (Allison, Puce, & McCarthy, 2000) and shows specific activity for goal-directed actions and configural and kinematic information from body movements (Bonda, Petrides, Ostry, & Evans, 1996; Grossman & Blake, 2002; Perrett et al., 1989; Thompson, Clarke, Stewart, & Puce, 2005).

Recent studies show that the neural network underlying whole body perception overlaps with the face network and confirm the involvement of the amygdala, fusiform gyrus, and superior temporal sulcus in face and body perception (Peelen & Downing, 2007; Meeren et al., 2008; van de Riet et al., 2009). But so far, these few direct comparisons have used static images. Chapter 2 describes an fMRI study in which participants› haemodynamic brain activity was measured while observing videos showing fearful, angry or neutral facial or bodily expressions.

Observing threatening actions (as compared to neutral or joyful actions) increases activity in regions involved in action preparation (Grèzes et al., 2007; Grosbras, Laird, & Paus, 2005; Pichon et al., 2008, 2009). Whereas some of us may fight back when confronted with aggression, others flee or freeze (Schmidt, Richey, Zvolensky, & Maner, 2008). The orbitofrontal cortex integrates information from regions of the cerebral cortex and subcortical areas and has strong connections to other organs of the body. Eisler and Levine (2002 adduced evidence that the orbitofrontal cortex is the pivotal area for choice between a fight or flight reaction in a threatening situation. Since the orbitofrontal cortex forms links between sensory events and positive or negative affective valuation, such choice among behaviors can be biased by an individual's personality and the presence of a stressor (Damasio, 1994; 2003; Rolls, 2004).

Specific abnormalities in the identification of emotionally salient information, together with misinterpretation of the intentions of others and impaired evaluation or regulation of one's emotional behavior, may underlie diverse symptoms in psychological disorders. Chapter 4 provides a review on emotion perception in different psychological disorders. In Chapter 5, I investigated how individual differences in personality in the healthy population may account for different brain responses following threatening stimuli. The key areas that are discussed above are visualized in figure 1.

Figure 1. The social brain



Schematic representation of brain areas involved in processing social signals.

Gender differences

Much evidence shows that women are better in identifying facial affect (Hall, 1978; Nowicki & Hartigan, 1988). Some research suggests, however, that differences depend on the type of emotion: women are better in recognizing fear and sadness (Nowicki & Hartigan, 1988), while men are superior at identifying anger (Mandal & Palchoudhury, 1985; Rotter & Rotter, 1988; Wagner, MacDonalda, & Mansteada, 1986). Sex differences are noticeable early in development. In a task which involved choosing a photograph that corresponded to a described emotion, 3.5-year-old girls were as accurate as 5-year-old boys (Boyatzis, Chazan, & Ting, 1993). The discrepancy between boys and girls is even higher in adolescence and it is most likely the result of functional maturation of affect related prefrontal-amygdala circuits.

Common sense intuitions view women as more emotional than men. Research suggests this presumed difference is based more on an expressive and less on an experiential difference (Kring & Gordon, 1998) and may be influenced by culture. Moore (1966) found that males reported more violent scenes than females during binocular rivalry, possibly because of cultural influences that socialize males to act more violently than females. While socialization of aggressiveness might involve learning to control and inhibit angry behavior, pressures for this may be stronger on females than on males (Eron & Huesmann, 1984).

A growing body of research demonstrates gender differences in the neural network involved in processing emotions (Dickie & Armony, 2008; Harwood et al., 1999; Hofer et al., 2006; Kemp, Silberstein, Armstrong, & Nathan, 2004; Wehrle et al., 2000). Two observations are a stronger right hemispheric lateralization but also higher activation levels in males as compared to females (Fine, Semrud-Clikeman, & Zhu, 2009; Killgore & Cupp, 2002; Schienle, Schafer, Stark, Walter, & Vaitl, 2005).

Armony and Sergerie found that the hemispheric laterality of the amygdala involvement in successful memory for emotional material was influenced not only by the sex of the subjects, as previously proposed, but also by the sex of the faces being remembered. So, another issue is whether how the gender of the person we observe influences our percept, depends on our gender. Evidence suggests that pictures of males expressing anger tend to be more effective as conditioned stimuli than pictures of angry females (Öhman & Dimberg, 1978). Previous behavioural studies indicate enhanced physiological arousal in men but not in women during the exposure to angry male as opposed to female faces (Mazurski, Bond, Siddle, & Lovibond, 1996). Moreover, Fischer et al (2004) observed that exposure to threatening male versus female faces activated the visual cortex and the anterior cingulate gyrus more in men than in women. Stronger activation in the superior temporal sulcus in men than women following dominant faces has been observed as well (Aleman & Swart, 2008).

Taken together, there are strong indications that males and females differ in the recruitment of cerebral networks following female and male emotional expressions. How these differences relate to bodily expressions is still unknown. Chapter 6 provides an extensive review of studies in the field of affective neuroscience on sex effects of the observer and observed. Next, chapter 7 describes the results of a study which investigated female and male participants' haemodynamic brain activity while they watched videos showing threatening or neutral facial or bodily expressions of emotion from female or male actors. In chapter 8 I elaborated on this study and investigated the perception of aggressive male body language in an aggressive male group of offenders and also discuss effects of the sex of the actor.

Aggression and delinquency

Aggression and other maladaptive antisocial behaviors may result from failure to be appropriately guided by the social cues of others. Persons who act in destructive or illegal ways are often described as lacking in empathic skills and as failing to be fully aware of the intentions of others. Research evidence has supported these clinical conclusions. For instance, several researchers have found delinquents to be less empathic than control subjects (Aleksic & Savitsky, 1974; Chandler, Greenspan, & Barenboim, 1974; Kurtiness & Hogan, 1972). In addition, it has been reported that delinquents are impaired in their recognition of facial expressions of emotion (Carr & Lutjemeier, 2005; McCown, Johnson, & Austin, 1986; Sato, Uono, Matsuura, & Toichi, 2009). In particular, the recognition of others' facial expressions has been shown to modulate aggressive behaviors (Savitsky, Izard, Kotsch, & Christy, 1974). This finding suggests that there may be a relationship between emotion recognition and conduct problems involving aggression.

Several researchers have reported a tendency among antisocial individuals to misperceive benign social situations as hostile, a phenomenon coined the "hostile attributional bias" (Nasby, Hayden, & DePaulo, 1980). In their study of aggressive adolescent boys in residential mental health treatment, aggressive participants were more likely to attribute hostile intent to the person in the photo than matched controls. Since then, over 100 studies have documented this phenomenon in a wide variety of aggressive juvenile populations, and a meta-analysis has revealed a robust phenomenon with a strong mean effect size (Orobio de Castro, Veerman, Koops, Bosch, & Monshouwer, 2002). Most of these studies focused on aggressive youth but the phenomenon has been observed in adults as well (Sato et al., 2009; Walz & Benson, 1996).

Real life situations are often much more ambiguous than the clear, obvious static facial expressions that previous research has used predominantly. So far, it is not known how offenders recognize emotions when they are embedded in a more naturalistic context and when they are expressed by the whole body (see chapter 8).

The role of a context in perceiving emotions

Facial expressions in the context of a bodily expression

In contrast to stimuli that are commonly used in lab situations, in our natural world, a face is usually encountered not as an isolated object but as an integrated part of a whole body situated in a scene. Moreover, we are often confronted with ambiguous signals. For example, when someone tells a sad story but cannot or does not want to show his true emotions and puts on a smile. In this example, the body language may be much more informative. Observers judging a facial expression are strongly influenced by emotional body language and research suggests a rapid neural mechanism sensitive to the degree of agreement between simultaneously presented facial and bodily expressions (Meeren et al., 2005). Chapter 3 deals with the questions whether in case of an incongruent body expression we attend more to the body and how much we empathize with people that show emotionally ambiguous signals.

Social context

We naturally encounter one another in a naturalistic scene, often with other people around. Scene context congruency facilitates the recognition of facial expressions (Righart & de Gelder, 2006, 2008a, 2008b). 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). Righart and de Gelder (2008a) replicated their findings by briefly (200 ms) presenting fearful faces in fearful versus happy scenes. The authors suggested that the affective gist congruency reflects an early and mandatory process.

But how we perceive another's emotion, may also depend on the people standing around that person, not just on the physical environment (Clarke, Bradshaw, Field, Hampson, & Rose, 2005). The influence of other peoples' emotions on the recognition of and fixations on one target figure has never been systematically investigated (see chapter 8).

Outline of the thesis

I will here briefly introduce the chapters that are included in this thesis. In chapter 2, the neural networks underlying emotional face and body perception are discussed, followed by a chapter on how we tend to look at and emotionally converge with people displaying congruent and incongruent facial and bodily expressions of emotion (chapter 3). Chapter 4 provides an overview of studies investigating emotion perception in the context of different psychological disorders. Chapter 5 deals with the question how the emotional brain responds differently to threat depending on personality factors. Chapter 6 provides a review on gender differences in emotion perception and underscores the importance of taking into account the sex of the observer as well as the sex of the observed. In chapter 7, the differences between male and female participants and how they are differentially influenced by the sex of the actor are described. In chapter 8, emotion perception deficits are investigated in a violent and offensive group. In chapter 9-11 I discuss the importance of a context in which we naturally perceive emotions. Chapter 12 presents an overview and integration of the findings of all chapters and a discussion of the strengths and limitations of these studies.

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Chapter 2

Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study.

This chapter is based on:
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Abstract

Neuroscientific research on the perception of emotional signals has mainly focused on how the brain processes threat signals from photographs of facial expressions. Much less is known about body postures or about the processing of dynamic images. We undertook a systematic comparison of the neurofunctional network dedicated to processing facial and bodily expressions. Two functional magnetic resonance imaging (fMRI) experiments investigated whether areas involved in processing social signals are activated differently by threatening signals (fear and anger) from facial or bodily expressions. The amygdala (AMG) was more active for facial than for bodily expressions. Body stimuli triggered higher activation than face stimuli in a number of areas. These were the cuneus, fusiform gyrus (FG), extrastriate body area (EBA), temporoparietal junction (TPJ), superior parietal lobule (SPL), primary somatosensory cortex (SI), as well as the thalamus. Emotion-specific effects were found in TPJ and FG for bodies and faces alike. EBA and superior temporal sulcus (STS) were more activated by threatening bodies.

Introduction

Perception of bodies and bodily expressions is a relatively novel topic in affective neuroscience, a field dominated so far by investigations of facial expressions. But faces and bodies are equally salient and familiar in daily life and often convey the same information about identity, emotion and gender. Therefore, it seems natural to expect that many of the same research questions arise about both (de Gelder, 2006; de Gelder et al., 2010). On the other hand, differences in the neural basis of body and face processing may be as interesting as the similarities. The goal of our study was to further our understanding of both by systematically comparing facial and bodily expressions of the same emotions.

The neural network underlying face perception is well known and includes the fusiform face area (FFA) (Kanwisher et al., 1997), the occipital face area (OFA) (Gauthier et al., 2000; Puce et al., 1996), the STS and the AMG(Haxby et al., 2000). Recent studies indicate that the neural network underlying whole body perception partly overlaps with the face network (de Gelder, 2006; de Gelder et al., 2010; Peelen and Downing, 2007). But so far, the few direct comparisons have used static images (Meeren et al., 2008; van de Riet et al., 2009). These studies mainly confirm the involvement of AMG, FG, and STS in face and body perception. Furthermore, it remains unclear how activity in these regions is influenced by dynamic information. Static body pictures may imply motion, but explicit movement information in dynamic stimuli may activate a richer and partly different, broader network.

Recent studies with dynamic stimuli have proven useful for better understanding the respective contribution of action and emotion related components. A study by Grosbras and Paus (2006) showed that video clips of angry hands trigger activations that largely overlap with those reported for facial expressions in the FG. Increased responses in STS and TPJ have been reported for dynamic threatening body expressions (Grèzes et al., 2007; Pichon et al., 2008, 2009). Whereas TPJ is implicated in higher level social cognitive processing (Decety and Lamm, 2007), STS has been frequently highlighted in biological motion studies (Allison et al., 2000) and shows specific activity for goal-directed actions and configural and kinematic information from body movements (Bonda et al., 1996; Grossman and Blake, 2002; Perrett et al., 1989; Thompson et al., 2005).

There are also some currently unanswered questions about the functional role of body and face selective areas. A body-sensitive area in the extra striate cortex (EBA) was first reported by Downing et al. (2001). Its role in processing dynamic stimuli and affective valence is not yet clear. Urgesi et al. (2007) attribute featural but not configural processing to EBA (see also Taylor et al., 2007; Hodzic et al., 2009). Previous studies using static stimuli failed to find evidence for emotion modulation (de Gelder et al., 2004; Lamm and Decety 2008; van de Riet et al., 2009), but studies of dynamic bodily expressions show that EBA is sensitive to affective information conveyed by the body stimulus (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008). This modulation by emotion may be compatible with EBA as a feature processor, in which case one would need to investigate which specific body part conveys the affective information. Alternatively, EBA does in fact process the configuration of the stimulus. This alternative is consistent with our findings that EBA is differentially sensitive to affective information in the body when videos are used. Originally, Hadjikhani and de Gelder (2003) compared neutral bodies and fear bodily expressions and reported sensitivity for fear bodies in FG. Consistent with this body sensitivity of FG, a later study using neutral bodies, defined a body-sensitive area in the FG labeled the fusiform body area (FBA) (Peelen and Downing, 2005). The role of the EBA and FG in emotional processing has not been fully understood yet, and it is too early to claim that EBA is specifically sensitive for bodily features and less or not sensitive to the configural representation of a body. The use of dynamic emotional stimuli and a direct comparison with facial expressions is likely to provide new insights in this matter.

We used fMRI to measure participants' haemodynamic brain activity while they were watching videos showing fearful, angry or neutral facial or bodily expressions. A major goal was to clarify the sensitivity of AMG, FG, EBA, STS and TPJ for affective valence of whole bodies and of faces. We used a ROI procedure to localize each of these regions. We predicted an increased BOLD response in these areas for facial and bodily expressions of emotion compared to neutral faces and bodies. A second goal was to clarify the emotion -sensitivity of EBA. Since studies that use dynamic stimuli find emotional modulation in this area, we expected to find this area especially active for threatening body expressions.

Methods

Participants

Twenty-eight (14 females, mean age 19.8 years old, range 18– 27 years old; 14 males; mean age: 21.6 years old, range 18–32 years old) took part in the experiment. Half of the participants viewed neutral and angry expressions and the other half viewed neutral and fearful expressions. Participants had no neurological or psychiatric history, were right-handed and had normal or corrected-to-normal vision. All gave informed consent. The study was performed in accordance to the Declaration of Helsinki and was approved by the local medical ethical committee. Two participants were discarded from analysis, due to task miscomprehension and neurological abnormalities and analyses were done over 26 participants.

Materials

Video recordings were made of 26 actors expressing six different facial and bodily emotions. All actors were dressed in black and filmed against a green background. For the facial videos, actors wore a green shirt, similar as the background color. To coach the actors to achieve a natural expression, pictures of emotional scenes were, with the help of a projector, shown on the wall in front of them and a short emotion inducing story was read out by the experimenter. Additionally, the stimulus set included neutral non expressive face and body movements (such as pulling up the nose, twitching/licking lips, coughing, fixing one's hair, or clothes).Recordings used a digital video camera under controlled and standardized lighting conditions in a recording studio. All video clips were computer-edited using Ulead and After Effects, to a uniform length of two seconds (50 frames). The faces of the body videos were masked with Gaussian masks so that only information of the body was perceived.

For each actor and emotion, a few different versions were filmed. These materials were given to five independent raters and they selected the best actors and of these the two best videos per emotion and per actor. The total number of video clips selected was sixty (five male and five female actors, three emotions and two videos each). These materials were then used in a validation study and presented twice to 20 independent raters. In the validation, participants selected among six emotion labels (anger, fear, surprise, sad, disgust and happy). Angry facial expressions were correctly recognized for 84% (SD 19), fearful facial expressions for 86% (SD 7), neutral facial expressions for 79% (SD 21) angry bodily expressions for 85% (SD 15), fearful body expressions for 83% (SD 16) and neutral body expressions for 80% (SD 20). The participants from the current study also had to label the selected videos after the scanning sessions. All expressions were recognized above 82% correct and there was no difference between anger and fear ($t(24)=.310$, ns).

To check for quantitative differences in movement between the movies, we estimated the amount of movement per video clip quantifying the variation of light intensity (luminance) between pairs of frames for each pixel (Grèzes et al., 2007; Peelen et al., 2007). For each frame (50 in total), these absolute differences were averaged across pixels that scored (on a scale reaching a maximum of 255) higher than 10, a value which corresponds to the noise level of the camera. These were then averaged for each movie. Student's two-tailed t-tests were conducted to check whether the amount of movement differed between neutral and threatening movies. Angry and fearful expressions contained equal movement (M=30.64, SD 11.99 vs. M=25,41, SD 8.71) [$t(19)=.776$, ns], but more than neutral expressions (M=10.17, SD 6.00) [$t(19)=3.78$, $p\leq.005$, $d=2.14$] and [$t(19)=4.09$, $p\leq.005$, $d=2.04$]. In addition, by using Matlab software, we generated scrambled movies by applying a Fourier-based algorithm onto each movie, a technique that has been used for pictures before (Hoffman et al., 2007). This technique scrambles the phase spectra of each movie's frames and allows to generate video clips served as low-level visual controls and prevents habituation to the stimuli.

Experimental design

The experiment consisted of a total of 176 trials (80 non scrambled (ten actors (five males) × two expressions (threat, neutral) × two runs × two repetitions) and 80 scrambled videos and 16 oddballs (inverted video clips)) which were presented in two runs in the MRI scanner. There were 80 null events (blank, green screen) with a duration of 2000 ms. These 176 stimuli and 80 null events were randomized within each run. A trial started with a fixation cross (500 ms), followed by a video (2000 ms) and a blank screen (2450 ms). An oddball task was used to control for attention and required participants to press a button each time an inverted video clip appeared so that trials of interest were uncontaminated by motor responses. Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head coil. Stimuli were centered on the display screen and subtended 11.4° of visual angle vertically for the body stimuli, and 7.9° of visual angle vertically for the face stimuli.

Procedure

Participants' head movements were minimized by an adjustable padded head-holder. Responses were recorded by an MR-compatible keypad, positioned on the right side of the participant's abdomen. After the two experimental runs, participants were given a functional localizer. Stimulus presentation of the main experiment and of the separate localizer study was controlled by using Presentation software (Neurobehavioral Systems, San Francisco, CA). After the scanning session, participants were guided to a quiet room where they were seated in front of a computer and validated the stimuli they had previously seen in the scanner by choosing between a threatening (fear or anger) or a neutral label.

fMRI data acquisition

Parameters of the functional scan

Functional images were acquired using a 3.0-T Magnetom scanner (Siemens, Erlangen, Germany). Blood Oxygenation Level Dependent (BOLD) sensitive functional images were acquired using a gradient echo-planar imaging (EPI) sequence (TR = 2000ms, TE = 30 ms, 32 transversal slices, descending interleaved acquisition, 3.5 mm slice thickness, with no interslice gap, FA = 90°, FOV = 224 mm, matrix size = 64 x 64 mm). An automatic shimming procedure was performed before each scanning session. A total of 644 functional volumes were collected for each participant (total scan time = ten minutes per run (2 runs with the anatomical scan in between)).

Parameters of the structural scan

A high-resolution T1- weighted anatomical scan was acquired for each participant (TR =2250 ms, TE = 2.6 ms, FA = 9°, 192 sagittal slices, voxel size 1 x 1 x 1 mm, Inversion Time (TI) = 900 ms, FOV = 256 × 256 mm2, 192 slices, slice thickness = 1 mm, no gap, total scan time = 8 minutes).

Statistical parametric mapping

Functional images were processed using the SPM2 software package (Wellcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm). The first five volumes of each functional run were discarded to allow for T1 equilibration effects. The remaining 639 functional images were reoriented to the anterior/ posterior commissures (AC–PC) plane, slice time corrected to the middle slice and spatially realigned to the first volume, subsampled at an isotropic voxel size of 2 mm, normalized to the standard MNI space using the EPI reference brain and spatially smoothed with a 6-mm full-width at half-maximum (FWHM) isotropic Gaussian kernel. Statistical analysis was carried out using the general linear model framework (Friston et al., 1995) implemented in SPM2.

At the first-level analysis, nine effects of interest were modeled: four represented trials where subjects perceived emotional expressions or neutral face and body videos, four represented the scrambled counterparts, and one represented the oddball condition. Null events were modeled implicitly. The BOLD response to the stimulus onset for each event type was convolved with the canonical haemodynamic response function over 2000 ms. For each subject's session, six covariates were included in order to capture residual movement related artifacts (three rigid-body translations and three rotations determined from initial spatial registration), and a single covariate representing the mean (constant) over scans. To remove low frequency drifts from the data, we applied a high-pass filter using a cutoff frequency of 1/128 Hz. We smoothed the images of parameter estimates of the eight contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel and estimated the following main effects and interactions at the first level:

1) Main effect of body vs. face [Emotion + neutral (body vs. face)];
2) Main effect of face vs. body [Emotion + neutral (face vs. body)];
3) Main effect of emotion vs. neutral [Emotion vs. neutral (face + body)]

At the second level of analysis, we performed between-subjects ANOVAs to isolate, in the main effects contrasts estimated at the first level, effects common to the fear and anger groups. Our goal was to study common modulations by threat in areas involved in processing faces and bodies, rather than studying specific modulations by fear and anger (see Pichon et al., 2009). Contrasts of main effects described above were entered in three between-subjects ANOVAs. The between factor corresponded here to group exposed to either fear or anger stimuli. A nonsphericity correction was applied for variance differences between conditions and subjects. Conjunction contrasts were estimated to reveal modulations common to both groups. For example, the ANOVA 'body vs. face' is a conjunction between the first-level contrasts 'body vs. face' estimated for subjects of Experiment 1 (anger) and Experiment 2 (fear). The conjunction allows rejection of the null hypothesis only if all comparisons in the conjunction are individually significant (Friston et al., 2005).

Given the conservative analyses based on the conjunction null hypothesis, we displayed activations that survived a threshold of T = 2.75 (<.005, uncorrected) with a minimum cluster extent of 20 contiguous voxels and report only p values that survived the threshold of T = 3.39 (<.001, uncorrected) with a minimum cluster extent of ten contiguous voxels. In addition, we indicate in tables, peaks that survived false discovery rate (FDR) correction (p<.05) (Genovese et al., 2002). Statistical maps were overlaid on the SPM's single subject brain compliant with MNI space, i.e., Colin27 (Holmes et al., 1998) in the anatomy toolbox www.fz-juelich.de/ime/spm_anatomy_toolbox, see Eickhoff et al. (2005) for a description). The atlas of Duvernoy was used for macroscopical labeling (Duvernoy, 1999).

Localization of face- and body-sensitive regions

Face- and body-sensitive voxels in the EBA, FFA/FBA, STS, AMG, and TPJ were identified using a separate localizer scan session in which participants performed a one backward task on face, body, house, and tool stimuli. The localizer consisted of 20 blocks of 12 trials of faces, bodies (neutral expressions, ten male, and ten female actors), objects, and houses (20 unique tools and 20 unique houses). Body pictures were selected from our large database of body expressions, and only the stimuli that were recognized as being absolutely neutral were included. To read more about the validation procedure of these stimuli, we refer the reader to the article of van de Riet et al. (2009). The tools (for example, pincers, a hairdryer etc.) and houses were selected from the Internet. All pictures were equal in size and were presented in a grayscale on a grey background. Stimuli were presented in a randomized blocked design and were presented for 800 ms with an ISI of 600 ms. Participants had to indicate whether the previous stimulus was the same as the one presented. We are currently preparing an extensive analysis of this localizer in a large sample of participants (van den Stock et al., in preparation).

Preprocessing was similar to the main experiment. At the first-level analysis, four effects of interest were modeled: faces, bodies, houses, and tools. For each subject's session, six covariates were included in order to capture residual movement-related artifacts (three rigid body translations and three rotations determined from initial spatial registration), and a single covariate representing the mean (constant) over scans. To remove low-frequency drifts from the data, we applied a high-pass filter using a cutoff frequency of 1/128 Hz. We smoothed the images of parameter estimates of the contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel. At the group level, the following t-tests were performed: face > house, body > house, and, subsequently, a conjunction analysis [body > house AND face > house]. The resulting images were thresholded liberal ($p < .05$, uncorrected) to identify the following face- and body-sensitive regions of the brain: FFA/FBA, AMG, STS, and EBA (see Table 1 for coordinates and the contrasts used). ROIs were defined using a sphere with a radius of 5 mm centred onto thegroup peak activation of the localizer. We did not detect TPJ with our localizer. All chosen areas appeared in the whole brain analysis and are well known to process facial and bodily expressions (see Fig. 1). However, since there is a lot of discussion about using the same data set of the main experiment for the localization of specific areas to make ROIs (Kriegeskorte et al., 2009), we defined TPJ by averaging the group peaks from our former studies (Grèzes et al., 2007; Pichon et al., 2008, 2009). The MNI coordinates of these voxels are shown in Table 1.

Table 1. Coordinates used to create regions of interest

		MNI coordinates				
Hemisphere	**Anatomical region**	**x**	**y**	**z**	**Reference**	**Contrast**
R	Fusiform face/body area	42	-46	-22	localiser	[body > house AND face > house]
L		-42	-46	-22	localiser	coordinate from right hemisphere
R	Amygdala	18	-4	-16	localiser	face > house
L		-18	-8	-20	localiser	face > house
R	Superior temporal sulcus	54	-52	18	localiser	[body > house AND face > house]
L		-54	-52	18	localiser	Coordinate from right hemisphere
R	Extrastriate body area	52	-70	-2	localiser	body > house
L		-50	-76	6	localiser	body > house
R	Temporo-parietal junction	62	-40	26	1+2+3	1+2+3
L		-60	-40	24	2+3	2+3

* average coordinate :
1. Grèzes et al., 2007 (fear body > neutral body)
2. Pichon et al., 2008 (anger body > neutral body)
3. Pichon et al., 2009 [anger body AND fear body]

The beta values of the ROIs were extracted for the following conditions: face threat, body threat, face neutral and body neutral. Since there were almost no differences across the left and right hemispheric ROIs and our interest does not concern hemispheric lateralization, we pool bilateral ROIs to reduce the total number of areas. Main and interaction effects were tested in SPSS in an ANOVA and were followed up with subsequent Bonferroni-corrected post-hoc 2-tailed t-tests.

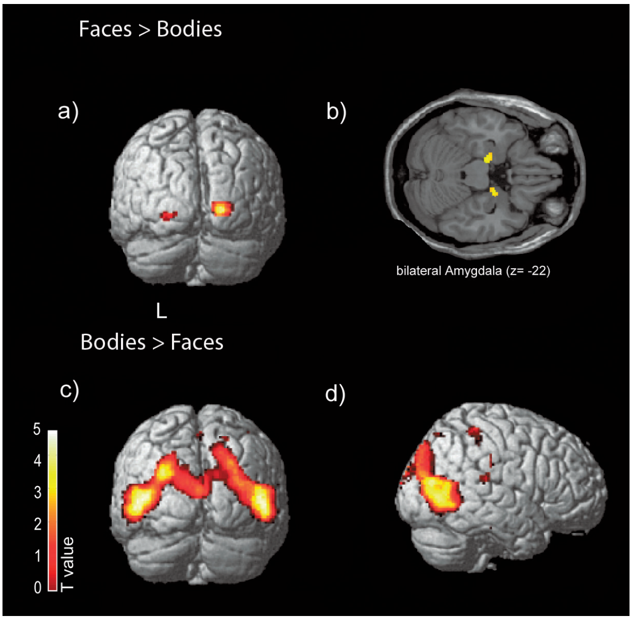
Results

fMRI results

Bodies vs. faces

The conjunction between body vs. face [(anger+neutral (BO vs. FA)] and [fear+neutral (BO vs. FA)] yielded a large increase of activity in both hemispheres including the cuneus, middle occipital/temporal gyrus, inferior temporal gyrus, and TPJ extending to the paracentral lobule and the posterior cingulate gyrus. This cluster included the FBA, EBA, and STS regions that were found in the localizer experiment. Other areas included the supramarginal gyrus, superior parietal lobule, left thalamus, primary somatosensory cortex (Brodmann area (BA) 3b/2), and intraparietal sulcus. The full list of activations is presented in Table 2 (see also Fig. 1).

Figure 1. Statistical maps of the whole brain analysis.



Statistical maps at p <.001, uncorrected, with a minimum cluster extent of 10 voxels showing a) common brain areas to fearful and neutral faces vs. bodies and angry and neutral faces vs. bodies, rendered on the Colin brain (SPM) and b) superimposed on SPM standard single-subject T1-weighted coronal section. AMG is sensitive to facial expressions. c) Statistical maps showing common brain areas to fearful and neutral bodies vs. faces and angry and neutral bodies vs. faces, rendered on the Colin brain (SPM),coronal view and d) sagittal view. Parietal and temporal regions were specifically involved in body stimuli. Results are listed in Table 2 and 3.

Faces vs. bodies

The conjunction between face vs. body [(anger+neutral (FA vs. BO)] and [fear+neutral (FA vs. BO)] showed activations in the occipital pole, left hippocampus, and right AMG (see Table 3 and Fig. 1).

Table 2. Body vs. Face stimuli

Hemi-sphere	Anatomical region	MNI coordinates x	y	z	z value	Size in voxels	
L	Middle occipital gyrus	-40	-80	6	5.54	7511	*
L/R	Middle temporal gyrus (MT/V5/EBA)	±50	-74	4	5.24/5.33	7511	↓*
R	Cuneus, dorsal part	18	-86	46	4.20	7511	↓*
L/R	Cuneus (BA 18)	±6	-92	16	4.93/5.11	7511	↓*
R	Intraparietal sulcus, middle part	32	-84	22	4.88	7511	↓*
L	Intraparietal sulcus, superior part	-22	-76	36	4.06	7511	↓*
L/R	Fusiform / lingual gyrus	±26	-58	-10	3.73/4.19	56/7511	↓*
R	Posterior middle cingulate cortex	12	-40	50	4.11	435	*
L	Paracentral lobule (BA 4)	-6	-38	50	2.45	7511	↓*
L/R	Posterior cingulate cortex	±16	-22	42	3.52/4.01	7511	↓*
R	Postcentral sulcus (BA 3b/2)	34	-36	54	3.84	435	↓*
L	Inferior parietal lobule (BA 2)	-30	-42	48	3.10	100	*
L	Temporo-parietal junction	-46	-38	20	3.75	140	*
R	Temporo-parietal junction (OP1)	56	-30	18	3.53	46	*
L	Supramarginal gyrus	-66	-32	20	3.23	12	*
R	Supramarginal gyrus (TPJ)	58	-26	34	3.45	21	*
L/R	Superior parietal lobule	±22	-72	56	3.01/3.23	129/18	*
R	Inferior temporal gyrus	46	-24	-26	3.54	16	*
L	Thalamus	-18	-28	4	3.46	40	*
R	Inferior temporal gyrus	52	-58	-4	4.93	7511	↓*
L		-52	-44	-20	3.03	41	*

$p < 0.001$ uncorrected, extend threshold 10 voxels
Results listed survived FDR correction p < 0.001
↓ subpeak

Table 3. Face vs. Body stimuli

Hemi-sphere	Anatomical region	MNI coordinates x	y	z	z value	Size in voxels
L/R	Occipital pole (BA 17)	±18	-100	0	3.46/4.98	48/225
L	Hippocampus	-14	-12	-22	3.30	47
R	Amygdala	20	-4	-22	3.20	28

$p < 0.001$, extend threshold 10 voxels

Emotion vs. neutral

The emotion vs. neutral conjunction [(anger vs. neutral (FA + BO)] AND [(fear vs. neutral (FA + BO)] showed bilateral activity in EBA and STS. Neither contrasting anger vs. fear (inclusively masked by anger vs. neutral, p=.05), nor fear vs. anger (inclusively masked by fear vs. neutral, p=.05) revealed significant activations (p=.001, uncorrected). See Table 4.

Table 4. Emotional vs. Neutral stimuli

Hemi-sphere	Anatomical region	MNI coordinates x	y	z	z value	Size in voxels
L/R	Middle occipital gyrus (MT/V5/EBA)	±50	-78	2	5.42	237
R	Superior temporal sulcus / gyrus	70	-38	14	4.22	128
L	Superior temporal sulcus / Middle temporal gyrus	-46	-48	10	3.07	44

p < 0.001, extend threshold 10 voxels

Facial and bodily expressions of emotion in different ROIs

To examine emotion effects in well known face- and body-selective areas, we extracted the beta values of predefined ROIs as described previously (see Fig. 2).

EBA showed a main effect of emotion (F(1,25)=45.343, p <.001, ηp 2 =.65) and category (F(1,25)=154.853, p <.001, ηp 2 =.86). This area was more active for threatening versus neutral expressions and for bodies than faces (both corrected, p <.001). EBA showed an interaction between category and emotion (F(1,25)=5.575, p <.05, ηp 2 =.18). Both faces and bodies induced more activity when expressing a threatening versus a neutral expression (faces: t(25) =3.362, p <.005, d=.43; bodies: t(25)=6.349, p <.001, d=.30), yet the difference in bodies versus faces was larger (t(25)=11.501, p <.001, d=1.46).

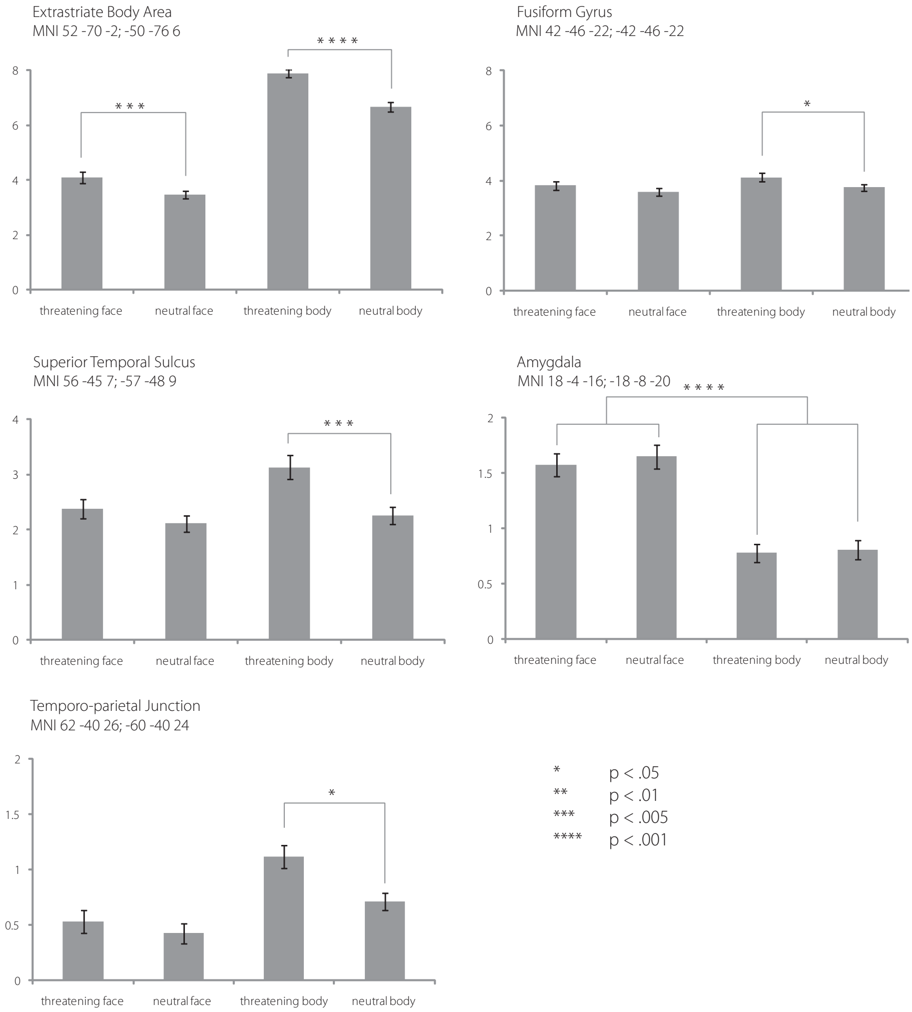
FFA/FBA showed a main effect of emotion (F(1,25)=9.463, p <.005, ηp 2 =.28). This area was more active for threatening than neutral expressions (corrected, p <.005), irrespective of the specific category.

STS showed a main effect of emotion (F(1,25)=21.404, p <.001, ηp 2 =.46) and category (F(1,25)=7.293, p <.05, ηp 2 =.23). This area was more active for threatening versus neutral expressions (corrected, p <.001) and for bodies than faces (corrected, p <.05). STS showed an interaction between category and emotion (F(1,25)= 7.874, p <.01, ηp 2 =.24). Whereas STS did not differentially respond to emotional versus neutral faces (p=.265), activity was higher for emotional versus neutral bodies (t(25)=4.386, p <.005, d=.45).

AMG showed a main effect of category (F(1,25)=18.568, p <.001, ηp 2 =.43). This area was more active for faces than bodies (corrected, p <.001), irrespective of the emotional component.

TPJ showed a main effect of category (F(1,24)=16.227, p <.001, ηp 2 =.39) and emotion (F(1,24)=4.374, p <.05, ηp 2 =.15). This area was more active for threatening than neutral expressions (corrected, p <.05) and for bodies than faces (corrected, p <.001).

Figure 2. Facial and bodily expressions of emotion.



Please note the differences in scale. EBA was more active for threatening versus neutral expressions and for bodies than faces. Both faces and bodies induced more activity when expressing a threatening versus neutral emotion yet the difference in bodies versus faces was larger. FFA/FBA was more active for threatening than neutral expressions, irrespective of the specific category, yet only significant for the bodies. STS was more active for threatening versus neutral expressions and for bodies than faces. Whereas STS did not differentially respond to emotional versus neutral faces, activity was higher for emotional versus neutral bodies. AMG was more active for faces than bodies, irrespective of the emotional component. TPJ was more active for threatening than neutral expressions and for bodies than faces.

Discussion

Our comparative study of the neurofunctional basis of perceiving video clips of facial and bodily expressions of threat (fear and anger) reveals similarities as well as differences between the neural basis of facial and bodily expression perception. The first major finding is that the AMG is more active for facial than for bodily expressions, but independently of the facial emotion. Secondly, a number of areas show higher activation for bodies than for faces. These are the cuneus, FG, EBA, TPJ, SPL, SI, as well as the thalamus. Thirdly, whereas EBA and STS show specific increased activity to threatening body expressions, FG responds equally to emotional faces and bodies.

Faces and amygdala activation

AMG was more active for facial than for bodily expressions. Our study provides the first direct comparison between dynamic facial and bodily expressions. The results show that AMG is responding to all face, and to a smaller extent, all body stimuli yet is not more sensitive to emotional than to neutral face videos. Other studies that used dynamic facial expressions did not find AMG activity either when contrasting emotional versus neutral faces (Grosbras and Paus, 2006; Kilts et al., 2003; Puce and Perrett, 2003; Simon et al., 2006; Thompson et al., 2007; van der Gaag et al., 2007; Wheaton et al., 2004). Hurlemann et al. (2008) found two clusters (b15 voxels) in the left AMG for happy but not for angry versus neutral facial animations. Sato et al. (2004) found left AMG in an ROI analysis by contrasting fearful but not happy morphed faces versus a mosaic pattern. Trautmann et al. (2009) report more left AMG activity for dynamic disgusted but not happy versus neutral faces. In earlier studies using still images (Hadjikhani and de Gelder, 2003; van de Riet et al., 2009), we also found the AMG responding similarly to facial and bodily fear expressions. On the other hand, the AMG activity found here with dynamic stimuli is not specific for threatening facial expressions.

One explanation for the lack of strong statistical evidence for increased AMG involvement in dynamic fear and anger expressions is that the difference between neutral and expressive faces may be smaller for dynamic than static stimuli. A dynamic neutral face has already by itself a strong social meaning. We know that AMG is responsive to ambiguity as exists when facial information is partly missing (Whalen et al., 1998; Hsu et al., 2005). In monkeys, increased AMG activity has been recorded during passive observation of social stimuli such as conspecifics facial expressions, gaze direction or social interactions (Logothetis et al., 1999; Gothard et al., 2007; Hoffman et al., 2007; Brothers et al., 1990). AMG activity is larger when during social communication with unpredictable consequences as compared to physical aggression (Kling et al., 1979). The BOLD response in AMG during the identity matching of neutral faces, was equally large as during matching the affect of faces (Wright and Liu, 2006). These studies suggest that the AMG response may be driven by neutral yet salient faces and fits with the notion that it encodes salience and modulates recognition and social judgment (Tsuchiya et al., 2009).

Body-specific activations and emotional body expressions

Recent fMRI studies using neutral stimuli have identified dedicated networks of face as well as of body-sensitive brain areas that are partly overlapping. STS as well as FG play a role in face as well as in body perception (for a review of currently available studies, see de Gelder et al., 2010). The role of FG in processing facial expressions is already well known, and evidence is accumulating that FG also plays a role in body perception. In line with our earlier studies with static stimuli (Meeren et al., 2008; van de Riet et al., 2009), we observe here that the FG is involved in processing dynamic bodies and faces. The sensitivity of FG to threat is not stimulus category specific. As expected, body videos trigger activity in EBA (Grèzes et al., 2007; Peelen and Downing, 2007; Pichon et al., 2008), especially when the expression was threatening. However, since the movement quantification method we used may not reflect the neural computation of movement, we cannot rule out that EBA reacts also to movement and threatening videos contained more movement than neutral videos.

TPJ is systematically associated with a variety of social cognitive tasks such as perspective-taking (Ruby and Decety, 2003), empathy (Jackson et al., 2006; Lamm et al., 2007), and theory of mind (Lawrence et al., 2006; Saxe and Wexler, 2005; for a review, see Decety and Lamm, 2007). In the current study, TPJ, although responsive to all social stimuli, was more responsive to bodies than to faces, and especially bodily expressions of emotion which is in line with our earlier studies (Grèzes et al., 2007; Pichon et al., 2008, 2009). It is not surprising that TPJ reacts more to bodies than to faces since bodily expressions, in contrast to facial expressions, imply action (de Gelder et al., 2004; de Gelder, 2006; 2010). TPJ is known to be involved in action understanding (Samson et al., 2004). Interestingly, Ruby and Decety (2001) observed greater TPJ activation when participants imagined another person performing an action than imagining themselves performing the action. The observed increased activity for bodily expressions, especially emotional ones, fits well with the literature on action understanding.

Conclusion

Our study yielded several important findings. The AMG was modulated more by faces than bodies. A number of crucial areas showed higher activation for bodies than for faces and some reflected affective stimulus meaning. Body specific activation increases were found in the FG, EBA, SPL, SI, thalamus, and TPJ. TPJ and FG showed more activity while processing emotional faces and bodies than neutral ones. There was an interaction between category selectivity and emotion in EBA and in STS. This area was specifically modulated by threatening body expressions. So, whereas EBA and STS show a specific activity pattern triggered by emotional bodies, FG is equally responsive to emotional faces and bodies. Altogether our findings underscore the importance of including investigations using bodily expressions for a better understanding of the neural basis of affective processes.

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Chapter 3

When faces and bodies do not match
Looking at emotional incongruency between a face and a body

Abstract

A face is usually encountered as part of a whole body. Facial and bodily expressions both contribute in conveying the emotional state of the individual. Previous research has shown that when briefly presented compound stimuli showing face and body cues with conflicting emotional information, judgement of the facial expression is hampered and becomes biased toward the emotion expressed by the body. This incongruency is noticed at a very early stage of processing. So far, it is not known how we observe emotionally ambiguous signals over longer stimulus presentation times and whether it affects our empathic responding. To this extent, we presented emotionally (in)congruent face-body compounds under different task instructions for 4 seconds. Overall, participants looked longer at threatening (fear/anger) than happy bodies and they spend more time observing the body when the face showed a non-threatening, happy expression. Participants' scan-path was longest in the presence of a happy face and/or body expression. Between 500-1000 ms, participants attended to the most emotionally informative parts: often the face, but also the hands. We found (in)congruency effects in manual responses: when categorizing the facial expression, participants were influenced by the body and when categorizing the body, they were influenced by the face. We observed influences of the facial expression on looking patterns on the body and influences of bodily expression on looking patterns on the face, along with differential EMG responses, but a clear congruency effect was not found.

Introduction

Communication signals used by higher organisms come in many shapes and forms and involve all sensory modalities. Among these signals, actions involving the whole body and expressing emotion by their saliency and frequency occupy a privileged position in many species (Darwin, 1872). Surprisingly, the most cursory glance at the literature on emotion in humans shows that over 95 per cent of them have used faces as stimuli. But emotions can easily be read from bodily expressions and in contrast to facial expressions, they imply action (de Gelder et al., 2009).

The eyes are richly informative and heavily relied upon in social communication. Emotions can easily be read from the eye region (Leppanen, Hietanen, & Koskinen, 2008). This region captures more attention than other areas of the face both in adults (Janik, Wellens, Goldberg, & Dell'Osso, 1978) and infants (Farroni, Csibra, Simion, & Johnson, 2002). Therefore, we tend to look immediately at the eye region of a face, and all the more so when the face expresses fear (Yarbus, 1967a). Visual cues provided by the eyes are particularly critical for the recognition of fear; other facial emotions can be recognized without looking at the eyes (Vuilleumier, 2005).

Whereas there exists a broad literature on how people look at faces, there is hardly any literature on how we look at bodily expressions of emotion. Bannerman et al (2008) investigated participants' orienting behavior using EOG electrodes measuring eye movements. Participants were instructed to make a saccade (or in another condition, a manual response), as fast as possible, to the side where the fearful body (or in another condition, the neutral body or face) appeared. In half of the trials, the stimuli were presented for 20ms, and in the other half for 500ms. The authors observed faster saccadic orienting to fearful bodily and facial expressions as compared to neutral ones, only at the shortest presentation time. For manual responses, faster discrimination of fearful cues was observed only at the longest duration (Bannerman, Milders, de Gelder, & Sahraie, 2009). Fridin et al (2009) found that people tend to fixate on the head when observing joyful pictures, whereas for pictures associated with anger and fear, most attention is devoted to the hands and arms (Fridin, Barliya, Schechtman, de Gelder, & Flash, 2009). A study by Grosbras and Paus (2006) confirmed that the hands are important in emotional communication. The authors showed that video clips of angry hands trigger activations that largely overlap with those reported for facial expressions in the fusiform gyrus (Grosbras & Paus, 2006). Whereas Fridin et al (2009) investigated fixation behavior averaged over 5 seconds of stimulus presentation, Bannerman focused on the first 500ms. Both studies provided insight in how we perceive emotions from whole bodies, but it is still unknown how participants' fixation durations develop over stimulus presentation time.

Emotional expressions play a fundamental role in social interactions, as shown by the spontaneous tendency to synchronize our facial expressions with those of another person during face-to-face situations, a phenomenon termed emotional contagion (Hatfield, Cacioppo, & Rapson, 1994). The phenomenon that observers tend to spontaneously produce facial movements similar to the facial expression of the person observed has been supported by a substantial number of electromyography (EMG) studies (Dimberg & Lundquist, 1990; Dimberg & Thunberg, 1998). Such studies typically record muscular reactions of the zygomaticus major, which pulls the corners of the mouth up and back, and the corrugator supercilii, which pulls the eyebrows together and downwards. Generally, corrugator supercilii activity is higher in response to frowning faces, whereas zygomaticus major activity is higher in response to smiling faces. Similar results have been obtained with bodily expressions indicating that we not simply mimic other people, but unconsciously synchronize emotionally with them (Tamietto et al., 2009).

In contrast to stimuli that are commonly used in lab situations, in our natural world, a face is encountered not as an isolated object but as an integrated part of a whole body situated in a scene (Kret & de Gelder, 2010). Moreover, in real life, we are often confronted with ambiguous signals. For example, when someone tells a sad story but cannot or does not want to show his true emotions and puts on a smile. Meeren et al. (2005) combined angry and fearful facial expressions with angry and fearful whole-body expressions to create 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 while 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 between happy and fearful were combined once with a happy and once with a fearful body expression (Van den Stock, Righart, & de Gelder, 2007). The resulting compound stimuli were presented for 150 ms. Again, the ratings of the facial expressions were influenced towards the emotion expressed by the body, and this influence was highest for ambiguous facial expressions (with an intermediate position on the morph continuum). The brain responded to this emotional face–body incongruency as early as 115 ms post-stimulus onset (Meeren, van Heijnsbergen, & de Gelder, 2005). We recently replicated the behavioural findings in a male violent offender group and a control group by presenting the stimuli (anger, fear, happy) even shorter (100 ms). Although the offender group suffered more from the incongruency when the body showed a threatening expression than the control group, effects of incongruency were observed in both groups (Kret & de Gelder, submitted).

So, observers judging a facial expression are strongly influenced by emotional body language and research suggests a rapid neural mechanism sensitive to the degree of agreement between simultaneously presented facial and bodily expressions. However, it is not known how these above described findings relate to situations where other people may be observed longer than 100-200 ms and be attended to consciously. What processes take over after the initial P1-peak at 115 ms as observed by Meeren et al (2005)? In fact, we earlier reported that similar effects of incongruency (between the emotion of a foreground figure and the social scene) on accuracy rates were not significant with unlimited presentation duration (strong effects were observed with 100 ms) (Kret & de Gelder, 2010). In order to further investigate this, we here presented face-body compound stimuli for 4000ms and investigated looking patterns and EMG responses as a function of stimulus presentation time. Another question is whether the earlier reported effects of incongruency are dependent on a task in which participants explicitly categorize another's emotion or whether they are also apparent in passive viewing tasks. A major goal of this research is whether we observe people with ambiguous emotional expressions differently and whether emotional incongruency between a body and a face obstructs emotional contagion. Finally, we aim to investigate if a facial expression influences the percept of a bodily expression. In five experiments, peoples' facial musculature reactions and eye gaze behavior were measured while they looked at facial and bodily expressions of emotion. In Experiment 1, participants passively viewed (in)congruent face-body pairs. In Experiment 2, they defined the facial expression of the same face-body pairs and in Experiment 3 the bodily expression. Experiment 4 and 5 served as control experiments in which participants categorized isolated facial and bodily expressions (faces without bodies and bodies with the facial features blurred).

Experiment 1. Passively viewing other people with emotional expressions

Methods

Participants

Twenty-eight participants (19 females, mean age 21.9 years old, range 18-27 years old; 9 males; mean age: 23.9 years old, range 20-32 years old) took part in the experiments. Participants had no neurological or psychiatric history, were right-handed and had normal or corrected-to-normal vision. All gave informed consent. The study was performed in accordance with the Declaration of Helsinki and was approved by the local medical ethical committee.

Materials

Facial stimuli were selected from the NimStim set of facial expressions of emotion and were all correctly recognized above 80% (Tottenham et al., 2009). Fearful, happy, and angry expressions were chosen from 6 male individuals. The bodies were selected from our large validated stimulus database (see (van de Riet, Grèzes, & de Gelder, 2009) for validation details). Face-body compound images were created by combining emotionally (in)congruent body expressions from six male actors with the facial expressions of 6 other male identities. The same identity-pairs were kept across the different conditions. Across all experiments that are described in this manuscript, stimuli were presented for 4 seconds. Because the human eye is differentially sensitive to light in the green, red, and blue spectrums (making it more difficult to estimate luminance for colour photographs), we presented pictures in greyscale, against a grey background. Luminance was controlled for by equating both the average luminance in each picture and in addition we measured the intensity with a light meter on the test computer screen.

Facial EMG

By using BioSemi flat-type active electrodes, facial EMG was measured bipolarly over the regions of the zygomaticus major and the corrugator supercilii on the right side of the face. Two additional electrodes, the common mode sense [CMS] active electrode and the driven right leg [DRL] passive electrode, were attached to the left cheek and used as reference and ground electrodes, respectively (http://www.biosemi/faq/cms&drl.htm). Before attachment, the skin was cleaned with alcohol and the electrodes were filled with electrode paste. The raw data were digitally filtered offline with a 20–500 Hz band-pass in Brain Vision Analyzer Version 1.05 (Brain Products GmbH), rectified and segmented into 5000 ms epochs, including a 1000 ms pre-stimulus baseline.

Data were then visually inspected for remaining artefacts by two independent raters that were blind to the specific condition of these trials. The problematic trials that were detected by both were immediately discarded and trials that were indicated as problematic by one rater were discussed, resulting in the exclusion of 4.36% (SD 6.06) of the trials from subsequent analysis in the passive viewing task, 4.40% (SD 7.07) in the compound-body categorization task, 6.30% (SD 6.40) in the compound-face categorization task, 6.69% (SD 8.41) in the isolated face categorization task, 8.60% (SD 10.06) in the body categorization task with blurred facial features. These trials were discarded due to abundant movement during baseline. The parameters for facial EMG acquisition and analysis were selected to conform to published guidelines for this psycho-physiological technique (DeLuca, 1997; van Boxtel, 2001). Due to technical problems, the EMG data of four participants in Experiment 1 and three in Experiment 3 were not recorded.

Eyetracking

Eye movements were recorded using the EyeLink Eye Tracking System which is a head mounted tracking device (SensoMotoric Instruments GmbH, Germany). Gaze position was sampled at a rate of 500 Hz. A drift correction was performed on every trial to ensure that eye movement data was adjusted for movement of the headset and/or body. The eye-event detection is based on an internal heuristic saccade detector built in the EyeLink tracker program. A blink is defined as a period of saccade-detector activity with the pupil data missing for three or more samples in a sequence. A saccade was defined as a period of time where the saccade detector was active for 2 or more samples in sequence and continued until the start of a period of saccade detector inactivity for 20 msec. The configurable acceleration (8000 degrees/sec/) and velocity (30 degrees/sec) threshold were set to detect saccades of at least 0.5 degrees of visual angle. A fixation is the maintaining of the visual gaze on a single location and is by default defined as any period that is not a blink or saccade.

To adjust for individual differences in fixation duration due to blinking or momentary distraction from the screen, analyses were performed on the proportion of time spent looking at each interest area within the time spent looking on the screen. The first 200ms were discarded from all analyses because since we used a fixation cross on a fixed location (between the shoulders) the first fixation automatically fell on that spot in the stimulus and was considered un-informative. Length of scan path is defined as the average saccade amplitude multiplied by the number of saccades on the whole screen as measured over the full four seconds of stimulus presentation.

Procedure

The order in which the five different tasks were completed was counterbalanced across subjects but the first two blocks always involved the passively viewing task. After every two blocks, participants were given a short break. Participants sat 1 metre from the PC monitor. The eye-tracking device was positioned on the participant's head and a 9-point calibration and validation routine of the eye tracker was performed before each block. Stimuli were presented using Eprime software on a PC screen with a resolution of 1024 by 768 and a refresh rate of 100 Hz. Each trial started with a white fixation-cross on a grey screen, shown for minimally 3000ms (until the participant fixated and a manual drift correction was performed) followed by a picture which was presented for 4000ms followed by a blank grey screen or, in case of the categorization tasks, a screen on which the emotion labels were presented (3000ms). To keep them naive regarding the purpose of the EMG, they were told that the electrodes served the recording of sweat. The eye tracking cameras were said to measure pupil dilation during the task, to conceal the recording of gaze (Kellough, Beevers, Ellis, & Wells, 2008).

There were first two blocks of 36 randomly presented trials with (in)congruent face-body compound stimuli. One block consisted of 18 emotionally congruent trials (three emotions * six actors) and 18 incongruent ones. In order to have an equal amount of incongruent as congruent trials, the 18 congruent trials were repeated in the second block, the 36 incongruent trials ((three facial expressions * three bodily expressions * six actors) – the congruent combinations = 36) were randomly distributed over the two blocks. An interest area was created around the head, the body (excluding the head) and both hands and eye tracking analyses were performed within these areas. The hand was chosen as additional region of interest because previous research has shown the importance of this region in communicating emotions (Fridin et al., 2009; Grosbras & Paus, 2006).

Participants were told that they were going to see other people at the computer screen and were instructed to attend to the fixation-cross and subsequently to look at the images any way they wanted. No reference was made to emotional expressions or ambiguous signals or what so ever (Experiment 1, two consecutive blocks). In Experiment 2 (two consecutive blocks), participants were instructed to categorize the facial expression and not to pay attention to the body expression. It was made very explicit that they had to make their judgments based on the facial expression only. In Experiment 3 (two consecutive blocks), they were instructed to categorize the emotion from the body posture. In Experiment 4, they categorized the facial expressions they saw earlier in Experiment 1-3, but this time in isolation. The faces were presented two times. An interest area was created around each eye, hence the inter-ocular space was not included (see also Moukheiber et al, 2010). In Experiment 5, participants categorized the earlier observed bodily expressions, now with blurred faces.

Data analysis

Congruent and incongruent face-body compounds- the influence of task

Yarbus (1967) is often referred to as evidence on how a task influences eye movements. The compound stimuli were used in three different experiments that differed in task instruction.

We divided the total stimulus presentation time into eight 500 ms timeslots. We first included all three tasks in one ANOVA per interest area (including the following factors: task (3), facial expression (3), bodily expression (3) and time (8)) and investigated the influence of task on looking patterns. To further investigate the interactions with task, we describe in separate paragraphs, the results per experiment. The effects that are similar across the different tasks are not repeated in each separate section (to avoid repeating the same results three times). To improve readability, the statistics are not reported in the text but all the results of the conducted statistical tests can be found in the tables. A Greenhouse-Geisser correction was applied when the sphericity assumption was not met (Greenhouse & Geisser, 1959). The results are divided in the following sections: 'looking at bodies', 'looking at hands', 'looking at faces', 'scan-path' in which the eye tracking data is discussed, followed by 'zygomaticus' and 'corrugator' (EMG data) and 'behavioural results' in which we describe the analyses of accuracy and reaction times. For the analyses regarding the EMG responses, we again first analyzed the influence of task before looking at the results within each task.

Results

Looking at bodies

Compund tasks

Relative fixation duration

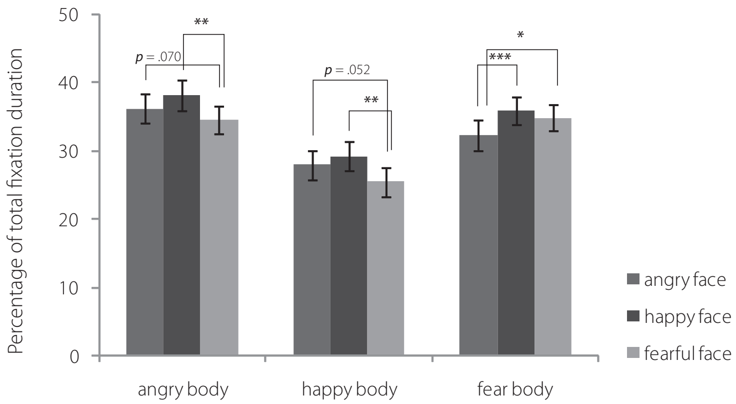
Task - Participants looked longest at the body in the body categorization task and shortest in the face categorization task (see Table 1, body area, main effect of task).

Independent of task

Facial expression – Longest fixations on the body were observed when the face showed a happy expression.

*Bodily * facial expression* - Whereas participants tended to look shorter at a body below a fearful versus angry face, an opposite effect was observed when the body expressed fear.

Figure 1. Relative fixation duration on bodies as a function of facial expression.



Pooled task, averaged over the whole stimulus presentation duration (except the first 200 ms). Participants looked shortest at a happy body and longest at a body with a happy face.

Interactions with task

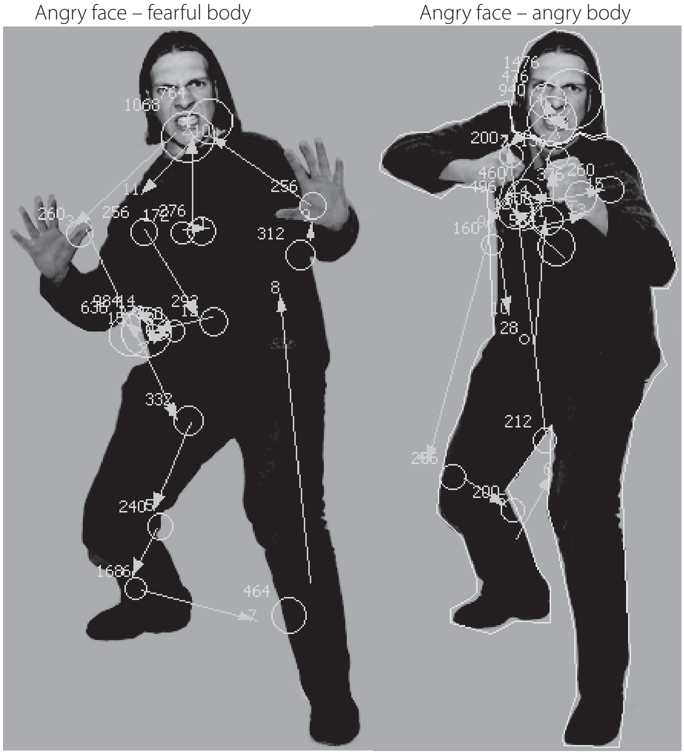
*Task * body expression* - Although participants across tasks looked shortest at happy bodies, this effect was particularly strong when categorizing the body emotion.

*Task * time* - After a drop in looking time at T2 (when participants mostly attended to the face), participants re-attended to the body. Interestingly, although participants in the face categorization task were instructed 'not to get distracted by the body', (and indeed they looked less at this region), their looking times on the body kept increasing whereas in the other two tasks this increase diminished in the final timeslots.

*Task * body expression * time* - In the first four timeslots fixation durations on fearful and angry bodies were similar. However, from that point on, looking times on angry bodies increased more than on fearful bodies. But the interaction between time and body expression was strongest in the body categorization task and there was no such interaction in the face categorization task (see figure 3c). Therefore, this effect was further investigated by including two tasks in one ANOVA. Because there was still a significant interaction [$F(14, 378) = 2.089$, $p < .001$], we discuss it below within the passive viewing task and within the body categorization task.

Figure 2. Scan-path on face-body compound (4 seconds)

Angry face – fearful body | Angry face – angry body



Fixation of one random participant during the passive viewing task. The size of the circles indicates the duration of the fixation. The lines are saccades and the numbers indicate the order in which these were made. In the picture on the right, the interest areas 'head' and 'body' are made visible with a line.

Table 1. Congruent and incongruent face-body compounds- the influence of task

	Fixation duration								
	Main effect				Interaction effect				
	Bodily expression	Facial expression	Task	Time	Body expression * Facial expression	Body expression * Time	Time *Task	Facial expression * Task	Body expression * Task	Task * Time * Body expression
Body area	F(2, 54) = 76.478**** A/F > H**** A > F, p = .055	F(2, 54) = 11.638**** H > F**** H > A*	F(2, 54) = 183.709**** Exp 3 > Exp1,2**** Exp 1 > Exp 2****	F(2.86, 77.11) = 17.159**** T2 > T1**** T3 > T2* T4> T3**** T5 > T4**	F(4, 108) = 2.791* BoA_FaA > BoA_FaF t(27)= 1.887, p = .07 BoA_FaH> BoA_FaF t(27)= 2.978** BoH_FaA > BoH_FaF t(27)= 2.032, p = .052 BoH_FaH> BoH_FaF t(27)= 3.531*** BoF_FaA < BoF_FaH/BoF_FaF t(27)≥2.215*	F(7.18, 378) = 1.938, p =.064 T1-8 BoA/F > BoH t(27)≥ 4.255**** T1, T5-T7 BoA > BoF t(27)≥ 1.752, p ≤ .091			F(3.29, 88.85) = 31.416**** Diff score (fear/anger) minus happy Exp 3 > Exp1,2 t(27) ≥ 9.942**** See Table 2	F(11.34, 306.09) = 2.629***
Face area		F(1.59, 42.86) = 8.174*** A > H** A > F*	F(2, 54) = 54.663**** Exp 2 > Exp1,3****	F(2.75, 74.20) = 34.045**** T2 > T1* T2 > T3**** T4> T3**** T5 > T4** T7 > T6*		F(7.09, 191.37) = 4.245**** T1 BoH > BoA/F t(27) ≥ 3.842*** T3 BoA/F > BoH t(27) ≥ 2.724*	F(5.07, 136.87) = 9.852**** Peak of attention at T2 for passive viewing	F(3.11, 83.92) = 10.597**** Diff score anger minus happy Exp 2 > Exp 1,3 t(27) ≥ 3.406*** Diff score anger minus fear Exp 2 > Exp 1,3 t(27) ≥ 3.258*** See Table 2	F(4, 108) = 3.595** See Table 2	F(11.38, 307.36) = 2.258*

Table 1. (Continued) Congruent and incongruent face-body compounds- the influence of task

	Fixation duration									
	Main effect				Interaction effect					
	Bodily expression	Facial expression	Task	Time	Body expression * Facial expression	Body expression * Time	Time *Task	Facial expression * Task	Body expression * Task	Task * Time * Body expression
Scanpath	F(2, 54) = 27.655**** H > A/F****	F(2, 54) = 40.441* H > A, *p* = .064	F(2, 54) = 20.490**** Exp 2 > Exp1*** Exp 2 > Exp3****	x		x	x	F(4, 108) = 3.690** Diff score happy minus (fear/anger) Exp3 > Exp2 t(27) = 3.568*** See Table 2	F(2.56, 69.20) = 12.648**** Diff score happy minus (fear/anger) Exp3 > Exp1,2 t(27) ≥ 2.760** Exp 2 > Exp 1 t(27) = 5.007**** See Table 2	x
	EMG response									
Zygomaticus				F(1.53, 29.02) = 5.866* T8 > T3-6)*						
Corrugator		F(1.28, 24.36) = 6.829** A/F > H*	F(2,38) = 6.373*** Exp 1 < Exp2,3*	F(2.57, 48.84) = 6.573*** T8 > T3-6)*						
								H = happy	Fa = face	*p* < .01 = **
								F = fear	Bo = body	*p* < .005 = ***
								A = anger	*p* < .05 = *	*p* < .001 = ****

Main and interaction effects were followed up by 2-tailed t-tests and Bonferroni corrected pairwise comparisons.

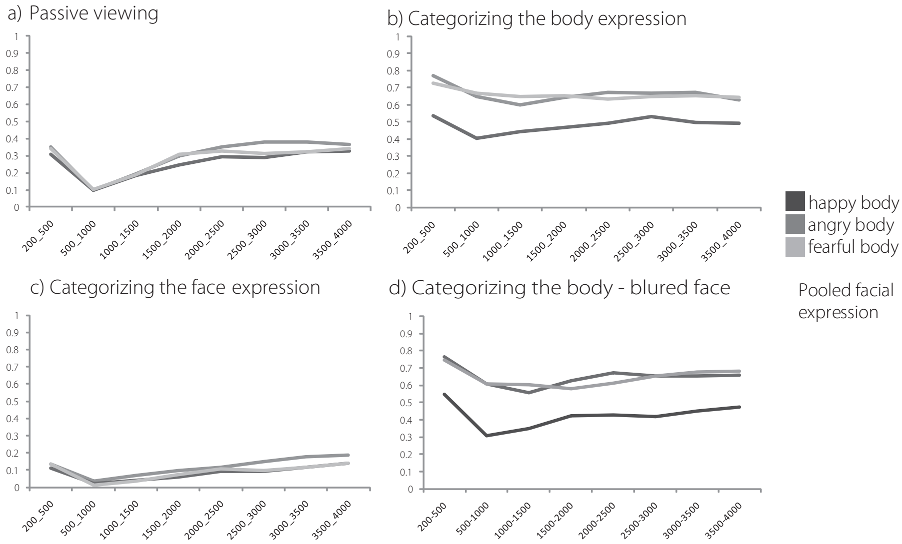
Experiment 1 Passive viewing

*Body expression * time* - Participants looked shorter at happy than fearful and particularly angry bodies, especially during the second half of stimulus presentation duration. At T2-3 and T8 there was no difference and between T5-7 the difference with fear was not significant. See figure 3a. See table 5, exp 1, body.

Experiment 3 Categorizing the body expression

*Body expression * time* - Although participants looked shorter at a happy than at an angry body, their pattern of fixation durations across time, looked similar. Fixation durations on fearful bodies were deviant since they did not show the clear drop in looking time at T2. Instead, fixation durations on fearful bodies remained relatively constant. See figure 3b. See table 5, exp 3, body.

Figure 3. Relative fixation duration on body.



500 ms timeslots on x-axis, proportion of total fixation duration on the y-axis. T2 (500-1000 ms) shows a drop in attention: in proportion, participants fixated relatively short on the body as compared to other timeslots. a-c) Pooled facial expression. d) whole bodies with all facial features blurred.

Experiment 5 Categorizing the body expression- blurred face

When looking at the relative fixation duration on the body, a main effect of emotion was observed; participants looked shorter at happy than fearful or angry bodies. The finding that happy bodies were worse recognized than angry ones was not related to the shorter fixation durations on the happy bodies; the two variables were not correlated (r = .093, p = .658). There was an interaction between time and emotion. Participants looked shorter at happy than fearful bodies during all timeslots and during T5 they looked shorter at fearful as compared to angry bodies. See figure 3d. See table 6, exp 5, body.

Looking at hands

Compund tasks

Relative fixation duration

When categorizing the bodily expression, participants looked about 10.10 % (SD .50) of the time at the hands, whereas this was only 2.90% (SD .20) in the passive viewing task and 0.50% (SD .10) in the face categorization task. Because of a floor effect in the latter two tasks, fixation behavior was only further analyzed in the body categorization task.

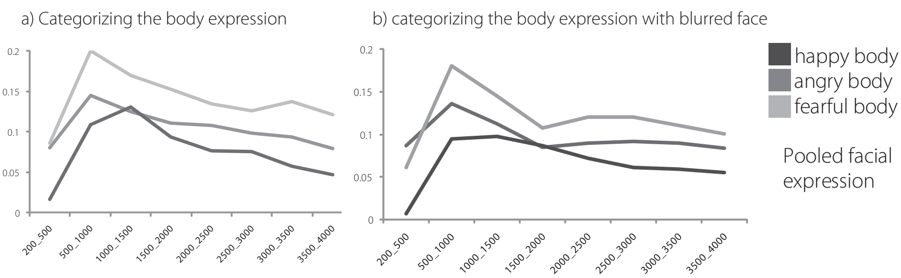
Experiment 3 Categorizing the body expression

There was an effect of body emotion; participants looked longest at fearful hands and longer at angry than happy hands. There was no difference between happy and anger between T3-4 resulting in an interaction with time. (see table 5, exp 3, hand).

Experiment 5 Categorizing the body expression- blurred face

Again, participants looked longer at fearful or angry hands than at happy ones. There was an interaction between time and body emotion. Participants looked longer at fearful than angry hands, significantly at T2-3, T5 but the inverse was true during T1. With the exception of T3-5, T7, angry hands were longer looked at than happy hands. See table 6, experiment 5, hand.

Figure 4. Relative fixation duration on the hands.



Timeslots on x-axis (total 4 seconds), proportion of total fixation duration on the y-axis. A clear peak in attention was observed at T2 (500-1000ms), with +/-20% of the total fixation duration in the condition fearful expressions, falling on the hands (as a comparison, +/-45% of the fixation duration fell on the head and +/-25% of the time was spent looking at the rest of the body (which of course covers a much larger area than just the hand region). The remaining 10% was spent on the background).

Table 2. Relative fixation duration on bodies.

			200 - 500		500 -1000		1000 - 1500		1500 - 2000		2000 - 2500		2500 - 3000		3000 - 3500		3500 - 4000	
	Body	Face	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Passive viewing	**angry**	angry	.32	.19	.08	.18	.19	.22	.30	.22	.32	.23	.36	.24	.36	.25	.34	.24
		happy	.39	.22	.12	.21	.21	.21	.28	.24	.35	.22	.41	.28	.39	.26	.38	.24
		fear	.34	.19	.09	.21	.18	.25	.32	.23	.38	.25	.37	.24	.38	.23	.39	.25
	happy	angry	.34	.21	.12	.20	.20	.25	.26	.26	.30	.24	.28	.26	.32	.24	.30	.23
		happy	.29	.17	.10	.19	.20	.21	.26	.21	.31	.24	.29	.21	.31	.23	.34	.23
		fear	.30	.21	.08	.20	.16	.21	.22	.23	.28	.25	.30	.24	.33	.23	.35	.25
	fear	angry	.37	.19	.11	.19	.18	.23	.28	.25	.31	.25	.29	.26	.34	.25	.31	.23
		happy	.34	.22	.10	.21	.19	.26	.34	.32	.35	.26	.33	.26	.34	.25	.39	.27
		fear	.32	.19	.09	.18	.19	.20	.31	.24	.33	.22	.33	.21	.29	.21	.33	.23
Face categorization	**angry**	angry	.12	.08	.04	.06	.08	.10	.09	.12	.14	.18	.16	.21	.17	.20	.19	.22
		happy	.16	.15	.04	.10	.08	.14	.13	.19	.13	.17	.17	.21	.22	.24	.22	.26
		fear	.13	.14	.02	.07	.04	.08	.07	.10	.09	.14	.12	.19	.14	.21	.16	.24
	happy	angry	.12	.13	.02	.06	.04	.10	.04	.09	.09	.14	.08	.14	.12	.15	.14	.19
		happy	.13	.12	.03	.07	.07	.09	.10	.10	.13	.13	.13	.11	.14	.16	.15	.16
		fear	.09	.09	.01	.03	.01	.03	.03	.07	.06	.09	.07	.10	.09	.12	.13	.16
	fear	angry	.13	.11	.01	.02	.03	.07	.05	.11	.06	.13	.05	.10	.04	.08	.07	.15
		happy	.14	.14	.01	.04	.04	.12	.09	.16	.15	.17	.12	.15	.17	.17	.20	.21
		fear	.13	.13	.02	.04	.04	.06	.09	.10	.11	.10	.13	.11	.14	.14	.16	.16

Table 2. (Continued) Relative fixation duration on bodies.

			200 - 500		500 -1000		1000 - 1500		1500 - 2000		2000 - 2500		2500 - 3000		3000 - 3500		3500 - 4000	
	Body	Face	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Body categorization	**angry**	angry	.78	.19	.64	.23	.58	.24	.66	.18	.69	.20	.69	.18	.71	.19	.66	.24
		happy	.75	.26	.66	.24	.63	.29	.66	.25	.71	.20	.70	.21	.72	.23	.63	.29
		fear	.78	.23	.66	.23	.59	.29	.62	.25	.62	.24	.61	.25	.59	.28	.60	.27
	happy	angry	.55	.21	.41	.22	.45	.27	.47	.25	.51	.19	.55	.21	.49	.20	.50	.32
		happy	.56	.21	.43	.21	.47	.21	.50	.19	.50	.20	.53	.21	.54	.17	.53	.23
		fear	.50	.26	.37	.23	.41	.23	.44	.20	.47	.24	.51	.23	.46	.21	.46	.23
	fear	angry	.71	.25	.66	.23	.66	.21	.62	.23	.61	.21	.62	.21	.60	.21	.65	.25
		happy	.76	.27	.66	.25	.64	.29	.66	.30	.63	.30	.68	.29	.67	.28	.64	.27
		fear	.71	.22	.69	.19	.64	.22	.69	.17	.66	.16	.65	.16	.69	.19	.64	.21

Means are followed by standard deviations. The 4 seconds of total stimulus presentation duration are divided in eight timeslots.

Looking at hands

Compund tasks

Relative fixation duration

We first included all three tasks in one ANOVA for the face/head interest area (including the following factors: task (3), facial expression (3), bodily expression (3) and time (8)) and investigated the influence of task on looking patterns, just as we did with the previously described body area. The statistics can be found in Table 1 under face area.

Interactions with task

*Task * time* - Participants looked shorter at the face when they were instructed to ignore its expression and categorize the body expression. Fixation duration peaked at T2 and decreased subsequently. This peak was most pronounced in the passive viewing task and absent in the body categorization task.

*Task * facial expression* - Participants looked longest at an angry face. This effect was very strong, especially when they had to rate the facial expression. This was numerically consistent in the passive viewing task. When categorizing the body (and when instructed to ignore the face), participants looked longer at a fearful face than at an angry one but that effect was mainly derived from the 'fear face-happy body condition' in which participants attended to the face 43% at T1 and 36% at T2 whereas in all the other conditions this was much lower (25% at T1 and 24% at T2 on average).

*Task * bodily expression* - The influence of the body on looking times on the face, was only apparent when participants rated the body expression. They looked longer at the face when accompanied with a happy versus fearful body.

*Task * bodily expression* time* -The interaction between time and body expression was strongest in the body categorization task and was absent in the face categorization task. We investigated this interaction further by including two tasks. Since the interaction remained after excluding the face categorization task [F (14, 378) = 6.174, $p < .001$], we investigated bodily expression * time within these two tasks.

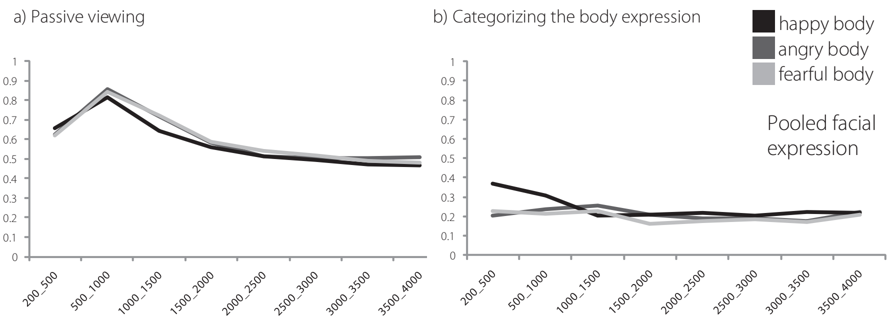
Experiment 1 Passive viewing

Bodily expression time* -Participants looked shorter at the faces of happy than at the faces of fearful or angry bodies during T3 and T6-8 but the opposite was true for T1. Whereas fixation duration on the heads of fearful and happy bodies decreased from T2 and onwards, fixation durations on the head of an angry body stabilized after T5. See Table 5, exp 1, face.

Experiment 3 Categorizing the body expression

Bodily expression time* - The major difference between the different body emotion categories was at T1 where participants looked longer at the heads above happy versus angry or fearful bodies. Participants were instructed to ignore the facial expression and categorize the bodily expression. Participants had difficulty disengaging from the face when the body showed a happy expression or were less "eager" to quickly attend to a happy versus threatening body. See Table 5, exp 3, face.

Figure 5. Relative fixation duration on face as a function of bodily expression



Timeslots on x-axis (total 4 seconds), proportion of total fixation duration on the y-axis. a) A clear peak in attention was observed in the passive viewing task at T2 (500-1000ms) (See also figure 3 and 4). b) Participants were instructed to ignore the facial expression but had difficulty disengaging from the face when the body showed a happy expression.

Experiment 4 Categorizing isolated facial expressions

Fixation duration-face

There was an interaction between time and emotion. In general, fixation duration decreased over time, especially between T3 and T4 on fearful expressions. By inspecting the graph, there appears to be a drop in fixation duration on fearful faces at T4. The second largest, yet only marginally significant decrease between two timeslots was for happy expressions between T6-7. See Figure 6a-d. For the statistical results see Table 6, experiment 4, face.

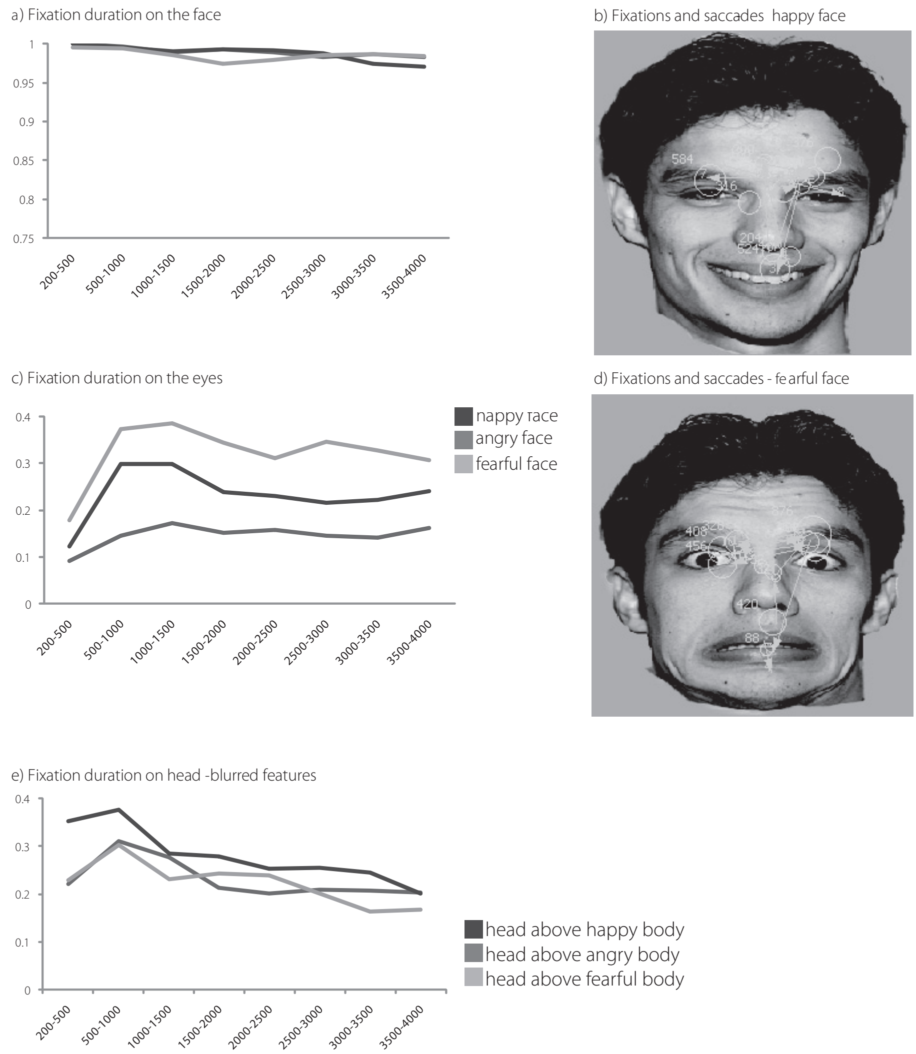
Fixation duration-eyes

A main effect of emotion was observed on the fixation duration on the eyes; participants looked shortest at angry eyes, and looked shorter at happy than fearful eyes. An interaction between time and emotion was observed. Angry eyes were shorter looked at than fearful eyes in all timeslots and fearful eyes were longer looked at than happy ones in all except the first timeslot. The decline in fixation duration between T3 and T4 was significant for happy eyes. See figure 6c and Table 6, experiment 4, eyes.

Experiment 5 Categorizing the body expression- blurred face

Interestingly, even though faces were blurred and facial features were not visible, a strong effect of body emotion on fixation duration on the head was observed; participants looked longer at the heads of happy than fearful bodies. There was an interaction between time and emotion. Participants looked longer at the heads of happy than fearful bodies during T1-2, T6-7 and during T4 at the heads of happy as compared to the heads of angry bodies. See Figure 6e. See Table 6, experiment 5, body.

Figure 6. Relative fixation duration on isolated faces, and bodies with blurred faces.



Length of scan path

Compound tasks

Task - Participants scanned the face-body compound pictures least in the face categorization task. For the statistics, see Table ,1 under scanpath.

*Bodily expression * task* - The scan path was longer for happy than angry or fearful bodies, especially in the body categorization task. The effect was not observed in the face categorization task.

*Facial expression * task* - The scan path was slightly longer when the face showed a happy versus an angry expression but this effect was only observed when participants categorized the face. See Table 5, outer right column, for the statistics per task.

Experiment 5 Categorizing bodily expressions-blurred face

The scan path on happy bodies was longer than that on angry or fearful bodies.

Zygomaticus

Compound tasks

Time -The zygomaticus response increased with stimulus presentation time, independently of task, facial or bodily expression. Since there were no interactions with task, we do not report the responses per task (see Table 3).

Experiment 4 Categorizing isolated facial expressions

Facial expression- The zygomaticus was most responsive to happy faces, more as compared to fearful faces and with a trend towards significance as compared to angry faces. See figure 7a.

Experiment 5 Categorizing the body expression- blurred face

Due to technical implications, the data of the first two participants was not recorded.

Bodily expression- There was a marginally significant effect of body emotion, but follow up comparisons did not reveal any significant effects.

Time - The response was increasing with time.

Corrugator

Compound tasks

Task - The corrugator was least responsive in the passive viewing task.

Facial expression- The corrugator responded more to angry and fearful than to happy faces (See Table 4).

Time - The response increased from T3 onwards and differed significantly from T8.

Experiment 4 Categorizing isolated facial expressions

Facial expression- The corrugator was most responsive to angry and fearful faces, more as compared to happy faces.

*Facial expression * time*- In all timeslots was the corrugator most responsive to angry and fearful faces but whereas the difference between fearful and happy faces was generally larger than between angry and happy faces, at T2, the difference with anger was larger. At T8, the difference between angry and happy expressions was not significant (See Table 6 and Figure 7b).

Table 3. Zygomaticus response to congruent and incongruent face-body compounds-independent of task

		0 -500		500 -1000		1000 - 1500		1500- 2000		2000 - 2500		2500 - 3000		3000-3500		3500 - 4000	
Body	Face	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
angry	angry	99.76	1.21	100.80	1.99	103.92	2.82	106.64	4.01	113.73	5.07	114.54	5.53	113.75	5.92	116.34	6.83
	happy	99.98	1.30	105.33	3.40	111.65	5.87	107.18	3.63	109.75	4.11	107.47	3.72	104.12	2.87	108.54	4.68
	fear	99.99	.72	100.05	0.92	105.98	2.71	110.93	5.34	112.75	5.30	117.10	7.51	118.02	7.88	112.23	4.96
happy	angry	100.30	1.21	100.54	1.57	107.38	4.15	110.71	4.54	111.37	6.69	114.69	8.53	116.00	9.33	116.27	9.51
	happy	101.78	1.99	104.05	2.23	113.51	10.09	112.00	5.26	111.86	3.46	117.53	6.90	123.68	10.93	116.31	5.33
	fear	100.05	.64	101.14	1.28	105.05	3.21	114.79	7.86	115.54	8.88	116.76	8.86	119.08	8.94	116.93	8.54
fear	angry	100.63	1.11	100.67	1.11	106.48	5.25	106.05	4.36	108.32	4.59	111.45	7.97	108.98	7.68	113.26	9.67
	happy	100.43	1.11	104.24	3.49	108.42	3.44	108.91	3.34	119.97	10.19	129.15	11.72	128.94	12.14	127.28	12.44
	fear	99.48	0.96	102.48	3.38	110.53	7.92	114.52	9.18	116.21	9.85	115.30	8.94	114.29	8.68	121.11	9.22

Since there were no interactions with task, the three experiments were pooled.

Table 4. Corrugator response to congruent and incongruent face-body compounds-per task.

			0 -500		500 - 1000		1000- 1500		1500- 2000		2000- 2500		2500- 3000		3000-3500		3500- 4000	
	Body	Face	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Passive viewing	angry	angry	101.36	1.01	98.75	1.29	97.84	1.25	96.90	1.49	97.00	1.78	98.08	1.83	99.51	1.45	98.68	1.53
		happy	98.95	1.15	98.44	1.85	96.08	2.02	96.65	2.26	96.71	2.30	95.46	1.58	98.30	2.38	97.18	1.57
		fear	99.08	.91	96.88	1.39	96.82	2.67	97.43	2.19	98.29	1.86	97.93	1.98	97.82	1.81	98.63	1.71
	happy	angry	98.37	1.15	97.68	1.70	96.75	1.75	98.41	1.62	98.61	1.79	99.46	1.96	98.08	1.43	98.72	1.60
		happy	98.80	.63	96.30	1.09	95.93	1.28	96.47	1.25	96.19	1.27	96.47	1.36	96.59	1.13	96.50	1.19
		fear	100.37	.94	99.07	1.93	98.28	1.35	98.23	1.72	100.80	1.75	101.02	2.24	100.58	2.18	100.91	2.21
	fear	angry	99.92	.91	96.46	1.15	98.01	1.70	98.20	2.49	99.76	2.12	99.75	2.12	102.39	2.01	105.15	3.87
		happy	99.24	1.03	94.47	1.54	92.35	2.37	93.77	2.68	93.63	2.41	94.91	2.18	93.78	2.57	93.12	2.84
		fear	98.86	.83	97.02	1.24	98.42	1.30	98.50	1.15	97.61	1.26	98.94	1.69	98.33	1.76	99.59	1.83
Body categorization	angry	angry	101.89	0.57	102.20	.76	101.54	.98	101.21	.93	102.03	1.06	101.31	1.41	101.39	.84	101.12	.90
		happy	100.10	1.39	100.91	1.99	100.21	2.13	98.80	2.57	100.33	2.00	99.62	2.14	101.81	2.46	103.01	2.80
		fear	100.59	.79	101.23	.98	100.34	1.10	100.82	1.37	100.76	1.22	101.36	1.26	103.05	1.95	103.79	1.30
	happy	angry	102.32	1.13	101.04	1.39	101.76	1.33	99.80	1.49	98.26	1.40	97.80	1.30	100.33	2.03	103.17	2.86
		happy	101.24	.68	98.64	1.20	98.24	1.62	98.03	1.59	99.64	1.31	102.54	2.11	101.27	2.02	100.94	2.10
		fear	100.09	1.19	99.28	1.16	98.30	1.29	99.92	1.44	98.55	1.52	99.61	1.81	99.85	1.71	100.19	1.62
	fear	angry	100.20	1.09	100.98	1.50	101.35	2.19	101.26	2.08	102.11	2.33	101.91	2.56	100.88	2.40	100.23	2.36
		happy	99.33	1.57	99.28	2.10	99.18	2.33	101.19	2.72	99.61	2.54	101.09	3.01	103.46	2.85	105.99	2.90
		fear	101.19	.80	101.25	1.11	100.56	1.21	102.27	1.55	102.98	1.39	101.87	1.68	100.98	.97	108.39	6.53

Table 4. (Continued) Corrugator response to congruent and incongruent face-body compounds-per task.

			0 -500		500 - 1000		1000- 1500		1500- 2000		2000- 2500		2500- 3000		3000-3500		3500- 4000	
Face categorization	**angry**	angry	101.93	1.06	101.57	1.67	101.35	1.80	101.16	1.88	100.68	1.73	102.10	2.00	103.27	2.10	104.96	3.42
		happy	101.22	1.02	98.34	2.24	98.74	3.11	99.02	4.17	99.60	3.55	100.21	2.34	100.98	2.82	101.13	2.50
		fear	101.06	1.48	100.64	1.96	101.59	1.88	103.45	3.37	102.33	2.52	102.42	2.68	103.61	3.04	103.27	2.01
	happy	angry	101.37	.82	100.17	1.89	102.12	2.25	103.85	3.32	102.84	3.09	105.43	3.21	107.10	4.32	106.52	2.89
		happy	101.05	.85	97.52	1.36	98.60	2.08	97.69	1.95	97.48	1.51	99.02	1.66	99.53	1.47	100.69	1.39
		fear	99.91	1.01	103.40	2.57	104.38	3.86	103.92	3.72	102.70	2.80	101.07	1.86	100.52	2.03	102.79	2.31
	fear	angry	102.44	1.76	100.28	1.38	100.12	1.65	102.03	2.67	100.30	1.97	104.70	2.11	106.49	3.15	108.92	4.31
		happy	100.61	.86	98.02	1.01	97.28	1.48	96.45	1.41	96.69	1.55	98.37	1.74	98.60	1.46	99.83	1.33
		fear	100.43	.83	100.08	1.07	99.98	1.11	101.16	1.43	101.25	1.55	102.94	1.41	104.35	1.66	105.49	2.01

Corrugator response. The 4 seconds of total stimulus presentation duration are divided in eight timeslots.

Table 5. Congruent and incongruent face-body compounds- statistical analyses per task

		Main effect fixation duration			Interaction effect fixation duration				Main effect
Exp	Area	Bodily expression	Facial expression	Time	Body expression * Facial expression	Body expression * Time	Facial expression * Time	Body expression* Facial expression* Time	Scan path length
1	Body	F(2, 54) = 8.587*** A > H****		F(2.67, 72.16) = 21.280**** T1 > T2-3*** T3 > T2, T4 > T3****		F(7.13, 192.49) = 1.945, p = .063 T6-7 A > F/H t(27) ≥ 2.153*			F(2, 54) = 11.099**** BoH >BoF**** BoH > BoA**
	Face			F(2.81, 75.88) = 31.344**** T2 > T1,3-8****		F(6.54, 176.53) = 1.896, p = .078 T1 H > F/A T3,T6-8 F/A > H t(27) ≥ 2.347			
Zygomaticus				F(1.40,27.97) = 3.869* T3 > T2					
Corrugator			F(1.36,27.23) = 6.059* F > H* A > H, p = .055		F(3.00,60.02) = 2.415, p = .075		F(6.25,124.90) = 2.138*		
2	Body	F(2, 54) = 5.930** A > H/F*	F(2, 54) = 7.134***	F(1.82, 49.09) = 15.012**** T4 > T3*, T5 > T4*	F(4, 108) = 3.358* BoH_FaH > BoH_FaF t(27) = 2.913** BoF_FaF > BoF_FaA t(27) = 3.577****		F(5.99, 161.85) = 2.158* T4-8 FaH > FaA T1, T3-8 FaH > FaF t(27) ≥ 2.100*		F(2, 54) = 15.649**** FaH > FaA**** FaH > FaF**
	Face		FF(2, 54) = 14.715****A > H/F****	F(2.20, 59.38) = 37.749**** T2 > T3-8****					
Zygomaticus				F(2.10,56.79) = 3.959*					

Table 5. (Continued) Congruent and incongruent face-body compounds- statistical analyses per task.sk

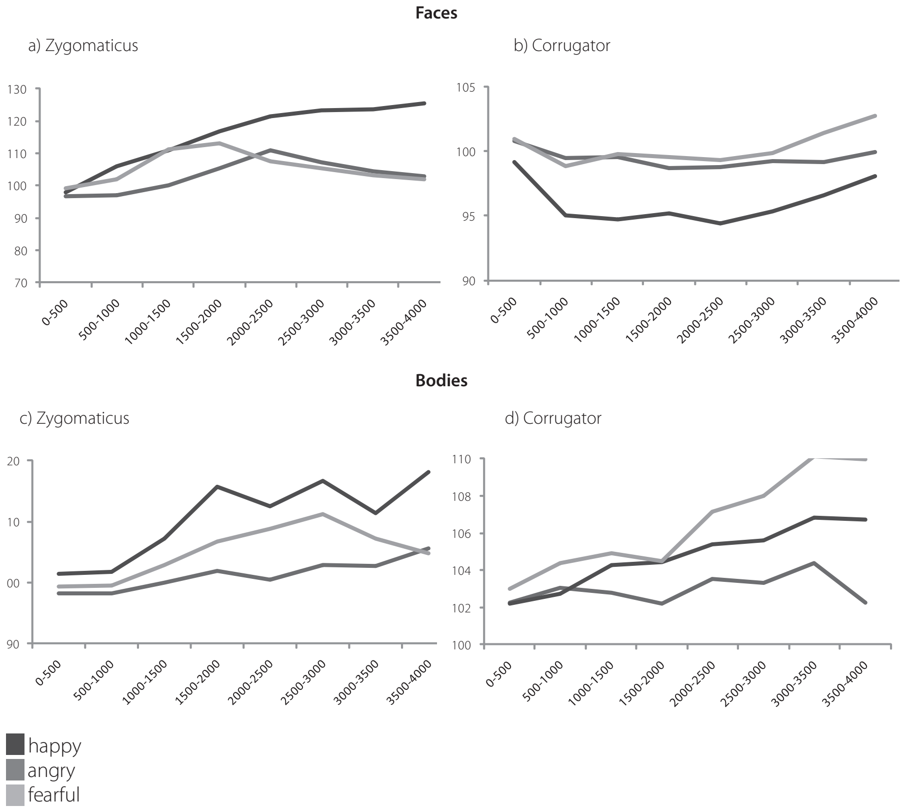
		Main effect fixation duration			Interaction effect fixation duration				Main effect
Exp	**Area**	**Bodily expression**	**Facial expression**	**Time**	**Body expression * Facial expression**	**Body expression * Time**	**Facial expression * Time**	**Body expression* Facial expression* Time**	**Scan path length**
Corrugator			F(2,54) = 2.687, *p* = .077	F(2.43,65.73) = 5.254** T8 > T3*	F(2.85,76.85) = 2.332, *p* = .084				
3	**Body**	F(2, 54) = 84.012**** F/A > H****	F(2, 54) = 3.890* H > F, *p* = .057	F(2.60, 70.07) = 2.273, *p* = .096 T1 > T2*		F(8.25, 222.73) = 3.030*** **»F**			F(2, 54) = 24.031**** BoH >BoF/A****
	Face	F(2, 54) = 6.394*** H > F** H > A, *p* = .069	F(2, 54) = 2.776, *p* = .071 F > A*			F(8.42, 227.36) = 5.651**** T1 H > A/F t(27) ≥ 6.636****			
	Hand	[F(54, 2) = 26.706**** F > A/H**** A > H*		F(3.06, 82.57) = 15.189**** T2 > T1*		F(7.12,192.30) = 2.439*** A/F > H *t* (27) ≥ 2.041, *p* < .001 but no difference between H and A at T3			
Zygomaticus		F(2, 48) = 2.928, *p* = .063		F(2.57,61.65) = 5.089** T8 > T1					
Corrugator				F(3.28,78.71) = 3.709*					
						H = happy F = fear A = anger	T = time Fa = face Bo = body	_i= incongruent _c = congruent	*p* < .05 = * *p* < .01 = ** *p* < .005 = *** *p* < .001 = ****

Main and interaction effects were followed up by 2-tailed t-tests and Bonferroni corrected pairwise comparisons.
» indicates that the effect is mainly driven by a certain factor.

Experiment 5 Categorizing the body expression- blurred face

Time -The corrugator response was increasing with time.

Figure 7. EMG response following isolated faces, and bodies with blurred faces



Please note the differences in scale.
a) the zygomaticus was activated following happy versus fearful faces
b) the corrugator was activated following angry versus happy faces.
c) There were no effects of emotion
d) the corrugator responded stronger to fearful than angry bodies.

Table 6. Isolated faces and bodies with blurred faces

Experiment 4. Isolated faces

		Fixation duration			
		Emotion	Time	Emotion * Time	Scan path length°
Eye tracking	Face		F(3.57, 96.25) = 4.931*** T1 > T6-8* T2 > T7*	F(5.26, 142.10) = 2.035, *p* = .074 F T3 > T4 t(27) = 2.016, *p* = .054 H T6 > T7 t(27) = 1.949, *p* = .062	
	Eyes	F(1.61, 43.54) = 53.091**** F/H > A**** F > H****	F(3.45,93.03) = 8.917**** T1 < T2-T8* T3 > T4*	F(6.54,176.53) = 2.212* all timeslots, F > A t(27) ≥ 3.054*** H T3 > T4 *t*(27) = 2.879** F > H T2-T8 t(27) ≥ 2.330*	x
EMG	Zygo	F(2, 54) = 5.100** H > A* H > F, *p*= .094	F(1.68, 45.36) = 3.221, *p* = .057 » nonsign. increase		
	Corru	F(2, 54) = 10.077**** A/F > H***	F(3.30, 89.03) = 2.326*** T1 > T2, *p* = .063 T7-8 > T5* T8 > T6*	F(7.17, 193.58) = 2.326*** T8 A > H *p* = .198	

Experiment 4. Isolated bodies

		Fixation duration			
		Emotion	Time	Emotion * Time	Scan path length°
Eyetracking	Body	F(2, 54) = 148.386**** F/A > H****	F(2.76,74.41) = 8.613**** T1 > T2-8* T7-8 > T3***	F(7.47,201.57) = 2.018* all timeslots, F > H t (27) ≥ 4.308**** T5 A > F, t (27) = 2.245*	F(2, 54) = 10.571 H > A/F**
	Head ♦	F(1.58,42.53) = 6.724*** H > F***	F(2.60,70.21) = 4.948** T2 > T7-8*	F(7.78,210.15) = 2.161* T1-2, T6-7 H > F *t*(27) ≥ 2.145* T4 H > A *t*(27) = 2.079*	x
	Hand	F(2, 54) = 15.819**** F > H**** F > A* A > H*	F(3.55,95.72) = 14.424**** T2 >T1, T5, T7-8*	F(6.80,183.64) = 3.224*** T1 A > F t(27) = 3.833*** T2-3,T5 F > A *t* (27) ≥ 2.719* T1-2, T6, T8 A > H *t*(27) ≥ 2.061	x
EMG	Zygo	F(2, 50) = 2.532, *p* = .09	F(3.57,89.22) = 6.547**** T8 > T1*		
	Corru		F(2.21,55.12) = 4.570*		

Zygo = zygomaticus Corru = corrugator

♦ *in experiment 5, facial expressions were blurred but nevertheless, an interest area was created from the head.*

Behavioural results

Experiment 2. Congruent and incongruent face-body compound expressions of emotion

Categorizing the facial expression

Accuracy- A main effect of face emotion was observed [F (2, 54) = 13.264, $p < .001$]. Angry facial expressions were better recognized than fearful ones ($p < .005$). There was an interaction between emotion of the body and emotion of the face [F (4, 108) = 7.505, $p < .001$]; facial expressions were better recognized in congruent versus incongruent combinations, significantly for fearful and angry faces t(27) ≥ 2.026, $p \leq .05$. Happy facial expressions were recognized at ceiling and the body expression was of no influence. See figure 8b.

Reaction time[1] There was a marginally significant effect of body emotion [F (2, 54) = 3.079, $p = .054$]; facial expressions were faster recognized on top of a happy versus a fearful body expression ($p < .05$).

Experiment 3. Congruent and incongruent face-body compound expressions of emotion

Categorizing the body expression

Accuracy- A main effect of body emotion was observed [F (2, 54) = 16.110, $p < .001$]. Angry body expressions were better recognized than happy ones ($p < .001$). A main effect of face emotion was observed on body emotion recognition [F (2, 54) = 4.450, $p < .05$]; if body expressions were paired with angry faces, accuracy dropped more than when paired with happy faces ($p < .05$). There was an interaction between emotion of the body and the face [F (4, 108) = 3.346, $p < .05$]; the body expressions were better recognized in congruent versus incongruent combinations, significantly for happy bodies with happy versus angry faces t(27) = 2.614, $p < .05$ or versus fearful faces t(27) = 2.357, $p < .05$. Fearful bodies were slightly better recognized with fearful than with angry faces t(27) = 1.695, $p = .10$. See figure 8d.

Reaction time- There was a nearly significant effect of body emotion [F (2, 54) = 3.102, $p = .053$] but pairwise comparisons did not reveal any difference ($p \geq .115$).

Experiment 4. Perceiving facial expressions of emotion

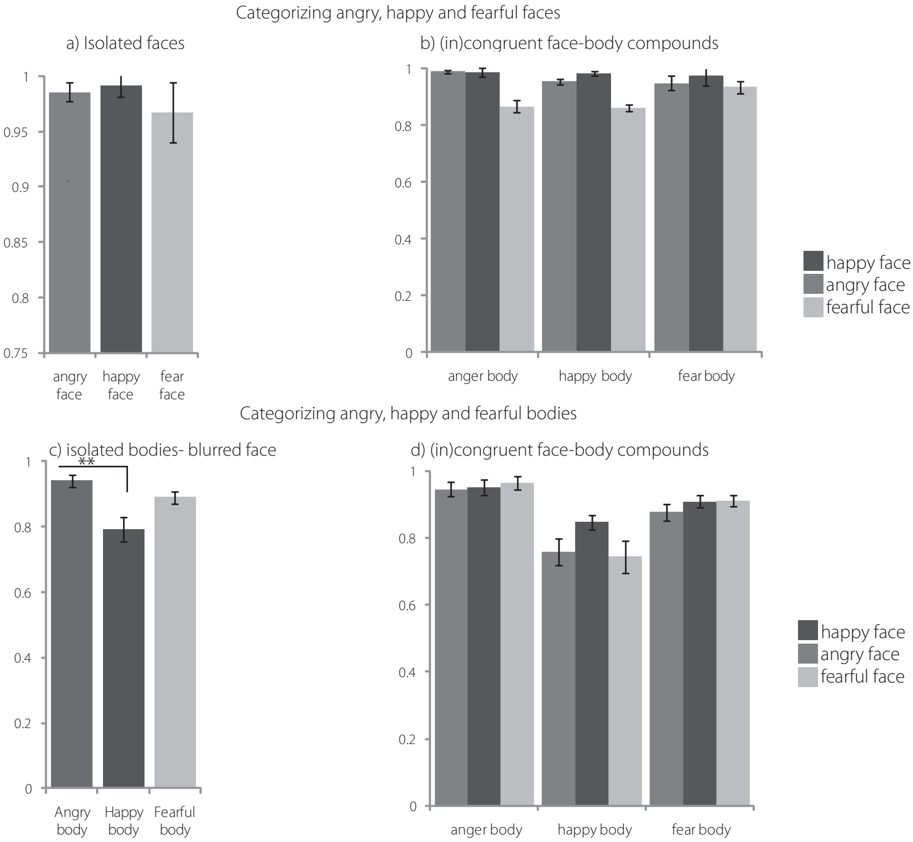
Accuracy & reaction time -There were no effects of emotion on accuracy or reaction times.

Experiment 5. Perceiving bodily expressions of emotion

Accuracy & reaction time- A main effect of emotion was observed on accuracy [F (2, 54) = 8.519, $p < .001$]. Angry bodies were better recognized than happy ones ($p < .005$). There were no effects of emotion on reaction times. See figure 8c.

[1] Please note that participants responded only after 4 seconds, after the stimulus had disappeared from the screen.

Figure 8. Accuracy rates in all categorization tasks



Proportion correct answer.

General Discussion

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 job interview, however annoying or unenlightening the questions may be. The perception of a facial expression is influenced by the body language of the observed and research suggests an early integration of these signals. However, this (in)congruency effect may be influenced by attention and how it affects facial EMG responses is so far unknown. To this end, we recorded eye movements and facial EMG activity while participants observed people with congruent or incongruent facial and bodily expressions of emotion under different task instructions. We were specifically interested how these signals developed over stimulus presentation time.

As observed earlier, angry and fearful faces were better recognized in the context of an angry or fearful body expression. With longer presentation durations (four seconds) than in our previous studies, happy faces were recognized at ceiling and the influence of the body expression was not measurable anymore. In contrast, happy bodies were least accurately recognized and therefore the influence of the facial expression was large.

As one would expect, task instructions influenced looking patterns. Participants attended more to the body when they were asked to do so and attended more to the face when they were instructed to ignore the bodily expression. As a consequence, the influence of the emotion of either the face or the body was larger when instructed to attend to either of the two. Interestingly, although participants in the face categorization task were instructed 'not to get distracted by the body', their looking times on the body kept increasing whereas in the other two tasks this increase diminished in the final timeslots. Looking times on the face decreased with time. After a drop in looking time on the body and an increase in looking time on the face at T2 (500-1000 ms), participants re-attended to the body, except when categorizing fearful body expressions in which attention remained constant over time. This peak at T2 was most pronounced in the passive viewing task.

Why do we immediately direct our attention to the face and after that become increasingly interested in the body? 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. However, the happy, angry and fearful faces we see leave room for interpretation, as is evidenced by the influence of the body language on the accuracy of categorizing facial expressions. However, the first thing we do when encountering another person is looking at his eyes (especially when they express fear). We here show that after T2, we increasingly attend to the body language, possibly to verify the emotion as observed in another's eyes or face. Another reason why we attend to bodies is to study the action plan of the observed and prepare our own response (de Gelder, 2006; de Gelder et al., 2009). Interestingly, when we look at the pattern of fixation durations that fell on the hands, a similar peak in attention was observed around T2 when categorizing body expressions. Moreover, when faces were presented in isolation, participants attended mostly to the eyes at T2-3. It seems that around that time, participants attend to the most informative parts.

Participants looked shortest at happy bodies and longer at threatening ones. It is interesting that this was observed across the total stimulus duration indicating that this result is not due to a relative decrease in attention for happy bodies. In the two body categorization tasks, participants attended more to the face in the first two timeslots in case of a happy body (as compared to fear and anger) and attention to the background increased in the first three timeslots, than stabilized but was higher than when the body expressed threat. Another interesting finding is that participants looked longest at bodies with happy faces. This effect was observed from T2 onwards. The total scanpath length was longest for happy bodies because participants attended more to the non-informative background. Interestingly, participants' scanpath was also longer when the face showed a happy versus angry expression (only when categorizing the face of a compound). In the compound-face categorization task, participants looked longest at an angry face, but when categorizing this body expression and when asked to ignore the face, they attended longest to a fearful face, especially in the first two timeslots and even more so when the body showed a non-threatening, happy expression.

It seems that overall participants attended more to threatening cues and when there was no threat, they scanned the whole picture in search of it. Indeed, previous studies also found longer fixations on threat-related expressions, including anger, compared to threat-irrelevant expressions (Green, Williams, & Davidson, 2003; Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009). Moreover, visual search studies have found that angry faces are typically detected more quickly and accurately than happy ones (Fox & Damjanovic, 2006; Lundqvist & Öhman, 2005). Adolphs et al (2005) showed that the fear recognition deficit as observed in a patient (SM) with bilateral amygdala damage was caused by her inability to make normal use of information from the eye region of faces. Although SM failed to look normally at the eye region in all facial expressions, her selective impairment in recognizing fear is explained by the fact that the eyes are the most important feature for identifying this emotion (Adolphs et al., 2005). Thus, attention allocation during interaction may reflect the need to prepare an adaptive response to social threat. Only the happy expression would signal safety and would therefore be the least interesting one, as indicated by shorter fixations.

Fridin et al (2009) reported earlier that when perceiving pictures associated with joy, people tend to fixate on the head, whereas for angry and fearful pictures, most attention was devoted to the hands and arms. Bannerman et al (2008) observed that faster localization of threatening bodies and faces. Our study confirms the results of both studies but also illustrates that a facial expression influences looking patterns on the body, and a bodily expression influences looking patterns on the face. Moreover, we studied attention towards bodily expressions of emotion over a longer time-span and observed that fixation duration is dependent on time.

As demonstrated decades ago by Buswell (Buswell, 1935) and Yarbus (Yarbus, 1967b), people look at informative regions when shown a picture of a scene or a face. Furthermore, when given more time to look at the picture, they return again and again to these informative regions rather than covering the whole area of the picture. It is especially under these conditions that it becomes obvious that eye movements do not reflect a passive type of perception but represent active, goal-directed movements. The fact that we hardly see effects of face-body (in)congruence suggests that the earlier observed effects that Meeren et al (2005) obtained with much shorter presentation times (200 ms) reflect an automatic mandatory process which cannot be seen in fixation behavior because it occurs much earlier in processing time. Aviezer et al (2008) demonstrated that characteristic fixation patterns previously thought to be determined solely by the facial expression are systematically modulated by emotional context already at very early stages of visual processing. However, a clear congruency effect was not observed (Aviezer et al., 2008). With a different experimental design, for example by presenting two stimuli at a time and the fixation cross in between (as in (Gamble & Rapee, 2010)), one can measure where participants attend to first: an emotionally congruent or incongruent face-body pair.

Categorizing isolated facial and bodily expressions of emotion gave the expected EMG response (zygomaticus for happy expressions, corrugator for anger and fear) but there were hardly any effects of emotion in the compound tasks. We think that this may be due to a fewer number of trials per condition as compared to the isolated face and body categorization tasks. The corrugator was least responsive in the passive viewing task. This suggests that task difficulty

influenced and possibly biased the natural response. The observation that the effect of facial expression was strongest in the passive viewing task gives further evidence for this hypothesis.
Intriguingly, measures of attention allocation and facial muscle activity demonstrate distinct reaction patterns at different stages of processing. We suggest that these patterns of reactivity subserve and contribute to the dynamic processes of person perception by constituting parts of the biological correlates of our propensity for social perception. This helps us to actively engage with others, to drive the allocation of attentional resources towards threatening cues and to inform higher-order cognitive functioning, thereby providing essential information to help us to understand others and plan our own actions.

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Chapter 4

Commonalities and differences in impaired emotional processing in psychological and neurological disorders

This chapter is based on:
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Introduction

Recognizing emotional meaning from others is vital and of crucial importance for normal communication. Distinct patterns of structural and functional abnormalities in neural systems, important for emotion processing are associated with specific symptoms in a range of disorders. Increased vigilance and enhanced autonomic activity are part of an adaptive response to threat. That said, in various pathological conditions, the anxiety response is disproportionate to the stressor, because of either a misinterpretation of threat, or hyper- or hypo-responsiveness at any of a variety of points in the complex network of neural pathways that serve the stress response.

There are high rates of co morbidity between and similar biochemical conditions with common genetic basis across different disorders such as anxiety and depression. Advances in our understanding of the features of responding that are shared across vs. unique to specific disorders will require dimensional approaches. Investigations of neurological and behavioral differences in emotion perception across different clinical populations will enrich basic clinical research, will help to understand emotion perception better in the healthy population and can lead to the development of new observational and diagnostic tools.

In this review, an overview of evidence is provided from studies employing a variety of techniques for the presence of specific abnormalities in emotion perception in depressive disorder and anxiety disorder, schizophrenia, autistic disorder, borderline personality disorder, eating disorder, Huntington's disease, and Parkinson's disease.

Anxiety and Depression

Of all adults in the USA, 9.5% have a depressive disorder and 18.1% an anxiety disorder. Anxiety disorders frequently co-occur with depression, substance abuse, and other types of anxiety disorders. The first episode often takes place around the age of twenty (Kessler et al., 2007; Kessler, Chiu, Demler, Merikangas, & Walters, 2005). Whereas imaging and neurochemistry data suggest important differences between anxiety and depression, both family studies and whole-genome surveys show that anxiety and depression share some of the same genes (Gorwood, 2004). Twin studies have shown a common, underlying genetic vulnerability but environmental factors seem to determine whether a twin becomes anxious or depressed (Franic, Middeldorp, Dolan, Ligthart, & Boomsma, 2010)

A normative function of the mechanisms underlying fear is to facilitate detection of danger in the environment and to help the organism respond effectively to threatening situations. Biases in processing threat-related information have been assigned a prominent role in the etiology and maintenance of anxiety disorders (Beck & Stoger, 1976; Eysenck, Mogg, May, Richards, & Mathews, 1991; Mathews, May, Mogg, & Eysenck, 1990). Bar-Haim et al. (2007) examined the threat-related attentional biases in anxiety in 172 different studies. They conclude that the bias is reliably demonstrated with diverse experimental paradigms and under a variety of experimental conditions. Impaired perception of facial expressions of emotion may underlie the interpersonal difficulties observed in depressed patients as well and it has even been proposed as a candidate marker for depression (Mikhailova, Vladimirova, Iznak, Tsusulkovskaya, & Sushko, 1996; Chan, Norbury, Goodwin & Harmer, 2009).

The serotonergic system has been widely implicated in stress related psychiatric disorders such as depression and anxiety. Mekli et al (2011) observed that the serotonin-1A receptor conveys vulnerability to these psychiatric disorders by modulating threat-related information processing (Mekli et al., 2011).

Amygdalar hyperactivity has been observed during negative emotional processing in patients with posttraumatic stress disorder (Rauch et al., 2000; Shin et al., 2004; Shin et al., 2005; Williams et al., 2006), social anxiety disorder (Phan, Fitzgerald, Nathan, & Tancer, 2006; Stein, Goldin, Sareen, Zorrilla, & Brown, 2002), specific phobia (Dilger et al., 2003; Schienle, Schafer, Walter, Stark, & Vaitl, 2005; Straube, Mentzel, & Miltner, 2006; Veltman et al., 2004) panic disorder (van den Heuvel et al., 2005), and obsessive-compulsive disorder (van den Heuvel et al., 2004; van den Heuvel et al., 2005). Although inconsistent findings across neuroimaging studies and between anxiety disorders have been reported, a meta-analysis revealed consistent amygdalar hyperactivity along with increased insula responses, in posttraumatic stress disorder, social anxiety disorder and specific phobia (Etkin & Wager, 2007).

Whereas some studies report increased amygdala response for threatening versus neutral expressions related to depressive symptoms (Canli et al., 2005; Peluso et al., 2009) others report decreased activity (Thomas et al., 2001) or no difference (Lee et al., 2008). A meta-analysis revealed that compared with healthy controls, individuals with major depressive disorder show increased neural activity in response to sad faces and diminished neural activity in response to happy faces in emotion-related brain circuits (e.g. amygdala and ventral striatum) (Leppanen, 2006).

Several studies report decreased cortico-limbic *connectivity* in response to emotional stimuli in depression, although antidepressant treatment can re-establish this connectivity (Anand, Li, Wang, Gardner, & Lowe, 2007). In a recent study, the brain activity of medication-free patients with a first major depressive episode, medication-free patients who had recovered from a first episode and a group of matched healthy individuals were compared in two emotion identification tasks. The depressed individuals performed worse than recovered and healthy individuals on an emotion-labeling but not an emotion-matching task. The labeling deficit was related to increased recruitment of the right amygdala, left inferior frontal gyrus and anterior cingulate cortex (van Wingen et al., 2010).

Depression has a murky border with psychosis, which involves (paranoid) delusions and hallucinations. Bipolar illness and schizophrenia have often been thought of as separate disorders. But genetic and brain-imaging studies over the past decade have undermined this separation (Ivleva, Thaker, & Tamminga, 2008). For example, both bipolar and schizophrenic patients exhibit anomalous brain waves and eye movements (Blackwood et al., 1996) for a review, see (Thaker, 2008).

Schizophrenia

Schizophrenia is characterized by abnormalities in the perception or expression of reality. Distortions in perception most commonly manifest as auditory hallucinations, paranoia, and bizarre delusions, or disorganized speech and thinking with social or occupational dysfunction.

Onset typically occurs in young adulthood, with 0.4 - 0.6% of the population being affected (Bhugra, 2005).

Social cognition has become a high priority area in schizophrenia research. Impaired recognition of facial expressions (Edwards, Pattison, Jackson, & Wales, 2001; Feinberg, Rifkin, Schaffer, & Walker, 1986; Whittaker, Deakin, & Tomenson, 2001); prosody (Edwards et al., 2001) and a correlation between emotion recognition and specific symptoms of the disease (Kohler, Bilker, Hagendoorn, Gur, & Gur, 2000) and the chronicity of illness (Mueser, Penn, Blanchard, & Bellack, 1997) have been reported. Other studies have suggested a greater differential impairment in negative affect recognition (Bell, Bryson, & Lysaker, 1997) including a superior ability in paranoid as compared to non-paranoid patients in negative affect identification (Kline, Smith, & Ellis, 1992). Schizophrenic patients with persecutory delusions demonstrated specific abnormalities in their viewing strategies for social scenes, depicting ambiguous rather than explicitly threatening information (Phillips, Senior, & David, 2000). Moreover, schizophrenia patients show deficits in gender discrimination and emotion identification from body shapes and motion (Bigelow et al., 2006).

Some studies have reported deficits in the categorization of emotional voices, and correlations between deficits in hearing and seeing emotions have been observed as well (de Gelder, Vroomen, Annen, Masthof, & Hodiamont, 2003; de Jong, Hodiamont, Van den Stock, & de Gelder, 2009; Hendrick et al., 2001; Suri, Burt, Altshuler, Zuckerbrow-Miller, & Fairbanks, 2001). In the healthy population, a vocal emotional expression influences the categorization of a facial expression (de Gelder, Vroomen, & Teunisse, 1995) and vice versa (de Gelder & Vroomen, 2000). In schizophrenics, the multisensory integration of facial and vocal emotional information is impaired (de Jong et al., 2009). Vaskinn et al., 2007 presented visual (facial pictures) and auditory (sentences) emotional stimuli for identification and discrimination in groups of participants with schizophrenia, bipolar disorder and healthy controls. Visual emotion perception was unimpaired in both clinical groups, but the schizophrenia sample, especially the males, showed reduced auditory emotion perception (Altshuler, Dudley, & McGuire, 2004).

Neuroimaging studies show structural and functional abnormalities in the ventral and dorsal neural systems, but inconsistent findings have been noted. Structural and functional abnormalities have been found in regions important for the appraisal and identification of positive and negative emotional stimuli and production of affective states, such as the amygdala, anterior insula, and ventral striatum. For example, the fusiform gyri have been shown to be smaller in schizophrenia patients, where volume reduction was proportional to impairment at remembering face identities (Lee et al., 2002; Onitsuka et al., 2006). Compared to controls, the extent of activation in the fusiform gyrus, amygdala, parahippocampal gyrus, right superior frontal gyrus, and lentiform nucleus was smaller in patients during facial emotion processing (for a meta-analysis, see Li, Chan, McAlonan, and Gong (2009)). Other studies have demonstrated that schizophrenic patients fail to activate the amygdala in response to emotional expressions (Gur et al., 2002; Phillips et al., 1999) but see (Altshuler et al., 2000; Chance, Esiri, & Crow, 2002; Kosaka et al., 2002; Rauch et al., 2010), aversive scenes (Taylor, Liberzon, Decker, & Koeppe, 2002), and during sad mood induction (Schneider et al., 1998). The abnormalities have also been associated with a misinterpretation of threatening, nonthreatening and ambiguous stimuli and with a decreased range of subsequent affective states and behaviors (Phillips, Drevets, Rauch, & Lane, 2003). A possibility is that there is a lowering of the threshold at which the amygdala responds to ambiguous stimuli but an attenuation of their responses to explicit displays of emotion, although further research is needed.

In sum, schizophrenia is associated with functionally important abnormalities in face processing in the domains of emotion recognition and complex social judgments (for a meta-analysis, see Marwick and Hall (2008)). Shared genetic and environmental risk factors have been identified for autistic spectrum disorders and schizophrenia. Social interaction, communication, emotion processing, sensorimotor gating and executive function are disrupted in both, stimulating the debate about whether these are related conditions (Cheung et al., 2010).

Autistic disorder

Autism is a neurodevelopmental disorder characterized by impaired social interaction and communication, and restricted and repetitive behavior. The signs appear before the age of three. One explanation for these deficits is a lack of interest in other people (Jemel, Mottron, & Dawson, 2006). However, much evidence suggests this explanation is too simplistic.

People with autism look less at faces than controls but when they do, perceptual processes and exploratory ocular movements focus much on irrelevant features (Senju & Johnson, 2009; Spezio, Adolphs, Hurley, & Piven, 2007). Individuals with Asperger's syndrome, an autistic disorder where linguistic and cognitive development is relatively preserved, have deficits in the recognition of identity, gender, age, and expressions in faces (Celani, Battacchi, & Arcidiacono, 1999). But the deficit extends beyond faces. For example, (Hubert et al., 2007) reported that autistic individuals performed worse than controls in recognizing bodily emotions from point-light displays, even though they performed as well as controls in recognizing simple actions and object manipulations.

Williams' syndrome is a rare genetic disorder where patients show propulsion toward social stimuli and interactions. (Riby & Hancock, 2009) tracked eye gaze of children with autism and those with Williams' syndrome when they were looking at pictures of socially relevant scenes. Children in the former group spent less time looking at faces than normally developed children. On the contrary, children with Williams' syndrome spent more time than controls on looking at faces. These different visual preferences for important social information indicate that both groups interpret the social cues differently. Moreover, when using video clips instead of pictures, the atypicalities in gaze remained.

Pictures of emotional social scenes were also used in a study comparing individuals with autism and schizophrenia with healthy controls. Just as persons with autism, schizophrenics did not look as much as controls at faces. For the former group, it did not even make a difference whether those faces were blurred or not, while people with schizophrenia, like healthy controls, oriented faster to informative face regions. However, they showed a delay in this orienting (Sasson et al., 2007).

The neural circuitry underlying deficits in emotion perception in autism remain poorly understood. One open question is whether individuals with autism have reduced neural sensitivity to emotional cues such as facial expressions or abnormally localized regions of face sensitivity. Abnormalities have been found in the amygdala and mirror neuron system in response to neutral (Kleinhans et al., 2008) and emotional faces (Dapretto et al., 2006). Moreover, several investigators have hypothesized that the fusiform face area is underdeveloped in autism because of the limited experience with faces that is a feature of this disorder (Critchley et al., 2000; Hubl et al., 2003; Pierce et al., 2001; Schultz et al., 2000). Decreased activation in the fusiform face areas has been observed in combination with increased activation outside of the lateral fusiform gyrus (Pierce, Muller, Ambrose, Allen, & Courchesne, 2001; Schultz et al., 2000). However, a lot of contradicting results have been published. One possible explanation for the inconsistencies in the literature is differences in eye-gaze patterns in autism, which we discussed in the previous paragraph. The relevance of this characteristic to fMRI studies of autism was identified by (Dalton et al., 2005) who reported a correlation between time spent fixating on the eyes and activation in the fusiform gyrus and amygdala. However, a recent study showed that individuals with autism failed to engage the subcortical brain regions involved in face detection while fearful faces were presented for 23.4 ms and were backwardly masked. This suggests a core mechanism for impaired socio-emotional processing in autism which is independent of looking patterns (Kleinhans et al., 2011).

To conclude, the neural circuitry underlying deficits in emotion perception in autism still remains poorly understood. Social deficits are strongly associated with autism spectrum disorders but are also common in borderline personality disorder.

Borderline personality disorder

Borderline personality disorder is the most common personality disorder, and is characterized by severe and persistent emotional, cognitive, behavioral and interpersonal impairments. The emotional instability in this disorder results from the interaction between an invalidating environment and an emotion vulnerability driven by biological factors. This biological vulnerability consists of a high sensitivity and reactivity to emotional stimuli, and a slow return to baseline level of emotional arousal (Linehan, 1993).

Borderline personality disorder patients show impairments in emotion regulation, resulting in affective instability in a social context. Impaired facial emotion recognition contributes to social disturbances. A particular facial emotion recognition pattern has been shown: impairments in basic emotion recognition and increased sensitivity to detect negative emotions. This is characterized by an enhanced sensitivity towards negative emotions and a tendency to label ambiguous or neutral stimuli more negatively (Domes, Schulze, & Herpertz, 2009).

Several brain imaging studies suggest that borderline personality disorder patients show structural and functional alterations in a frontolimbic network, in particular reduced amygdala volume and enhanced amygdala responding to emotional stimuli (for a meta analysis, see Domes et al. (2009). However, some controversy remains. For example, impaired recognition of disgusted faces has been observed, along with elevated activation in the posterior temporal cortex, but not the amygdala (Guitart-Masip et al., 2009).

To conclude, borderline personality disorder patients show impairments in processing emotions, associated with emotional hyper-reactivity, resulting in affective instability in social context and negative biases when observing emotions.

Eating disorders

Eating disorders include the syndrome of anorexia nervosa, which is characterized by a classic triad of amenorrhea, weight loss, and psychiatric disturbance (Klein & Walsh, 2003). Bulimia nervosa is often related to previous anorectic behavior and is characterized by gorging followed by periods of severe food restriction. Unusual methods are employed to lose weight, including vomiting and abuse of diuretics or laxatives. Some eating disorders are classified as an eating disorder not otherwise specified and may be associated with excessive exercise (DSM-IV, 2000). Eating disordered patients have many problems in their emotional and social functioning, but also with regulating their emotions (Schmidt & Treasure, 2006).

Although emotion perception studies have mainly focused on eating- and weight-related issues, some studies have looked at emotional processing at a more general level. As compared to a healthy control group, eating disordered patients show an attentional bias to faces, especially angry ones (Harrison, Sullivan, Tchanturia, & Treasure, 2010). It has been observed that patients with anorexia nervosa, in contrast to a control group, showed no modulation of emotional face processing and displayed significantly increased N200 amplitudes in response to all emotional categories. Moreover, they showed decreased visual-evoked potentials in response to unpleasant emotional faces in the P300 time range. They also made more mistakes in emotional face recognition, in particular, for neutral, sad, and disgusted faces (Pollatos, Herbert, Schandry, & Gramann, 2008).

Differences in brain dynamics might contribute to difficulties in the correct recognition of facially expressed emotions, deficits in social functioning, and in turn the maintenance of eating disorders. Imaging studies have revealed different neural responses in eating disordered patients versus controls following high caloric food pictures and photographs of one's own body versus other female bodies (Santel, 2006; Vocks, 2010). As far as we know, there has not been any imaging study investigating whether these differential responses extend to the perception of emotional cues from other people, such as for example facial expressions. Another difficulty with anorexia nervosa is that it is difficult to pull apart the effects of underweight and the underlying disease. In fact, the state of our body greatly influences how we perceive emotions. We address this issue further in the next paragraph.

Our body posture and facial expression influence our emotional responsiveness

Research suggests a close relationship between motor abilities and activation of the emotion circuit. Adopting facial expressions of specific emotions affects emotional judgments and memories (Schnall & Laird, 2007). Similarly, ones' body posture can affect behavior: slumped postures lead to more 'helpless behaviors' (Riskind & Gotay, 1982). More evidence comes from a study by Harmon-Jones and Peterson (2009) in which participants heard insulting remarks about an essay they had written. Those who were sitting in a chair exhibited more left frontal cortex activity (which correlated with experiencing anger) than those who were lying flat on their backs (Harmon-Jones & Peterson, 2009). Hennenlotter et al. (2009) studied women who had received cosmetic botox injections, thus rendering them unable to flex the corrugator muscle. For imitating anger, activity in the left amygdala was lower in those who had received botox compared to those who had not (Hennenlotter et al., 2009). If patients with a movement disorder cannot *produce* emotional expressions, it may be that they also have a deficit in *perceiving* the emotion.

Huntington's Disease

Huntington's disease is a rare neurodegenerative genetic disorder that is the most common genetic cause of repetitive abnormal movements called chorea. The prevalence varies from one person per million in populations of Asian and African descent, to 70 per million in Western European populations. The earliest symptoms, appearing around the age of 40, are a lack of coordination and unsteady gait. As the disease advances, uncoordinated movements become apparent, along with a decline in mental abilities and an increase in behavioral and psychiatric problems (Walker, 2007). The disease attacks primarily the caudate nucleus and putamen, leading to an impairment in motor (Vonsattel et al., 1985) and emotional tasks (Kampe, Frith, Dolan, & Frith, 2001).

Deficits in the perception of emotions have been widely reported, especially for disgust (Gray, Young, Barker, Curtis, & Gibson, 1997). But the deficits extent to positive emotions as well, including amusement and sensual pleasure (Robotham, Sauter, Bachoud-Levi, & Trinkler, 2011). Snowden et al. (2008) employed ten different tasks assessing recognition of emotion from facial and vocal cues in patients with manifest Huntington's disease. They found that patients were impaired in the recognition of several negative emotions across their extensive battery of tasks and concluded that Huntington's disease may cause a general impairment in the identification of negative emotions.

Moreover, Huntington's disease patients are impaired in recognizing instrumental and angry whole body postures and this deficit correlated with measures of motor deficit (de Gelder, Van den Stock, Balaguer Rde, & Bachoud-Levi, 2008). Research has clearly indicated that action recognition involves similar brain areas that are involved in performance of that same action by the observer (Rizzolatti & Craighero, 2004). The observed impairment in recognition of instrumental actions evokes the concept of motor resonance at the center of motor cognition abilities, which are implemented in the premotor cortex, parietal cortex, and superior temporal sulcus. Degeneration of the motor areas in Huntington's disease, predominantly striatum and its connections to parietal areas, premotor cortex and superior temporal sulcus is consistent with the importance of action representation for intact recognition of whole body postures.

A recent study examined context effects in Huntington patients while categorizing emotional faces. Disgust faces were embedded in images of people conveying sadness and anger as expressed by body language and additional paraphernalia. Additionally, sad and angry faces were embedded in context images conveying disgust. Despite the deficient explicit recognition of isolated disgust and anger faces, the perception of the emotions expressed by the faces was affected by context in Huntington patients in a similar manner as in controls. These findings suggest that despite their impaired explicit recognition of facial expressions, Huntington patients display relatively preserved processing of the same facial configurations when embedded in a context (Aviezer et al., 2009).

To conclude, these studies show that Huntington patients have reduced sensitivity in the identification of emotional signals. Given the motor symptomatology in Huntington disease, one candidate mechanism may be affective motor representations, which have been suggested to underlie emotion recognition across modalities (Niedenthal, 2007).

Parkinson's Disease

Parkinson's disease is another degenerative disorder of the central nervous system, characterized by muscle rigidity, tremor, and a slowing of or even complete loss of physical movement. The primary symptoms result from decreased stimulation of the motor cortex by the basal ganglia, caused by a deficient dopamine system. While many forms of the disease are idiopathic, secondary cases may result from toxicity most notably caused by drugs, head trauma, or other medical disorders (Jankovic, 2008). Prevalence rate estimates range from 65.6 / 100.000 to 12.500 / 100.000 (for a meta-analysis, see von Campenhausen et al. (2005)).

It is generally argued that the loss of dopaminergic neurons, resulting in dysfunction of fronto-subcortical systems, not only leads to motor disturbances but also to emotional information processing deficits (Altshuler et al., 2001; Dujardin et al., 2004). Parkinson's disease patients have a reduced ability in making spontaneous emotional expressions and have monotonous, flat, and poorly inflected speech. They are impaired in imaging, perceiving, and expressing emotional faces (Jacobs, Shuren, Bowers, & Heilman, 1995; Wieser et al., 2006). Kan et al. (2002) observed that Parkinson's disease patients had no problems recognizing emotions in voices and words, but had deficits in emotion recognition from facial expressions, particularly fear and disgust (Kan, Kawamura, Hasegawa, Mochizuki, & Nakamura, 2002). In line with this, (Suzuki, Hoshino, Shigemasu, & Kawamura, 2006) also showed that these patients were impaired at recognizing disgusted expressions. However, others have failed to demonstrate differences between patients and controls in facial emotion recognition tasks (Adolphs, Schul, & Tranel, 1998). Dujardin et al. (2004) established that early in the course of Parkinson's disease, emotional facial processing is disturbed and untreated patients are significantly impaired in decoding these. It has recently been observed that men compared to women with Parkinson's disease and healthy control men display specific impairments in the recognition of fearful expressions (Clark, Neargarder, & Cronin-Golomb, 2008). A recent meta-analysis of emotion recognition in Parkinson disease concluded that the identification of negative emotions is disproportionately impaired in this group of patients (Gray & Tickle-Degnen, 2010).

Sprengelmeyer et al. (2003) investigated the effect of dopamine medication and observed that the recognition of anger and fear was disrupted in medicated Parkinson's disease participants, but that non-medicated patients in addition showed impairments in the recognition of sadness and disgust (Sprengelmeyer et al., 2003). Lawrence, Goerendt, and Brooks (2007) reported that the recognition of anger was impaired in Parkinson's disease patients who had been temporarily removed from dopamine replacement therapy. Not surprisingly, reduced dopaminergic-binding sites in the orbitofrontal cortex and amygdala (Ouchi et al., 1999), and abnormal clumps of degenerating neurons in the amygdala of Parkinson's disease patients (Mattila, Rinne, Helenius, & Röyttä, 1999) have been reported. Tessitore et al. (2002) observed that in these patients, an emotional task was not associated with amygdala activation, but dopaminergic repletion was shown to restore this response (Tessitore et al., 2002).

Research in Huntington and Parkinson disease patients add further evidence to the existence of a close relationship between motor abilities and the processing of emotion.

Future directions

In this review, we gave a selective overview of emotional processing in relation to psychological and neurological disorders. Emotion perception is disrupted in different clinical samples. Whereas clinical diagnosis is often based on behavioral symptoms and course of illness, the interest in neurobiological markers of psychiatric disorders has grown substantially in recent years.

Disrupted emotion recognition is associated with anomalous activity levels of and reduced connectivity between different areas of the brain. For example, the amygdala plays a clear role in processing emotions, and many abnormalities in its functioning have been observed among the disorders discussed in this article. In anxiety disorders, over-activation of the amygdala and insula has been observed, whereas depressive disorder is mainly characterized by decreased cortico-limbic connectivity. Schizophrenia is marked by under recruitment of the amygdala, accompanied by a substantial limitation in activation throughout a ventral temporal-basal ganglia-prefrontal cortex when processing facial emotion. Main areas affected in autistic disorder are the amygdala, insula and fusiform face area. Characteristics of borderline personality disorder are the structural and functional alterations in a frontolimbic network and enhanced amygdala responding to emotional stimuli. Degeneration of the motor areas in Huntington's disease, predominantly the striatum and its connections to parietal areas, premotor cortex and superior temporal sulcus may contribute to impaired emotion recognition. Parkinson patients also have deficits in emotion recognition from facial expressions, particularly fear and disgust. These impairments may be associated with malfunctioning of fronto-subcortical connectivity.

Despite considerable evidence that certain activity patterns are disrupted in various disorders, controversy often persists over what place disrupted processing should take within our understanding of these diseases. For example, are connectivity problems best seen as "central", "core" or "primary" in these diseases, or are they one of numerous "downstream" features of disrupted system performance? Attempts to answer this question have been frustrated by the considerable difficulties involved in studying early development in these disorders, prior to diagnosis. Subjects tend to present with a host of already developed symptoms, making causal pathways hard to untangle.

Genetic variation in the receptors associated with oxytocin, vasopressin, dopamine and serotonin has been intensively studied in human and animal models. Based on the enormous advances in animal models of the role of neuropeptides in social cognition and behavior, recent human studies suggest that the basic social effects of oxytocin and arginine vasopressin from animal research may also be applicable to human social interaction. Although the translation of behavioral and neurobiological findings from animal studies to humans generally bears the risk of drawing oversimplified parallels between rodents and humans, the initial findings are encouraging in terms of providing a better understanding of the neurobiology and neurogenetics of human social behavior. Moreover, these translational findings suggest that oxytocin and arginine vasopressin may play an important role in the etiology and treatment of a number of clinical disorders involving social deficits. Recent findings are building an increasingly coherent picture of these regulatory mechanisms (Skuse & Gallagher, 2011). Therefore, future research on impaired emotion perception should attempt to compare the severity and nature of these abnormalities across different psychiatric disorders and integrate new findings with animal, human lesion, genetic and developmental studies to identify the neural bases of the different neuropsychological processes important to the understanding of human emotional behavior.

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Chapter 5

The role of negative affectivity and social inhibition in perceiving social threat: an fMRI study

this chapter is based on:
Kret, M.E. & Denollet, J., Grèzes, J. & de Gelder, B., (2011). The role of negative affectivity and social inhibition in perceiving social threat: an fMRI study. *Neuropsychologia, 49(5),* 1187-1193.

Abstract

Personality is associated with specific emotion regulation styles presumably linked with unique brain activity patterns. By using functional magnetic resonance imaging (fMRI) in 26 individuals, the neural responses to threatening (fearful and angry) facial and bodily expressions were investigated in relation to negative affectivity and social inhibition. A negative correlation was observed between negative affectivity and activation of the amygdala, fusiform gyrus, insula and hippocampus. Increased activation following threatening stimuli was observed in the left temporo-parietal junction and right extrastriate body area correlating with more social inhibition traits. Interestingly, the orbitofrontal cortex, superior temporal sulcus, inferior frontal gyrus (Brodmann area 45) and temporal pole correlated negatively with negative affectivity and positively with social inhibition. Whereas individuals with increased negative affectivity tend to de-activate the core emotion system, socially inhibited people tend to over-activate a broad cortical network. Our findings demonstrate effects of personality traits on the neural coding of threatening signals.

Individual differences in emotion perception

Social communication includes intuitively grasping signals of hostility and reacting with empathy to signals of distress. Humans are especially sensitive to the gestural signals and facial expressions made by other people, and use these signals as guides for their own behavior. Previous research has largely focused on the perception of emotions from static faces (Adolphs, 2002b; Haxby, Hoffman, & Gobbini, 2000). But our communicative ability also relies heavily on decoding messages provided by body movements. Dynamic presentations of facial stimuli facilitate processing (Sato, Fujimura, & Suzuki, 2008; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). Moreover, dynamic information is useful for a better understanding of the respective contribution of action components in body expressions (Grèzes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grèzes, 2008).

People vary in how they perceive emotions and their brain activity patterns differ. For example, healthy individuals with high trait anxiety show increased amygdala activity when they look at threatening faces (Etkin et al., 2004). People not only differ in how they perceive emotions, but also in how they act in threatening situations. Whereas some of us may fight back when confronted with aggression, others flee or freeze (Schmidt, Richey, Zvolensky, & Maner, 2008). These differences may be mediated by the orbitofrontal cortex (Rolls, 2004). Eisler and Levine (Eisler & Levine, 2002) provided evidence that the orbitofrontal cortex is the pivotal area for choice between a fight or flight or other responses in a threatening situation. Since the orbitofrontal cortex plays a role in linking sensory events and positive or negative affective valuation, behavioral selection may be biased by an individual's personality and by the presence of a stressor (Damasio, 1994; Rolls, 2004).

Socially anxious people are afraid of possible scrutiny and negative evaluation by others and strive towards social acceptance. Research supports a positive link between anxiety levels and orbitofrontal cortex activity during threat perception (Stein, Simmons, Feinstein, & Paulus, 2007). Observing another person in a distressed or aggressive state evokes stress in the observer (Hatfield, Cacioppo, & Rapson, 1994). The stress response includes facilitation of neural pathways that subserve acute, time limited adaptive functions, such as arousal, vigilance and focused attention, and inhibition of neural pathways that subserve acutely nonadaptive functions (Chrousos, 2009). However, this response can become maladaptive when the anxiety response is disproportionate to the situation 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. Through its mediators, stress can lead to acute or chronic pathological, physical and mental conditions (Chrousos, 2009).

Individuals with a Type D (distressed) personality (21% of the general population) are more likely to experience feelings of depression and anxiety (Denollet, 2005). They tend to experience negative emotions across time and situations (negative affectivity component of Type D) but also inhibit the expression of these emotions due to fear of rejection or disapproval (social inhibition component of Type D). Type D personality is associated with hyper-reactivity of the hypothalamic-pituitary-adrenal axis, increased inflammatory activity, decreased endogenous neural progenitor cells and eventually, poor prognosis in cardiovascular patients (Denollet, Martens, Nyklicek, Conraads, & de Gelder, 2008; Denollet, Pedersen, Vrints, & Conraads, 2006; Denollet, Schiffer et al., 2009; Denollet, Schiffer, & Spek, ; Habra, Linden, Anderson, & Weinberg, 2003; Molloy, Perkins-Porras, Strike, & Steptoe, 2008; Sher, 2005; Van Craenenbroeck et al., 2009). Because Type D personality affects the course and treatment of cardiovascular conditions (Denollet et al.), this personality construct qualifies for the DSM-IV classification Psychological Factors Affecting Medical Condition (DSM-IV, 2000). Whereas depression is an episodic risk marker, Type D is a chronic risk marker for clinical manifestations of coronary disease (Denollet, de Jonge et al., 2009). Type D and depression are partly overlapping (for a recent meta analysis, see (Denollet, Schiffer et al., 2009) .

Type D refers to the combination of negative affectivity with social inhibition, but these two subcomponents may be reflected differently in the brain. Learning more about how the two subscales independently and jointly influence emotion processing in the brain will provide new insights into the Type D construct. Still very little is known about the neurofunctional basis of negative affectivity and social inhibition. A study by de Gelder et al (de Gelder, van de Riet, Grèzes, & Denollet, 2008) reports a negative correlation between negative affectivity and amygdala activation following static threatening versus neutral facial and bodily expressions. The authors focused only on the amygdala as region of interest but other effects may be detected in a whole brain analysis and also in relation to the social inhibition personality trait.

The amygdala is viewed as a key area in the social brain network and responds to salient signals such as faces (Adolphs, 2009). We recently compared the neurofunctional network of dynamic facial expressions with that of dynamic bodily expressions and showed that the amygdala was more active for facial than bodily expressions. But bodily expressions triggered higher activation than face stimuli in a number of regions including the cuneus, fusiform gyrus, extrastriate body area, temporo-parietal junction, superior parietal lobule, primary somatosensory cortex as well as the thalamus. We found no major differences between fearful and angry expressions. Emotion related activations were primarily observed in the superior temporal sulcus and gyrus as well as in the extrastriate body area and the middle temporal gyrus. The absence of the amygdala here may be surprising. However, most studies using dynamic naturalistic expressions (not morphs between a neutral and emotional static face), reported similar results (Grosbras & Paus, 2006; Kilts, Egan, Gideon, Ely, & Hoffman, 2003; Simon, Craig, Miltner, & Rainville, 2006; van der Gaag, Minderaa, & Keysers, 2007), possibly because of the relevance of a dynamic neutral face (these results are in detail discussed in (Kret, Pichon, Grèzes, & de Gelder, 2011)). But this explanation may not be complete.

The current study investigates the relation between negative affectivity and social inhibition and the neural responses to threatening signals provided by videoclips of facial and bodily expressions in a healthy population. Our main questions were threefold. First, we wanted to know whether the earlier reported decrease in amygdala activation associated with threat perception in high negative affectivity scorers (de Gelder et al., 2008) would persist when using dynamic, more naturalistic stimuli and examine whether this decreased activity would extend to other brain areas known to be important for emotion perception. Second, we wanted to examine whether socially inhibited individuals would over activate the cortical social brain network including temporo-parietal junction (which is involved in mentalizing) and the orbitofrontal cortex (which is involved in social decision making). Third, since Type D personality is associated with a broad range of health issues and somatic responses, we were specifically interested in the combined influence of social inhibition and negative affectivity because these subscales together have much predictive value in health outcomes.

Methods

Participants

Twenty-eight students (14 females, mean age 19.73 years old, range 18-27 years old; 14 males; mean age: 21.69 years old, range 18-32 years old) were recruited via an advertisement at Maastricht university. The advertisement stated that we were looking for healthy, right-handed students without a neurological or psychiatric disease or psychological problems. As part of the standard protocol at Maastricht university, before inviting them to participate in the experiment, they were sent additional information about fMRI in general and they had to fill out a standard medical questionnaire developed at Maastricht university, in order to check if their psychological or medical condition was normal and if they were medication free. In addition, the experimenter asked all participants whether they had been diagnosed with a psychiatric disorder or whether they suffered from psychological problems. All were eligible and took part in the experiment in September 2007. None of the participants reported having a neurological or psychiatric history, all were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), healthy, and had normal or corrected-to-normal vision. The students were randomly assigned to one version of the experiment (anger-neutral or fear-neutral). The two groups did not differ in age (M = 21.81, SD = 5.63 versus M = 19.83, SD = 1.80, $t(26) = 1.168$, $p = .253$) and male and female participants were equally distributed. All participants gave informed consent. The study was performed in compliance with national legislation and in accordance with the declaration of Helsinki and was approved by the local ethics committee. Two participants were discarded from analysis, due to 1) task miscomprehension and attention deficit disorder 2) neurological abnormalities, so 26 participants were included.

Stimuli and validation

Video recordings were made of 26 actors expressing six facial and bodily emotions. For the body video sessions all actors were dressed in black and filmed against a green background. For the facial videos, actors wore a green shirt, similar as the background color. Recordings used a digital video camera under controlled and standardized lighting conditions. To coach the actors to achieve a natural expression, pictures of emotional scenes were, with the help of a projector, shown on the wall in front of them and a short emotion inducing story was read out by the experimenter. The actors were free to act the emotions in a naturalistic way as response on the situation described by the experimenter and were not put under time restrictions. Fearful body movements included stretching the arms as if to protect the upper body while leaning backwards. Angry body movements included movements in which the body was slightly bended forward, some actors showed their fists, whereas others stamped their feet and made resolute hand gestures. Additionally, the stimulus set included neutral face and body movements (such as pulling up the nose, coughing, fixing one's hair or clothes). Distance to the beamer screen was 600 mm. All video clips were computer-edited using Ulead and After Effects, to a uniform length of two seconds (50 frames).

We filmed several versions per actor and condition. A total of 380 face and body videos of all six basic emotions and in addition neutral stimuli were included in a large validation study. The face and body videos were validated separately. All videos were presented twice to 20 independent raters who had to categorize the emotion (and choose among seven categories) and rate its intensity (how intense is the emotion being displayed?) on a 5-point scale. The in this experiment included angry facial expressions were recognized for 84% (SD 19) with intensity 2.90 (SD .23), fearful facial expressions for 86% (SD 7) with intensity 3.31 (SD .22), neutral facial expressions 79% (SD 21) with intensity 1.99 (SD .30), angry bodily expressions for 85% (SD 15) with intensity 3.56 (SD .62), fearful bodily expressions for 83% (SD 16) with intensity 3.64 (SD .47) and neutral bodily expressions for 80% (SD 20) with intensity 2.09 (SD .21). Angry and fearful expressions were rated as more intense than neutral ones [t(19) = 6.417, $p < .001$] and [t(19) = 6.028, $p < .001$] respectively. Intensity scores did not differ between fearful and angry expressions [t(19) = 1.532, $p = .165$]. Actors' age closely matched that of the participants.

The faces of the body videos were covered with Gaussian masks so that only information of the body was perceived. To check for quantitative differences in movement between the movies, we estimated the amount of movement per video clip by quantifying the variation of light intensity (luminance) between pairs of frames for each pixel (Grèzes et al., 2007). For each frame, these absolute differences were averaged across pixels that scored (on a scale reaching a maximum of 255) higher than ten, a value which corresponds to the noise level of the camera. These were then averaged for each movie. Angry and fearful expressions contained equal movement ($M = 30.64$, SD 11.99 vs. $M = 25.41$, SD 8.71) [$t(19) = .776$, $p = .88$] but more movement than neutral expressions ($M = 10.17$, SD 6.00) [$t(19) = 3.78$, $p < .005$] and [$t(19) = 4.093$, $p < .005$]. By using Matlab software, we generated scrambled movies by applying a Fourier-based algorithm onto each movie, a technique that has been used before for pictures (Hoffman, Gothard, Schmid, & Logothetis, 2007). This technique scrambles the phase spectra of each frame and generates video clips that served as low level visual controls and prevented habituation to the stimuli.

Experimental design

The experiment consisted of 176 trials, presented in two runs, with 80 non-scrambled (10 actors * 2 expressions (threatening (fear or anger), neutral) * 2 runs * 2 repetitions), 80 scrambled videos and 16 oddballs. There were 80 null events (blank, green screen) with a duration of 2000 ms. These 176 stimuli and 80 null events were randomized within each run. A trial started with a fixation cross (500 ms), followed by a video (2000 ms) and a blank green screen (2450 ms). An oddball task was used to control for attention and required participants to press a button on a keypad, positioned on the right side of the participant's abdomen each time an inverted video-clip appeared so that trials of interest were uncontaminated by motor responses. Half of the participants viewed neutral and angry expressions and the other half neutral and fearful expressions. They were pseudo-randomly assigned to one of the two versions of our experiment but we made sure that the male-female distribution was exactly equal. In this way, the participants saw an equal number of emotional and neutral movies and this design allowed us to pool two different types of threat. The stimulus was centred on the display screen and subtended 11.4° of visual angle vertically and 10.0° horizontally for the body stimuli and 7.9° of visual angle vertically and 4° horizontally for the face stimuli. After the scanning session, participants were guided to a quiet room where they were seated in front of a computer and categorized the stimuli they had previously seen in the scanner by choosing between a threatening (fear or anger) or a neutral label. The accuracy rates were as follows: anger (M = 95% (SD 8), fear (M = 94% (SD 9)), neutral (M = 95% (SD 11).

Description of the Type D questionnaire

After the scanning session participants completed the DS14 scale as a standard measure of Type D personality (Denollet, 2005). The 14 items are answered on a five-point scale ranging from zero (false) to four (true). Seven items refer to 'negative affectivity' or the tendency to experience negative emotions ('I am often down in the dumps', 'I often find myself worrying about something'). The other seven items refer to the participants' level of 'social inhibition' or the tendency to inhibit the expression of emotion/behaviour in social relationships ('I am a closed kind of person', 'I often feel inhibited in social interactions'). People who score ten points or more on both dimensions are classified as Type D and have the tendency to experience increased negative emotions across time and situations and tend not share these emotions with others, because of fear of rejection or disapproval. These personality scales were earlier found reliable (Cronbach's = 0.88/0.86) and stable over time (Denollet, 2005; Martens, Kupper, Pedersen, Aquarius, & Denollet, 2007).

fMRI data acquisition

Parameters of the functional scan

Functional images were acquired using a 3.0-T Magnetom scanner (Siemens, Erlangen, Germany). Blood Oxygenation Level Dependent (BOLD) sensitive functional images were acquired using a gradient echo-planar imaging (EPI) sequence (TR = 2000ms, TE = 30 ms, 32 transversal slices, descending interleaved acquisition, 3.5 mm slice thickness, with no interslice gap, FA = 90°, FOV = 224 mm, matrix size = 64 x 64 mm). An automatic shimming procedure was performed before each scanning session. A total of 644 functional volumes were collected for each participant (total scan time = ten minutes per run (2 runs with the anatomical scan in between)).

Parameters of the structural scan

A high-resolution T1- weighted anatomical scan was acquired for each participant (TR = 2250 ms, TE = 2.6 ms, FA = 9°, 192 sagittal slices, voxel size 1 x 1 x 1 mm, Inversion Time (TI) = 900 ms, FOV = 256 × 256 mm2, 192 slices, slice thickness = 1 mm, no gap, total scan time = 8 minutes).

Statistical Parametric Mapping

Functional imaging data were preprocessed and analysed using SPM2 Functional images were processed using SPM2 software (Wellcome Department of Imaging Neuroscience; see www.fil.ion.ucl.ac.uk/spm). The first five volumes of each functional run were discarded to allow for T1 equilibration effects. The remaining 639 functional images were reoriented to the anterior/posterior commissures (AC-PC) plane, slice time corrected to the middle slice and spatially realigned to the first volume, subsampled at an isotropic voxel size of 2 mm, normalized to the standard MNI space using the EPI reference brain and spatially smoothed with a 6 mm full width at half maximum (FWHM) isotropic Gaussian kernel. Statistical analysis was carried out using the general linear model framework implemented in SPM2 (Friston et al., 1995).

At the first level analysis, nine effects of interest were modelled: four represented the trials where subjects perceived emotional expressions or neutral face and body videos; four represented the scrambled counterparts and one the oddball condition. Null events were modelled implicitly. The BOLD response to the stimulus onset for each event type was convolved with the canonical haemodynamic response function over a duration of 2000 ms. For each subject's session, six covariates were included to capture residual movement-related artefacts (three rigid-body translations and three rotations determined from initial spatial registration), and a single covariate representing the mean over scans. To remove low frequency drifts from the data, we applied a high-pass filter using a cut-off frequency of 1/128 Hz. We smoothed the images of parameter estimates of the eight contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel and estimated the following main effects at the first level:

1) Main effect of body vs. face [Emotion + neutral (body vs. face)];
2) Main effect of face vs. body [Emotion + neutral (face vs. body)];
3) Main effect of emotion vs. neutral [Emotion vs. neutral (face + body)]

At the second level of analysis, we performed within-subjects correlation analyses examining the contrast between threatening and neutral videos and social inhibition and negative affectivity scores. Social inhibition and negative affectivity were included in the same regression model. We performed a correlation analysis with social inhibition and one with negative affectivity and four conjunction analyses to investigate areas that are 1) positively correlated with both scales, 2) negatively correlated with both scales, 3) positively correlated with social inhibition and negatively with negative affectivity and 3) negatively with social inhibition and positively with negative affectivity. Our goal was to study common modulations by threat in areas involved in processing faces and bodies, rather than studying specific modulations by fear and anger or faces and bodies (Kret et al., 2011). A nonsphericity correction was applied for variance differences between conditions and subjects.

For all statistical maps, we report activations that survived the threshold of $p < .001$, uncorrected, with a minimum cluster extent of 15 contiguous voxels. Statistical maps were overlaid on the SPM's single subject brain compliant with MNI space, i.e., Colin27 (Holmes et al., 1998) in the anatomy toolbox (www.fz-juelich.de/ime/spm_anatomy_toolbox (Eickhoff SB et al., 2005). The atlas of Duvernoy (Duvernoy, 1999) was used for macroscopical labeling.

Results

Scores on the negative affectivity trait ranged from 0-19 (*M* = 6.54, SD = 4.28), five individuals scored ≥ 10. Scores on the social inhibition trait ranged from 1-16 (*M* = 7.65, SD = 4.41), eight individuals scored ≥ 10. The two trait subscales were correlated ($r = .402$, $p < .05$). The scores on the questionnaire of the participants who participated in the anger-neutral version of the experiment were similar to the scores from the students that participated in the fear-neutral version (negative affectivity: *M* = 6.21, SD = 4.08 versus *M* = 6.92, SD = 4.66. t(24) = .410, p = .69; social inhibition: *M* = 7.50, SD = 5.33 versus *M* = 7.83, SD = 3.25 t(24) = .188 p = .85. Three individuals met criteria for Type D personality. These scores are similar to norms for this age group. In a study that included 167 students, scores were as follows: negative affectivity: *M* = 7.49, SD = 5.34, social inhibition: *M* = 9.06, SD = 5.24 (Kupper & Denollet, 2007).

Negative affectivity

We observed a negative correlation between the negative affectivity score and activity in amygdala, right hippocampus, orbitofrontal cortex, cingulate cortex, temporal pole, right insula, inferior frontal gyrus (including Brodmann area 44/45), fusiform gyrus, superior temporal sulcus, temporo-parietal junction and other areas in the temporal and frontal lobes. To further investigate the effect in the amygdala we investigated the average response of the whole cluster (including all 102 voxels) to the neutral and the emotional stimuli in a multiple regression analysis in SPSS including social inhibition and negative affectivity. The correlation in the amygdala was derived from a negative correlation with threat ($r^2(2, 23) = .170$, $p = .042$) rather than from increased activity for neutral stimuli ($r^2(2, 23) = .007$, $p = .88$). There were no positive correlations with negative affectivity. See Figure 1 and Table 1 for the full list of activations.

Social Inhibition

A broad network was positively related to social inhibition; orbitofrontal cortex, left superior frontal gyrus, inferior frontal gyrus pars Triangularis (Brodmann area 45), right medial temporal pole, right primary somatosensory cortex (Brodmann area 3a), superior temporal sulcus, left temporo-parietal junction, inferior temporal gyrus, right fusiform gyrus, left middle occipital gyrus and the visual cortex. See Figure 1 and Table 2 for the full list of activations.

Negative affectivity and social inhibition

We did not find areas similarly correlating with social inhibition and negative affectivity. However, a conjunction between a negative correlation with negative affectivity and a positive correlation with social inhibition showed common patterns in the orbitofrontal cortex, inferior frontal gyrus

(Brodmann area 45), primary somatosensory cortex (Brodmann area 3b), right medial temporal pole, left middle temporal gyrus, superior temporal sulcus and left temporo-parietal junction (see Table 3). There were no regions that were positively correlated with negative affectivity and negatively with social inhibition.

Table 1. Negative correlation with negative affectivity

Brain regions	MNI Coordinates	cluster	z-value
Left/right superior medial gyrus	+/-14 62 -14	2585*	3.48
Left/right rectal gyrus	8 50 -14	44	2.98
Left middle frontal gyrus	-30 52 16	2585	3.58
Right/left orbitofrontal cortex	+/-24 30 -10	2585*	3.66/3.49
Right middle frontal gyrus	26 42 6	2585*	3.51
Left middle frontal gyrus	-36 34 50	35	3.11
Right inferior frontal gyrus Pars Triangularis (BA 45)	48 30 14	2585*	4.00
Right/left temporal pole	44 16 -22	599	3.16
Right insula	34 -2 22	138	3.75
Right insula	44 -10 10	56	3.03
Right Rolandic Operculum (BA 3a)	54 -12 26	299	4.69
Left/Right anterior cingulate gyrus	+/ -6 8 26	2585*	4.01/335
Left/right posterior cingulate gyrus	-14 -32 26	193/403	4.41/3.88
Left/right amygdala	22 -8 -12	102	3.20
Right hippocampus	32 -28 -10	619	3.95
Right hippocampus	48 -44 -10	34	3.31
Right hippocampus	26 -48 12	40	3.29
Right medial temporal gyrus	54 -32 -2	599*	3.12
Left/right superior temporal sulcus	-64 -16 -10	149/599*	3.69/3.14
Right/left superior temporal sulcus	42 -44 6	75/202	3.73/3,08
Left temporo-parietal junction	-50 -50 30	118	3.39
Left/right inferior temporal gyrus	-42 -38 2	202/619	3.82/3.22
Right fusiform gyrus	28 -36 -20	619	3.98
Left fusiform gyrus	-26 -60 -10	69	3.03
Right/Left cerebellum	46 -56 -42	2434	4.00/ 3.28
Right primary visual cortex	20 -74 10	503	3.38

* subpeak
MNI coordinate: + = right hemisphere
MNI coordinate: - = left hemisphere

Table 2. Positive correlation with social inhibition

Brain regions	MNI Coordinates	cluster	z-value
Left orbitofrontal cortex	-16 62 -16	47	2.97
Right/left inferior frontal gyrus pars Triangularis (BA 45)	+/-52 12 6	403*/144	3.29/3.00
Right inferior frontal gyrus pars Orbitalis (BA 45)	52 30 2	403	3.36
Right medial temporal pole	42 8 -30	46	3.03
Right parietal operculum/Rolandic Operculum (BA3a) (SI)	54 -12 26	131	3.93
Right/left superior temporal sulcus	+/-54 -32 -2	1107/968*	4.58/3.34
Left middle temporal gyrus	-44 -38 2	968	3.56
Left posterior superior temporal sulcus	-54 -60 10	968*	3.45
Left temporo-patietal junction	-50 -48 30	968*	3.36
Right extrastriate body area	44 -78 0	180	3.57
Right fusiform gyrus	48 -40 -22	22	3.04
Left middle occipital gyrus	-36 -68 12	63	3.08
Left/right primary visual cortex	-14 -96 6	187	3.45

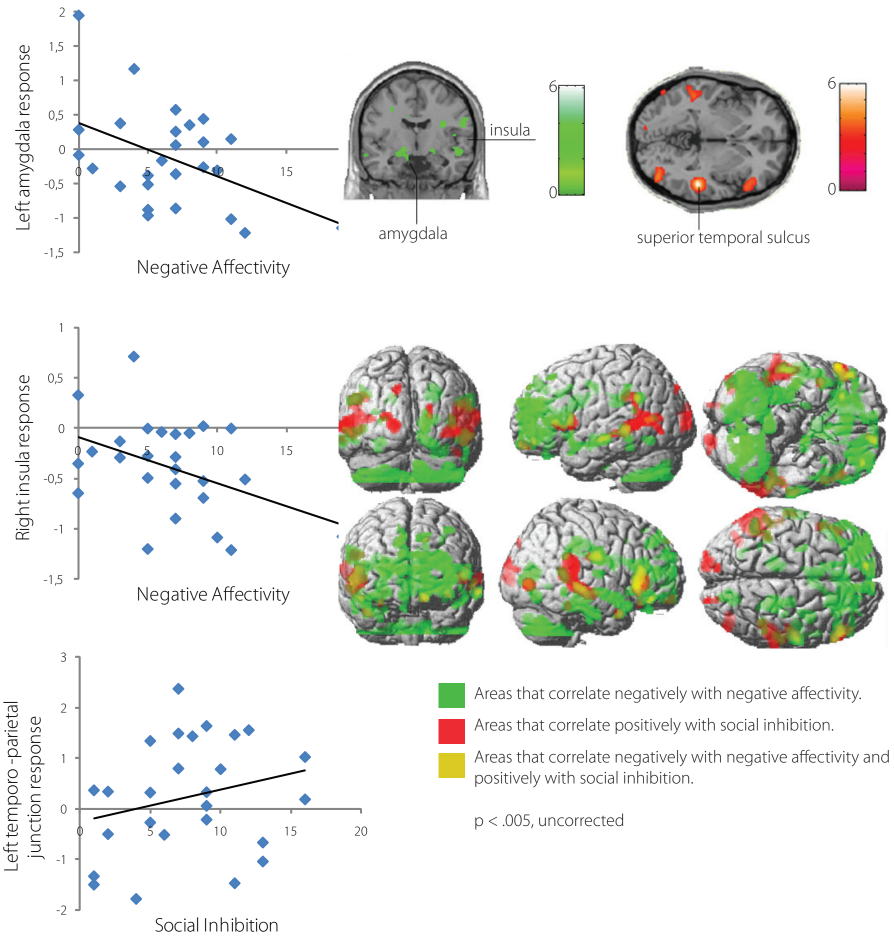
* subpeak
MNI coordinate: + = right hemisphere
MNI coordinate: - = left hemisphere

Table 3. Negative correlation with negative affectivity AND Positive correlation with social inhibition

Brain regions	MNI Coordinates	cluster	z-value
Left orbitofrontal cortex	-16 62 -16	42	2.97
Right inferior frontal gyrus pars Triangularis (BA 45)	50 30 10	235	3.29
Right rolandic operculum (area 3b)	54 -12 26	118	3.93
Right medial temporal pole	42 10 -30	40	2.98
Left middle temporal gyrus	-64 -16 -10	40	3.10
Right superior temporal sulcus	54 -32 -2	142	3.12
Right superior temporal sulcus	42 -44 6	66	3.73
Left superior temporal sulcus	-44 -38 2	134	3.56
Left temporo-parietal junction	-50 -50 30	50	3.21

MNI coordinate: + = right hemisphere
MNI coordinate: - = left hemisphere

Figure 1. Neural correlates with negative affectivity and social inhibition.



A negative correlation between negative affectivity and activity following threatening stimuli was observed in amygdala (r2(2, 23) = .338 and insula (r2(2, 23) = .378. The correlations appear to be driven by an outlier (an individual with an negative affectivity for threatening versus neutral stimuli score beyond that of the group mean). However, these results are to be considered very robust, since after this subject was removed and the analysis was performed again, the correlations remained significant. Increased activation following threatening stimuli was observed in the left temporo-parietal junction with more social inhibition traits (r2(2, 23) = .372. See Tables 1-3 for the full list of activations.

Discussion

A growing literature demonstrates that different personality traits are associated with specific activity patterns in the brain when people are faced with threat (Campbell-Sills et al., ; Canli et al., 2001; Cremers et al., ; Ewbank et al., 2009; Jimura, Konishi, Asari, & Miyashita, ; Kugel et al., 2008; Perez-Edgar et al., 2007; Reker et al., 2010). Our main results are threefold. First, the observed amygdala decrease in high negative affectivity scorers for threatening facial and bodily expressions is similar to what we found earlier by the use of static stimuli. Second, the orbitofrontal cortex, left temporo-parietal junction and right extrastriate body area showed increased activity for threatening stimuli in high scorers on the social inhibition scale. Third, the orbitofrontal cortex, superior temporal sulcus, inferior frontal gyrus (Brodmann area 45) and temporal pole correlated negatively with negative affectivity and positively with social inhibition. The first two findings are in line with our expectations, but the third one is different from what we first predicted. Below we elaborate on these findings in more detail.

In line with our expectations, we observed decreased activity for threatening videos in the amygdala in a whole brain analysis along with right hippocampus, orbitofrontal cortex, cingulate cortex, temporal pole, right insula, inferior frontal gyrus (including Brodmann area 44/45), fusiform gyrus, superior temporal sulcus, and temporo-parietal junction. These areas are widely reported in the emotion literature and also in studies on structural abnormalities in depression (including a reduced volume of the orbitofrontal and cingulate cortex, insula and amygdala /parahippocamal region) (Lee et al., 2007). Whereas some studies report a decrease in activity (Thomas et al., 2001) or no difference (Lee et al., 2008), others report increased amygdala response to threatening versus neutral expressions related to depressive symptoms (Canli et al., 2005; Peluso et al., 2009). Beesdo et al. (Beesdo et al., 2009) observed amygdala *hypo* activation in major depressive disorder patients while passively viewing fearful faces, and amygdala *hyper* activation when actively rating how afraid they were when seeing a fearful face. Similarly, healthy behaviorally inhibited adolescents, relative to non-inhibited peers, showed exaggerated amygdala response during subjective fear ratings and deactivation during passive viewing of emotional faces (Perez-Edgar et al., 2007). These inconsistencies may thus originate from differences in the specific task and attention load between studies. Importantly, our results are in line with those using implicit tasks and show that deactivation of the amygdala was paired with deactivation of other emotion areas in the brain.

Whereas we found cortical but also subcortical structures correlating negatively with negative affectivity, we found a broad but exclusively cortical network which activity pattern was positively correlated with social inhibition. These regions (including temporo-parietal junction, superior temporal sulcus, inferior frontal gyrus (Brodmann area 45) and orbitofrontal cortex) are jointly involved in perceiving the action goal of the observed (Van Overwalle & Baetens, 2009). Observing and imitating facial expressions both activate the inferior frontal gyrus (Brodmann area 45) similarly (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). The temporo-parietal junction plays an important role in mentalizing and computes the orientation or direction of the observed behavior in order to predict its goal (Decety & Lamm, 2007). As predicted, we observed a positive correlation between threat-related activity in these areas and scores on the social inhibition scale. Pelphrey et al. (Pelphrey, Morris, & McCarthy, 2005) report that observing whole-body motion and gaze engage the posterior superior temporal sulcus and most likely reflect an orientation response in line with the action or attention of the observed. So, the observed increased activity in the superior temporal sulcus may indicate increased vigilance in individuals who have a tendency to inhibit socially. This explanation is plausible since there was also a positive correlation with V1 which may point to increased attention (Somers, Dale, Seiffert, & Tootell, 1999). Hyperactivity in these cortical structures does not necessarily mean, and probably does not mean, better function.

Since Type D personality is associated with a broad range of health issues and somatic responses, we were specifically interested in the combined influence of social inhibition and negative affectivity on threat-related brain activity. We did not find areas with activity patterns correlating positively or negatively with both social inhibition and negative affectivity. Instead, whereas the orbitofrontal cortex and somatosensory cortex correlated positively with social inhibition, they correlated negatively with negative affectivity.

The orbitofrontal cortex is connected with areas that underlie emotional function and empathy (Hynes, Baird, & Grafton, 2006) and interprets somatic sensations (Bechara, Tranel, & Damasio, 2000) mediated by internally generated somatosensory representations that simulate how the other person would feel when displaying a certain emotion (Adolphs, 2002a). Without the ability to re-activate emotion-related somatic markers in the orbitofrontal-limbic circuit, behavior lacks planning. Whereas the orbitofrontal cortex and somatosensory cortex correlated positively with social inhibition, they correlated negatively with negative affectivity. The function of the orbitofrontal cortex is complex and dependent on the exact location, and functional asymmetry in emotional processing has been reported earlier (Kringelbach & Rolls, 2004). With fMRI, we can never be sure of the exact time frames of the two networks underlying social inhibition and negative affectivity. It may well be that the decrease in activity as observed in high negative affectivity scorers in a number of (subcortical) regions preceded the increase in cortical regions in participants with higher social inhibition scores.

A number of limitations should be considered when interpreting the results of our study. A limitation of our study is the small sample size which resulted in statistical comparisons which lost most significance when correcting for multiple comparisons. A bigger sample size would have allowed us to investigate the full Type D personality construct in more detail and also differentiate between fear and anger. Further research is needed to link threat related brain activity in different personality traits including the Type D personality trait which is characterized by high negative affectivity *and* high social inhibition. In a follow-up experiment it would be interesting to include participants based on their scores on the DS14 and compare participants that score high on social inhibition and high on negative affectivity with participants that score low on both scales, but also with participants that score extreme on one scale and not on the other. Moreover, further studies need to demonstrate the validity of present findings in clinically relevant samples. One of our participants, whom we excluded from the analyses, reported suffering from ADD. It turned out later, that he misunderstood the task instructions (he pressed a button following each scramble instead of during the presentation of inverted videos). To prevent this from happening again in future studies, we strongly recommend a clinical interview such as the SCID (Structured Clinical Interview for DSM-IV Axis I Disorders) (Gibbon, Spitzer, Williams, Benjamin, & First, 1997) beforehand, and the use of additional questionnaires such as the Beck Depression Inventory (Beck, 2006).

To summarize, the current study investigates the normal variance in negative affectivity and social inhibition scores in healthy participants and relate the between-subject differences to between-subject differences in brain reactivity. This makes clear that subclinical individual when perceiving threat. Altogether, this study demonstrates that negative affectivity and social inhibition are differentially related to emotion-specific brain activation that may be relevant to both physical and mental health. Our results support that the network of brain regions involved in emotion regulation may be relevant to the relationship between medical and psychological disorders. Therefore, their assessment should be considered in neuroimaging studies on emotion regulation and stress reactivity.

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Chapter 6

Sex differences in processing emotions

this chapter is submitted

Abstract

Sex-related functional differences in the brain may be at the heart of the complementary social roles that men and women have in human society. These differences may be one way that evolution has capitalized on the capacity of homologous brain regions to process information differently and shaped our brains to meet the demands of two sexes with unique reproductive and social roles. There are several anatomical, physiological, and biochemical differences between men and women but these differences have so far mostly been ignored in affective neuroscience research. Furthermore, available studies have looked at gender impact as a function of the observer, without paying much attention to the gender of the stimulus and its interaction with that of the observer. This article highlights some of the more important investigations and their implications related to gender differences in emotional processing. The results indicate that it is crucial to take gender differences into account, at least when emotional paradigms are used.

Introduction

Recognizing emotions

Men and women show differences in recognizing facial expressions of emotion. Much of the evidence shows that women are better in identifying various displays of facial affect (Campbell et al., 2002; Collignon et al., 2009; Hall, 1978; Hampson, van Anders, & Mullin, 2006; Miura, 1993; Thayer & Johnsen, 2000). But there is still controversy about the specificity of the female advantage (Derntl, Finkelmeyer et al., 2009; Grimshaw, Bulman-Fleming, & Ngo, 2004; Rahman, Wilson, & Abrahams, 2004). It has been suggested that sex differences in the reaction to face stimuli may be greatest when the intensity of the emotions portrayed is maximal (Wild, Erb, & Bartels, 2001). A recent study advocates that these differences may be explained by different looking patterns of male and female participants on emotional faces. For example, women looked longer at the eyes (Vassallo, Cooper, & Douglas, 2009). That said, women were even more accurate than men under conditions of minimal stimulus information, when the expression was shown for less than 200 ms on a neutral face (Hall & Matsumoto, 2004) but see (Matsumoto et al., 2000).

Other studies suggest that these sex differences depend on the type of emotion. Women are better in recognizing facial expressions of fear and sadness (Mandal & Palchoudhury, 1985; Nowicki & Hartigan, 1988), while men are superior at identifying anger (Mandal & Palchoudhury, 1985; Rotter & Rotter, 1988; Wagner, MacDonalda, & Mansteada, 1986). Note that all the above studies used photographs. In real life, emotional expressions are highly dynamic and researchers recently explored the influence of movement in emotional paradigms. Sex differences have again been observed: in women, dynamic expressions were associated with higher intensity ratings for anger and happiness. In men, dynamics' influence was limited to anger (Biele & Grabowska, 2006).

The results of the studies above favor the possibility of an evolved computational mechanism for emotion recognition. The female advantage may be an evolved adaptation related to the care of preverbal offspring.

Are women more emotional than men?

Common sense views women as more emotional than men. Yet research suggests this presumed difference is based more on an expressive and less on an experiential difference (Dimberg & Lundquist, 1990). Kring and Gordon (1998) assessed the expressive, experiential, and physiological emotional responses of men and women in two studies. In Study 1, participants viewed emotional films. Compared with men, women were more expressive, did not differ in reports of experienced emotion, and showed a different pattern of skin conductance responding. In Study 2, men and women viewed emotional films and completed self-report scales of expressivity, gender role characteristics, and family expressiveness. Results replicated those from Study 1, and gender role characteristics and family expressiveness modulated the relation between sex and expressivity (Kring & Gordon, 1998). Wagner et al (1986) videotaped participants' facial expressions as they watched emotional slides. After each slide, participants nominated the emotion term that best described their affective reaction. Similar nominations of emotion terms were later made by another group who watched the videotaped expressions. Females were found to be better senders than males. Although neither sex was found to be better at receiving facial expressions, female subjects better recognized females' than males' expressions. Females' neutral and surprised expressions were more accurately recognized than those of males (Wagner et al., 1986).

The findings that men feel anger more frequently (Biaggio 1980), that they smile less and are more aggressive than women (Hall 1984) provide further evidence against the idea that women are more emotional than men. Of course, many of these gender differences are socialized in accordance with display rules, prescriptive social norms that dictate how, when and where emotions can be expressed by males and females, at which point stereotypes may take over (Underwood, Coie, & Herbsman, 1992). Moreover, gender differences in emotional expressiveness depend on the context, including for example the presence of other people and social pressure including that of peers. This is illustrated by a study of Fischer et al (2003) in which it was shown that females' responses to advertisements that contain happiness or excitement or sentimentality and warmth were not influenced by social context effects. In contrast, the presence of another male in the viewing environment affected male responses only when the emotional appeal was incongruent with gender stereotypes. Under private viewing conditions, male participants' self-reports were similar to that of females.

Evolution versus culture

In an older study using an interesting relatively bias-free technique, Moore (1966) found that males reported more violent scenes than females during binocular rivalry. One explanation may be that cultural influences socialize males to act more violently than females. While socialization of aggressiveness might involve learning to control and inhibit angry behavior, pressures for this may be stronger on females than on males (Eron & Huesmann, 1984). In contrast, men who display sadness, depression, fear, or dysphoric self-conscious emotions including shame and embarrassment are evaluated more negatively than females (Siegel & Alloy, 1990), and are less likely to be comforted than women (Barbee, Cunningham, Winstead, & Derlega, 1993). On the opposite side, anger and aggression are seen as socially acceptable for men and aggressive boys have been found to be judged as more likable and socially competent than non-aggressive boys (Hart, de Wol & Burts, 1993; Serbin, Marchessault, 1993), whereas this is not the case for girls (Crick, 1997).

On the other hand, sex differences on emotion categorization tasks are noticeable very early in development. In a task which involved choosing a photograph that corresponded to a described emotion, 3.5-year-old girls were as accurate as 5-year-old boys (Boyatzis, Chazan, & Ting, 1993). To examine developmental sex differences in affective processing, Killgore et al (2001) investigated children and adolescents' hemodynamic response while viewing pictures of fearful faces. Males and females differed in the pattern of their amygdala versus prefrontal activation during adolescent maturation. With age, females showed a progressive increase in prefrontal relative to amygdala activation in the left hemisphere, whereas males failed to show a significant age related difference (Killgore, Oki, & Yurgelun-Todd, 2001). McClure et al (2000) reviewed studies on sex differences in facial expression processing from infancy through adolescence and indicate a female advantage (McClure, 2000).

The results suggest that in men anger is an emotion of greater evolutionary significance than happiness whereas this may be the opposite for women. A growing body of research demonstrates gender differences in the neural network involved in processing emotions (Lee et al., 2002). Two observations are a stronger right hemispheric lateralization but also higher activation levels in males as compared to females.

Hemispheric lateralization in affective neuroscience

Some studies suggest that the cerebral activation differences in face processing depend on sex. Killgore et al (2001) observed that happy faces produced greater right than left amygdala activation in males but not females. Both sexes showed greater left amygdala activation following fearful faces (Killgore & Yurgelun-Todd, 2001). Another study examined amygdala responses to fearful faces in men and women. This study also reported significantly different patterns of amygdala responsiveness depending both on the sex of the subjects and on whether the right or left amygdala was being studied (Williams, Barton, Kemp, Liddell, Peduto, Gordon, Bryant, 2005). Kesler-West and associates (Kesler-West et al., 2001) found greater left hemispheric activation in men, but not women, with the presentation of sad faces. Hall et al (2004) observed that the recognition of facial expressions resulted in bilateral frontal activation in women, and unilateral right-sided activation in men (Hall, Witelson, Szechtman, & Nahmias, 2004). A meta analysis of neuroimaging studies on valence, gender and lateralization in functional brain anatomy in emotion concluded that lateralization of emotional activity is complex and region-specific (Wager, Phan, Liberzon, & Taylor, 2003) see also (Wager & Ochsner, 2005). However, more recent studies (predominantly EEG) continue to find sex-related lateralization effects in emotion research.

In an electrophysiological study using a task of judging facial expressions and pictures of infants, Proverbio and colleagues found an asymmetrical activation of the visual cortex in men (with right-hemisphere predominance), and bilateral activity in women (Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006). Gasbarri et al (2007) observed similar sex-related hemispheric lateralization of electrical potentials evoked by arousing negative pictures. Negative pictures elicited more robust P300 effects, as indexed by both amplitude and latency measures, in the left hemisphere in women than in men, yet elicited a stronger P300 component in the right hemisphere in men (Gasbarri et al., 2007).

Some recent fMRI studies provide further insight into the lateralization question. For example, increased functional connectivity with the right amygdala of men and the left amygdala of women has been observed (e.g., Kilpatrick, et al., 2005). In another fMRI study, Fine et al (2009) presented pictures of facial expressions and video vignettes of positive and negative social interactions and also found that males were more lateralized than females (Fine, Semrud-Clikeman, & Zhu, 2009). However, controversy around the lateralization hypothesis remains and a new meta-analysis is required (Schienle, Schafer, Stark, Walter, & Vaitl, 2005).

Higher activation levels in males as compared to females?

Elevated activation of the amygdala in males compared to females following emotional stimuli has been observed consistently. While viewing pictures of attacks by humans or animals, men exhibited greater activation in the bilateral amygdala and the left fusiform gyrus than women (Schienle et al., 2005). Male subjects demonstrated right amygdala activation compared to baseline while observing sad faces which was not present in females. Moreover, in male subjects, signal intensities in the right amygdala increased with intensified subjective experience of sadness. The same could not be confirmed for women and also not for the left amygdala (Schneider et al., 2009). Elevated activation in males versus females has also been observed outside the amygdala. For example, Fine et al (2009) showed greater male than female activation following photos and videos of positive and negative content in a range of frontal and temporal areas, and in the cingulate cortex. Remarkably, there was only one single, small area in the left middle temporal gyrus that showed more activation in females versus males. Kesler-West et al (2001) reported a sex-by-facial expression of emotion-by-hemisphere interaction. Five ROIs were included in the analysis: the fusiform gyrus, inferior frontal gyrus, precentral sulcus, the medial part of the superior frontal gyrus and the superior temporal sulcus. Post hoc comparisons revealed that in men, angry faces elicited more activation than did happy faces in both hemispheres. Sad faces caused more activation than happy ones in the left hemisphere, and angry faces showed more activation than sad faces in the right hemisphere. Women showed no differences between the emotions in either the right or the left hemisphere (Kesler-West et al., 2001). Wrase et al. (2003) reported that men showed more activity than women in the amygdala, inferior frontal gyrus, medial frontal gyrus and fusiform gyrus following exposure to emotional pictures. Again, there were no areas that responded stronger in female than male participants (Wrase et al., 2003). Also Lee et al (2005) observed enhanced activity in male participants during emotion recognition, in the right insula and left thalamus (Lee, Liu, Chan, Fang, & Gao, 2005).

In contrast, Derntl et al (2009) observed that females and males showed equal bilateral amygdala activation following emotional faces but calculation of correlation coefficients for females and males separately revealed a significant association between recognition accuracy and amygdala activation to fearful faces only in the male group (Derntl, Habel et al., 2009). Schneider et al. (2000) observed a significant correlation between mood parameters and amygdala activation during sad mood induction only in the male subjects, while no significant gender difference in mood parameters were found. While viewing fearful versus neutral facial expressions, male but not female observers showed attenuation of tonic arousal across early to late phases of the experiment. By contrast, when amygdala responses to fear perception were averaged across the experiment, females showed a relatively greater extent (area) of amygdala activity than males, but there were no differences in the magnitude of the response (Williams, Barton, Kemp, Liddell, Peduto, Gordon, Bryant, 2005).

Above we discussed male-female differences in brain activity. In the previous section, we shortly discussed differences in connectivity possibly leading to lateralization effects. However, these connectivity differences are not fixed factors and certain male-female differences can only be observed when participants are brought into a stressful state. A recent study shows that acute stress affects face perception in opposite ways for men and women. Mather et al (2010) did not report differences in activity, but specifically focused on the connectivity question. They observed that both in the stress and in the control conditions, women showed greater functional connectivity between the insula and a visual region specialized for face processing (FFA) and the amygdala when viewing angry faces than men did. FFA activity was greater under stress for women but diminished under stress for men, a relationship that was correlated with baseline testosterone but not estrogen levels (Mathera, Lighthalla, Ngaa, & Gorlickb, 2010). These findings are particularly interesting in the light of another recent study by Ino et al (2010). They suggested that the reduced activation of women's brains during processing emotions suggest that the relevant neural systems are more efficiently recruited in women than in men (Ino, Nakai, Azuma, Kimura, & Fukuyama). However, the limited temporal resolution of fMRI may be important to take into account when interpreting these results and moreover, these differences may not always relate to effects of emotion. For example, (Levin et al., 1998) reported that by applying photic stimulation, lower BOLD responses in women than in men were observed. There may be a possible influence of baseline hemoglobin concentration in blood on the BOLD effect. Thus, the lower baseline hemoglobin concentration of women could release a greater and earlier signal increase compared to men to compensate, resulting in an early amygdala response not detected with the temporal resolution of fMRI. Consequently, this limited temporal resolution presumably allowed to map only delayed activation in men.

EEG cannot give us much insight into amygdala activation. But in line with the above described explanation, some EEG studies found enhanced activity in females versus males. Especially when looking at visual areas, women tend to have a larger beta response when observing facial expressions, yet independent of the type of emotion (O2, Guntekin & Basar, 2007; P300, Proverbio et al., 2010). Female subjects have been found to generate significantly longer latency and higher amplitude P450 components than male subjects to both happy and sad faces (Orozco & Ehlers, 1998). Moreover, the N2b component, functionally considered as an attentional orienting mechanism, was delayed in men for happy stimuli as compared with fearful ones in a task in which they had to quickly detect deviant happy or fearful faces amongst a train of neutral ones (Campanella et al., 2004). However, this finding may not be related to facial expressions specifically, since it has also been shown in studies where simple shapes were presented (Guntekin & Basar, 2007). Moreover, Hoffman and Polich (1999) found that males produce smaller P200, P300, and N200 components during a classical odd-ball paradigm.

As indexed by both amplitude and latency measures emotional pictures elicited more robust P300 effects in the left hemisphere in women than in men, while a stronger P300 component was elicited in the right hemisphere in men compared to women. A set of slides was accompanied by a narrative of a simple story – a neutral version and an arousing one. Men, but not women, recalled the arousal version of the story more than the neutral version (Arnone, 2010). There is a broad literature suggesting that sex hormones may play an important role in these processes. We will give a brief overview of these in the next paragraph.

Hormones and the stress response

In males, the fight-or-flight response is characterized by the release of vasopressin. The effects of vasopressin are enhanced by the presence of testosterone and influence the defense behavior of male animals (Taylor et al., 2002). Testosterone level is a good predictor of the presence of aggressive behavior and dominance (van Honk and Schutter, 2007) and amygdala activity to threatening faces in men (Derntl et al., 2009). Testosterone inhibits the release of oxytocin as shown in Jezova et al. (1996; for a discussion, see Taylor et al., 2000). In addition to the increased quantity of oxytocin released in females as compared to males, McCarthy (1995) has found that estrogen enhances the effects of oxytocin. Therefore, oxytocin may be vital in the reduction of the fight-or-flight response in females.

Ovarian hormones play an important role in cognition, emotion and nonverbal behavior (Williams, 1998). Oxytocin has caused relaxation and sedation as well as reduced fearfulness and reduced sensitivity to pain (Uvnas-Moberg, 1997). Moreover, Pearson and Lewis (2005) reported highest accuracy for fear during the late preovulatory phase, when estrogen levels are high, and lowest accuracy during menstruation, when estrogen levels are low (Pearson & Lewis, 2005). Several studies investigating facial emotion processing have indicated that women's ability on this task differs significantly over the course of the hormonal cycle, with better performance found in the late follicular or preovulatory phase, relative to the luteal phase (Derntl et al., 2008; Guapo et al., 2009; Pearson & Lewis, 2005). Derntl et al. (2008) additionally observed a negative correlation of progesterone levels with emotion recognition accuracy. Analysis of error tendencies showed that raised progesterone levels bias behavioral tendencies towards threatening stimuli (Derntl, Kryspin-Exner, Fernbach, Moser, & Habel, 2008). In line with this result, Conway et al. (2007) reported a significant effect of progesterone levels on intensity ratings of disgusted and fearful but not happy faces in healthy female subjects (Conway et al., 2007). Increases in neural activation in the amygdala in response to aversive affective pictures during the early follicular phase (low estrogen) compared with midcycle timing (high estrogen) have been reported (Derntl, Windischberger et al., 2008; Goldstein et al., 2005) as well as following reward-related stimuli (Dreher et al., 2007).

Over human history, women have been mostly responsible for child care. Accordingly, selection pressures for responses to threat that benefit both self and offspring would have been greater for females than for males, favoring social responses to threat in women. Research shows that women are, in fact, more likely to seek the company of others in times of stress, compared to men. Male behavior under stress may be better characterized by the fight or flight response. The effects of circulating sex hormones cannot fully account for all sex differences observed in the human brain, as many sex differences persist even in the absence of these hormones. Yet, although both men and women show the biological fight or flight pattern of arousal (e.g., elevated heart rate and blood pressure), men's behavior under stress is better characterized by fight (aggression) and by flight (social withdrawal, substance abuse) in response to stress (Geary & Flinn, 2002; Taylor et al., 2000).

Gender of the actor

Evidence suggests that pictures of males expressing anger tend to be more effective as conditioned stimuli than pictures of angry females (Ohman & Dimberg, 1978). Marinkovic and Halgren (1998) showed that male faces evoked a larger late negativity than female faces (Marinkovic & Halgren, 1998). Research suggests that especially male participants respond to threatening male cues. For example, behavioural studies indicate enhanced physiological arousal in men but not in women during exposure to angry male as opposed to female faces (Mazurski, Bond, Siddle, & Lovibond, 1996). However, whereas anger posed by males was more accurately perceived than anger posed by females, this was not related to testosterone levels (Goos & Silverman, 2002).

Fischer et al (2004) observed that exposure to angry male as opposed to angry female faces activated the visual cortex and the anterior cingulate gyrus significantly more in men than in women. A similar sex-differential brain activation pattern was present during exposure to fearful but not neutral faces (Fischer, Fransson, Wright, & Backman, 2004). In line with these results, Aleman and Swart (2008) report stronger activation in the superior temporal sulcus in men than women in response to faces denoting interpersonal superiority (Aleman & Swart, 2008). Kret et al (2011) observed that men, as compared to women, showed a higher BOLD response following fearful and angry male bodily expressions in several regions of interest: extrastriate body area, fusiform gyrus, superior temporal sulcus and the premotor and supplementary motor area (Kret, Pichon, Grèzes, & De Gelder, 2011).

These studies suggest a defensive response in men during a confrontation with threatening males. Not surprisingly, aggression in men is often directed towards their own sex. In the evolutionary history, men were more often engaged in aggressive behavior, especially in situations connected with reproduction. Brutal rivalization between males is a part of human evolution and in most cultures men not only commit more violent offences, but also become their victims (Daly & Wilson, 1988). Therefore, it may be especially relevant for men to recognize anger in other men.

Same-versus-opposite sex effects

There is a large literature on the own race bias, the finding that people are better at recognizing faces of people from their own race. Recent studies suggest that there may also be an own gender bias. There is some literature reporting same-versus-opposite sex effects. For example, Armony and Sergerie (2007) found that the left amygdala was more active for successfully remembered female fearful faces in women, whereas in men the right amygdala was more involved in memory for male fearful faces. On the behavioral level, they observed that female participants better remembered fearful female versus male faces whereas female participants did not show enhanced performance for neutral or happy female faces. Male participants remembered all face categories equally but the activation within the right amygdala was associated with stronger activity for successful memory for male, compared to female, fearful faces (Armony & Sergerie, 2007). Fischer et al (2004) found that although men and women rated male and female faces as being equally expressive and although no differences between the participating men and women regarding the degree of expressiveness in the overall ratings were observed, an increased fMRI signal was found in the left amygdala and adjacent anterior temporal regions in men, but not in women, during exposure to faces of the opposite versus the same sex (Fischer, 2004). In an EEG study, Doi et al (2010) observed a late positive component that was larger to neutral but not to happy expressions of own-sex faces than to that of opposite-sex faces. Furthermore, the late positive component amplitude to male neutral expressions was significantly larger in the male viewers than in the female viewers (Doi, Amamoto, Okishige, Kato, & Shinohara, 2010).

Conclusion

In the past decades we have witnessed something like a pendulum swing with interest in gender differences going through alternative phases of stressing and denying these. New research methods including brain imaging and hormone manipulations make it possible to get a closer and closer view of the issues at stake. Taken together, there are strong indications that males and females differ in the recruitment of cerebral networks following female and male emotional expressions. This clearly suggests that in order to generalize findings about the neural correlates of processing emotions, we definitely should consider the gender of the subjects.

The reasons of these functional differences between men and women are numerous. A complete discussion about the many structural differences between the sexes is beyond the scope of this article. But nevertheless, several researchers have reported anatomical differences in limbic areas such as the amygdala and the caudate in male and female children (Durston et al., 2001) as well as in regions of the cingulate, hippocampus, parietal, and occipital regions in adults (Raz et al., 2004). It has also been reported that women have a greater proportion of grey matter, in comparison to men; although brain volume rather than sex may be the main variable in the determination of grey matter volume (Luders et al., 2002). Gur et al. (1999) have also reported a disconnect in the percentages of grey and white matter between the two sexes.

The basis of this sexual dimorphism in brain structure may lie in exposure to androgens by influencing neuronal survival and connections (De Vries et al. 2002; Negri-Cesi et al. 2004). There is evidence to support an endocrine effect upon functional brain activity and brain perfusion. A review of the literature on this issue suggests that estrogen replacement may decrease brain white matter lesions, increase cerebral blood flow, alter regional brain activation patterns during cognitive processing, and have modulatory effects on various neurotransmitter systems. Overall, this points to a functional plasticity in higher order brain processing that can be altered by sex steroids (Smith & Zubieta, 2001).

We already discussed at length the effects of circulating sex hormones in the human brain's response to emotional stimuli. It has been suggested that fetal testosterone comes into prominence when its priming is experimentally activated by testosterone administration in adulthood. More precisely, van Honk et al (2011) showed that a single administration of testosterone in female subjects lead to an impairment in the ability to infer emotions, intentions, and mental states of others. However, the 2D:4D ratio fetal testosterone marker predicted more than 50% of the variance in this effect; i.e., sizable effects of testosterone on cognitive empathy were only seen in subjects who were highly prenatally primed by testosterone (van Honk et al., 2011).

Finally, we must consider the physiological differences involved in the generation of the BOLD signal contrast between females and males. Aforementioned structural differences may influence the BOLD response, as well as regional cerebral blood flow, blood volume, and cerebral metabolic rate of oxygen (Kastrup et al., 1999). Moreover, recent studies investigating simple visual stimulation in males and females have suggested that a greater number of undetectable BOLD signals are present in males versus females (Marcar et al., 2004; Hedera et al., 1998). However, Marcar et al. (2004) conclude that females higher cerebral glucose metabolism is not reflected in the peak of the BOLD signal amplitude. In a similar investigation, Levin et al. (1998) found a decreased BOLD signal response in females during binocular visual stimulation, compared to males. They conclude that this is most likely based on a variety of factors influencing blood flow, volume, and oxygenation and also possibly by the fact that lower levels of hemoglobin are observed in females than in males.

Future studies should further address the issue what it, from an evolutionary perspective and in the current society means that, in emotional tasks, women often show enhanced connectivity between different brain areas and enlarged EEG responses whereas in men enlarged activity in fMRI studies and more lateralized distributions are observed? How do possible differences in baseline activity and hormonal differences influence these differential brain activity patterns? Not much is known about the relationship between connectivity and activity levels (Pietrini, 2011). Another topic currently under debate is whether a larger brain area means it is better connected. Striedter (2005) suggests so: a brain region with more volume has an enhanced ability to modulate processing in its target regions. A full discussion about this issue is beyond the scope of this article. But an open question is whether we should, when looking at male-female differences in brain activity, somehow correct for these differences when comparing the two sexes.

To conclude, many studies observed strong effects of threatening stimuli, ranging from recognition performance effects to enhanced physiological arousal and brain activity in male observers. Research has also shown that males use more physical aggression, especially towards other males. Future studies should further investigate the interaction between gender of the observer and observed in various emotion paradigms.

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Chapter 7

Men fear other men most: gender specific brain activations in perceiving threat from dynamic faces and bodies – an fMRI study

This chapter is based on:

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Abstract

Gender differences are an important factor regulating our daily interactions. Using functional magnetic resonance imaging we show that brain areas involved in processing social signals are activated differently by threatening signals send from male and female facial and bodily expressions and that their activation patterns are different for male and female observers. Male participants pay more attention to the female face as shown by increased amygdala activity. But a host of other areas show selective sensitivity for male observers attending to male threatening bodily expressions (extrastriate body area, superior temporal sulcus, fusiform gyrus, pre-supplementary motor area, and premotor cortex). This is the first study investigating gender differences in processing dynamic female and male facial and bodily expressions and it illustrates the importance of gender differences in affective communication.

Introduction

Facial and bodily expressions are among the most salient affective signals regulating our daily interactions and they have a strong biological basis (de Gelder, 2006, 2010). Therefore it stands to reason that gender figures prominently among factors that determine affective communication. Previous studies have already reported gender differences in how the brain processes facial emotions. But it is not known whether gender differences also influence how emotional expressions of the whole body are processed. It is also unclear whether there is a relation between the gender of the observer and that of the image shown. The goal of this study was to address both issues. We first give a systematic overview of the core areas that underlie the perception of facial and bodily expressions of emotion (Kret et al., 2011) and then outline the implications for gender differences.

The cortical network underlying face perception is well known and includes the fusiform face area (FFA; Kanwisher et al., 1997), the occipital face area (Puce et al., 1996; Gauthier et al., 2000), the superior temporal sulcus (STS) and the amygdala (AMG; Haxby et al., 2000). Recent studies show that the brain areas involved in whole body perception overlap with the face network and confirm the involvement of AMG, fusiform gyrus (FG), and STS in face and body perception (Hadjikhani and de Gelder, 2003; de Gelder et al., 2004; Peelen and Downing, 2007; Meeren et al., 2008; van de Riet et al., 2009; Kret et al., 2011). Two areas in the body perception network have been the targets of categorical selectivity research. The one reported first is an area at the junction of the middle temporal and middle occipital gyrus, labeled the extrastriate body area (EBA; Downing et al., 2001). A later added one is in the FG, at least partly overlapping with FFA (Kanwisher et al., 1997) and termed the fusiform body area (FBA; Peelen and Downing, 2005). Recent evidence suggests that these areas are particularly responsive to bodily expressions of emotion (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008).

Yet so far the relation between categorization by the visual system and emotion perception is not clear. Furthermore, photographs of bodily expressions also trigger areas involved in action perception (de Gelder et al, 2004). Recent studies with dynamic stimuli have proven useful for better understanding the respective contribution of action and emotion-related components. A study by Grosbras and Paus (2006) showed that video clips of angry hands trigger activations that largely overlap with those reported for facial expressions in the FG. Increased responses in the STS and the temporo-parietal junction (TPJ) have been reported for dynamic threatening body expressions (Grèzes et al., 2007; Pichon et al., 2008, 2009). Different studies have demonstrated a role for TPJ in "theory of mind", the ability to represent and reason about mental states, such as thoughts and beliefs (Saxe and Kanwisher, 2003; Samson et al., 2004). Other functions of this area involve reorienting attention to salient stimuli, sense of agency, and multisensory body-related information processing, as well as in the processing of phenomenological and cognitive aspects of the self (Blanke and Arzy, 2005). Whereas TPJ is implicated in higher level social cognitive processing (for a meta-analysis, see Decety and Lamm, 2007), STS has been frequently highlighted in biological motion studies (Allison et al., 2000) and shows specific activity for goal-directed actions and configural and kinematic information from body movements (Perrett et al., 1989; Bonda et al., 1996; Grossman and Blake, 2002; Thompson et al., 2005). Observing threatening actions (as compared to neutral or joyful actions) increases activity in regions involved in action preparation: the pre-supplementary motor area (pre-SMA; de Gelder et al., 2004; Grosbras and Paus, 2006; Grèzes et al., 2007) and premotor cortex (PM; Grosbras and Paus, 2006; Grèzes et al., 2007; Pichon et al., 2008, 2009). To our knowledge, it is still unclear whether these above described regions relate to gender differences.

Common sense intuitions view women as more emotional than men. Yet research suggests this presumed difference is based more on an expressive and less on an experiential difference (Kring and Gordon, 1998). For example, Moore (1966) found that males reported more violent scenes than females during binocular rivalry, possibly because of cultural influences that socialize males to act more violently than females. A growing body of research demonstrates gender differences in the neural network involved in processing emotions (Kemp et al., 2004; Hofer et al., 2006; Dickie and Armony, 2008). Two observations are a stronger right hemispheric lateralization but also higher activation levels in males as compared to females (Killgore and Cupp, 2002; Schienle et al., 2005; Fine et al., 2009).

A different issue is whether how the gender of the person we observe influences our percept, depends on our gender. Evidence suggests that pictures of males expressing anger tend to be more effective as conditioned stimuli than pictures of angry females (Öhman and Dimberg, 1978). Previous behavioral studies indicate enhanced physiological arousal in men but not in women during exposure to angry male as opposed to female faces (Mazurski et al., 1996). Fischer et al. (2004) observed that exposure to angry male as opposed to angry female faces activated the visual cortex and the anterior cingulate gyrus significantly more in men than in women. A similar sex-differential brain activation pattern was present during exposure to fearful but not neutral faces. Aleman and Swart (2008) report stronger activation in the STS in men than women in response to faces denoting interpersonal superiority. These studies suggest a defensive response in men during a confrontation with threatening males.

Evolutionary theorists suggest that ancestral males formed status hierarchies, and that dominant males were more likely to attract females. Men's position within these hierarchies could be challenged, possibly explaining why men use physical aggression more often than females (Bosson et al., 2009). While socialization of aggressiveness might involve learning to control and inhibit angry behavior, pressures for this may be stronger on females than on males (Eron and Huesmann, 1984). Moreover, there are many studies reporting a relationship between high levels of testosterone and increased readiness to respond vigorously and assertively to provocations and threats (Olweus et al., 1988). A physically strong male expressing threat with his body is likely to represent a large threat and may be more relevant for the observer. It is thus conceivable that the perception of and reactivity to emotional expressions depends on the gender of the observer and observed.

Taken together, there are strong indications that males and females differ in the recruitment of cerebral networks following female and male emotional expressions. We tested this hypothesis here by measuring female and male participants' hemodynamic brain activity while they watched videos showing threatening (fearful or angry) or neutral facial or bodily expressions of female or male actors. First, we expected male observers to react more strongly to signals of threat than females. Second, since threatening male body expressions are potentially harmful, we expected the male as compared to female videos to trigger more activation in regions involved in processing affective signals (AMG), body-related information (EBA, FG, STS, and TPJ), and motor preparation (pre-SMA and PM; de Gelder et al., 2010).

Materials and Methods

Participants

Twenty-eight participants (14 females, mean age 19.8 years old, range 18–27 years old; 14 males; mean age: 21.6 years old, range 18–32 years old) took part in the experiment. Half of them viewed neutral and angry expressions and the other half neutral and fearful expressions. Participants had no neurological or psychiatric history, were right-handed and had normal or corrected-to-normal vision. All gave informed consent. The study was performed in accordance to the *Declaration of Helsinki* and was approved by the local medical ethical committee. Two participants were discarded from analysis, due to task miscomprehension and neurological abnormalities.

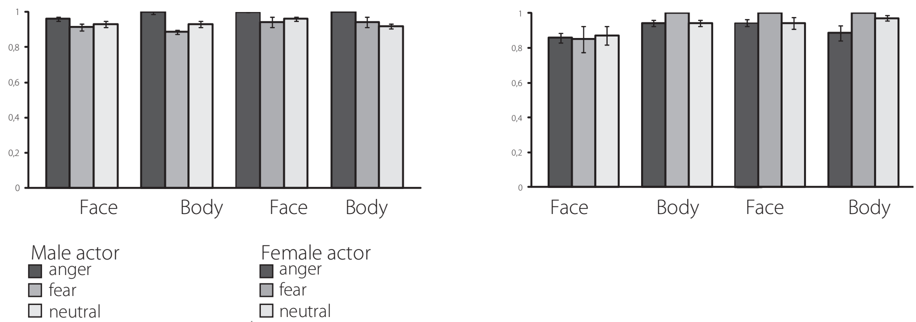
Materials

Video recordings were made of 26 actors expressing six different facial and bodily emotions. For the body video sessions all actors were dressed in black and filmed against a green background. For the facial videos, actors wore a green shirt, similar as the background color. Recordings used a digital video camera under controlled and standardized lighting conditions. To coach the actors to achieve a natural expression, pictures of emotional scenes were, with the help of a projector, shown on the wall in front of them and a short emotion inducing story was read out by the experimenter. The actors were free to act the emotions in a naturalistic way as response on the situation described by the experimenter and were not put under time restrictions. Fearful body movements included stretching the arms as if to protect the upper body while leaning backward. Angry body movements included movements in which the body was slightly bended forward, some actors showed their fists, whereas others stamped their feet and made resolute hand gestures. Additionally, the stimulus set included neutral face and body movements (such as pulling up the nose, coughing, fixing one's hair, or clothes). Distance to the beamer screen was 600 mm. All video clips were computer-edited using Ulead and After Effects, to a uniform length of 2 s (50 frames). The faces of the body videos were masked with Gaussian masks so that only information of the body was perceived. Based on a separate validation study, 10 actors were included in the current experiment. To check for quantitative differences in movement between the movies, we estimated the amount of movement per video clip by quantifying the variation of light intensity (luminance) between pairs of frames for each pixel (Peelen et al., 2007). For each frame, these absolute differences were averaged across pixels that scored (on a scale reaching a maximum of 255) higher than 10, a value which corresponds to the noise level of the camera. These were then averaged for each movie. Angry and fearful expressions contained equal movement (M = 30.64, SD 11.99 versus M = 25.41, SD 8.71) [$t(19)$ = 0.776, ns] but more movement than neutral expressions (M = 10.17, SD 6.00) [$t(19) = 3.78$, $p < 0.005$] and [$t(19) = 4.093$, $p < 0.005$]. Threatening male and female video clips did not differ in the amount of movement (M = 31.48, SD 10.89 versus M = 29.16, SD 11.05) [$t(19) = 2.07$, ns] and neutral male versus female videos were also equal in terms of movement (M = 26.70, SD 9.68 versus M = 24.11, SD 7.92) [$t(9) = 1.26$, ns]. In addition, we generated scrambled movies by applying a Fourier-based algorithm onto each movie. This technique scrambles the phase spectra of each movies' frames and allows to generate video clips served as low level visual controls and prevents habituation.

Figure 1. Recognition rates per condition and gender of the observer-validation afterward.

a) Female participants

b) Male participants



a) Mean recognition rate across conditions in the female observers.
b) Mean recognition rate across conditions in the male observers. There were no significant differences between accuracy rates for male or female participants and neither between the recognition of male or female actors.

For a full description of the validation, see Kret et al. (2011). Importantly, in order to ascertain that the participants of our study could also recognize the emotional expressions they had seen in the scanner, they completed a small validation study shortly after the scanning session. They were guided to a quiet room where they were seated in front of a computer and categorized the non-scrambled stimuli they had previously seen in the scanner. They were instructed to wait with their response until the end of the video when a question mark appeared in the middle of the screen and were then required to respond as accurate as possible. Two emotion labels were pasted on two keys of the computer keyboard and participants could either choose between a neutral and angry label or between a neutral and fearful label. There were three practice trials included with emotions from different actors than the ones used in the experiment. A trial started with a central fixation cross (800 ms) after which the video was presented (2 s) which was followed by a blank screen with a central question mark, with a duration of 1–3 s. Main and interaction effects were tested in SPSS in an ANOVA with three within-subject variables, [emotion (threat and neutral), category (face and body), gender of actor (female and male)] and one between subject variable, [gender of observer (female and male)]. One male participant pressed the same button for all stimuli and was excluded from analysis. There were no main or interaction effects. See Table 1.

Table 1. Experimental design.

Version 1. Anger – Neutral (N = 14)								
Run 1								
		Non-scrambled		Scrambled		Oddball*		Blank screen
		Anger	Neutral	Anger	Neutral	Anger	Neutral	80
Faces	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
Bodies	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
total		40	40	40	40	8	8	
Run 2								
		Non-scrambled		Scrambled		Oddball		Blank screen
		Anger	Neutral	Anger	Neutral	Anger	Neutral	80
Faces	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
Bodies	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
total		40	40	40	40	8	8	
Version 2. Fear – Neutral (N = 14)								
Run 1								
		Non-scrambled		Scrambled		Oddball		Blank screen
		Fear	Neutral	Fear	Neutral	Fear	Neutral	80
Faces	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
Bodies	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
total		40	40	40	40	8	8	
Run 2								
		Non-scrambled		Scrambled		Oddball		Blank screen
		Fear	Neutral	Fear	Neutral	Fear	Neutral	80
Faces	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
Bodies	Male	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
	Female	5 * 2	5 * 2	5 * 2	5 * 2	2	2	
total		40	40	40	40	8	8	

*The oddball condition consisted videos that were presented upside down. 5*2: 5 unique identities that were presented twice. All stimuli were presented in random order.*

Experimental Design

The experiment consisted of 176 trials {80 non-scrambled [10 actors (five males) * two expressions (threat, neutral) * two categories * two repetitions] and 80 scrambled videos and 16 oddballs (inverted videos)] which were presented in two runs. There were 80 null events (blank, green screen) with a duration of 2000 ms. These 176 stimuli and 80 null events were randomized within each run (see Table 1). A trial started with a fixation cross (500 ms), followed by a video

(2000 ms) and a blank screen (2450 ms). An oddball task was used to control for attention and required participants to press a button each time an inverted video appeared so that trials of interest were uncontaminated by motor responses. Stimuli were back-projected onto a screen positioned behind the subject's head and viewed through a mirror attached to the head coil. Stimuli were centered on the display screen and subtended 11.4° of visual angle vertically for the body stimuli, and 7.9° of visual angle vertically for the face stimuli.

Procedure

Participants' head movements were minimized by an adjustable padded head-holder. Responses were recorded by a keypad, positioned on the right side of the participant's abdomen. After the two experimental runs, participants were given a functional localizer. Stimulus presentation was controlled by using Presentation software (Neurobehavioral Systems, San Francisco, CA, USA). After the scanning session participants were given a 10-min break. They were then guided to a quiet room where they were seated in front of a computer and categorized the non-scrambled stimuli they had previously seen in the scanner.

fMRI Data Acquisition

Parameters of the functional scans

Functional images were acquired using a 3.0-T Magnetom scanner (Siemens, Erlangen, Germany). Blood oxygenation level dependent (BOLD) sensitive functional images were acquired using a gradient echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, 32 transversal slices, descending interleaved acquisition, 3.5 mm slice thickness, with no interslice gap, FA = 90°, FOV = 224 mm, matrix size = 64 mm × 64 mm). An automatic shimming procedure was performed before each scanning session. A total of 644 functional volumes were collected for each participant [total scan time = 10 min per run (two runs with the anatomical scan in between)].
The localizer scan parameters were: TR = 2000 ms, TE = 30 ms, FA = 90°, 28 slices, matrix size = 256 mm × 256 mm, FOV = 256 mm, slice thickness = 2 mm (no gap), number of volumes = 328 (total scan time = 11 min).

Parameters of the structural scan

A high-resolution T1-weighted anatomical scan was acquired for each participant (TR = 2250 ms, TE = 2.6 ms, FA = 9°, 192 sagittal slices, voxel size 1 × 1 × 1 mm, Inversion Time (TI) = 900 ms, FOV = 256 mm × 256 mm, 192 slices, slice thickness = 1 mm, no gap, total scan time = 8 min).

Statistical Parametric Mapping

Functional images were processed using SPM2 software (Wellcome Department of Imaging Neuroscience)[1]. The first five volumes of each functional run were discarded to allow for T1 equilibration effects. The remaining 639 functional images were reoriented to the anterior/posterior commissures plane, slice time corrected to the middle slice and spatially realigned to the first volume, subsampled at an isotropic voxel size of 2 mm, normalized to the standard MNI space using the EPI reference brain and spatially smoothed with a 6 mm full width at half maximum (FWHM) isotropic Gaussian kernel. Statistical analysis was carried out using the general linear model framework (Friston et al., 1995) implemented in SPM2.

At the first level analysis, eight effects of interest were modeled: face threat (fear or anger, depending on the version of the experiment) female, face neutral female, body threat female, body neutral female, face threat male, face neutral male, body threat male, body neutral male. Null events were modeled implicitly. The BOLD response to the stimulus onset for each event type was convolved with the canonical hemodynamic response function over a duration of 2000 ms. For each subject's session, six covariates were included in order to capture residual movement-related artifacts (three rigid-body translations and three rotations determined from initial spatial registration), and a single covariate representing the mean (constant) over scans. To remove low frequency drifts from the data, we applied a high-pass filter using a cut-off frequency of 1/128 Hz. Statistical maps were overlaid on the SPM's single subject brain compliant with MNI space, i.e., Colin27 (Holmes et al., 1998) in the anatomy toolbox[2] (see Eickhoff et al., 2005 for a description). The atlas of Duvernoy was used for macroscopical labeling (Duvernoy, 1999).

The beta values of the ROIs (see next paragraph) were extracted for the following conditions: face threat male and female, body threat male and female, face neutral male and female, and body neutral male and female. The reason for combining two studies into one analysis was because the overall pattern of responses to these two types of threat stimuli was similar. Since there were almost no differences across the two hemispheric ROIs and our interest does not concern hemispheric lateralization, we pool bilateral ROIs to reduce the total number of areas. Main and interaction effects were tested in SPSS in an ANOVA with three within-subject variables [emotion (threat and neutral), category (face and body), gender of actor (female and male)] and one between subject variable (gender of observer) and were further investigated with Bonferroni-corrected paired comparisons and Bonferroni-corrected two-tailed *t*-tests.

Localization of Face- and Body-Sensitive Regions

Face- and body-sensitive voxels in EBA, FG, STS, and AMG were identified using a separate localizer scan session in which participants performed a one backward task on face, body, house, and tool stimuli. The localizer consisted of 20 blocks of 12 trials of faces, bodies (neutral expressions, 10 male, and 10 female actors), objects, and houses (20 tools and 20 houses). Body pictures were selected from our large database of body expressions and we only included the stimuli that were recognized as being absolutely neutral. To read more about the validation procedure, we refer the reader to the article of van de Riet et al. (2009). The tools (for example pincers, a hairdryer etc.) and houses were selected from the Internet. All pictures were equal in size and were presented in grayscale on a gray background. Stimuli were presented in a randomized blocked design and were presented for 800 ms with an ISI of 600 ms.

Preprocessing was similar to the main experiment. At the first level analysis, four effects of interest were modeled: faces, bodies, houses, and tools. For each subject's session, six covariates were included in order to capture residual movement-related artifacts (three rigid-body translations and three rotations determined from initial spatial registration), and a single covariate representing the mean (constant) over scans. To remove low frequency drifts from the data, we applied a high-pass filter using a cut-off frequency of 1/128 Hz. We smoothed the images of parameter estimates of the contrasts of interest with a 6-mm FWHM isotropic Gaussian kernel. At the group level, the following *t*-tests were performed: face > house, body > house, and subsequently a conjunction analysis [body > house AND face > house]. The resulting images were thresholded liberal ($p < 0.05$, uncorrected) to identify the following face- and body-sensitive regions: FG, AMG, STS, EBA (see Table 2). ROIs were defined using a sphere with a radius of 5 mm centered onto the group peak activation. All chosen areas appeared in the whole brain analysis (faces and bodies versus scrambles) and are well known to process facial and bodily expressions (de Gelder, 2006; de Gelder and Hadjikhani, 2006; Grèzes et al., 2007; Meeren et al., 2008; Pichon et al., 2008, 2009; van de Riet et al., 2009; for a recent review, see de Gelder et al., 2010). We were also interested to investigate gender differences in TPJ (Van Overwalle and Baetens, 2009), which is involved in higher social cognition and pre-SMA and the PM that are involved in the preparation of movement and environmentally triggered actions (Hoshi and Tanji, 2004; Nachev et al., 2008). These three areas could not be located with our localizer. However, since there are arguments against using the same data set of the main experiment for the localization of specific areas (Kriegeskorte et al., 2009), we defined TPJ, PM, and pre-SMA by using coordinates from our former studies (Grèzes et al., 2007; Pichon et al., 2008, 2009). In Kret et al. (2011), we revealed that FG was equally responsive to emotional faces and bodies, and therefore we chose to pool FFA and FBA. Also, our localizer showed a considerable overlap between the two areas and our whole brain analysis on the main experiment revealed that the FG as a whole responded much more to dynamic bodies than to dynamic faces.

Table 2. Coordinates used to create regions of interest.

Hemi-sphere	Anatomical region	x	y	z	Reference	Contrast
R	Fusiform face/body area	42	-46	-22	localizer	
L		-42	-46	-22	»	[body > house AND face > house]
R	Amygdala	18	-4	-16	localizer	face > house
L		-18	-8	-20	localizer	face > house
R	Superior temporal sulcus	54	-52	18	localizer	
L		-54	-52	18	»	[body > house AND face > house]
R	Extrastriate body area	52	-70	-2	localizer	body > house
L		-50	-76	6	localizer	body > house
R	Temporo-parietal junction	62	-40	26	1+2+3	
L		-60	-40	24	2+3	
R	Premotor cortex	42	2	44	2	
L		-46	10	54	2	
R	Pre-supplementary motor area	8	18	66	1	
L		-8	18	66	»	

** average coordinate :*

1. *Grèzes et al., 2007 (fear body > neutral body)* — *R = right*
2. *Pichon et al., 2008 (anger body > neutral body)* — *L = left*
3. *Pichon et al., 2009 [anger body AND fear body]* — *» coordinate was taken from the other hemisphere*

The localization of functional regions may differ between participants and there are arguments to define a fROI per participant and not base its location on the group level. However, the fROIs that we chose are very different from one another in terms of the location but also of the activity level and specific function. We opted for the group level for a number of reasons. First, group localization may be preferable for testing the behavior of a functional ROI if the region is small or if the criteria response is weak (for example in case of the AMG; Downing et al., 2001). Second, not all the ROIs were detectable in each participant. Localization at the individual level risks that one fails to identify an ROI in some individuals. Third, participants often show multiple peaks in one area and it is sometimes arbitrary to decide which one to take if the stronger peak lies further away from the group peak than the weaker peak. Fourth, not all our fROIs were easy to localize with our localizer and we therefore for some areas use a coordinate from the literature (see Table 2). Our definition of the ROIs has the advantage that their anatomy is easy to report. In tables, we specify exactly around which peak the sphere was drawn which may be meaningful for meta-analyses.

Results

In order to examine gender differences in face and body responsive areas, we specified the *gender of the actors and observers* by extracting the beta values of pre-defined ROIs. We checked the patterns of both fear and anger to ensure that both factors contributed the same way to the common effects that are reported below (See Figure 3).

1. *Extrastriate body area* showed a main effect of emotion ($F(1,24) = 44.597$, $p < 0.001$) and category ($F(1,24) = 147.764$, $p < 0.001$) and was more active for threatening versus neutral and for bodily versus facial expressions ($p < 0.001$). An *interaction between actor and emotion* was found ($F(1,24) = 4.706$, $p < 0.05$). Both male and female actors induced more activity when expressing threatening versus neutral emotions (female actors: $t(25) = 4.206$, $p < 0.001$; male actors: $t(25) = 6.412$, $p < 0.001$). Since we expected more brain activity in response to threatening male than threatening female actors, we conducted two planned comparison *t*-tests. First, we compared the difference between threatening and neutral expressions in male actors versus female actors and found a significant difference ($t(25) = 2.216$, $p < 0.05$, one-tailed). Second, to ascertain that the interaction was mainly driven by male threat, we compared threatening male versus threatening female expressions, which yielded a difference ($t(25) = 1.760$, $p < 0.05$, one-tailed). EBA showed an *interaction between category and emotion* ($F(1,24) = 8.775$, $p < 0.01$). Faces and bodies induced more activity when expressing a threatening versus neutral emotion (faces: $t(25) = 3.362$, $p < 0.05$; bodies: $t(25) = 6.349$, $p < 0.001$) yet this difference was larger in bodies versus faces ($t(25) = 11.501$, $p < 0.001$). An *interaction between category, emotion, and observer* was found ($F(1,24) = 9.499$, $p < 0.005$). Male observers showed more activity for threatening than neutral bodies ($t(11) = 7.481$, $p < 0.001$), threatening bodies than faces ($t(11) = 8.662$, $p < 0.001$), and neutral bodies than faces ($t(11) = 7.661$, $p < 0.001$). Female observers showed more activity for threatening than neutral faces ($t(13) = 3.987$, $p < 0.05$), threatening bodies than faces ($t(13)$

= 7.688, $p < 0.001$), and neutral bodies than faces ($t(13) = 8.353$, $p < 0.001$). The interaction was partly driven by female observers' enhanced activity for threatening versus neutral faces but this difference was not significantly larger in female than male observers ($p = 0.227$).

Since we expected more brain activity in response to threatening male body expressions in male observers, we conducted two planned comparisons. First, we compared male observers response to threatening versus neutral male body expressions ($t(11) = 5.601$, $p < 0.001$, one-tailed). Second, we expected this difference to be larger in male than female observers and therefore we compared the difference between threatening minus neutral male body expressions between male and female observers which yielded a difference ($t(24) = 1.716$, $p < 0.05$, one-tailed).

In summary, EBA not only processes bodies but is also sensitive to emotion. Moreover, highest activity was observed in male participants while watching threatening male body expressions.

2. *Fusiform gyrus* showed a main effect of emotion ($F(1,24) = 10.430$, $p < 0.005$) and was more active for threatening than neutral expressions ($p < 0.005$). There was an *interaction between category, emotion, and observer* ($F(1,24) = 4.695$, $p < 0.05$). Male observers showed more activity for threatening than neutral bodies ($t(11) = 5.106$, $p < 0.001$).

Since we expected more brain activity in response to threatening male body expressions in male observers, we conducted two planned comparisons. First, we compared male observers response to threatening versus neutral male body expressions ($t(11) = 3.054$, $p < 0.05$, one-tailed). Second, we expected this difference to be larger in male than female observers and therefore we compared the difference between threatening minus neutral male body expressions between male and female observers which yielded a difference ($t(24) = 1.835$, $p < 0.05$, one-tailed).

Fusiform gyrus was responsive to emotional expressions from faces and bodies and most responsive to threatening male bodies in male observers.

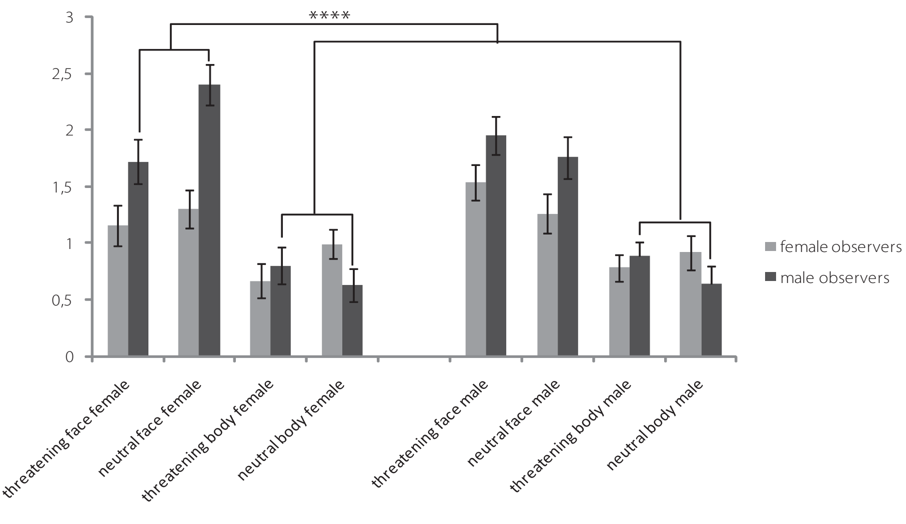
3. *Superior temporal sulcus* showed main effects of emotion ($F(1,24) = 21.191$, $p < 0.001$) and category ($F(1,24) = 6.846$, $p < 0.05$) and was more active for bodies than faces ($p < 0.05$) and for emotional than neutral videos ($p < 0.001$). An *interaction between emotion and category* was observed ($F(1,24) = 10.799$, $p < 0.005$). Whereas STS did not differentially respond to emotional versus neutral faces ($p = 0.371$), activity was higher for emotional versus neutral bodies ($t(25) = 4.571$, $p < 0.005$). The *gender of the actor interacted with emotion* ($F(1,24) = 7.632$, $p < 0.05$). STS was more active following male threatening than neutral expressions ($t(25) = 4.669$, $p < 0.001$) and threatening male versus female stimuli ($t(25) = 2.881$, $p < 0.05$). An *interaction between category, emotion, and observer* was observed ($F(1,24) = 6.498$, $p < 0.05$). Male observers showed more activity for threatening versus neutral bodies ($t(11) = 5.536$, $p < 0.001$) threatening bodies versus faces ($t(11) = 4.178$, $p < 0.05$) and females did not ($p = 0.420$; $p = 0.882$). The interaction was partly driven by female observers' enhanced activity for threatening versus neutral faces but this was not significantly different ($p = 0.230$). The difference between threatening versus neutral faces was not significantly larger in female versus male observers ($p = 0.810$).

Since we expected more brain activity in response to threatening male body expressions in male observers, we conducted two planned comparisons. First, we compared male observers response to threatening versus neutral male body expressions ($t(11) = 4.251$, $p < 0.001$, one-tailed). Second, we expected this difference to be larger in male than female observers and therefore we compared the difference between threatening minus neutral male body expressions between male and female observers which yielded a marginally significant difference ($t(24) = 1.454$, $p = 0.079$, one-tailed).

Similar to EBA and FG, STS was responsive to emotional expressions from faces and bodies and was most responsive to threatening male bodies in male observers.

4. *Amygdala* showed a main effect of category ($F(1,24) = 22.402$, $p < 0.001$) andwas more active for faces than bodies ($p < 0.001$). An *interaction between category and observer* was found ($F(1,24) = 4.325$, $p < 0.05$). Male observers only showed more activity for faces than bodies (male observers: $t(11) = 4.914$, $p < 0.001$ female observers: $p = 0.294$). Inspecting the graph (see Figure 2) gives more insight into this effect. The enhanced response in the male observers for facial expressions, was only significant in case of female faces (female faces versus all bodies $t(11) = 5.185$, $p < 0.001$); male faces ($p = 0.813$). In contrast to our expectations, and in contrast to the activity pattern in the regions described above as well as with TPJ, the AMG was not more responsive to emotional than neutral stimuli but showed enhanced activity for faces, in particular in the male observers, but only when they observed female faces.

Figure 2. The amygdala.



The amygdala showed more activity for faces than bodies as was shown by a main effect. However, an interaction between category and observer revealed that this increased activity for faces was specific to male observers. Although there was no interaction with gender of the actor, the enhanced response in the male observers for facial expressions, was only valid in case of female faces. The amygdala was not more responsive to emotional than neutral stimuli but showed enhanced activity for faces, in particular in the male observers, especially when they observed female faces.

5. *Temporo-parietal junction* showed a main effect of category ($F(1,24) = 16.227$, $p < 0.001$) and emotion ($F(1,24) = 4.374$, $p < 0.05$) and was more active for threatening than neutral expressions ($p < 0.05$) and for bodies than faces ($p < 0.001$). There was an *interaction between gender of the actor and observer* ($F(1,24) = 4.351$, $p < 0.05$). Follow-up comparisons did not yield any significant effects.

6. *Premotor cortex* showed a main effect of category ($F(1,24) = 4.670$, $p < 0.05$) and responded more to bodies than to faces ($p < 0.05$). There was an *interaction between gender of the actor and emotion* ($F(1,24) = 5.764$, $p < 0.05$) but follow-up *t*-tests did not yield significant differences. Since we expected more brain activity in response to threatening male than threatening female actors, we conducted two planned comparison *t*-tests. First, we compared the difference between threatening and neutral expressions in male actors versus female actors and found a marginally significant difference ($t(25) = 1.514$, $p = 0.07$, one-tailed). Second, to ascertain that the interaction was mainly driven by male threat, we compared threatening male versus threatening female expressions, which yielded a difference ($t(25) = 1.720$, $p < 0.05$, one-tailed). Moreover, an *interaction between gender of the actor and gender of the observer* was found ($F(1,24) = 4.670$, $p < 0.05$) but follow-up *t*-tests did not yield significant differences. Since we expected more brain activity in response to threatening male body expressions in male observers, we conducted two planned comparisons. First, we compared the difference in brain activity between threatening minus neutral male body expressions versus this difference for female actors which yielded a significant difference in the male observers ($t(11) = 1.853$, $p < 0.05$, one-tailed). Second, we compared the difference between threatening minus neutral male body expressions in male versus female observers which yielded a difference ($t(24) = 1.827$, $p < 0.05$, one-tailed).

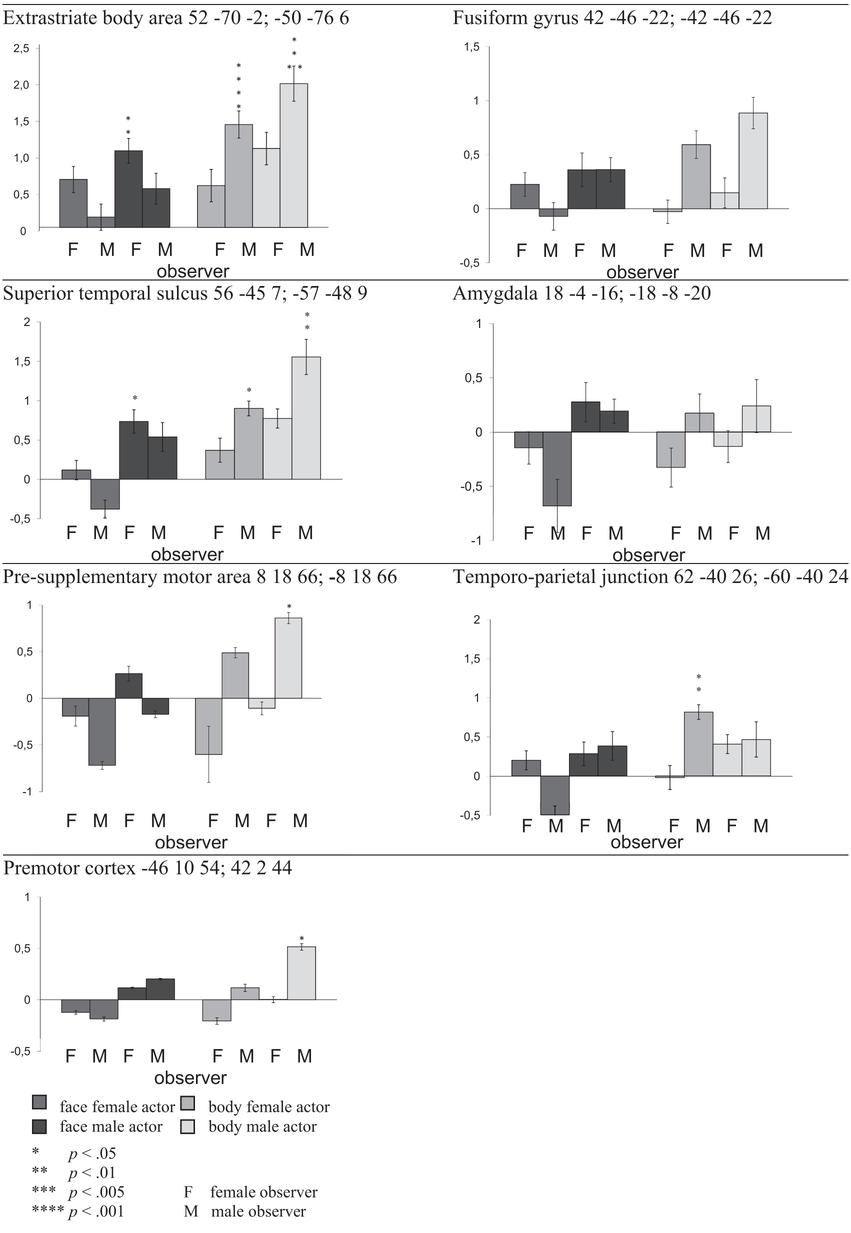
Even though there was no significant interaction between category, observer and emotion, the activity pattern looks very similar to EBA, FG, and STS and again, responds mostly to male threatening body expressions in male observers.

7. *Pre-supplementary motor area* showed a main effect of gender ($F(1,24) = 9.215$, $p < 0.01$) and responded more to male than female expressions ($p < 0.01$). There was an *interaction between gender of the actor and emotion* ($F(1,24) = 6.438$, $p < 0.05$). Pre-SMA was more responsive to threatening expressions from males than females ($t(25) = 3.555$, $p < 0.05$). Moreover, an *interaction between gender of the actor and gender of the observer* was found ($F(1,24) = 6.157$, $p < 0.05$). Although female observers were equally responsive as male observers, they showed more activity for male versus female actors, irrespective of emotion ($t(25) = 3.982$, $p < 0.05$). There was an interaction between *category * emotion * gender of the observer* ($F(1,24) = 6.239$, $p < 0.05$). In contrast to females, male observers were more responding to threatening than neutral bodies (female observer: ($p = 0.236$) male observer: $t(11) = 4.170$, $p < 0.05$).

Further analysis revealed that this effect in male observers was derived from threatening male versus neutral male bodies $t(11) = 3.130$, $p < 0.005$, one-tailed). We expected this difference to be larger in male than female observers and consequently compared the difference between threatening minus neutral male body expressions between male and female observers which yielded a significant difference ($t(24) = 1.944$, $p < 0.05$, one-tailed).

Pre-supplementary motor area responded mostly to male threatening body expressions in male observers.

Figure 3. Threatening facial and bodily expressions as a function of gender.



Difference scores between threatening and neutral videos. t-Tests are two-tailed, Bonferroni-corrected. Planned comparisons are described in the text and are not indicated in this figure. Regions are followed by the MNI coordinate. EBA, STS, pre-SMA, and PM were active following bodily expressions, especially when threatening, even more so when expressed by a male actor and above all when observed by a male participant. FG was equally responsive to faces and bodies but the interaction between category, emotion, and observer revealed more activation for threatening than neutral male bodies in male participants. AMG was more active for faces than bodies, specifically for male observers watching female faces. TPJ showed an effect of emotion and was more responsive to bodies than faces.

Discussion

Previous studies showed gender differences in how the brain processes facial emotions. The present study has three innovative aspects. First, we used facial expressions but also whole body images. Second, all stimuli consisted of video clips. Third, we investigated the role of the gender of the observer as well as that of the stimulus displays.

Overall, we found a higher BOLD response in STS, EBA, and pre-SMA when participants observed male versus female actors expressing threat. But interestingly, in these regions, as well as in FG, there was an interaction between category, emotion, and observer. There was more activation for male threatening versus neutral body stimuli in the male participants. Threatening bodies and not faces triggered highest activity in STS, especially in the male participants.

Whereas male observers responded more to threatening body expressions than females did, the opposite tendency was observed in the EBA for female observers. Females were not more responsive to faces than males, but the difference in brain activity following a threatening versus neutral face was significant in this region in female observers only. However, this difference score between threatening minus neutral faces was not significantly larger in female than in male observers. So, the three-way interaction between category, emotion, and observer in EBA was mainly driven by male observers' response to threatening body expressions. Ishizu et al. (2009) found that males showed a greater response in EBA than females when imagining hand movement. Our male subjects possibly imagined themselves reacting to the threatening male actor more than females did. Alternatively, there was an automatic, increased response to threatening body expressions (Tamietto and de Gelder, 2010). This latter explanation is plausible because the male observers additionally showed a clear motor preparation response in the PM and the pre-SMA toward threatening male body expressions.

Our results are similar to previous studies that show male observers to be more reactive to threatening signals than female observers (Aleman and Swart, 2008; Fine et al., 2009). Hess et al. (2004) finds that facial cues linked to perceived dominance (square jaw, heavy eyebrows, high forehead) are more typical for men, who are generally perceived as more dominant than women. So far, nothing is known about bodily cues and perceived dominance in humans but the physical differences between men and women may be important for interpreting our results. If there is a significant difference in power or status between men and women, then threat from an anger expression can elicit different responses depending on the status or power of the angry person.

The AMG was more active for facial than bodily expressions, independent of emotion. This effect was specifically for male observers watching female faces. This is consistent with earlier findings. Fischer et al. (2004) reported an increased response in the left AMG and adjacent anterior temporal regions in men, but not in women, during exposure to faces of the opposite versus the same sex. Moreover, AMG activity in male observers was increased for viewing female faces with relatively large pupils indicating an index of interest (Demos et al., 2008). Possibly, female faces provide more information to relevant males than male faces, whereas the distinction at the level of the face between male and female faces is less important for female observers. Other studies have reported that the AMG is face but not emotion specific (Van der Gaag et al., 2007; see Kret et al., 2011 for further discussion). But the striking fact here is that all the other areas that reflect sensitivity of the male observers are emotion sensitive, in contrast with the AMG results. This disjunction between AMG face-gender and STS, EBA, PM, pre-SMA gender–emotion sensitivity indicates that the AMG indeed plays a different role than being at the service of emotion encoding and fits with the notion that it encodes salience and modulates recognition and social judgment (Tsuchiya et al., 2009).

In our study males showed a clear motor preparation response to threatening male body language, and females did not. In males, the fight-or-flight response is characterized by the release of vasopressin. The effects of vasopressin are enhanced by the presence of testosterone and influence the defense behavior of male animals (Taylor et al., 2002). Testosterone level is a good predictor of the presence of aggressive behavior and dominance (van Honk and Schutter, 2007) and AMG activity to angry but also to fearful faces in men (Derntl et al., 2009). In contrast, oxytocin has caused relaxation and sedation as well as reduced fearfulness and reduced sensitivity to pain (Uvnas-Moberg, 1997). Testosterone inhibits the release of oxytocin as shown in Jezova et al. (1996; for a discussion, see Taylor et al., 2000). In addition to the increased quantity of oxytocin released in females as compared to males, McCarthy (1995) has found that estrogen enhances the effects of oxytocin. Therefore, oxytocin may be vital in the reduction of the fight-or-flight response in females. Although we cannot report any measure that could support such an interpretation, it is well known that the endocrine system plays an important role in modulating behavior. Comparing the levels of these hormones with specific neuronal responses may give more insight in these gender effects.

Conclusion

Increased activation in FG, STS, EBA, PM, and pre-SMA was observed for threatening versus neutral male body stimuli in male participants. AMG was more active for facial than bodily expressions, independent of emotion, yet specifically for male observers watching female faces. Human emotion perception depends to an important extent on whether the stimulus is a face or a body and whether observers and observed are male or female. These factors that have not been at the forefront of emotion research are nevertheless important for human emotion theories.

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Chapter 8

Violent offenders are impaired in recognizing emotional face and body expressions

This chapter is submitted

Abstract

Previous reports have suggested impairment in facial expression recognition in violent offenders. So far, it is unknown whether these findings extend to other nonverbal cues such as bodily expressions of emotion and whether they are still impaired when these expressions are placed in a context. Our goal was to test how aggressive males perceive aggressive body expressions from other males and whether they are more distracted by task irrelevant threatening cues. We used direct and indirect emotion recognition tasks and tested 29 aggressive incarcerated offenders and 31 control participants, matched on age, education level and cultural background. Violent offenders performed similarly to controls on matching either facial or bodily expressions of emotion. But in contrast to the controls, offenders often misinterpreted dynamic fearful body expressions as angry. This bias toward interpreting emotions as hostile angry expressions was clear in the indirect tasks. Violent offenders were impaired in recognizing a happy facial expression when the body showed a different, threatening expression (fear or anger). Moreover, they had great difficulty in categorizing the happy body expression of a target figure when it was presented against the background of a violent scene. These results indicate that one of the underpinnings of aggression and violent offences may be impaired recognition of emotional expressions, with a specific bias toward interpreting emotions as hostile angry expressions, especially when a threatening context was provided.

Introduction

In everyday life, we are continuously confronted with other people. One of the most important sources of social information is facial expressions: we spend a great deal of time looking at and analyzing faces. People often use the information communicated by emotional facial expressions as cues for modulating social behaviors (Frijda, 1986). In particular, the recognition of others' facial expressions has been shown to modulate aggressive behaviors (Savitsky, Izard, Kotsch, & Christy, 1974). However, bodily expressions are just as well recognized as facial expressions, they can be seen from a distance and are, from an evolutionary perspective, much older than facial expressions. Body language, therefore, has a high communicative role, albeit we are less aware of it (de Gelder, Van den Stock, Meeren, Sinke, Kret & Tamietto, 2010). So far, it is not known whether there is a relation between the ability to recognize bodily expressions of emotion and aggressive behavior.

Previous research suggests that there may be a relationship between facial expression recognition and conduct problems involving aggression (Blair, 2003). McCown et al. (1986) investigated the recognition of the six basic emotions among incarcerated juvenile delinquents. They found that, compared with control participants, the delinquents were less accurate in the recognition of facial expressions of disgust, sadness, and surprise. On the other hand, Cadesky et al. (2000) investigated the recognition of facial and vocal expressions of anger, fear, happiness, and sadness in children with conduct problems. They reported that these children were impaired in the recognition of fear, happiness, and sadness and tended to mislabel other emotions as anger. Sato Uono, Matsuura, and Toichi (2009) compared the performance of adolescent/young adult delinquents incarcerated in correctional facilities with those of age- and gender-matched control participants. Using photographs of facial expressions illustrating six basic emotions, participants matched each emotional facial expression with an appropriate verbal label. The findings revealed that delinquents were less accurate in the recognition of facial expressions that conveyed disgust than were control participants. The delinquents misrecognized this expression as anger more frequently than did controls (Sato et al., 2009). Impairments in processing emotions among personality disordered or psychopathic offenders have also been widely reported (see (Marsh & Blair, 2008) for a meta-analysis). Although the previous studies have consistently indicated the impairment of facial expression recognition in delinquents, it remains unclear whether these findings may generalize to whole body expressions of emotion.

In our natural world, a face is usually not encountered as an isolated object but as an integrated part of a whole body situated in a scene. Knowledge of the social situation (Carroll & Russell, 1996), body postures (Aviezer et al., 2009; Meeren, van Heijnsbergen, & de Gelder, 2005; Van den Stock, Righart, & de Gelder, 2007), voices (B. de Gelder & Vroomen, 2000; Van den Stock et al., 2007), emotional scenes (Righart & de Gelder, 2006, 2008a, 2008b), the presence of other emotional people (Kret & de Gelder, 2010; Russel & Fehr, 1987) and dynamic cues (Grèzes, Pichon, & de Gelder, 2007; Pichon, de Gelder, & Grèzes, 2008; Sato, Fujimura, & Suzuki, 2008; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004) all influence emotion perception. Real life situations are often much more ambiguous than the clear, obvious static facial expressions that previous research has used predominantly. So far, it is not known how offenders recognize emotions when they are embedded in a more naturalistic context.

About 95% of the imprisoned population in the Netherlands is male and a third of them have been convicted for a violent, aggressive offence (CBS, 2007). Many offenders grew up in violent environments with aggression in their daily routine (Lansford, 1995). In turn, individuals exposed to a chronic early aversive history manifest significantly higher levels of trait anger and anger reactivity than individuals who have not been exposed to such a harsh early history (Gardner, 2008). Their environment possibly conditioned them to detect and use physical aggression promptly, maybe almost reflexively, leaving little room for careful reflection in ambiguous situations. It is very natural that one's attention is immediately attracted towards a threatening situation (LeDoux, 1996). However, the degree to which we are distracted by it may depend on our prior experiences and what we learned from them (MacLeod, Mathews, & Tata, 1986). Whereas some of us may flee for threat, others may freeze and violent offenders may use aggression. In a situation where aggressive body language speaks against a smiling face or where a happy body posture seems out of place in an aggressive scene, their behavior may be guided disproportionally towards the threat.

In this study we were specifically interested in male aggression and especially in males who fight a lot, who tend to act impulsively and who seem to lack brakes. So, our aim was not primarily to include offenders who completely lack empathy or any sense of morality or reality. We only included violent offenders with a male victim, i.e., individuals who tend to act aggressively towards other men. Therefore, our sample may be slightly different from other studies that included for example psychopaths, sexual offenders or personality disordered offenders. Of particular interest to us was how aggressive males perceive aggressive body expressions from other males who are situated in a naturalistic scene. Whereas most former studies used explicit, static facial expression recognition tasks, we combined implicit tasks with explicit emotion categorization experiments and took the possible influence of a context into account. In five experiments, we tested whether violent offenders can 1) match facial and 2) bodily expressions of emotion 3) recognize emotions from dynamic bodies 4) recognize facial expressions when the body expression is incongruent 5) recognize bodily expressions when the social scene is incongruent.

Since we carefully matched the two groups on education level, age and cultural background, we did not expect a difference in performance with standard still images (experiment 1 and 2) (Pham & Philippot, 2010). Rather, we expected major differences to be revealed by more indirect task settings. Our main hypothesis was that the performance of the offender group would suffer from an emotionally incongruent context especially when the distracting context emotion was aggressive. We furthermore predicted that emotionally congruent face-body (experiment 3) and body-scene stimuli (experiment 4) would be better recognized than incongruent compounds. We expected a gender effect in the sense that the presence of angry male faces and bodies would interfere more with the matching task than female expressions of emotion, especially in the violent offender group. We hypothesized that this interference of angry male cues would be higher in the offender group. Finally, we expected that the two groups may differ on recognizing *dynamic* body expressions and that the violent offender group would recognize fearful and happy expressions more often as being angry (experiment 5). Recent studies with dynamic stimuli have proven useful for better understanding the respective contribution of action and emotion-related components (Grosbras & Paus, 2006; Kret, Pichon, Grèzes, & de Gelder, 2011). Therefore, this action component may be particularly interesting to reveal differences between the offender group and the controls.

Methods

Participants

Twenty-nine male violent incarcerated offenders (mean age: 31.76 years, range 19-61 years old) participated in this study. They were incarcerated in three prisons in the Netherlands, Z (N = 11), K (N = 11), D (N = 7) and were convicted for (a) violent crime(s) including murder with (N = 6) and without malice aforethought (N = 3), armed robbery, paired with aggravated assaults, threats and extreme violence (N = 20). In this study, our aim was to test the most aggressive males, in particular those who got into fights with other man often, who were perceived as aggressive by the staff and who had a history of recidivism. We did not include males with female or juvenile victims and neither did we aim to include psychopaths. Prisons in the Netherlands have a separate department for psychopathic and personality disordered individuals and we deliberately did not test participants from those departments. The psychologist of the prison created a list based on these criteria and approached possible candidates. In one prison, the first author was authorized to recruit them herself, with the help of a social worker. At the time of testing they were 2 to 8 years in prison and were convicted for 5 to 20 years.

The control group consisted of thirty-one males who were age- (mean age: 32.31 years, range 18-62 years old; t-test, $t(58) = .186$, $P > 0.1$) and education level matched. Since the offender group consisted of different minority groups, we additionally matched the control group on this factor; the control group consisted of as many different nationalities and cultural backgrounds as the offender group. In the current study we matched the two groups on these three factors. See Table 1 for more details. All participants lived in the Netherlands. The controls were recruited among the technical and maintenance staff of the university, via advertisements in community centers, via an integration course for ethnic minorities, via a reintegration course for unemployed people and via personal connections. Exclusion criteria of the control group involved a neurological or psychiatric history or a criminal record (based on self report only). All participants had normal or corrected-to-normal visual acuity. The study was conducted in accordance with the ethical provisions of the institutes and the Declaration of Helsinki.

Table 1.

Offender group				Control group		
Location	Age	Nationality (mother tongue)	Education level	Age	Nationality (mother tongue)	Education level
K	32	Republic of Cape Verde #	0	19	Iraq (Arab) #	0
Z	43	Turkey #	0	36	Turkey #	1
Z	49	The Netherlands	0	23	The Netherlands	2
D	19	Morocco #	1	17	Germany	a*
Z	33	The Netherlands	1	18	Armenia #	a*
D	39	The Netherlands	1	18	Moluccan (Malay) ##	a*
K	30	Morocco	1	18	Turkey ##	a*
D	34	Republic of Surinam (Papiamentu) #	1	32	Republic of Surinam	a
K	23	The Netherlands	2	38	Turkey #	a
K	21	Trinidad and Tobago (Spanish) #	2	39	The Netherlands	a
Z	28	Netherlands Antilles (French) #	2	41	Moluccan Islands (Malay) ##	a
Z	29	Netherlands Antilles	2	45	Turkey #	a
Z	40	Turkey #	a*	48	Iraq (Arab) #	a
D	48	The Netherlands	a*	51	Belgium	a
D	39	The Netherlands	a*	23	Republic of Surinam (Papiamentu) ##	a
D	19	Turkey #	a*	23	The Netherlands	a
K	21	The Netherlands	a*	25	Canada ##	a
K	19	Surinam (Hindi) #	a*	31	The Netherlands	a
K	19	Dominican Republic (Spanish) #	a*	20	Nepal (Hindi) #	b*
K	22	Iraq (Arabic) #	a*	24	Canada ##	b*
Z	41	Yugoslavia #	a*	28	The Netherlands	b
Z	22	Morocco (Arab) #	a*	28	The Netherlands	b
Z	61	Republic of Suriname	a*	37	The Netherlands	b

Table 1. (Continued)

Offender group				Control group		
Location	Age	Nationality (mother tongue)	Education level	Age	Nationality (mother tongue)	Education level
K	24	Serbia #	a	47	The Netherlands	b
D	31	Republic of Suriname	a	22	Serbia #	b
K	22	Netherlands Antilles (Papiamentu) #	a	24	Indonesia	b
Z	43	Pakistan #	a	50	Indonesia	c*
K	25	Republic of Suriname (Sranantongo) #	a	62	The Netherlands	c*
Z	45	Italy (French & Italian) #	c	25	Republic of Cape Verde	c
				45	France #	c
				45	Ireland #	unknown

Education Level

0 primary school
1 VMBO — *a a MBO*
2 HAVO — *b b HBO*
3 VWO — *c c WO*
** not (yet) finished*

bilingual
 # Dutch was not the mother tongue

K, D and Z refer to the three different locations of the prisons.

n the Netherlands, secondary education, which begins at the age of 12 until the age of 18, is offered at three levels. The two programs that lead to higher education are HAVO (five years) and VWO (six years). The HAVO diploma is the minimum requirement for admission to HBO (universities of professional education). The VWO curriculum prepares pupils for WO (research universities). 55% of all students are enrolled in VMBO (four years). Tertiary education also consists of three levels: MBO (after VMBO), HBO (after HAVO) and WO (after VWO).
20.3% of the population has a foreign background (1. Turkish; 2 Moroccan). (ref: CBS, 2009)

Materials and procedure

Questionnaires

Our sample included many individuals that had another language than Dutch as their mother tongue. Some participants indicated that they had difficulties filling out the questionnaires and requested help. For this reason, the results of the questionnaires should be interpreted with caution and the results will not be discussed in detail (see Table 2).

After the experiments, participants filled out the following questionnaires:
1). The Aggression Questionnaire (Buss & Perry, 1992) translated into Dutch by (Meesters, Muris, Bosma, Schouten, & Beuving, 1996) provides a global measure of aggression and four subscales: physical aggression, with nine items ('Given enough provocation, I may hit another person.'), verbal aggression, with five items ('I often find myself disagreeing with people'), anger, with seven items ('Some of my friends think I'm a hothead.') and hostility, with eight items ('At times I feel I have gotten a raw deal out of life.'). Participants rated each question on a Likert scale of 1 (extremely like me) to 5 (extremely unlike me). Scores on the scale may range from 29 to 145. This questionnaire has been shown to reliably differentiate aggressive individuals in normal, forensic, and clinical samples (Harris, 1995, 1997; Williams, 1996).

2) *The Emotional Contagion Scale* assesses people's susceptibility to 'catching' joy and happiness, love, fear and anxiety, anger, and sadness and depression, as well as emotions in general (Hatfield, Cacioppo, & Rapson, 1994). The eighteen-item scale contains items such as 'When someone laughs hard, I laugh too.' The participant indicated his response to an item on a four-point scale (never, often, rarely, always). The higher the total score, the more susceptible to emotional contagion the person is. The maximum score of the scale is 72. To our knowledge, no earlier study has reported using this questionnaire in an offender group.

3) *The NEO Five Factor Inventory* (Costa, 1985) translated into Dutch by (Hoekstra, 1996) measures the five major domains of personality; 1) Neuroticism: anxiety, anger, depression, shame, impulsivity and vulnerability 2) Extraversion: warmth, sociability, dominance, energy, cheerfulness, adventurism. 3) Openness to: fantasy, aesthetics, feelings, changes, ideas, values.

4) Altruism: trust, honesty, caring, compromise, humility, compassion. 5) Conscientiousness: efficiency, orderliness, dependability, ambition, self-discipline, thoughtfulness. The instrument uses a five-point Likert response format (strongly disagree, disagree, neutral, agree, strongly agree). Twelve items related to each of the five personality domains measured by the scale. Item scores ranged from 0-4, and the maximum total score for each domain was 48. Numerous findings support the role for personality in models of the etiology and persistence of conduct disorder and aggressive behavior (Anderson, 2007; Miller, 2003).

4) *Mood states* were rated on 100-mm Visual Analogue Scale (VAS), ranging from 'not at all' to 'extremely' (tense, tired, down, anxious, active, motivated, concentrated) based on the subscales of the Profile of Mood States (Pollock, Cho, Reker, & Volavka, 1979). We included these scales in the test battery in order to be able to control, if necessary, for differences on these scales.

5) *The State Trait Anger Inventory* (STAXI) (Spielberger, Jacobs, Russell, & Crane, 1983), in Dutch the SPI-DA (van der Ploeg, Defares, & Spielberger, 1980) contains ten items with a four-point scale (from 'not at all' to 'very much'). The scale measures the current experience of angry feelings. This questionnaire has been proposed as an effective tool for screening participants for anger management interventions, for treatment planning, and for evaluating the effectiveness of therapeutic interventions individuals in normal, forensic, and clinical samples (Deffenbacher, 1996; Foley, 2002; Mansfield, 2008).

Table 2. Mean scores (with SD) for the different questionnaires.

	Violent offenders		Controls	
	Mean	**SD**	**Mean**	**SD**
Aggression Questionnaire*	82.39	15.66	74.90	10.70
Physical aggression ***	27.79	8.27	22.60	4.17
Verbal aggression	14.57	3.33	14.70	2.67
Anger/rage	17.50	5.67	18.33	4.79
Hostility *	22.54	5.50	19.27	4.33
Emotional Contagion Questionnaire	43.86	4.81	45.39	6.34
Joy/Happiness	8.21	1.77	9.00	1.41
Love	9.96	1.45	9.10	1.94
Fear/anxiety	5.46	2.22	5.61	2.16
Anger	5.79	1.20	6.39	1.61
Sadness/depression	6.79	1.69	6.32	1.54
General *	7.64	2.15	8.97	1.76
NEO-FFI				
Neuroticism	16.68	5.80	17.89	5.89
Extraversion	30.32	6.09	30.81	4.49
Openness	27.36	7.07	25.26	5.09
Agreeableness	28.14	5.18	27.56	4.41
*Conscientiousness**	30.57	7.69	35.59	6.68
State Trait Anger Inventory (state only)	10.93	2.40	10.57	1.22
Visual Analogue Scale				
Tension	4.83	5.34	4.48	3.15
Tired	5.28	6.25	8.19	5.67
Down/dark	4.07	4.27	3.74	3.51
Anxious	1.66	2.45	1.94	3.10
Active	9.86	6.13	11.58	4.94
Motivation	15.17	4.76	13.90	4.66
Trouble concentrating	4.41	5.42	6.18	5.32

** P < .05*
**** P < .005*

Mean is followed by the standard deviation (SD)

General procedure

The experiments were administered in quiet consulting rooms in three different prisons in the Netherlands, at Tilburg University and in an empty class room. The experimenter was allowed to share the consulting room with the participant without the presence of another person such as a guard. The testing situation for the control group was kept as similar as possible. For this reason, we deliberately did not test the control group in a soundproof booth in which we usually test participants. The events were controlled by E-prime (Psychology Software Tools, Inc., Sharpsburg, USA) (Experiment 1-4) and Presentation (Neurobehavioral Systems, San Francisco, CA) (Experiment 5), implemented on a laptop (Latitude E5500, Dell) with a 60 Hz refresh rate. Distance to the computer screen was 60 cm. In order to counterbalance for fatigue and for handedness we changed the order of the experiments across participants as well as the labels on the response box that was used in the experiments in which reaction time data was important. Experiment 5 was programmed in Presentation because of good experiences with this program with dynamic stimuli. Before each experiment, participants completed five practice trials to become familiarized with the procedure. In Experiment 2, 3 and 5, the faces were blurred so that the emotion could be read from the body only.

Data Analysis across experiments

The data were analyzed using SPSS 17.0 (SPSS, Japan). Main effects were always followed up by Bonferonni corrected pairwise comparisons and interaction effects were further explored with 2-tailed t-tests. Trials with reaction times below 250 ms or above 6000 ms and then those with an incorrect response were discarded from the reaction time analyses. A second filter was used to exclude reaction times above or below two standard deviations per participant, per target emotion condition. Because this second filter is based on the correct responses only, it was not applied to the accuracy data.

Experiment 1. Matching two facial expressions

Materials and procedure

Participants were asked to match a validated set of facial expressions in a two-alternative forced choice task. A matching task was used here in order to investigate how the different emotions were recognized on the basis of similarities with other stimuli from the same category, while not being mediated by the use of verbal labels. Three different identities of the same gender were shown per trial: one in the middle upper part of the screen (1.6 cm below the upper part of the screen), one in the left down corner and the other in the right down corner (5.3 cm from the left or right and 2.4 cm from below). Stimuli were 200 pixels in width and 271 pixels in height. The task was to indicate whether the left or the right down face showed the same expression as the one presented at the top. No time limits were set, and no feedback was provided about performance during the test trials. Participants saw ten unique identities per emotional expression category, resulting in a total of 60 trials for each participant. After button-press, a gray screen appeared for 500 ms after which the next trial started.

Data analysis

Main and interaction effects of facial expression of the target and distracter expression for mean accuracy and reaction time were tested in repeated measures analyses of variance (ANOVA) with two within-subject variables 'target expression' (Anger, Disgust, Fear, Happy, Sad, Surprise) or 'distracter expression' (Anger, Disgust, Fear, Happy, Sad, Surprise) and 'gender' (Male or Female actor) and 'group' (Violent offender or Control) as between-subjects variable.

Results

Accuracy: There was a main effect of target expression [$F(5, 290) = 37.920$, $P < .001$]. Accuracy was lowest for fear ($P < .001$). Happy faces were more accurately matched than all other expressions except anger ($P < .05$). There was an effect of gender [$F(5, 290) = 14.014$, $P < .001$]; male emotions were more accurately matched than female ones ($P < .001$). The interaction between gender of the actor and facial expression [$F(5, 290) = 13.269$, $P < .001$] indicated that anger, disgust and sadness were better matched if the actor was male versus female ($t(59) \geq 3.106$, $P < .005$). Fear was better matched from female versus male actors ($t(59) = 2.942$, $P < .005$).

There was a main effect of the emotion of the distracter [$F(5, 290) = 25.337$, $P < .001$]. Happy and surprised faces were less distracting than the four negative emotions ($P < .05$). Angry faces distracted most ($P < .05$), especially angry male actors, as was revealed by an interaction between gender of the actor with the emotion of the distracter [$F(5, 290) = 21.016$, $P < .001$]. Angry male faces affected accuracy more than angry female faces ($t(59) = 3.361$, $P < .001$) and more so than all other male emotions ($t(59) \geq 6.721$, $P < .001$). There was an interaction between emotion of the distracter and group [$F(5, 290) = 2.348$, $P < .05$] but further t-tests did not yield significant effects. In both groups, fearful and sad faces were more interfering with accuracy when the gender of the actor was feminine instead of masculine ($t(59) \geq 5.774$, $P < .01$).

Reaction time: There was a main effect of target expression [$F(5, 290) = 18.148$, $P < .001$]. Happy expressions were fastest matched ($P < .001$). Fearful and angry expressions were slower matched than disgusted, happy and surprised faces ($P < .001$). There was an interaction between the gender of the actor and the target emotion [$F(5, 290) = 2.327$, $P < .05$]; disgust was faster matched if the actor was male rather than female ($t(59) = 2.312$, $P < .05$). There was an interaction between gender of the actor and distracter expression [$F(5, 290) = 3.165$, $P < .01$]; whereas a disgusted distracting face affected reaction times more in case of a male versus a female actor ($t(59) = 2.870$, $P < .01$), the opposite was true for fear ($t(59) = 3.041$, $P < .005$). See Table 3.

Table 3. Matching facial expressions of emotion.

		Target emotion							
		Violent offender				**Control**			
		ACC		RT		ACC		RT	
Facial expression	Gender actor	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Anger	M	.92	.11	2203.53	737.21	.92	.13	2233.77	882.73
	F	.85	.18	2344.36	858.85	.85	.17	2256.91	953.47
Disgust	M	.91	.16	1933.80	667.39	.93	.11	1997.00	772.61
	F	.75	.22	2067.39	674.51	.81	.19	2166.65	850.26
Fear	M	.62	.18	2251.39	850.46	.64	.20	2408.64	878.12
	F	.75	.18	2346.41	798.77	.69	.17	2347.69	1034.89
Sad	M	.88	.20	2476.41	928.53	.88	.13	2212.20	993.15
	F	.76	.17	2306.89	726.09	.69	.20	2142.27	941.10
Surprise	M	.85	.20	2236.82	833.83	.89	.14	2043.95	752.09
	F	.86	.18	2124.31	857.68	.90	.13	1929.18	764.05
Happy	M	.91	.17	1876.44	669.64	.94	.12	1686.66	548.90
	F	.90	.19	1855.53	669.38	.95	.15	1620.18	484.54
		Distracting emotion							
Anger	M	.71	.19	2211.87	826.17	.66	.21	2040.23	774.67
	F	.83	.14	2191.70	700.20	.76	.17	2117.06	921.11
Disgust	M	.88	.18	2338.20	849.99	.88	.14	2173.41	776.85
	F	.80	.20	2259.22	788.13	.85	.15	1951.37	679.58
Fear	M	.88	.16	2040.54	708.52	.93	.11	1890.50	670.12
	F	.73	.24	2167.47	711.77	.73	.21	2170.57	959.18
Sad	M	.89	.17	2218.20	727.61	.89	.17	2160.29	807.25
	F	.73	.21	2221.90	766.21	.70	.15	1954.24	595.47
Surprise	M	.88	.14	2077.75	762.34	.95	.09	2112.78	839.92
	F	.89	.13	2181.11	722.47	.94	.10	2040.83	799.08
Happy	M	.86	.18	2144.86	669.62	.90	.13	2081.96	658.17
	F	.92	.18	2047.46	660.16	.95	.10	1973.76	748.53

Discussion

As predicted, the offender group was not impaired in matching facial expressions of emotion when compared to a carefully matched control group. In both groups, accuracy for anger, disgust and sadness was higher if the actor was male rather than female and the inverse was observed for fear. These findings are in line with the literature on gender emotion stereotypes (Hess, Adams, & Kleck, 2004). Happy and surprised faces had a smaller interfering effect on judging the target expression than angry, disgusted, fearful and sad faces. These latter emotions indicate distress in the observed and it may have a strong evolutionary importance to attend to them. In contrast, happy and surprised faces have a strong social meaning and are used on a daily basis (Hess & Bourgeois, 2009). In line with this hypothesis, angry male faces were most distracting. Fearful and sad faces interfered most with accuracy when the actor was female. These effects may be trade-offs from the higher accuracy rates for these three emotions from either male or female faces. Whereas a disgusted distracting face affected reaction times more in case of a male versus a female actor, the opposite was true for the emotion fear. Whether these findings will extend to bodily expressions of emotion will be investigated in the next experiment.

Experiment 2. Matching bodily expressions of emotion

Materials and procedure

Materials consisted of 72 gray-scale photographs representing semiprofessional actors (half male) expressing different emotions with their whole body (anger, fear, happiness, and sadness) with the face blurred (310 pixels in height). The expressions disgust and surprise were not included because they resemble fear and happiness (de Gelder, 2006). Selection of materials for use in the present experiment was based on the results of a validation study in which the images were shown one by one for 4000 ms with a 4000 ms interval. 120 participants were instructed to categorize each stimulus in a forced choice procedure choosing one among four emotion categories. We here included images that were correctly recognized above 70%. A trial consisted of a target body posture presented at the top and two different identities of the same gender left and right underneath 1.4 cm from the bottom of the screen. 72 unique images were used. Task instructions were the same as in Experiment 1.

Data analysis

Main and interaction effects of facial expression of the target and distracter for mean accuracy and reaction time were tested in two ANOVAs with one within-subject variable 'gender of the actor' (Male or Female), and 'target body expression' or 'distracter expression' (Anger, Fear, Happy, Sad) and 'group' (Violent offender or Control) as between-subjects variable.

Results

Accuracy: There was a main effect of target body expression [$F(3, 174) = 9.933$, $P < .001$]; sad expressions were most accurately matched ($P < .05$). There was a main effect of gender [$F(3, 174) = 17.446$, $P < .001$] ; female bodies were more accurately matched ($P < .001$) but again this was a function of the specific emotion [$F(3, 174) = 13.917$, $P < .001$]; anger was more accurately matched if the actor was male rather than female $t(59) = 2.020$, $P < .05$ and fear, happy and sad expressions more accurately matched from female versus male bodies $t(59) \geq 2.615$, $P < .05$.

Table 4. Matching bodily expressions of emotion.

		Target emotion							
		Violent offender				Control			
		ACC		RT		ACC		RT	
Bodily expression	Gender actor	M	SD	M	SD	M	SD	M	SD
Anger	M	.93	.14	2068.52	556.72	.95	.12	2023.56	798.89
	F	.88	.17	1873.31	734.90	.89	.16	1797.76	779.83
Fear	M	.86	.17	2333.47	800.39	.80	.17	2247.51	822.08
	F	.91	.16	2043.95	857.66	.94	.13	1886.12	823.45
Sad	M	.93	.14	2108.79	817.21	.92	.17	2115.53	885.14
	F	.97	.10	1791.98	699.51	.99	.06	1773.86	694.22
Happy	M	.85	.18	2375.84	682.62	.75	.21	2163.19	823.15
	F	.94	.16	1817.20	647.35	.99	.06	1719.13	733.23
		Distracting emotion							
Anger	M	.77	.27	2282.17	923.19	.74	.24	2199.66	991.85
	F	.87	.17	1933.22	923.73	.89	.21	1762.72	776.59
Fear	M	.89	.23	1811.53	665.53	.96	.14	1931.04	752.27
	F	.89	.16	2182.86	881.51	.82	.17	2116.62	861.09
Sad	M	.93	.19	1980.15	730.85	.98	.08	1752.03	648.24
	F	.95	.15	1972.93	718.18	.97	.10	1828.18	607.37
Happy	M	.91	.18	1953.50	568.60	.90	.15	1883.78	689.92
	F	.94	.16	2176.45	797.15	.97	.10	2153.88	852.53

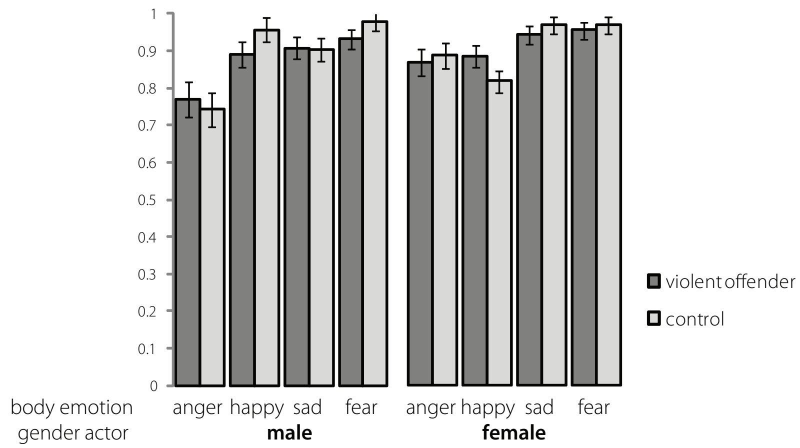
Matching performance of the gender of the actor was also a function of group [$F(1, 58) = 4.747$, $P < .05$]; whereas the control group matched female emotions better than male ones $t(30) = 4.625$, $P < .001$ there was no difference in the offenders group ($P = .18$).

There was a main effect of distracter expression [$F(3, 174) = 19.580$, $P < .001$]; angry bodies were most distracting and the matching accuracy was lowest when the distracting body was an angry one ($P < .05$). There was a main effect of gender [$F(1, 58) = 5.007$, $P < .05$]; male bodies were more distracting than female bodies ($P < .05$). The gender of the actor interacted with the emotion of the distractor [$F(1, 58) = 5.007$, $P < .05$]; in line with our hypothesis and with the findings of Experiment 1, angry male body expressions were most distracting $t(59) \geq 2.783$, $P < .01$. A female fearful body expression interfered more with target body recognition accuracy than a fearful male body expression $t(59) = 2.566$, $P < .05$.

Reaction time: There was a main effect of target body expression [$F(3, 174) = 4.667$, $P < .005$]; angry and sad expressions were faster correctly matched than fearful expressions ($P < .05$). There was a main effect of gender [$F(1, 58) = 66.870$, $P < .001$]; female bodies were faster matched than male bodies ($P < .001$).

There was a main effect of distracter expression [F(3, 174) = 3.273, $P < .05$]; reaction times of target body expression recognition were fastest when accompanied with a sad distracting body expression, faster than happy bodies ($P < .05$). Interestingly, we again found a strong interaction between the gender of the actor and the body emotion [F(3, 174) = 16.687, $P < .001$]; angry male body language slowed down matching performance much more than angry female bodies or than other male expressions $t(59) \geq 3.216$, $P < .005$. Fear and happy bodies were more distracting when expressed by a female versus a male $t(59) \geq 3.085$, $P < .005$.

Figure 1. Proportion correct answer as a function of the distracting image.



Proportion correct answer of mathcing bodily expressions of emotion as a function of the distracting male or female body expression.

Discussion

Angry expressions were more accurately matched in case of a male than female actor and fear, happy and sad expressions were more accurately matched from female rather than male bodies. These findings are similar to what we observed in Experiment 1 except for sadness. We again found that angry bodies were most distracting and recognition accuracy was lowest and reaction time highest when the distracting body was an angry one, especially when male. However, this interference was not larger in the offender group, as we had predicted. A female fearful body expression interfered more with task performance than a fearful male body expression. Happy bodies were also more of influence on reaction times when female rather than male. To conclude, violent offenders are not impaired in matching two emotional bodily expressions. Previous studies have predominantly used static facial expressions and sometimes found impairments on explicit emotion recognition tasks. How these and the above described results relate to dynamic body expressions is unknown.

Experiment 3. Dynamic bodily expression of emotion

Materials and procedure

Video recordings were made of 45 actors (27 male identities) expressing six different facial and bodily emotions. All actors were dressed in black and filmed against a green background. To coach them to achieve a natural expression, pictures of emotional scenes were presented with a beamer projecting on the wall in the front and a short emotion-inducing story was read out by the experimenter. The actors were free to act the emotions in a naturalistic way as response on the situation described by the experimenter and were not put under time restrictions. Fearful body movements included stretching the arms as if to protect the upper body while leaning backwards. Angry body movements included movements in which the body was slightly bended forward, some actors showed their fists, whereas others stamped their feet and made resolute hand gestures. Additionally, the stimulus set included neutral non-expressive face and body movements (such as pulling up the nose, twitching/licking lips, coughing, fixing one's hair or clothes). Recordings used a digital video camera under controlled and standardized lighting conditions in a recording studio. All video clips were computer-edited using Ulead and After Effects, to a uniform length of two seconds (50 frames). The faces of the body videos were masked with Gaussian masks so that only information of the body was visible. The videos were 504 pixels in height. For each actor and emotion, a few different versions were filmed. The whole stimulus database was split in two and 30 students categorized the videos, choosing among the six basic emotions and a neutral label. Based on these results, we selected angry, fearful and happy bodily expressions from 10 male identities for inclusion in the current experiment. Angry bodies were recognized for 93% (SD 12), fearful bodies for 93% (SD 9), and happy bodies for 91%, (SD 12).

Participants were instructed that a series of short video clips with bodies expressing emotion would be presented on the computer screen. They were asked to categorize the emotion and choose among four options: anger, fear, happy or neutral. The decision to add "neutral' as an additional response option was made to provide participants with more of an open choice and not restrain them to choices limited to the target emotions (Hastings, Tangney, & Stuewig, 2008). In addition, if they did not find the video emotional, they could choose 'neutral'. Participants were provided unlimited time to complete the task. After the end of a video, a blank screen with a question mark appeared. Once a participant made a response, a blank screen appeared which lasted between 1 and 3 seconds after which a fixation cross was presented.

Data analysis

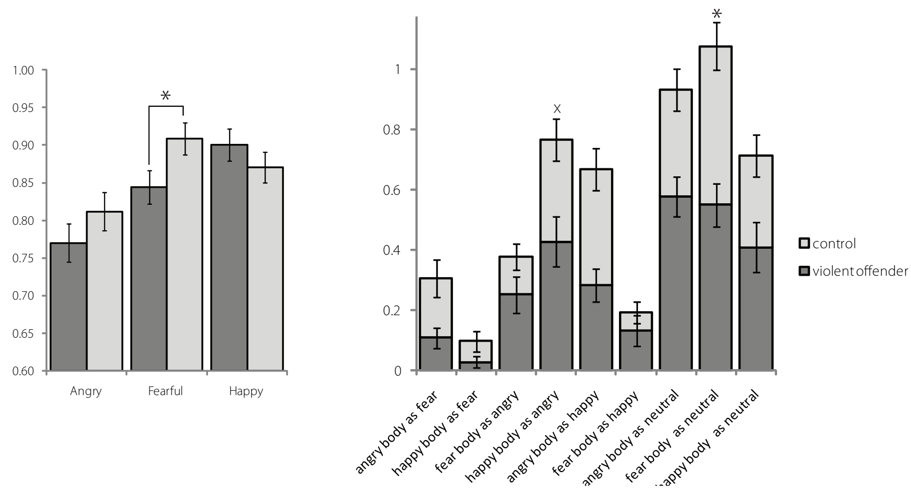
Main and interaction effects of bodily expression for mean accuracy were tested in an ANOVA with one within-participant variable 'body expression' (Anger, Fear or Happy) and 'group' (Violent offender or Control) as between-subjects variable. Reaction time data was not analyzed because in order to make sure that participants watched the whole video, they were instructed to wait with their response until the 2 second video ended.

Results

Accuracy: There was a main effect of dynamic body expression [F(2, 116) = 18.046, $P < .001$]; happy expressions were more accurately recognized than angry ones ($P < .001$). There was an interaction between body expression and group [F(2, 116) = 3.872, $P < .05$]; violent offenders were worse than controls in recognizing fearful bodies t(58) = 2.254, $P < .05$) than controls. The violent offenders, but not the control group showed a difference in accuracy for the recognition of happy versus angry body expressions t(28) = 5.349, $P < .001$.

Violent offenders had a small tendency to more often misinterpret fearful body expressions as angry than the control group t(58) = 1.692, $P = .09$ (number of this specific error divided by the total number of errors). The violent offender group more often erroneously interpreted an angry signal as being neutral than the control group t(58) = 2.271, $P < .05$.

Figure 2. Recognition rates of dynamic bodily expressions of emotion.



a) Proportion correct answer.
b) Proportion error (of total number of errors)
** = P < .05, two-tailed x = P < .10, two-tailed*

Discussion

Happy expressions were more accurately recognized than angry ones. Violent offenders were worse than controls in recognizing dynamic fearful body expressions. This is in line with the literature about facial expressions (Marsh & Blair, 2008). Both groups recognized fearful expressions better than angry ones but violent offenders were worse than the control group in the recognition of fear. The violent offenders, but not the control group showed a difference in accuracy for the recognition of happy versus angry body expressions. Violent offenders somewhat more often misinterpreted fearful body expressions as angry as the control group and also more often erroneously interpreted an angry signal as a neutral signal than the control group.

Experiment 4. Facial expression recognition with congruent or incongruent body expression

Materials and procedure

Face-body compound images were created by pasting emotionally (in)congruent body expressions below the facial expressions of six male actors. We did not include sad bodies since these contain less action than happy, angry and fearful bodies (Kret et al., 2011). In order to create a naturalistic looking image, the faces and bodies were turned to grayscale. The stimuli were 532 pixels in height. Face and body stimuli had different identities than the ones in Experiment 1 and 2. The face stimuli were taken from the well-validated McArthur set and were all recognized above 80% (http://www.macbrain.org/resources.htm) (as described in Experiment 2). The bodies were selected from our validated stimulus database. The body images were presented for 4000 ms and students (N = 80) correctly recognized the angry bodily expressions (with faces blurred) for 95% (SD 10.00) happy body expressions for 73% (SD 26), fearful body expressions 92% (SD 28). The compound images were presented to the same students (random block order); facial expression of the congruent compounds for 97% (SD 4.42) and the incongruent ones for 93% (SD 10.84). In a different block, they categorized the body expressions from the compound images and recognized the bodies of the congruent combinations for 88% (SD 17.67) and the incongruent combinations for 80% (SD 22.04). In the current experiment, the compound stimuli were briefly (100 ms) presented against a grey background. Participants were asked to categorize the facial expression only and ignore the body posture as much as possible. It was made very explicit that they should base their judgment on the facial expression only. After button press, a gray screen appeared on which after 5700 ms, a fixation cross was presented for 300 ms. In total 72 pictures were shown.

Data analysis

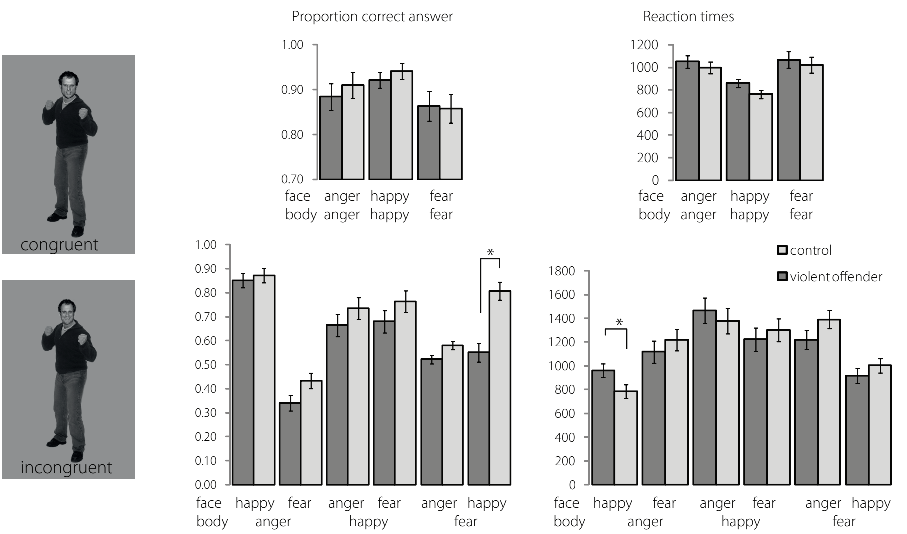
Main and interaction effects of group and emotion on accuracy and RT were tested in a 3 x 3 repeated measures ANOVA with two within-subject variable 'facial expression' (Anger, Happy or Fear) and 'bodily expression' (Anger, Happy or Fear) and 'group' (Violent offender or Control) as between-subjects variable.

Results

Accuracy: There was a main effect of facial expression [$F(2, 116) = 25.899$, $P < .001$]; happy expressions were most accurately recognized ($P < .001$) and angry faces were better recognized than fearful ones ($P < .05$). There was a main effect of body expression [$F(1, 116) = 10.389$, $P < .001$]; facial expression recognition was best when the accompanied body showed a happy expression ($P < .001$). There was a trend towards a main effect of group [$F(1, 58) = 3.205$, $P = .079$]; violent offenders were generally less accurate than the control group, but only for the incongruent face-body compounds $t(58) = 1.998$, $P < .05$; there was no difference between the two groups for the congruent compounds $t(58) = .413$, $P = .681$. An interaction between emotion of the face and emotion of the body was observed [F(4, 232) = 66.475, $P < .001$]; facial expressions were better recognized when accompanied by a body that showed the same expression. This was significant for all possible combinations (t(59) ≥ 3.479, $P < .001$). There was an interaction between emotion of the face, emotion of the body and group [F(4, 232) = 3.199, $P < .05$]. Violent offenders were worse in recognizing happy facial expressions when accompanied with fearful bodies than the controls (t(58) = 2.167, $P < .05$). When looking at the errors that were made, it becomes clear that violent offenders when looking at a happy face with a fearful body expression, more often than controls erroneously answer that the facial expression is fearful (t(58) = 1.936, $P = .058$). Moreover, for this condition, healthy controls more often pressed the button 'happy' (i.e. gave the correct response) than the violent offenders (t(58) = 2.385, $P < .05$).

Reaction time: There was a main effect of facial expression [F(2, 116) = 47.580, $P < .001$]; happy expressions were fastest recognized ($P < .001$) and fearful faces were faster recognized than angry ones ($P < .05$). There was a main effect of body expression [F(1, 116) = 10.544, $P < .001$; facial expression recognition was fastest when the accompanied body showed an angry expression ($P < .05$). An interaction between emotion of the face and emotion of the body was observed [F(4, 232) = 14.167, $P < .001$]; facial expressions were faster recognized when accompanied by a body that showed the same emotion expression. This was significant for all combinations (t(59) ≥ 2.098, $P < .05$). There was an interaction between emotion of the face, emotion of the body and group [F(4, 232) = 2.562, $P < .05$]. Violent offenders were slower in recognizing happy facial expressions when accompanied with angry bodies than the controls (t(58) = 2.157, $P < .05$).

Figure 3. Emotionally congruent and incongruent face-body compounds.



Proportion correct anser and reaction times (ms). Pictures were presented for 100 ms. Participants defined as fast and accurate as possible the emotion of the face.
** = P < .05, * * = P < .01, *** = P < .005, **** = P < .001, x = P < .10, all two-tailed.*

Discussion

Facial expression recognition was most accurate when the accompanied body showed a happy, non-threatening expression. In line with our previous studies, facial expressions were more accurately and faster recognized when accompanied by a body that showed the same emotional expression (Meeren et al., 2005; Kret et al., in prep). Violent offenders were less accurate than the control group in recognizing facial expressions from incongruent face-body compounds. Accuracy rates for happy facial expressions when accompanied with fearful bodies were lower in the offender than in the control group. The response of the former group went into the direction of the body expression (fear). Facial expression recognition was fastest when the accompanied body showed an angry expression. Violent offenders were slower in recognizing happy facial expressions when accompanied with angry bodies than the controls.

Experiment 5. Bodily expression recognition in congruent or incongruent social scenes

We briefly describe the construction and validation of the target body stimuli. Eight happy and fearful body images from the same set as in Experiment 2 (but different actors), on average correctly recognized at 91% (SD 10), were included in the experiment. Angry (fights), happy (party) and neutral (sports) scenes were selected from the Internet. Emotionally congruent and incongruent body postures were pasted in the social emotional scenes. For a detailed description of the validation procedure of these stimuli, see (Kret et al., 2011). Participants were given a two-alternative forced choice task over two emotions and were instructed to focus on the main figure in the middle of the screen, to ignore the scene, and to categorize as accurately and rapidly as possible the body emotion, to respond with their right index and middle finger and not to change the position of their fingers during the experiment. A trial started with a white fixation cross on a gray screen (300 ms), a stimulus (100 ms), followed by a gray screen shown until button press (with a maximum duration of 8 s).

Data analysis

Main and interaction effects of bodily expression recognition in congruent and incongruent scenes for mean accuracy and reaction times were tested in an ANOVA with three within-participant variables 'body expression' (Anger or Happy), 'scene emotion ' (Anger, Neutral or Happy) 'gender of the actor' (Male or Female) and 'group' (Violent offender or Control) as a between-subjects variable. The data of one offender could not be collected because this participant had to go back to his cell due to strict time schedule regulations in prison.

Results

Accuracy: There was a main effect of body emotion [$F(1, 58) = 6.512$, $P < .05$]; happy expressions were more accurately recognized than angry ones ($P < .001$). There was an interaction between the emotion of the scene and the emotion of the body [$F(2, 116) = 32.191$, $P < .001$]; happy bodies were best recognized in a happy scene t(58) ≥ 3.328, $P < .001$ and angry bodies were best recognized in an angry scene t(58) ≥ 4.739, $P < .001$. There was an interaction between group, the emotion of the scene and the emotion of the body [F(2, 116) = 4.476, $P < .05$]; in both groups, there was a strong effect of (in)congruency, but interestingly, this effect was much stronger in the violent offenders. We calculated a difference score between 1) the accuracy rates of happy bodies in happy scenes minus happy bodies in angry scenes and 2) angry bodies in angry scenes minus angry bodies in happy scenes and compared the two groups. The first comparison yielded a significant difference t(58) = 2.617, $P = .011$. The second comparison was marginally significant t(58) = 1.806, $P = .076$. The interaction was mainly driven by the drop in recognition accuracy in the violent offender group for happy bodies that were presented in an angry scene. When we split up the gender of the actor, it turned out that this difference between the two groups in this condition was especially true when the actor was male t(58) = 2.826, $P = .006$; female t(58) = 1.849, $P = .070$.

The actors' gender interacted with body emotion [F(1, 58) = 8.389, $P < .005$]; angry males were better recognized than angry females t(58) = 2.224, $P < .05$ and happy females were better recognized than angry males t(58) = 2.607, $P < .05$. Female bodies were better recognized when happy than when angry t(58) = 2.124, $P < .05$ but for male bodies there was no difference between the two emotions t(58) =.999, $P = .322$. See figure 3.

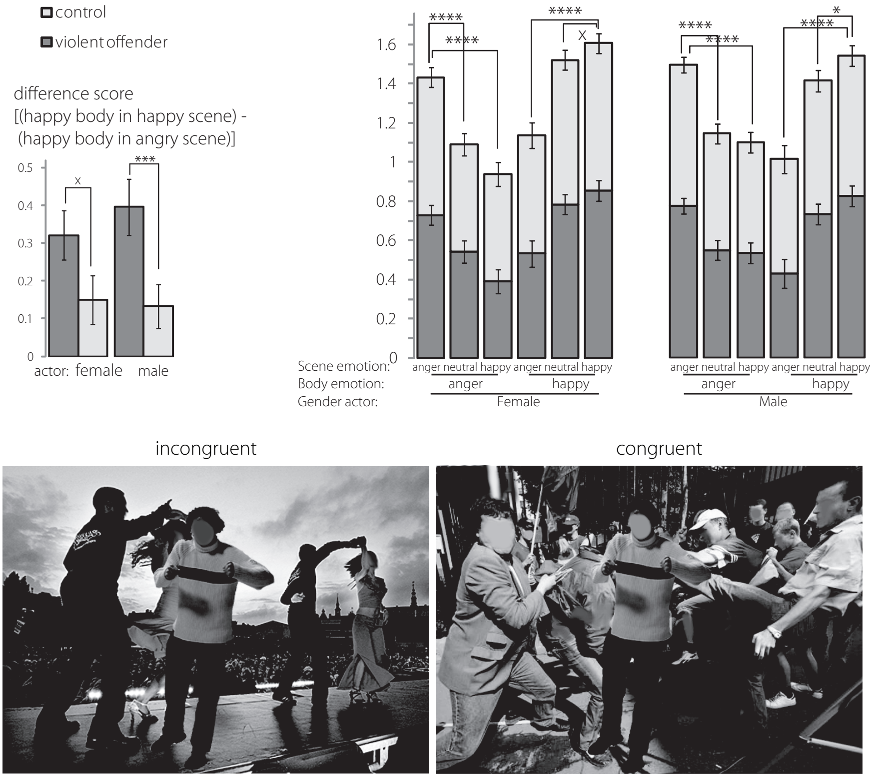
Reaction times: There was an interaction between body emotion and scene emotion [F(2, 116) = 3.672, $P < .05$]. Angry bodies were faster recognized in an angry than happy scene t(58) = 2.434, $P < .05$ or than in a neutral scene t(58) = 1.796, $P = .078$ (marginally significant). Although numerically consistent with our hypothesis, happy body expressions were not significantly faster recognized in a happy than in an angry context $P = .140$.

The actors gender interacted with body emotion [F(1, 58) = 10.566, $P < .005$]; angry males were faster recognized than angry females t(58) = 3.199, $P < .005$ and happy females were faster recognized than angry males t(58) = 2.581, $P < .05$. Female bodies were faster recognized when happy than when angry t(58) = 2.124, $P < .05$ but there was no difference for male bodies being faster recognized when angry than when happy t(58) = 1.453, $P = .152$. See Table 5.

Discussion

In both groups, there was a strong effect of (in)congruency, but interestingly, this effect was much stronger in the violent offenders who showed a drop in recognition accuracy for happy bodies that were presented in an angry scene versus a happy scene, especially when the actor was male.

Figure 4. Recognition rates of bodily expressions in congruent and incongruent social scenes



*Stimulus examples. Proportion correct anser and reaction times (ms). Pictures were presented for 100 ms. Participants defined as fast and accurate as possible the emotion of the foreground body. x = P < .1, * = P < .05, *** = P < .005, **** = P < .001, all two-tailed.*

Table 5. Reaction times of bodily expressions in congruent or incongruent social scenes

			Violent offender		**Control**	
Gender actor	Emotion body	Emotion scene	*M*	*SD*	*M*	*SD*
F	Anger	Anger	936.14	406.37	922.15	348.71
		Neutral	961.06	452.20	980.64	281.53
		Happy	1011.35	439.85	1102.26	465.67
	Happy	Anger	1011.90	547.11	929.50	333.14
		Neutral	917.29	452.08	904.28	246.31
		Happy	886.71	482.31	852.40	290.82
M	Anger	Anger	873.78	415.34	853.40	294.72
		Neutral	915.84	400.46	984.67	339.34
		Happy	931.29	553.59	938.78	400.10
	Happy	Anger	967.84	419.70	911.36	389.52
		Neutral	911.10	344.87	1064.33	418.90
		Happy	971.01	475.55	921.53	285.71

General Discussion

In this study, we investigated the performance of violent offenders on decoding facial and bodily expressions of emotion and the influence of a context in which they are naturally perceived. Our major finding is that violent offenders are particularly impaired in recognizing emotions in an incongruent, threatening context. We further observed that violent offenders were worse in recognizing dynamic fearful body expressions than the control group and more often categorized these as angry.

Misinterpretation of social cues such as emotional expressions can result in the generation of inappropriate social responses, such as reacting aggressively or violently. Several studies have reported an impaired recognition of emotional expressions in offenders. Sato et al (2009) reported that delinquents were less accurate in categorizing facial expressions of disgust and misrecognized this emotion more frequently as anger than controls did. Other studies found a relationship between psychopathic traits and recognition deficits of fearful and sad faces (Marsh & Blair, 2008) but see (Pham & Philippot, 2010).

We here show that violent offenders with high aggression scores can match two faces or bodies from different identity but with the same emotional expression as accurately as the control group. In line with the literature on gender emotion stereotypes (Hess et al., 2004) we found that angry faces and bodies were more accurately matched and were most distracting if the actor was male rather than female. We reasoned that, since our group of interest often gets into fights with other males, it may be that they get distracted more by aggressive signals from other males. However, violent offenders' performance was equal to that of the controls.

In real life, emotions are highly dynamic and contain a clear action component. When comparing violent offenders with the control group on their performance of recognizing dynamic bodily expressions, we observed that they were worse in the recognition of fearful cues and more often misinterpreted these as angry. In contrast, angry body expressions were more often erroneously interpreted as a neutral signal by the violent offender group. Very few studies provide error information and the ones that do, do not reveal a clear, consistent error pattern (Blair, Colledge, Murray, & Mitchell, 2001; Hoaken, Allaby, & Earle, 2007; Matheson & Jahoda, 2005; Sato et al., 2009; Walz & Benson, 1996). The finding that offenders had more difficulties categorizing fearful expressions is in line with the literature on emotion recognition deficits in antisocial populations from static facial expressions (Marsh & Blair, 2008).

Perceiving emotions in context

In Experiment 1-3, clear, explicit emotions were presented. However, in real life, we are often confronted with ambiguous signals. For example, when someone tells a sad story but cannot show his true emotions and puts on a smiling face. Males in particular tend to hide their emotions and instead act aggressively in a stressful situation (Taylor et al., 2000; van Honk & Schutter, 2007). Therefore, in Experiment 4, compound images were presented that consisted of emotionally congruent or incongruent face and body emotions. In line with our previous studies, facial expressions were better recognized when accompanied by a body that expressed the same emotion (Meeren et al., 2005). Interestingly, whereas violent offenders performed equally well on the congruent trials as the control group, they were impaired in recognizing facial expressions from incongruent face-body compounds and their response pointed into the direction of the body expression, especially when it showed a threatening expression (fear or anger).

We always encounter other people in a certain context, often with the presence of other people and consequently recognize emotions in a social environment. In line with our previous studies in students (Kret & de Gelder, 2010), we here find similar (in)congruency effects of the social scene. An emotionally congruent social scene helps recognizing the emotion of a central figure and an incongruent scene impairs recognition. However, this effect was much stronger in the offender group, in particular when the background showed a fight and especially when the foreground figure was male. The violent scenes, albeit very briefly presented (100 ms) and albeit explicitly instructed to ignore, interfered more in the offender group than in the control group. Due to the incongruence of the violent scene with the happy (male) body expression, the violent offenders had great difficulties correctly categorizing the happy body expression and performed at chance level.

In order to explain the results, we need to stress the importance of the factor aggression. The offenders in our study were convicted for an extremely violent crime against another man. They were screened by the staff in order to include the most aggressive ones who got into fights a lot (including with the other prisoners) and with a history of other violent crimes. Their self reports further confirmed that they were more physically aggressive and hostile than the control group. Criminal populations have often been confronted with violence during their life and were often raised in a violent environment (Cima, Smeets, & Jelicic, 2008; Driessen, Schroeder, Widmann, von Schonfeld, & Schneider, 2006; Heide & Solomon, 2006; Hosser, Raddatz, & Windzio, 2007; Kopp et al., 2009; Lindberg et al., 2009; Poythress, Skeem, & Lilienfeld, 2006). Attending and reacting to a threatening male expression has high evolutionary significance. However, this reactivity to threat may be fed by the specific background we come from and our current environment. If we in daily life are surrounded by violence, we may be continuously looking out for danger, ready to quickly respond whenever we think someone is attacking us and this behavior has probably often been positively reinforced. This leaves little room to recognize someone's facial expression when the body expression is not matching or let alone recognize a happy person when the social scene is aggressive. Earlier studies have suggested an interpretative bias in offenders. For example, Copello and Tata (1990) observed that offenders were more likely to interpret violent ambiguous sentences (e.g. "The painter drew the knife") in a threatening fashion, with the opposite being shown by the non-offender group. The tendency to infer violent threat was found to correlate with hostility.

The finding that offenders often responded with 'fear' or 'anger' labels when the face, in contrast to the body, expressed happiness and in addition, with 'anger' when the body expressed happiness but the scene aggression, is consistent with the *hostile attributional bias* identified in aggressive children (Dodge, 1993). Such a bias has also been reported in case studies with aggressive individuals (Black, Cullen, & Novaco, 1997). In our study, the smiling face may have been perceived as a fake, dominant smile (bordering contempt), a laugh in the face or even expressing defy for/an invitation to a fight. These results may also be explained by the *low-fear model*, which posits that psychopaths fail to effectively process threat or punishment cues (Lykken, 1957). The current findings are partly consistent with the low-fear model in that violent offenders had a decreased recognition of dynamic body expressions of fear (a similar tendency was observed for anger but not happy bodies). However, they could match threatening body expressions and recognized them in a congruent or neutral context, equally well as the control group. The low-fear model may only be applicable in explicit, non-ambiguous, clear situations. The current findings that included implicit tasks as well as explicit categorization tasks are of particular importance because they reinforce the view that such a bias is a cognitive distortion in the interpretation of emotional cues, possibly strengthened by dynamic cues, and not purely a labeling bias.

Future directions

In the current study, we did not measure the IQ of the participants. Some previous studies have shown the impact of low IQ on crime (Hirschi & Hindelang, 1977) and on emotion recognition (Rojahn, 1995). Although we did not measure IQ, we carefully matched the two groups on education level. The control group participants were not selected among the societal upper class but rather from low social economic status groups. Nonetheless, in the future a non-violent, cognitively matched population would make for a better control population.

Another limitation of our study is that we, with the narrow range of tests used in this study, were not able to rule out the possibility that the results are explainable by aberrations in other cognitive processes rather than emotional ones, such as executive functioning. However, we think an alternative explanation is more likely. In a recent review, van Honk et al (2010) discuss that reactive aggression is essentially subcortically motivated by an imbalance in the levels of the steroid hormones cortisol and testosterone. This imbalance not only sets a predisposition for social aggression, but also down-regulates cortical-subcortical communication, hence diminishing control by cortical regions that regulate socially aggressive inclinations (van Honk, Harmon-Jones, Morgan, & Schutter, 2010). The finding that violent offenders faced more difficulties to ignore threatening irrelevant cues (threatening body expressions in experiment 4 and threatening scenes in experiment 5) fits with this theory. It is possible that these to be ignored threatening cues were first processed via the subcortical route, thereby facilitating immediate action towards the threat. In line with this possible explanation, it is not surprising that the offenders were more guided towards the threat and we only found this effect of incongruence in the case of a threatening emotion and not a happy one. Therefore, these deficits could be significantly accounted for by a compromised mechanism such as "cortical-subcortical communication". The psychobiological mechanisms underlying human social aggression are still poorly understood but research suggests positive correlations between testosterone and aggression (Terburg, Morgan, & van Honk, 2009). Future research should take into account these biological factors underlying aggression and violent behavior and possibly investigate these paradigms further by using connectivity analyses in fMRI.

A violent environment in which anti-social responses to threat were learned, in combination with an imbalance in the levels of the steroid hormones may the 'perfect' recipe for a violent offence. Fortunately, learned responses can still be modified. In recent years, cognitive-behavioral interventions including aggression regulation courses have been increasingly developed and implemented in Dutch forensic institutions. This approach seems successful since the number of prisoners is declining ever since (CBS, 2009). We believe that the new insights from our study can help to improve aggression regulation protocols. Future studies should investigate how best to implement emotion recognition training in a clinical setting.

Conclusion

We here show that violent offenders with high aggression scores are impaired in recognizing dynamic fearful body expressions and tended to misinterpret these as angry. Moreover, they had difficulties recognizing a happy facial expression when the body showed a threatening expression (fear or anger). Similarly, they were impaired in recognizing a happy body expression situated in an incongruent, violent scene. Importantly, when asked to match expressions, they were not impaired at all. In sum, we show that especially ambiguous, threatening cues interfere with emotion categorization in aggressive, offensive individuals.

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Chapter 9

Social context influences recognition of bodily expressions

This chapter is based on:
Kret, M.E., & de Gelder, B. (2010). Social context influences recognition of bodily expressions. *Experimental Brain Research 203*(1), 169-180.

Abstract

Previous studies have shown that recognition of facial expressions is influenced by the affective information provided by the surrounding scene. The goal of this study was to investigate whether similar effects could be obtained for bodily expressions. Images of emotional body postures were briefly presented as part of social scenes showing either neutral or emotional group actions. In Experiment 1, fearful and happy bodies were presented in fearful, happy, neutral and scrambled contexts. In Experiment 2, we compared happy with angry body expressions. In Experiment 3 and 4, we blurred the facial expressions of all people in the scene. This way, we were able to ascribe possible scene effects to the presence of body expressions visible in the scene and we were able to measure the contribution of facial expressions to the body expression recognition. In all experiments, we observed an effect of social scene context. Bodily expressions were better recognized when the actions in the scenes expressed an emotion congruent with the bodily expression of the target figure. The specific influence of facial expressions in the scene was dependent on the emotional expression but did not necessarily increase the congruency effect. Taken together, the results show that the social context influences our recognition of a person's bodily expression.

Introduction

Facial expressions are by far the most frequently used stimuli in human emotion perception research. Over decades, a large body of evidence has been published showing that emotion perception is not just based on facial information alone (Hunt, 1941). Indeed, in our natural world, a face is usually encountered not as an isolated object but as an integrated part of a whole body. The face and the body both contribute in conveying the emotional state of the individual. Meeren et al. (2005) show that observers judging a facial expression (fear or anger) are strongly influenced by emotional body language; an enhancement of the occipital P1 component as early as 115 ms after stimulus presentation onset points to the existence of a rapid neural mechanism sensitive to the agreement between simultaneously presented facial and bodily emotional expressions. Aviezer et al. (2008a) positioned prototypical pictures of disgust faces on torsos conveying different emotions. Their results showed that placing a face in a context induced striking changes in the recognition of emotional categories from the facial expressions to the extent where the "original" basic expression was lost when positioned on an emotionally incongruent torso (for the interested reader see Aviezer et al. 2008b). Knowledge of the social situation (Carroll and Russell 1996), body postures (Meeren et al., 2005; Van den Stock et al. 2007; Aviezer et al., 2008a), voices (de Gelder & Vroomen, 2000; Van den Stock et al. 2007), scenes (Righart & de Gelder, 2006, 2008a, b), linguistic labels (Barrett et al., 2007), or other emotional faces (Russel & Fehr, 1987) all influence emotion perception.

Research on context effects has a long tradition in object but not in face recognition. Because of repetitive co-occurrence of objects or co-occurrence of a given object in a specific context, our brains generate expectations (Bar & Ullman, 1996; Biederman et al., 1974). A context can facilitate object detection and recognition (Biederman et al., 1982; Boyce & Pollatsek, 1992; Boyce et al., 1989; Palmer, 1975), even when glimpsed briefly and even when the background can be ignored (Davenport and Potter 2004). Joubert et al. (2008) observed that context incongruence induced a drop of correct hits and an increase in reaction times, affecting even early behavioral responses. They conclude 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.

In line with the evolutionary significance of the information, the effects of the emotional gist of a scene may occur at an early level and it has been suggested that the rapid extraction of the gist of a scene may be based on low spatial frequency coding (Oliva & Schyns, 1997). We previously showed scene context congruency effects on the perception of facial expressions (Righart & de Gelder, 2006, 2008a, b). They were seen when participants explicitly categorized the emotional expression of the face (Righart & de Gelder, 2008a) but also when they focused on its orientation (Righart & de Gelder, 2006). This indicates that affective gist congruency reflects an early and mandatory process and suggests a perceptual basis. Our EEG studies support this view: the presence of a fearful expression in a fearful context enhanced the face-sensitive N170 amplitude when 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). Righart and de Gelder (2008a) replicated this finding by briefly (200 ms) presenting fearful faces in fearful versus happy scenes.

Similar context effects have already been found for bodies. Using point-light displays, Thornton and Vuong (2004) have shown that the perceived action of a walker depends upon actions of nearby "to-be-ignored" walkers. The task-irrelevant figures could not be ignored and were processed unconsciously to a level where they influenced behavior. Another point-light study demonstrates that the recognition of a person's emotional state depends upon another person's presence (Clarke et al., 2005).

If indeed we recognize a person's emotional behavior in relation to that of the social group, it is important to focus on the specific aspects of group behavior. Group behavior may be considered at different levels, of which three are relevant for understanding the visual process at stake: (1) the relative group size, (2) the dynamic motor and action aspects of the group and (3) the affective significance of the group's activity (Argyle 1988). Context effects may take place along all three dimensions and therefore require appropriate control conditions. First, group size is not considered as a variable in our study as the different group scenes used all have similar group sizes. The second and third aspects relating to action and effect were the focus of our recent brain imaging studies (de Gelder et al., 2004; Grèzes et al., 2007; Kret et al., 2011; Pichon et al., 2008) and see de Gelder et al. (2010) for an overview.

Here we investigated whether briefly viewed information from a task-irrelevant social scene influences how observers categorize the emotional body expression of the central figure. For this purpose, we selected scenes that represent a group of people engaged in an intense action either neutrally or affectively laden. By contrasting the affective meaning and keeping the action representation similar, we manipulated specifically the affective dimension of the social scenes. Our main interests were threefold. First, we aimed to investigate the influence of a congruent versus incongruent scene on body expression recognition. We expected enhanced performance in the congruent conditions. Second, we were interested in disambiguating the contribution from the emotion versus the action component. Our hypothesis was that the similarity along the emotion dimension of the social rather than along the action dimension influences recognition of the target body expression. If so, bodily expressions may be recognized faster in an emotionally congruent than in a neutral action scene indicating that the effect derives from target-scene emotional congruency. Third, we aimed to investigate the contribution of facial expressions visible in the scene to the recognition of emotional body expressions. Based on previous studies that report strong mutual influence of face and body expressions, we expected the strongest context effects when scenic facial expressions were visible.

In Experiment 1, these predictions were tested by presenting fearful and happy bodies in fearful, happy, neutral and scrambled contexts. In Experiment 2, we compared happy with angry body expressions. Experiment 3 was similar to Experiment 1, but the faces in the background were blurred to ascertain that possible effects were a result of the body expressions visible in the scene and not of bystanders' facial expressions. In Experiment 4, faces in the scenes were blurred and the same design as Experiment 2 was kept. We used naturalistic color photographs as color has been shown to improve object and scene recognition (Oliva & Schyns 2000; Wurm et al., 1993). Based on previous results (Righart & de Gelder, 2006, 2008a, b) and on studies of rapid scene recognition (Bar et al., 2006; Thorpe & Fabre-Thorpe, 2002; Maljkovic & Martini, 2005), we used short presentation times.

Angry, fearful, sad and happy expressions are the emotions that are most often used in emotion research (de Gelder, 2006). Here we specifically wanted to contrast a positive versus negative body expression in a positive/ welcoming versus negative/threatening social scene that one wants to avoid. As an opponent of the positive, happy emotion, we could choose among angry, disgusted, fearful or sad stimuli. We did not opt for sad bodies and scenes since these contain less action than happy bodies and scenes, whereas angry and fearful stimuli contain comparable action intensity. Whereas disgust can be expressed very clearly via the face, the body expressions are more ambiguous and resemble fearful expressions (de Gelder, 2006). We did not include anger and fear in one design since that would result in twice as many negative versus positive emotions. With the current design, we had an equal amount of positive and negative body expressions in each experiment.

The influence of a social context on the perception of an emotional body expression

Experiment 1. Fearful and happy bodies in a social emotional context including faces

Method

Images of emotional body postures were briefly presented in scenes showing intense group activities with either neutral or emotional valence. Participants rapidly categorized the target body expression.

Participants

Twenty-four students of Tilburg University (7 men; mean age: 20 years, range 17–25 years old) with no neurological or psychiatric history and normal or corrected-to-normal vision participated in the study. The experimental procedures were in accordance with the Helsinki Declaration and approved by Tilburg University.

Apparatus, Design and Procedure

We briefly describe the construction and validation of the target body stimuli. A total of 38 male and 46 female amateur actors were recruited. Prior to the photography session, they were instructed with a standardized procedure and received payment. As part of the instructions, the actors were familiarized with a typical scenario corresponding to each emotion; the fearful scenario was an encounter with an aggressive dog and the happy scenario was an encounter with a friend. A total of 869 body stimuli (consisting of fearful, happy, angry, sad, disgusted and neutral instrumental actions) were included in the validation study and were shown to 120 participants. Stimuli were presented for 4 s with an inter-stimulus interval of 7 s. Participants were instructed to categorize the emotion displayed by circling the correct answer on an answer sheet. Eight happy and fearful body images, correctly recognized on average for 91% (standard deviation, SD 10), were included in the experiment.

Scenes were selected from the Internet. We took care to make them gender balanced (for example, the neutral condition included a soccer field with male players; therefore, we also included a female hockey team playing). In a separate validation study, we measured affective gist recognition by presenting each image twice for 100 ms in random order. Fearful (people running away for danger), happy (people dancing at a party) and neutral scenes (people involved in sports) were correctly recognized for 87, 97, and 92%, respectively. Scenes showing bodies involved in neutral actions served as baseline.

We also validated the stimuli as they were used in the experiments described in this paper. The selected bodies were pasted on fearful, angry, happy and neutral scenes. These were presented with unlimited duration to 24 participants who had to categorize the emotion of the middle target body. The mean (M) recognition rates and SDs were as followed: angry bodies in angry scenes (M = 91%, SD 8), angry bodies in happy scenes (M = 89%, SD 11), angry bodies in neutral scenes (M = 91%, SD 9), fearful bodies in fearful scenes (M = 97%, SD 6), fearful bodies in happy scenes (M = 98%, SD 4), fearful bodies in neutral scenes (M = 96%,SD8), happy bodies in happy scenes (M = 75%, SD 21), happy bodies in fearful scenes (M = 73%, SD 23), happy bodies in angry scenes (M = 75%, SD 22) and happy bodies in neutral scenes (M = 77%, SD 21). Body expressions were not better or worse recognized in a congruent versus incongruent or in a congruent versus neutral scene when stimuli were presented with unlimited duration. See Fig. 1 for stimulus examples.

Mosaic squared scrambles (38 x 28) were created using MATLAB, containing identical luminance, color and contrast as the originals. For each scene category, eight similar scenes were included. There were two emotions (fearful and happy) shown by eight actors (half man), four context categories (fearful, happy, neutral, scrambles) and eight different scenes (versions) per context category, yielding eight conditions of 64 stimuli each (512 stimuli). Stimuli were arranged in two equivalent blocks to allow participants a 2-min break in between. Each block thus contained 256 randomized trials. In order to have the scrambles equally represented in the experiment and not to fatigue the participant with superfluous trials, we included 64 of the 384 scrambled counterparts of all unscrambled stimuli. Since we controlled for handedness by counterbalancing two versions of the experiment across the participants (in version 1, fear was button nr.1 on the response box and happy button nr. 2 and in version 2 the inverse), we were able to select different scrambles per version and use as many different ones as possible. Initially, we meant to use the scrambled condition as a non-emotion, non-action condition. However, across all experiments, bodies were significantly better recognized in these scrambled contexts than in non-scrambled contexts (possible pop-out effect or due to the semantic information content of the background) ($t(175) = 2.58$, $P < .01$) similar to the results for faces in scrambled context observed in Righart and de Gelder (2006). Therefore, the neutral condition was considered as a more viable baseline (see also Sommer et al., 2008). Compared to the scrambled scenes, neutral scenes still contain action (without emotion) and were therefore considered a better baseline.

Figure 1. Incongruent, congurent, neutral.

a) The upper left figure shows a man who is joyfully surprised and greets an old friend. Strangely, this man is in the middle of a fight.
b) The upper right figure shows a man who is threatening another person that also wants to join the fight.
c) Middle left: the woman on the foreground is frightened at something but the other people in the scene do not experience the situation as threatening and are still enjoying the party, as can be read from their body language. The incongruence makes recognition of the emotion of the foreground figure difficult.
d) Middle right: the girl on the foreground is happily welcoming a new visitor/a friend at the party. Her emotion matches the social situation and the emotion of the other people.
e-f) The figure below shows a man (left) and women (right) who are frightened at something. The people in the scene are involved in sports. Body expressions are easier to recognize when congruent with the social scene.

Participants were seated at a table in a dimly lit, soundproof booth. Distance to the computer screen was 60 cm. Stimuli were presented on a PC screen with a 60 Hz refresh rate and subtended 19.9° of visual angle vertically and 30.8° horizontally. Instructions were given verbally and via an instruction screen. Participants were given a two-alternative forced choice task over two emotions and were instructed to focus on the main figure in the middle of the screen, to categorize as accurate and rapid as possible its emotion, to respond with their right index and middle finger and not to change the position of their fingers during the experiment. A trial started with a white fixation cross on a gray screen (300 ms), a stimulus (100 ms), followed by a gray screen shown until button press (with a maximum duration of 8 s).

Results

Trials with reaction times (RT) below 200 ms or above 2,000 ms were discarded from the analysis, leading to 2.1% outliers. Trials were also excluded from the RT analyses if the response was incorrect. Main and interaction effects of scene and body emotion for mean accuracy (ACC) and RT were tested in a 2 9 3 repeated measures analysis of variance (ANOVA) with two within-participant variables, "body emotion" (fear and happy) and "context emotion" (fear, happy, neutral). T-test planned comparisons were used to test our hypothesis of congruency effects and to compare the perception of an emotional body expression in a congruent emotional scene with a scene that contains action but is emotionally neutral. We expected that a congruent social scene would not only enhance recognition, it would also speed up recognition when compared to an incongruent and also when compared to a neutral scene. All statistical information can be found in Table 1.

Accuracy

There was a main effect of context emotion [$F(2, 46) = 5.39$, $P< .01$, $\eta p2 = .19$] and for body emotion [$F(1, 23) = 4.30$, $P < .05$, $\eta p2 = .16$]. Bonferroni corrected pairwise comparisons revealed that bodies were better recognized in a neutral context than in a happy context ($P < .05$). Happy bodies were better recognized than angry bodies ($P < .01$). An interaction effect was observed for body emotion 9 context emotion [$F(2, 46) = 5.39$, $P < .01$, $\eta p2 = .19$]. Bodies, irrespective of the specific emotion, were more accurately recognized in a congruent context versus incongruent context and in a neutral context versus in an incongruent context. There was a trend toward significance for enhanced body recognition in a congruent context versus in a neutral context. Fearful body expressions were more accurately recognized in a fearful context than in a happy context or than in a neutral context. Happy bodies were better recognized in a happy versus in a fearful context but not versus in a neutral context.

Reaction time

An interaction was found for body emotion 9 context emotion [$F(2, 46) = 3.83$, $P < .05$, $\eta p2 = .14$]. Bodies were faster recognized in a congruent context versus in a neutral one. There was a trend toward significance for faster recognition of body expressions in a congruent versus neutral context but there was no difference between a neutral and incongruent context. There was a faster response for a fearful body in a fearful context than for a fearful body in a happy or neutral context. A happy body in a happy context when compared to in a fearful context did not yield a significant difference and neither when compared to in a neutral context.

Discussion

Target body expressions were more accurately recognized in congruent social scenes than in incongruent or baseline social scenes. Recognizing a fearful expression was more accurate in a context of people fleeing from danger and a happy body expression was best recognized in a context consisting of people dancing at a party. An emotionally congruent scene possibly speeds up the recognition process of fearful body expressions. Although fearful bodies were recognized faster in a fearful context, we cannot draw the conclusion that happy bodies were also faster recognized in the congruent condition. Importantly, the ACC congruency effects were no speed-accuracy trade-offs.

Experiment 2. Angry and happy bodies in a social emotional context including faces.

Our goal was to measure whether the observed effects of Experiment 1 would generalize to angry expressions. Therefore, we replicated the previous experiment with angry rather than fearful bodily expressions in an angry (congruent), happy (incongruent) or neutral context.

Methods

Participants

A new group of 22 students participated (5 men; range 18–25 years old, Mean: 21 years old).

Apparatus, Design and Procedure

Apparatus, design and procedure were identical to the former experiment with the difference of angry rather than fearful stimuli. Angry scenes (people on strike) were 88% correctly recognized as was measured subsequent to the main experiment in a separate validation of the scenes without foreground bodies. Eight angry body images that were on average correctly recognized for 92% (SD 10) replaced the fearful body images that were used in the previous experiment.

Results

ACC and RT were calculated after exclusion of two participants due to recognition at chance level and extremely fast RTs. 2.5% of the trials fell out of the range of 200–2,000 ms and were treated as outliers. Trials were also excluded from the RT analyses if the response was incorrect.

Accuracy

A main effect was found of body emotion [$F(1, 21) = 6.31$, $P < .05$, $\eta p2 = .23$]. Bonferroni corrected pairwise comparisons revealed that happy bodies were better recognized than angry bodies (M

= 86, SD 17 vs. M = 75, SD 16) ($P < .05$). There was no main effect of scene emotion. There was a significant interaction between body emotion and context emotion [$F(2, 42) = 17.41$, $P < .001$, $\eta p2 = .45$]. Bodies were better recognized in a congruent versus in an incongruent and versus in a neutral context and also in a neutral versus in an incongruent context. Angry bodies in an angry context were better recognized than in a happy context or in a neutral context. Happy bodies were better recognized in a happy context than in an angry context. Happy bodies were not better recognized in a happy than in a neutral context, although a trend toward significance was observed.

Reaction time

There was a main effect for body emotion [$F(1, 21) = 4.32$, $P < .05$, $\eta p2 = .17$]. Bonferroni corrected pairwise comparisons revealed that angry bodies were recognized faster than happy bodies (M = 649, SD 157 vs. M = 687, SD 210) ($P = 0.05$). An interaction effect between body emotion and context emotion was found [$F(2, 42) = 3.36$, $P < .05$, $\eta p2 = .14$]. Bodies were recognized faster in a congruent versus in an incongruent context and in a neutral context versus in an incongruent context. Target body expressions were not faster recognized in a congruent context versus in a neutral context. Angry bodies were recognized faster in an angry versus in a happy context but not versus in a neutral context. There was a trend toward significance for happy bodies in a happy versus in an angry context, but not when compared to in a neutral context.

Discussion

The congruency effect we found in Experiment 1 was also present for angry expressions. Angry bodies were more accurately and faster recognized in an angry context. Happy body expressions were better recognized in a happy context. We cannot rule out, however, the possible confounding influence of the presence of faces in the scenes.

The role of facial expressions in interactions between emotion of the context and body expression

Experiment 3. Fearful and happy bodies in a social emotional context with blurred faces

We repeated the first experiment but blurred the facial expressions that were still visible in the scenes that may have confounded the obtained results in Experiment 1. Blurring the faces allowed us to measure the influence of pure bodily expressions of bystanders on the recognition of one individual's body expression.

Method

Participants

A new group of 22 students participated (6 men; range 18–41 years old, Mean: 22 years old).

Apparatus, Design and Procedure

The single difference from Experiment 1 was the blurring of faces in the scenes.

Results

The trials that fell out of the pre-defined range that was used in the former experiments were considered as outliers (2.5%). Trials were also excluded from RT analyses if the response was incorrect.

Accuracy

An interaction effect was observed of body emotion 9 context emotion [F (2, 42) = 5.14, $P < .01$, $\eta_p^2 = .20$]. Bodies were better recognized in a congruent context versus in an incongruent context and in a congruent context versus in a neutral context. Moreover, bodies were better recognized in a neutral context versus in an incongruent context. Recognition of fearful bodies was better in a fearful context than in a happy context or than in a neutral context. Happy bodies were better recognized in a happy context than in a fearful context but not than in a neutral context, although a trend was observed.

Reaction time

A trend toward significance was found for the interaction body emotion 9 context emotion [F (2, 42) = 2.41, $P < .1$, $\eta_p^2 = .11$]. Body expressions were when compared to baseline facilitated by a congruent context and slowed down by an incongruent versus a congruent context. There was no difference between a neutral and incongruent context. RTs in the congruent fear condition were shorter than in the incongruent happy context and were also shorter than in the neutral context. Happy bodies were not recognized faster in a happy context when compared to in a fearful context or in a neutral context.

Discussion

The enhanced recognition ACC of body postures in congruent versus incongruent scenes found in Experiment 1 obtains when faces in the scenes were blurred. Happy bodies were best recognized in a happy context, fearful bodies in a fearful context. RTs in the congruent fear condition were shorter than fearful bodies in the happy or neutral scenes, but there was only a trend toward significance for the interaction body emotion * context emotion. The results indicate that the emotional congruency effect that we found in Experiment 1 cannot be attributed to the presence of facial expressions. The presence of people expressing emotions via bodily postures influences the perception of body emotion from the target figure. Our next question is whether the same conclusion can be drawn for angry expressions.

Experiment 4. Angry and happy bodies in a social emotional context with blurred faces

Method

Participants

A new group of twenty students participated (7 men; range 19–30 years old, Mean: 22 years old).

Apparatus, Design and Procedure

Apparatus, design and procedure were identical to the former experiment that used blurred faces with the sole difference of angry instead of fearful stimuli.

Results

Due to recognition at chance level, three participants were excluded from analysis. Moreover, 2.4% of the trials were excluded since they fell out of the pre-defined range that was maintained across all experiments. Trials were also excluded from the RT analyses if the response was incorrect.

Accuracy

A main effect was found of context emotion [F (2, 38) = 4.57, $P < .05$, ηp2 = .19]. Bonferroni corrected pairwise comparisons revealed that bodies were better recognized in a happy context than in an angry context ($P < .05$). There was an interaction effect between body and context emotion [F (2, 38) = 5.22, $P < .01$, ηp2 = .22]. Bodies were better recognized in a congruent context versus in a neutral or incongruent context and in a neutral context versus in an incongruent context. Angry bodies in an angry context were better recognized than in a happy context but not than in a neutral context. Happy bodies in a happy context were more accurately recognized than in an angry context or than in a neutral context.

Reaction time

There were no main or interaction effects. In the perspective of the former experiments, we had clear expectations about a possible facilitating influence of a congruent scene and therefore, we conducted planned comparison paired samples t-tests. These revealed that RTs in the congruent anger condition were shorter than in the happy context but not than in the neutral context. Happy bodies were not recognized faster in happy contexts when compared to in angry or neutral contexts.

Discussion

After having blurred the faces, all effects remained in the ACC data and for the angry but not happy body expressions in the RT data. The results were not related to speed-accuracy trade-offs. See Fig. 2.

The presence of facial expressions

Difference scores of congruent and incongruent conditions were calculated and independent sample t-tests conducted to compare the context congruency effect in the experiments where faces were still visible versus where they were not.

Angry body expressions

The congruency effects in the ACC data of angry body expressions were stronger in the experiments where facial expressions were visible: ACC anger non-blurred congruent—incongruent (M difference = .13, SD .10) versus anger blurred congruent— incongruent (M difference = .04, SD .12) ($t(40) = 2.61$, $P < .05$, $d = .80$). Subsequent t-tests revealed the origin of this effect; angry body expressions were better recognized in a happy context where faces were blurred than where they were visible (M = 77%, SD 18 vs. M = 70%, SD 17) ($t(40) = 1.38$, $P = .09$, $d = .43$). This was not due to the specific presence of happy facial expressions since a similar effect was observed for the presence of neutral facial expressions (blurred vs. non-blurred (M = 72%, SD 13 vs. M = 80%, SD 15) ($t(40) = 1.89$, $P < .05$, $d = .58$). The presence of angry facial expressions did not influence ACC or RT.

Fearful body expressions

A numerically consistent but non-significant trend as with angry body expressions was observed.

Happy body expressions

The congruency effect in the ACC data of happy bodies (in happy or angry context) was larger when facial expressions were invisible (M difference = -.09, SD .25 vs. M difference = .11, SD .16) ($t(40) = 2.97$, $P < .01$, $d = .93$). Subsequent t-tests did not reveal any differences. There were no differences in the RTs.

In conclusion, the influence of facial expressions in the scene was dependent on the specific emotional expression. The presence of facial expressions was not the crucial factor toward a congruency effect. In all four experiments, the body expressions in the scene influenced how the target body expression was perceived.

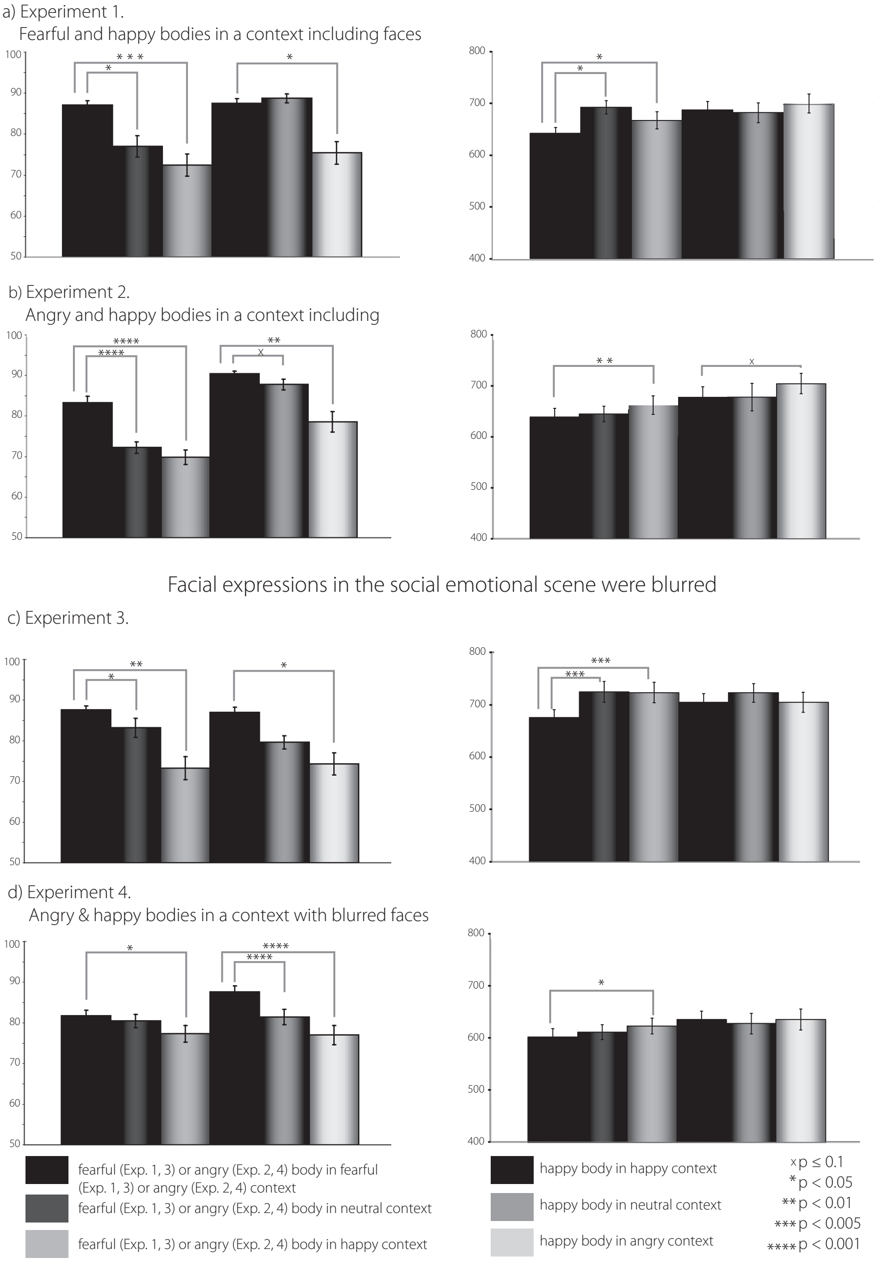
Table 1.

Experiment 1 (N = 24)										
			Accuracy				**Reaction time**			
Congruent context	vs.	Incongruent context	*M* 87 SD 10	vs.	74 26	$t = 2.43, p < .05, d = .31$	665 110	vs.	682 129	$t = 1.59, p = .063, d = .14$
Congruent context	vs.	Neutral context	*M* 87 SD 10	vs.	83 15	$t = 1.53, p = .07, d = .32$	665 110	vs.	688 137	$t = 1.97, p < .05, d = .19$
Neutral context	vs.	Incongruent context	*M* 83 SD 15	vs.	74 26	$t = 3.17, p < .005, d = .42$	688 137	vs.	682 129	$p = .650$
Fearful body in fearful context	vs.	Fearful body in happy context	*M* 87 SD 10	vs.	72 26	$t = 2.76, p < .005, d = .76$	643 108	vs.	668 129	$t = .79, p < .05, d = .21$
Fearful body in fearful context	vs.	Fearful body in neutral context	*M* 87 SD 10	vs.	77 26	$t = 1.89, p < .05, d = .51$	643 108	vs.	693 162	$t = 2.52, p < .01, d = .36$
Happy body in happy context	vs.	Happy body in fearful context	*M* 88 SD 12	vs.	75 27	$t = 2.08, p < .05, d = .64$	687 115	vs.	696 138	$p = .228$
Happy body in happy context	vs.	Happy body in neutral context	*M* 88 SD 12	vs.	89 10	$p = .160$	687 115	vs.	682 124	$p = .276$
Experiment 2 (N = 22)										
			Accuracy				**Reaction time**			
Congruent context	vs.	Incongruent context	*M* 87 SD 8	vs.	74 16	$t = 4.07, p < .001, d = 1.03$	659 170	vs.	683 196	$t = 3.02, p < .005, d = .13$
Congruent context	vs.	Neutral context	*M* 87 SD 8	vs.	80 9	$t = 5.68, p < .001, d = .82$	659 170	vs.	661 174	$p = .302$
Neutral context	vs.	Incongruent context	*M* 80 SD 9	vs.	74 16	$t = 2.53, p < .01, d = .46$	661 174	vs.	683 196	$t = 3.19, p < .01, d = .12$
Angry body in angry context	vs.	Angry body in happy context	*M* 83 SD 15	vs.	70 17	$t = 6.13, p < .001, d = .81$	639 160	vs.	662 146	$t = 2.54, p < .01, d = .15$
Angry body in angry context	vs.	Angry body in neutral context	*M* 83 SD 15	vs.	72 13	$t = 9.45, p < .001, d = .78$	639 160	vs.	645 170	$p = .240$
Happy body in happy context	vs.	Happy body in angry context	*M* 90 SD 7	vs.	79 24	$t = 2.70, p < .01, d = .62$	678 189	vs.	705 256	$t = 1.32, p = .101, d = .12$
Happy body in happy context	vs.	Happy body in neutral context	*M* 90 SD 7	vs.	88 13	$t = 1.34, p = .096, d = .19$	678 189	vs.	678 187	$p = .485$

Experiment 3 (N = 22)										
			Accuracy				**Reaction time**			
Congruent	vs.	Incongruent	*M* 87 SD 8	vs.	74 25	$t = 2.47, p < .05, d = .70$	691 145	vs.	714 174	$t = 1.98, p < .05, d = .14$
Congruent	vs.	Neutral	*M* 87 SD 8	vs.	81 14	$t = 2.09, p < .05, d = .52$	691 145	vs.	724 166	$t = 3.00, p < .005, d = .21$
Neutral	vs.	Incongruent	*M* 81 SD 14	vs.	74 25	$t = 2.63, p < .01, d = .35$	724 166	vs.	714 174	$p = .288$
Fearful body in fearful context	vs.	Fearful body in happy context	*M* 88 SD 9	vs.	73 27	$t = 2.69, p < .01, d = .77$	676 142	vs.	724 183	$t = 3.12, p < .005, d = .29$
Fearful body in fearful context	vs.	Fearful body in neutral context	*M* 88 SD 9	vs.	80 22	$t = 1.92, p < .05, d = .48$	676 142	vs.	725 186	$t = 3.27, p < .005, d = .30$
Happy body in happy context	vs.	Happy body in fearful context	*M* 87 SD 11	vs.	74 26	$t = 2.22, p < .05, d = .65$	705 180	vs.	705 157	$p = .499$
Happy body in happy context	vs.	Happy body in neutral context	*M* 87 SD 11	vs.	83 16	$p = .105$	705 180	vs.	723 168	$p = .118$
Experiment 4 (N = 20)										
			Accuracy				**Reaction time**			
Congruent context	vs.	Incongruent	*M* 85 SD 10	vs.	77 18	$t = 2.54, p < .01, d = .55$	619 140	vs.	626 139	$p = .178$
Congruent context	vs.	Neutral context	*M* 85 SD 10	vs.	81 13	$t = 2.72, p < .01, d = .34$	619 140	vs.	624 145	$p = .250$
Neutral context	vs.	Incongruent context	*M* 81 SD 13	vs.	77 18	$t = 1.85, p < .05, d = .25$	624 145	vs.	626 139	$p = .713$
Angry body in angry context	vs.	Angry body in happy context	*M* 82 SD 12	vs.	77 18	$t = 1.67, p < .05, d = .29$	603 120	vs.	624 130	$t = 2.35, p < .05, d = .17$
Angry body in angry context	vs.	Angry body in neutral context	*M* 82 SD 12	vs.	80 15	$p = .253$	603 120	vs.	612 126	$p = .150$
Happy body in happy context	vs.	Happy body in angry context	*M* 88 SD 13	vs.	77 21	$t = 3.01, p < .005, d = .63$	636 166	vs.	628 154	$p = .449$
Happy body in happy context	vs.	Happy body in neutral context	*M* 88 SD 13	vs.	81 17	$t = 3.74, p < .001, d = .46$	636 166	vs.	636 172	$p = .493$

Congruent = happy body in happy context + anger (or fearful) body in anger (or fearful) context; Incongruent = happy body in anger (or fearful) context + anger (or fearful) body in happy context; Neutral = happy body in neutral context + anger (or fearful) body in neutral context; M = mean (in percentage correct or milliseconds); SD = standard deviation.

Figure 2. Percentage correct and reaction times.



a) Recognition was more accurate and faster for a fearful body in a fearful versus happy or neutral context. A happy body in a happy versus fearful context was better recognized.
b) Angry bodies in an angry context were more accurate and faster recognized than in a happy context and happy bodies in a happy versus angry (or neutral for ACC data) context.
c) Congruency effects in the ACC data for both body emotions were observed. Moreover, fearful bodies were better and faster recognized in a fearful versus neutral and happy context.
d) Angry bodies in an angry context were more accurately and faster recognized than in a happy context. Happy bodies in a happy context were better recognized versus in an angry or neutral context. In sum, individual body expressions were best recognized in emotionally congruent social scenes.

General Discussion

The aim of this study was to investigate the influence of social contexts on the recognition of a single emotional body expression. The effects of congruency on emotional body perception were investigated using manipulated photographs containing a foreground figure that was either displaying the same or a different emotion than the people in the background. In the first experiment, participants categorized as fast as possible the emotion of the actor (fear and happy). In the second experiment, the task was similar, but we used different emotions (anger and happy). The third experiment was similar to Experiment 1, but the faces of the people in the scene were blurred to ascertain that the obtained effects were specifically related to the congruence of the body expressions seen in the background. In the fourth experiment, angry and happy expressions were used and faces in the scenes were blurred. Finally, the effect of the presence of facial expressions was tested by comparing reaction times and accuracy rates of all conditions of Experiment 1 with 3 and 2 with 4.

In the human emotion literature, there is thus far no answer to the question of whether our recognition of an individual's emotional body language is influenced by bodily expressions of other individuals as perceived in a naturalistic scene. It is known that an emotional scene influences the perception of facial expressions. Body expressions, in contrast to facial expressions, represent and implement emotion, but in addition also direct action. Therefore, we go beyond our prior studies by investigating the role of the social emotional scene representing actions from other people on the perception of an individuals' emotional body expression. During our life span, we are confronted more often with situations where people express similar (group) emotions and therefore it is likely that we are quicker and better in reacting to less ambiguous situations since this has survival value. Therefore, we predicted an enhanced recognition of body expressions in an emotionally congruent versus incongruent and neutral social action scene especially when facial expressions in the scenes were visible.

Indeed, fearful, angry and happy body expressions were more accurately recognized in congruent social emotional scenes. We observed a significant contribution to a congruency effect of the presence of facial expressions in Experiment 4 versus 2. This was merely due to increased incongruence for an angry body in a happy and neutral context with facial expressions visible. The presence of facial expressions did not increase ACC in the congruent conditions and neither specifically speeded up processing. However, different participants were involved in the different experiments. For the interested reader, see Meeren et al. (2005); Van den Stock et al. (2007); Aviezer et al. (2008a, b).

The actions we see going on in the background may automatically trigger action representation. We hypothesized that when the actions seen in the background have emotional significance similar to that of the central character, the target recognition would speed up. In Experiment 1 and 3, we indeed found that fearful bodies were recognized faster in a fearful than in a happy or neutral context. Furthermore, the presence of other angry people in the scene speeded up the RT in the observer when compared to when the angry body expression was perceived in a happy context (Experiment 2). After having blurred the faces in Experiment 4, we lost the interaction between body and scene emotion in the RTs, but a congruency effect for angry expressions was still present. All predicted effects were present in the ACC data. We found the strongest congruency effects for the RT data in the fearful body scene compounds. Although we expected to find it as clearly for the other emotions, thinking about how fast mass panic can spread out over many people versus observers' ambivalent behavior in an aggressive situation(fight, help or flight?) or the time it takes to "warm up/ drink in" at a party, this might not be a strange result after all.

Our study is in line with earlier studies about scene congruency effects in object recognition. For example, if there is high probability that a certain context surrounds a visual object, the processing of that object is facilitated, whereas unexpected contexts tend to inhibit it (Palmer, 1975; Ganis & Kutas, 2003; Davenport & Potter, 2004; but see also Hollingworth & Henderson 1998). Studies of scene recognition and context effects show that scenes can be processed and scene gist recognized very rapidly (Thorpe & Fabre-Thorpe, 2002; Maljkovic & Martini, 2005; Bar et al., 2006; Joubert et al., 2007). ERPs recorded from the visual cortices demonstrate differences between emotional and neutral scenes as early as 250 ms from stimulus onset (Junghöfer et al., 2001). In a recent study, Joubert et al. (2008) investigated the time-course of animal/context interactions in a rapid go/no-go categorization task. They conclude that the congruence facilitation is induced by the customary co-activation of "congruent" populations of neurons, whereas interference would take place when conflicting populations of neurons fire simultaneously.

However, our study includes the factor 'emotion'. Emotions are intimately linked to action preparation. The results of the current study are in line with the few experimental studies that currently exist on the influence of emotional scenes on the perception of faces and bodies and imply that the facilitating effect of context congruence reflects a mandatory process with an early perceptual basis (Righart & de Gelder 2006).

There is a possibility that the congruency effect occurs at the response level. Especially in case of a more ambiguous stimulus participants may attend to the context. However, there is not much time for that and it is against the task instructions. A presentation time of 100 ms (although not masked) is too short to make saccades from the fixation point. Biederman et al. (1982) and Davenport and Potter (2004) have shown that 100 ms is sufficient to expect pop-out effects between background and foreground object. In the current experiment, the foreground figure is pasted on the background and although we tried to make the scene as naturalistic as possible, some pop-out effect of the foreground figure may have come through. However, if so, this will be true as much in all conditions since all the foreground bodies were combined with all scenes. Moreover, when stimuli were presented with unlimited presentation duration, and scenes processed consciously, body expressions were not better or worse recognized in a congruent versus in an incongruent or neutral scene that also speaks against a response conflict.

Finally, yet other processes than the ones measured here 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, consequently, to converge emotionally may play a role (de Gelder et al., 2004; Hatfield et al., 1994). The same brain areas are involved when subjects experience disgust (Wicker et al., 2003) or pain (Jackson et al., 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. This incongruity may create a conflict in emotional contagion processes triggered by the target figure and help to explain the slower and less accurate reaction of the observer. This explanation needs further testing using EMG measurements.

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Chapter 10

Measuring the influence of the social context on individual motion expressions with eye gaze and EMG recordings

Abstract

Previous studies have shown that recognition of facial and bodily expressions is influenced by the affective information from the surrounding scene. For example, recognition of a central bodily expression is hampered when the scene context represents an emotion different from the target figure. Although attention is drawn to the central figure, important aspects of a scene, including threatening or ambiguous cues, are generally looked at for longer periods than less important parts of the scene. To clarify this issue we measured participants' eye movements and EMG responses while watching emotionally (in)congruent body-scene compounds. Fixations were longer for angry than for happy body expressions situated in a neutral scene, thereby suggesting that attention is preferentially allocated to cues indicating potential threat in social situations. Fixation duration on happy bodies was influenced by the emotion depicted in the scene. There was no interaction between the emotion of the body and the emotion of the scene in the EMG data, but an angry scene increased the corrugator response and a happy scene the zygomaticus.

Introduction

Sitting on a terrace in the sun, it is always amusing to look at the people passing by and to spot those that look attractive, strange or pop out for some other reason. However, when a man suddenly starts yelling angrily, making heated gestures, people tend to look away from this person. In fact, we are experts in detecting people that seem to be 'out of place' and observing their body language is richly informative in that respect (de Gelder, 2006). Recent technologies including eye movement and gaze pattern recordings have been used to further the understanding of this ability.

Ousov-Fridin (2009) observed that people tend to fixate on the head when looking at joyful pictures, whereas for threatening pictures, most attention was devoted to the hands and arms. The legs almost never drew the observers' attention. Bannerman et al (2008) investigated participants orienting behavior using EOG electrodes measuring eye movements. Participants were instructed to make a saccade (or in another condition, a manual response), as fast as possible, to the side where the fearful body (or in another condition, the neutral body or face) appeared. In half of the trials, the stimuli were presented for 20 ms, and in the other half for 500 ms. The authors observed faster saccadic orienting to fearful body and face emotions compared with neutral, only at the shortest presentation time. For manual responses, faster discrimination of fearful cues was observed only at the longest duration (Bannerman, Milders, de Gelder, & Sahraie, 2009). We recently observed that participants looked shortest at happy bodies and longer at threatening ones. Moreover, looking patterns on the face were influenced by the bodily expression and looking patterns on the body were influenced by the facial expression (Kret et al., in prep).

Emotional expressions play a fundamental role in social interactions, as shown by the spontaneous tendency to synchronize our facial expressions with those of another person during face-to-face situations, a phenomenon termed emotional contagion (Hatfield, Cacioppo, & Rapson, 1994). The phenomenon that observers tend to spontaneously produce facial movements similar to the facial expression of the person observed has been supported by a substantial number of electromyography (EMG) studies (Dimberg & Lundquist, 1990; Dimberg & Thunberg, 1998). Such studies typically record muscular reactions of the zygomaticus major, which pulls the corners of the mouth up and back, and the corrugator supercilii, which pull the eyebrows together and downwards. Generally, corrugator supercilii activity is higher in response to frowning faces, whereas zygomaticus major activity is higher in response to smiling faces. Similar results have been obtained with bodily expressions indicating that we not simply mimic other people, but unconsciously synchronize emotionally with them (Tamietto et al., 2009).

In contrast to stimuli that are commonly used in lab situations, in our natural world, a face is usually encountered not as an isolated object but as an integrated part of a whole body situated in a scene (Kret & de Gelder, 2010). We immediately notice an emotion that seems out of place and often perceive these situations as embarrassing, rude or even anxious (laughing when someone falls, acting angrily in a sad situation etc). We recently showed that we recognize briefly (100 ms) presented images of bodily expressions situated in an emotion scene more accurately in an emotionally congruent versus incongruent situation (Kret & de Gelder, 2010).

It is not known how the above findings relate to situations where other people can be observed much longer and be attended to consciously. In fact, the earlier reported effects of incongruency on recognition performance were not significant with an unlimited presentation duration (Kret & de Gelder, 2010). In order to further investigate this finding, we presented emotionally (in)congruent body-scene compound stimuli for 4000ms and investigated looking patterns and EMG responses over the total stimulus presentation duration.

One main question of this research is whether we observe emotional people differently when their expression does not match with the surrounding social scene. Another key question is whether emotional incongruency between a body and a scene obstructs emotional contagion. In Experiment 1, we measured peoples' facial musculature reactions and eye gaze behavior while they looked at bodily expressions of emotion that were presented in emotionally congruent or incongruent social scenes. In Experiment 2, the same scenes were presented again, but this time much shorter (100ms) and participants categorized the bodily expressions by ignoring as much as possible the background (same experiment, but with a new group of participants as in (Kret & de Gelder, 2010)).

Experiment 1. Passively viewing other people with emotional expressions in congruent or incongruent social, emotional scenes

Methods

Participants: Twenty-eight participants (19 females, mean age 21.9 years old, range 18-27 years old; 9 males; mean age: 23.9 years old, range 20-32 years old) took part in the experiments. Participants had no neurological or psychiatric history, were right-handed and had normal or corrected-to-normal vision. All gave informed consent. The study was performed in accordance with the Declaration of Helsinki and was approved by the local medical ethical committee.

Materials: We briefly describe the construction and validation of the target body stimuli. Eight happy and fearful body images, on average correctly recognized at 91% (SD 10), were included in the experiment. Angry (fights), happy (party) and neutral (sports) scenes were selected from the Internet. Emotionally congruent and incongruent body postures were pasted in the social emotional scenes. For a detailed description of the validation procedure of these stimuli, see (Kret & de Gelder, 2010).

Data analysis: Main and interaction effects of bodily expression in congruent and incongruent scenes recognition performance (mean accuracy and reaction times), EMG (zygomaticus and corrugator muscle), fixation duration and scanpath were tested in an ANOVA with three within-participant variables 'body expression' (Anger or Happy), 'scene emotion' (Anger, Neutral or Happy) and in the case of fixation durations, 'time' (4 seconds were divided in 500 ms timeslots).

Facial EMG

By using BioSemi flat-type active electrodes, facial EMG was measured bipolarly over the regions of the zygomaticus major and the corrugator supercilii on the right side of the face. Two additional electrodes, the common mode sense [CMS] active electrode and the driven right leg [DRL] passive electrode, were attached to the left cheek and used as reference and ground electrodes, respectively (http://www.biosemi/faq/cms&drl.htm). Before attachment, the skin was cleaned with alcohol and the electrodes were filled with electrode paste. The raw data were digitally filtered offline with a 20–500 Hz band-pass in Brain Vision Analyzer Version 1.05 (Brain Products GmbH), rectified and segmented into 5000 ms epochs, including a 1000 ms pre-stimulus baseline. Data were then visually inspected for remaining artefacts by two independent raters that were blind to the specific condition of these trials. The problematic trials that were detected by both were immediately discarded and trials that were indicated as problematic by one rater were discussed, resulting in the exclusion of 0.061% of the trials from subsequent analysis. These trials were discarded due to abundant movement during baseline. The parameters for facial EMG acquisition and analysis were selected to conform to published guidelines for this psychophysiological technique (DeLuca, 1997; van Boxtel, 2001).

Eyetracking

Eye movements were recorded using the EyeLink Eye Tracking System which is a lightweight head mounted tracking device (SensoMotoric Instruments GmbH, Germany). Gaze position was sampled at a rate of 500 Hz. A drift correction was performed on every trial to ensure that eye movement data was adjusted for movement of the headset and/or body. The eye-event detection is based on an internal heuristic saccade detector built in the EyeLink tracker program. A blink is defined as a period of saccade-detector activity with the pupil data missing for three or more samples in a sequence. A saccade was defined as a period of time where the saccade detector was active for 2 or more samples in sequence and continued until the start of a period of saccade detector inactivity for 20 msec. The configurable acceleration (8000 degrees/sec/) and velocity (30 degrees/sec) threshold were set to detect saccades of at least 0.5 degrees of visual angle. A fixation is the maintaining of the visual gaze on a single location and is defined as any period that is not a blink or saccade. To adjust for individual differences in fixation duration due to blinking or momentary distraction from the screen, analyses were performed on the proportion of time spent looking at each interest area within the time spent looking on the screen. The first 200ms were discarded from all analyses because since we used a fixation cross on a fixed location, the first fixation automatically fell on that spot in the stimulus and is thus not informative. Length of scan path is defined as the average saccade amplitude multiplied by the number of saccades on the whole screen as measured over the full four seconds of stimulus presentation.

Procedure

Participants sat 1 metre from the PC monitor. The eye-tracking device was positioned on the participant's head and a 9-point calibration and validation routine of the eye tracker was performed. Stimuli were presented using Eprime software on a PC screen with a resolution of 1024 by 768 and a refresh rate of 100 Hz. Each trial started with a white fixation-cross on a grey screen, shown for minimally 3000ms (until the participant fixated and a manual drift correction was performed) followed by a picture presented for 4000ms followed by a blank grey screen (3000ms). Participants were given a short break after this task. In the second task, participants were given a two-alternative forced choice task over two emotions (happy and anger) and were instructed to focus on the main figure in the middle of the screen and ignore the scene, and to categorize as accurately and rapidly as possible the body emotion, to respond with their right index and middle finger and not to change the position of their fingers during the experiment. A trial started with a white fixation cross on a gray screen (300 ms), a stimulus (100 ms), followed by a gray screen shown until button press (with a maximum duration of 8 s). Eye movements were not recorded because of the short presentation time. To keep them naive regarding the purpose of the EMG, they were told that the electrodes served the recording of sweat. The eye tracking cameras were said to measure pupil dilation during the task, to conceal the recording of gaze (Kellough, Beevers, Ellis, & Wells, 2008).

In experiment 1, there were 48 randomly presented trials with (in)congruent unique body-scene compound stimuli (8 actors (half male), 2 bodily expressions (anger and happy), 3 context emotions (anger, happy neutral). An interest area was created around the body (including the head) and both hands and eye tracking analyses were performed within these areas (left and right hand pooled). Participants were told that they were going to see other people at the PC screen and were instructed to attend to the fixation-cross and subsequently to look at the images any way they wanted. No reference was made to emotional expressions or ambiguous signals.

In Experiment 2, the stimuli were presented much shorter (100 ms) and they were presented twice, resulting in 96 trials. Participants were instructed to categorize the middle bodily expression and not to pay attention to the scene. It was made very explicit that they had to make their judgments based on the target bodily expression only (Kret & de Gelder, 2010).

Data analysis

We divided the 4 seconds of total stimulus presentation time in the passive viewing task into eight 500 ms timeslots. We analyzed the influence of the following factors: bodily expression, scene emotion and time on looking patterns on the body and EMG responses. A Greenhouse-Geisser correction was applied when the sphericity assumption was not met (Greenhouse & Geisser, 1959).

Results

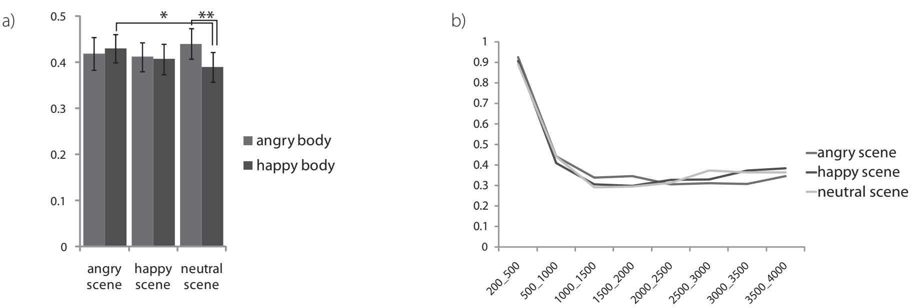
Experiment 1. Eye-tracking and EMG responses towards bodily expressions in social scenes

Relative fixation duration

There was a main effect of time [F(3.04, 82.14) = 158.538, $p < .001$, corrected]; looking times decreased between T1-T3 ($p < .001$) but were slightly increasing from T5 onwards, with a marginally significant difference with T8 ($p = .095$). The interaction between body and scene emotion [F(2, 54) = 3.581, $p < .05$] showed that happy bodies were longer looked at in an angry than neutral scene t(27) = 2.443, $p < .05$. Moreover, in a neutral scene, participants attended more to the bodies with threatening than happy postures t(27) = 2.756, $p < .01$.

The influence of the scene on looking patterns on the body depended on time (time * scene emotion) [F(8.66, 233.96) = 2.260, $p < .05$, corrected]. At T4, participants looked longer at a body situated in an angry versus happy or neutral scene [t(27) = 2.416, $p < .05$; t(27) = 2.610, $p < .05$ respectively]. However, inspection of figure 1b shows that after 2000-2500 ms, the pattern inverses, yet no further significant effects of scene emotion were observed.

Figure 1. Relative fixation duration on bodies.



a) Relative fixation duration on bodies as a function of bodily expression and emotion of the scene, averaged over stimulus presentation duration (4000 ms, except the first 200 ms). b) Relative fixation duration on bodies as a function of emotion of the scene, independent of bodily expression.

Length of scan-path (number of saccades * average amplitude of saccade)

Participants scanned the whole picture more when the body showed a happy versus angry expression [F(1, 27) = 7.405, $p < .05$]. See figure 2.

Zygomaticus

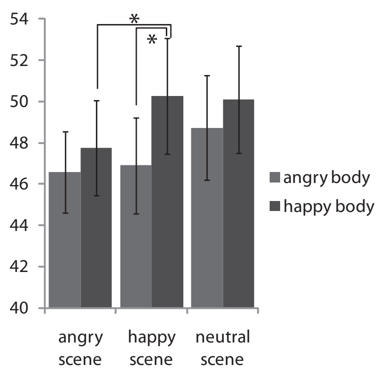
There was an effect of scene emotion [F(2, 54) = 5.059, $p < .01$]. The zygomaticus responded more following a happy than angry ($p < .05$) or neutral scene ($p = .09$).

Figure 2. Scanpath on bodies in scenes.

a) happy body in happy scene

b) angry body in happy scene

c)



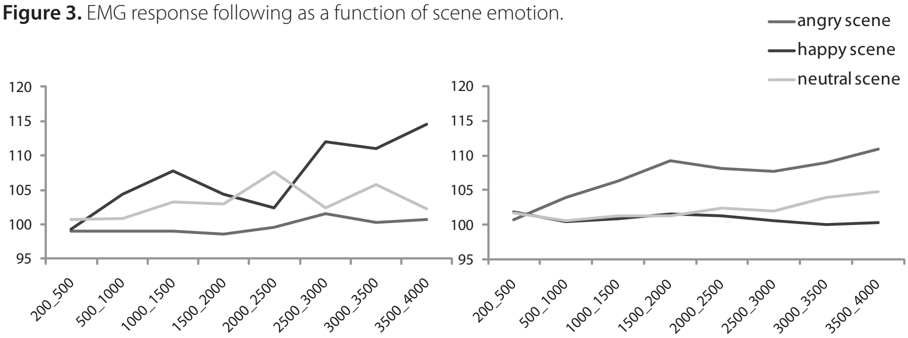
a-b) Fixations and saccades of one participant. The size of the blue circles indicates the duration of the fixation. The yellow lines are saccades and the yellow numbers indicate the order in which these were made. The yellow line around the body shows how the interest area was created.

c) length of scanpath (number of saccades multiplied by their average amplitude).

Corrugator

There was an interaction between time and emotion of the scene [$F(2.93, 79.03) = 3.558$, $p < .05$, corrected]. Whereas the corrugator response was relatively stable over time for happy and neutral scenes, it increased for angry scenes, making the difference between the emotion categories larger with time. Comparing the corrugator response for angry versus happy scenes averaged over the last two seconds of total stimulus presentation duration, yielded a significant difference $t(27) = 2.489$, $p < .05$.

Figure 3. EMG response following as a function of scene emotion.



a) the zygomaticus was most active following happy versus angry and neutral scenes.

b) the corrugator was most active following angry versus happy or neutral scenes, but only significantly in the second half of stimulus presentation time.

Table 1. EMG response following bodily expressions in emotional scenes

	Time (ms)	0-500		500-1000		1000-1500		1500-2000		2000-2500		2500-3000		3000-3500		3500-4000	
Body	**Scene**							**Zygomaticus**									
	angry	99.41	5.82	100.03	10.03	99.72	14.98	99.15	14.83	101.46	20.37	101.12	20.11	101.23	19.22	102.71	21.96
	happy	98.29	7.58	101.64	16.49	102.39	19.51	97.72	16.13	100.12	18.62	113.84	44.81	108.70	36.63	118.16	66.24
angry	neutral	101.03	11.09	100.28	11.51	101.66	12.07	101.90	12.17	104.77	35.81	97.63	10.59	99.35	17.55	97.31	14.46
	angry	98.53	7.78	97.93	11.45	98.27	15.83	98.12	17.15	97.68	19.08	102.10	23.91	99.47	18.52	98.82	15.98
	happy	100.38	6.61	107.14	33.00	113.29	50.43	110.92	34.24	104.70	19.11	110.14	28.51	113.48	36.09	110.90	27.47
happy	neutral	100.49	11.85	101.32	15.17	104.72	25.79	103.91	27.02	110.37	46.40	107.11	38.84	112.17	63.59	107.20	36.65
								Corrugator									
	angry	100.19	4.18	103.73	11.96	104.12	14.34	106.30	18.83	104.63	16.98	106.16	18.66	108.36	24.84	108.27	25.97
	happy	102.11	4.26	100.28	3.76	99.46	6.31	100.10	6.60	101.27	11.92	100.37	10.07	99.96	10.52	99.11	10.06
angry	neutral	101.64	5.47	101.83	6.70	101.79	7.89	102.59	7.62	103.40	8.65	102.06	7.88	104.60	9.79	106.20	12.67
	angry	101.30	3.52	104.05	9.00	108.62	17.66	112.26	23.10	111.58	23.91	109.36	23.76	109.56	19.43	113.64	26.21
	happy	101.49	3.78	100.73	6.01	102.34	7.45	103.03	10.06	101.28	8.53	100.74	9.64	100.02	12.77	101.51	13.24
happy	neutral	101.82	4.86	99.51	7.61	100.80	8.47	99.89	7.03	101.54	6.64	101.97	7.30	103.18	9.72	103.41	10.90

Experiment 2. Recognition of bodily expressions of emotion presented in emotionally (in)congruent social scenes

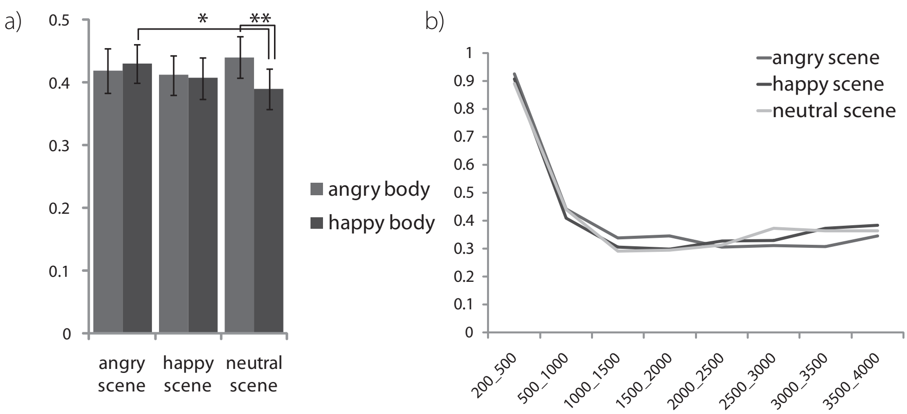
Accuracy

A main effect of body emotion was observed [F (1, 27) = 20.480, $p < .001$]. Angry bodies were better recognized than happy ones ($p < .001$). There was an interaction between emotion of the body and emotion of the scene [F (2, 54) = 3.740, $p < .05$]. As expected, angry body expressions were more accurately recognized in an angry versus happy scene [t(27) = 1.988, $p < .05$, one tailed] and happy body expressions better in a happy than angry scene, although only a marginally significant effect was observed [t(27) = 1.628, $p = .054$, one-tailed].

Reaction time

There was an interaction between emotion of the body and emotion of the scene [F (2, 54) = 3.974, $p < .05$]. As expected, angry body expressions were faster recognized in an angry versus happy scene, although the effect was only marginally significant [t(27) = 1.514, $p = .070$, one tailed].

Figure 4. Proportion correct answer and Reaction times.



a) angry body expressions were more accurately recognized in an angry versus happy scene and happy body expressions in a happy versus angry scene.
b) angry body expressions were somewhat faster recognized in an angry versus happy scene.

General Discussion

The perception of a bodily expression is influenced by the social scene and research suggests an early integration of these signals (Kret & de Gelder, 2010). To investigate whether the effects of incongruency remain over longer stimulus presentation duration, we recorded eye movements and facial EMG activity while participants observed people situated in emotionally congruent or incongruent social scenes.

Threatening versus happy body postures inside a neutral scene were looked at longer. This finding, along with the finding that participants scanned the whole picture more when the body showed a happy versus an angry expression are consistent with our previous results in which different actors were presented in isolation (without a scene) (Kret, Roelofs, Stekelenburg, & de Gelder, in prep.). It seems that overall, participants attended more to threatening cues and when there was no threat, they scanned the whole picture in search of it. Indeed, previous studies also found longer fixations on threat-related expressions, compared to threat-irrelevant expressions (Green, Williams, & Davidson, 2003; Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009). In fact, it has been demonstrated decades ago that people look at informative regions in a picture and they return again and again to these informative regions rather than covering the whole area of the picture (Buswell, 1935; Yarbus, 1967). One very important general finding is that viewers are able to acquire scene gist in a single glance. That is, the gist of the scene is understood so quickly, it is thought to be processed even before the eyes begin to move (De Graef, Christiaens, & d'Ydewalle, 1990). Castelhano and Henderson (2007) showed that when viewers were shown a scene for as little as 40 ms, they were able to extract enough information to understand the scene gist (Castelhano & Henderson, 2007).

Thus, attention allocation during interaction may reflect the need to prepare an adaptive response to social threat. Only the happy expression would signal safety and would therefore be the least interesting one, as indicated by shorter fixations and more explorative viewing behavior. However, the fact that happy bodies were longer looked at in an angry than in a neutral scene, does not fit with this idea. One explanation may be that the interpretation of the bodily expression changes as a function of scene emotion. For example, an angry body posture in a happy scene may be perceived as playful. However, when a person expresses happiness with his body whereas at the background, a serious fight is visible, the whole situation may be more threatening and participants may worry about the safety of the observed person, who does not seem to notice the fight taking place behind its back. This person may seem more 'out-of-place' and therefore holds the attention over longer stimulus presentation duration. This explanation is plausible because an object that is out-of-place in a scene also tends to attract many and longer fixations (Friedman, 1979; Loftus & Mackworth, 1978). Future studies should further investigate this, for example by asking participants to describe what they think is going on in the observed and what his intentions are.

We expected that body-scene ambiguity would hamper responses of the zygomaticus and corrugator muscle. However, in contrast to our earlier findings using isolated stimuli neither the zygomaticus, nor the corrugator showed an effect of bodily expression. Instead, both muscles reflected the emotion depicted in the scene. This finding is in line with the original Dimberg results (Dimberg, 1982). The zygomaticus responded more to happy than to angry or neutral scenes. The corrugator responded in the last two seconds of stimulus presentation duration more to angry versus happy scenes.

We replicated earlier findings by showing effects of an emotional scene on the recognition of target body expressions. The effects on accuracy and reaction times in the current study are slightly weaker than we previously observed (Kret & de Gelder, 2010), possibly because the participants during this task, had already seen the stimuli in the passive viewing task. The reason why we gave the passive viewing task first was because we did not want to refer to emotions. We simply asked them to watch the pictures which showed 'people'.

Intriguingly, measures of attention allocation and facial muscle activity demonstrate distinct reaction patterns at different stages of processing. We suggest that these patterns of reactivity subserve and contribute to the dynamic processes of person perception by constituting parts of the biological correlates of our propensity for social perception. This helps us to actively engage with others, to drive the allocation of attentional resources and to inform higher-order cognitive functioning thereby providing essential information to help us to understand individuals in a crowd.

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Chapter 11

Islamic context influences how emotional information from the eyes is recognized

This chapter is submitted

Abstract

Facial expressions and even isolated eyes strongly convey emotional information. Whether or not emotion recognition from the eyes is sensitive to contextual information is presently a matter of debate. Research has shown that we show a negative bias in the perception of emotions from out-group members. We therefore expect that a cultural context can robustly influence the interpretation of emotions, even when only the eyes are visible. The goal of this study was to investigate whether recognition of the expression conveyed by the eyes is influenced by the surrounding visual information covering the rest of the face. In four experiments we tested whether emotions can be recognized from a face partly covered by Islamic headdresses including a hijāb and a niqāb which define the out-group versus a cap or a scarf that are often worn by in-group members. Our results indicate that the type of headdress influences the recognition of emotions. Fear was recognized best when the face was partly hidden by a niqāb suggesting that a niqāb facilitates the fear response in a group of participants from non-Islamic background. Participant's performance was related to self-ratings of attitudes towards and experience with Islamic group members.

Introduction

We spontaneously divide our social world into a manageable number of categories (Macrae & Bodenhausen, 2000). Social psychology identity shows that group membership helps to define the social identity of the individual (Tajfel, 1978; Turner et al., 1987). For example, emotions are recognized better from in-group than from those of out-group members (Elfenbein & Ambady, 2002). Subjects with prejudices tend to make anger judgments when the target is a black (Hugenberg & Bodenhausen, 2003) versus a white in-group male. Moreover, emotion recognition is typically faster for positive than negative emotions, but the reverse obtains when Caucasians judge Black (Hugenberg, 2005) or Arab (Moroccan) targets (Bijlstra, 2010). Weisbuch and Ambady (2008) reported that negative automatic responses were activated in response to out-group expressions of joy and in-group expressions of fear. Emotion, context and race influence perception unconsciously and trigger automatic affective responses (Amodio et al., 2004; Devine et al., 2002; Fazio et al., 1995; Righart & de Gelder, 2006). If information concerning group memberships and emotion can be processed non-consciously, it is conceivable that the two interact to produce unique affective responses. Thus far, in-out-group membership has always been defined by features in the face itself such as for example skin color. It is not known whether these biases hold when in-out-group membership is purely defined by a context that is provided by the observed individual him/herself but not by his/her face features.

Adults are experts at processing faces. They can recognize thousands of individual faces and can quickly decode a variety of emotional expressions and direction of gaze. There is a large consensus in the literature that like the face itself, facial expressions are processed configurally, a processing style that presumably enables speed and efficiency (Tanaka & Farah, 1993). The hallmark of this processing routine is the inversion effect (Yin, 1969; for a review, see Maurer et al., 2002) or the loss in recognition performance when the face is shown upside down. To illustrate, the inversion effect is also observed with facial expressions (de Gelder, Teunisse, & Benson, 1997). There is a consensus that we process a facial expression as an integrated whole rather than serially accessing information from its individual features, but there is in fact very little evidence about the relative role of different face parts for different emotions. The available results suggest that some face parts are relatively more important than others for emotion identification. For example, face inversion did not hinder identification of a smiling expression but reduced accuracy for fearful, sad, and angry expressions (McKelvie, 1995). In contrast, identification of emotions was easier when only the upper part of the face carried the affective messages and the lower part was neutral than when the full face was shown. This effect was obtained for fearful, sad and angry but not happy faces (de Gelder et al., 1998). White (2000) has proposed that both the parts and the overall configuration play a role in emotion identification. The Bubbles paradigm which was invented by Gosselin and Schyns in 2001 has provided many new insights regarding which image locations and spatial frequencies are critical for discriminating between stimuli. This paradigm has later been widely applied in the field of face perception (Caldara, 2005; Langner, Becker, & Rinck, 2009; Langner, Becker, Rinck, 2009; Spezio, 2007)

Research on the perception of emotions from isolated face parts has mostly stressed the importance of the eye region. Indeed, the eyes are richly informative and are important in understanding emotion and communicative intention of other individuals (Emery, 2000; Senju & Csibra, 2008). Emotion-driven complex musculature changes such as the raising and lowering of eyelids and eyebrows enables perceivers to decode emotions from just the eye region (Baron-Cohen et al., 1997; Nummenmaa, 1964). Additionally, participants perform equally well at decoding complex mental states when only shown the eye region as when shown the whole face (Baron-Cohen et al., 1997). They capture more attention than other areas of the face in adults (Janik et al., 1978; Adolphs, 2005) as well as in infants (Haith et al., 1977; Farroni et al, 2002) and this bias may reflect an innate predisposition (Baron-Cohen et al., 1995; Argyle & Cook, 1976) that proved adaptive in evolution and is not uniquely human (Keating & Keating, 1982; Hirata et al., 2010). Focusing on the nose and mouth impairs fear recognition much more than that of other emotions. Recognition of a happy expression depends on the visibility of the mouth. People cannot recognize happiness from the eyes alone. Yet on the other hand, people express fear almost entirely with their eyes (Morris, de Bonis, & Dolan, 2002; Vuilleumier, 2005).

In view of this, one may expect that information from the eyes is robust such as to resist influence from the surrounding context including for example a cultural or religious context. Is the expression of the eyes sensitive to visual context factors or is the expression conveyed by a pair of eyes seen when the rest of the face is hidden recognized similarly whatever the context (helmet, medical mask, beard or a hat etc.). There is some evidence that emotion categorization from the eye region is a process that is automatically triggered in a bottom-up fashion on the basis of the information available from the position of the eyebrows (Sadrô, Jarudi, Sinha, 2003; Leppänen, Hietanen & Koskinen, 2008) and the eye white (Whalen et al., 2004). On the other hand, recent evidence suggests that as far as the whole face is concerned, the perception of expressions is influenced by context more than had previously been assumed. In fact, under certain conditions, the presence of a task-irrelevant naturalistic scene can dramatically shift the emotional category recognized in basic facial expressions and bias the valence judgment of facial expressions toward this information (e.g., Meeren et al., 2005; Righart & de Gelder, 2006; Van den Stock et al., 2007; Aviezer et al., 2008; Koji & Fernandes, 2010). Therefore it seems premature to rule out that context does play a role in eye perception expression.

Except for the studies that focused on race bias, other studies that took context into account provided a context which was not directly related to the observed individual, or, in other words, was not informative about the type of person one observed (for example an emotional scene showing a car crash and one individual standing in front of that, does not say something about that person's identity). In the case of race bias studies, as we mentioned before, the clear racial characteristics of the observed were defined by facial features. It is not known how a more subtle context, provided by the observed individual himself influences how people look at him or her. For example, people who are not used to see niqābis (a niqāb is the Arabic word for "mask") in everyday life, get an uneasy feeling about them. Is this because the face is covered and therefore, emotions are less visible? If so, they should have the same eerie feeling observing women wearing a cap and a scarf covering the same face areas. If they do not, it may be that negative associations with headdresses play a role. We would like to investigate the idea whether a cultural context which is provided by the observed individual herself influences how her emotions are perceived.

In four experiments we investigated if headdresses influence emotion recognition from the eyes and whether this depends on the type of headdress. We included the niqāb, a veil that covers the face, worn by some Muslim women as a part of a sartorial hijāb. In the current study we use the term hijāb for a headscarf that leaves the full face visible but covers the hair. With a niqāb, we refer to a veil that covers hair, nose and mouth and a burqa, which covers the whole face, including the eyes. In Experiment 1 we tested whether emotions can be read from the eyes when a veil covers the rest of the face. In Experiment 2, we added random noise to the eye region in the niqāb condition to make it resemble a burqa. In Experiment 3, we investigated the importance of seeing the whole face versus the eye region and additionally compared the hijāb and niqāb condition with a cap and scarf. In Experiment 4, we additionally used self-ratings and looked at correlations with 'negative attitudes towards the Islam'.

Experiment 1

Earlier studies have described the effects of context on emotion recognition from whole faces and have investigated emotion recognition from face parts. However, the contexts that were provided in these earlier studies were very explicit and not directly related to observed individual. Moreover, the role of contextual information on emotion perception from face parts has never been discussed before. The goal of experiment 1 was to test whether emotions can be read from the eyes when an Islamic veil covered all other parts.

Method

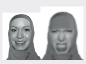
Participants

Fifteen students of Tilburg University participated (seven male; mean age: 20 years, range 17 - 25 years) with no neurological or psychiatric history and with normal or corrected-to-normal vision. The experimental procedures were in accordance with the Helsinki Declaration and approved by Tilburg University.

Stimuli

We used six female identities showing happy, angry, sad and fearful expressions taken from the well-validated McArthur set and all recognized above 80% (http://www.macbrain.org/resources.htm). The great advantage of this face set is that the actors appear to have a quite ambiguous cultural background. We tested this in a preliminary experiment. From the female actors that we included, three had brown eyes and three green/blue eyes. The neutral faces of these identities were shown to 12 independent raters who were asked which country they thought these women came from. The answers varied greatly but 41% of the answers included non-western countries such as Peru, Mexico, Syria, Armenia, Turkey, Pakistan, Bulgaria, Hungary, Bosnia and Herzegovina. We modified the stimuli and created a 'whole face' condition, an 'eyes only' condition in which the face was covered with a niqāb and a 'mouth only' condition in which only the mouth was visible. The visible face parts had the same size in terms of the number of pixels. Stimuli measured 16.4° x 12.0° visual angle. The newly created stimuli were used in another validation study in which all stimuli that are discussed in this article were included. In this validation, 27 students of Tilburg University watched the randomly presented stimuli for a maximum of 5 seconds and made a choice among an angry, happy, fearful or sad label. (see Table 1 for accuracy rates (ACC) and stimulus examples).

Table 1. Stimulus examples and their validation.

		Emotions							
		anger		**fear**		**happy**		**sad**	
		M	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**
Experiment 1									
Eyes niqāb		86	35	94	23	85	36	78	41
Mouth		82	38	72	45	96	19	92	27
Experiment 2									
Hijab		95	22	89	31	100	0	95	22
Niqāb		86	35	94	23	85	36	78	41
Burqa 80%		86	35	94	25	32	37	58	49
Burqa 90%		75	43	85	36	29	46	53	50
Experiment 3/4									
Hijab		93	26	94	23	99	10	86	35
Niqāb		88	33	94	23	77	42	78	41
Cap		92	27	96	19	99	7	87	34
Cap & scarf		87	34	93	25	83	38	80	40

The table gives mean (M) recognition rates followed by the standard deviation (SD). Experiment 1) Six female identities showing happy, angry, sad and fearful expressions were included in the experiment. Experiment 2) The actresses wear an Islamic headscarf in all conditions. The burqa conditions are similar to the niqāb condition but noise has been put on the eye region. Experiment 4) The actresses wear greyscale Islamic and non-Islamic headdresses.

Procedure

Participants were seated at a table in a dimly lit sound reduced booth. Distance to the computer screen was 60 cm. Instructions were given verbally and via an instruction screen. Participants were given a forced choice categorization task using four emotions and were instructed to respond as accurately and rapidly as possible, to use their index and middle fingers and not to change the position of their fingers during the experiment. They were told that the stimuli consisted of female faces with different emotions. A trial started with a white fixation cross (positioned at the height of the actors nose) on a grey screen (300 ms), a stimulus (100 ms), followed by a grey screen shown until response (with a maximum duration of 8 s). Stimuli were randomly presented on a PC screen with a 100 Hz refresh rate.

Data analysis

Recognition performance as a factor of emotion and type of headdress depends on both the reaction time and error data. To evaluate recognition performance accounting for speed-accuracy tradeoffs and shifts in criterion, inverse efficiency scores (IES: mean reaction times divided by proportion correct responses) (Townsend & Ashby, 1983) were analyzed in a 4 * 3 ANOVA (4 emotions, 3 face parts (whole face, mouth, eyes). Incorrect responses and responses < 200 or > 2500 ms were discarded from the reaction times. Lower values on the IES indicate better recognition performance. Main effects were followed up by Bonferroni corrected pairwise comparisons and interactions by two-tailed t-tests.

Results

There was an effect of emotion [$F(3, 42) = 11.33$, $p < .001$, $\eta p2 = .45$]. Angry faces were better recognized than happy ($p < .005$) and sad faces ($p < .05$) and fearful faces better than happy ones ($p < .01$). Face part and emotion interacted [$F(6, 84) = 13.26$, $p < .001$, $\eta p2 = .49$]. Happy and sad expressions were recognized more accurately when the whole face and not only the eyes were visible ($t(14) \geq 3.435$, $p < .005$). This was not the case for angry ($p = .348$) and fearful expressions ($p = .447$). Whereas fear and happiness were recognized better from the whole face than the mouth ($t(14) = 3.563$, $p < .005$; $t(14) = 3.286$, $p < .01$), there was no difference for sad expressions ($p = .383$) and only a trend towards significance was observed for angry expressions. See Table 2 for accuracy and reaction time data.

Discussion

The results demonstrate that we can recognize emotional expressions when we only see parts of the face due to partial coverage of an Islamic headscarf. However, performance depended on the specific emotion. Angry and fearful faces were not better recognized when the whole face versus only the eyes were visible. Sad faces were not better recognized when the whole face versus only the mouth was visible.

Experiment 2

In order to further investigate the importance of the eye region in recognizing emotions, an additional condition was included where even less facial information was visible than in the niqāb condition: a burqa, that covers the whole face, including 80 or 90% of the eye region. The whole face stimuli were covered with a hijāb so that the actress wore a headdress in all the conditions. See figure 1 for stimulus examples of the niqāb and burqa conditions. See table 1 for information regarding the validation of the stimuli.

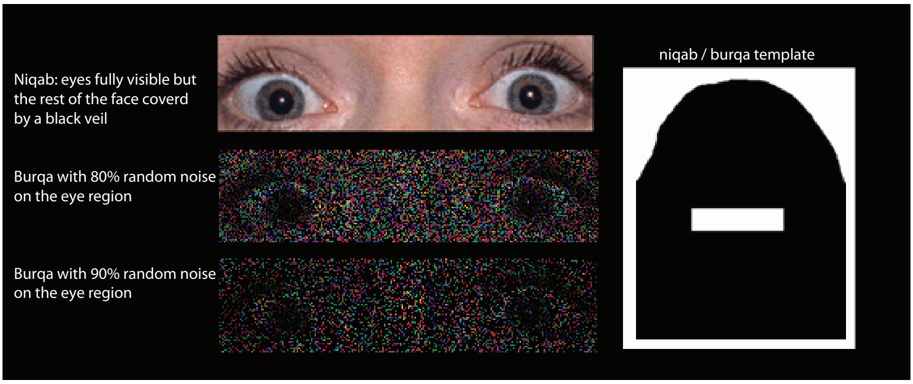
Participants

Twenty-five new students participated (seven male; mean age: 20 years, range 18-25 years). To avoid interactions between cultural background of the participant and stimulus, two Muslim participants were excluded from analyses.

Materials and Procedure

Pictures of one actor were replaced due to lower ACC compared to the other actors and replaced with a new actor from the same set that had a recognition rate above 80%. There were four types of headdresses, a hijāb where the whole face was visible, a niqāb where only the eyes were visible, a niqāb with 80% or 90% random noise on the eye region, i.e., a burqa. Stimuli were presented twice. IES were analyzed in a 4*4 ANOVA (4 emotions, 4 face parts).

Figure 1. Perception of emotion from the eye region in a cultural context.

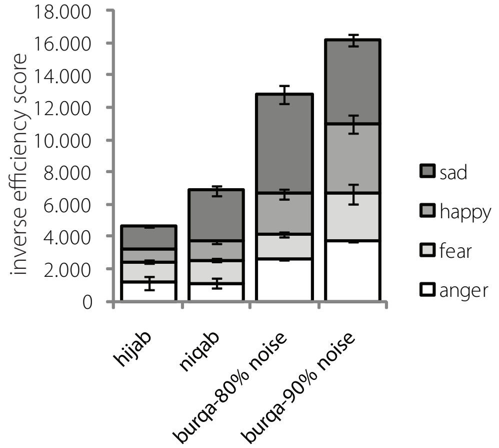


The eye region was presented in four different contexts: 1. as part of a whole face (which is not shown in this figure but is depicted in table 1), 2. in the context of a niqab (a headscarf which only leaves the eyes visible), 3. in the context of a burqa where 80% of this region consisted of random noise and 4) a burqa with 90% random noise.

Results

Main effects were found for emotion [$F(3, 72) = 34.096$, $p < .001$, $\eta p2 = .59$] and face part [$F(3, 72) = 98.23$, $p < .001$, $\eta p2 = .80$]. Sadness was recognized worst ($p < .001$). The more covered the faces were, the worse recognition was ($p < .005$). Face part and emotion were interacting [$F(9, 216) = 7.140$, $p < .001$, $\eta p2 = .23$]. Faces were recognized best in the hijāb, than in the niqāb and than in the two burqa conditions. However, fearful and angry faces were equally well recognized in the hijāb as in the niqāb condition (p ≥ .390). Fear was still recognized well in the burqa conditions and recognition did not differ between the two noise levels (p = .413). Sadness was recognized poorly from just the eye region, especially when random noise was added. See Figure 2.

Figure 2. Inverse efficiency scores for the recognition of facial expressions in an Islamic context.



Fearful and angry faces were equally well recognized in the hijāb as the niqāb condition. Fear was still recognized well in the burqa conditions and recognition did not differ between the two noise levels. Sadness was recognized poorly from the eye region, especially when random noise was added.

Discussion

Angry and fearful faces were not recognized better when the whole face versus only the eyes were visible. Recognizing sadness and happiness was hard from just the eyes. Although most emotions could be recognized in the niqāb condition, recognition in the burqa conditions was impaired; especially for sadness, where perceivers rely on the mouth. Recognition of fear from the eyes in the context of a burqa was very high. Visibility of the eye-white may have played a facilitating role, as earlier studies that presented 'cut out eyes' already suggested (Whalen et al., 2004). Alternatively, the participants may have more readily associated fearful expressions with women wearing Islamic headdresses.

Experiment 3

To investigate whether some emotions may be associated with group membership, we created in- and out-group headdresses. A pilot experiment is described in the supplementary materials.

Participants

Twenty-eight new students participated (five male; mean age: 20 years, range 17-25 years).

Procedure

One extra identity with an ACC over 80% was taken from the same set and was included in order to increase the number of trials. Four different headdresses in greyscale were used; a hijāb; a niqāb; a fleece cap; a fleece cap and knitted scarf. The latter two conditions represented the in-group. Grey colour of the headdresses was chosen to soften the contrast with skin colour and, although we did not test this assumption, grey could be perceived as more neutral than black. To make the stimuli more realistic, we cut out the headdresses from photographs and we specifically choose fabrics with visible texture. A hijāb and niqāb picture were found on the Internet and the cap and scarf, while being worn by a person, were photographed by the first author. These pictures were edited in Photoshop: the faces from the original pictures were erased. The cap and scarf were repositioned so that the distance from the actress' eye to the border of the cap was equal to the niqāb condition and the distance from the eye to the border of the scarf was also exactly similar as the niqāb condition. The space beside the outer corners of the eyes was kept constant. Stimuli were turned to greyscale to make them less culturally definable by skin colour. Two extra conditions were included in which a niqāb and a cap and scarf were shown, but the eye region was blurred to specifically test the emotions that students associate with these headdresses. After the experiment, students filled out a questionnaire on 'negative attitudes towards the Islam'.

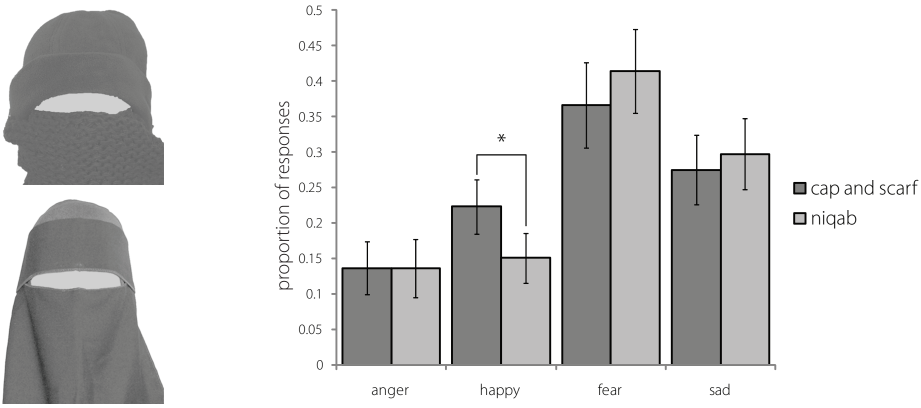
Results

A cap and scarf were more often associated with happiness than the niqāb ($t(27) = = 2.57$, $p < .05$). See figure 3.

Performance

Main effects were observed for emotion [$F(3, 81) = 18.47$, $p < .001$, $\eta p2 = .41$] and face part [$F(1, 27) = 36.39$, $p < .001$, $\eta p2 = .57$]. Sad faces were recognized worst ($p < .01$). Anger was better recognized than happiness ($p < .05$). Expressions were recognized best in the whole face condition ($p < .001$). Face part and emotion interacted [$F(3, 81) = 13.22$, $p < .001$, $\eta p2 = .33$]. In contrast to the other emotions, fear was not better recognized in the whole face than eyes only condition ($p = .518$). Happiness was better recognized from women wearing a cap and a scarf than from niqābis ($t(27) = 2.55$, $p < .05$). Importantly, there were no correlations between the responses that were given to the cap and scarf and niqāb templates and the responses to the images that contained emotion expressions.

Figure 3. Proportion of answers that were given to the headgear templates.



A cap and scarf were more often associated with happiness than a niqab. However, these answers did not correlate with the responses that were given to the pictures that contained emotional expressions.

Discussion

A cap and scarf were more often associated with happiness than a niqāb and happiness was better recognized from women wearing a cap and a scarf than a niqāb. The fact that these results were not related to the responses that were given to the cap and scarf and niqāb templates add to the idea that it is the interaction between the emotional expression and the specific type of headgear that contributes to the observed in-out-group biases. Our study adds to the literature on for example out-group and racial bias (Maddox, 2004) but the important point is that compared to previous literature the concept out-group is here purely defined by the context and not by facial features (i.e. a black versus a white man's face).

Experiment 4

This experiment serves as a further control for the visible facial surface and uses self-ratings to relate the perceptual data to participants' attitudes.

Participants

Twenty-eight new students participated (six male; mean age: 21 years old, range 19-36 years old).

Procedure

In the original version of the hijāb that we used in the previous experiment, more forehead was visible than in the niqāb, cap and cap/scarf conditions, as can be seen in Table 1. Therefore, we combined the upper part of the niqāb template with the lower part of the hijāb template. To increase task difficulty, stimulus presentation duration was brought back to 40 ms. After the experiment, students filled out a questionnaire about their attitudes towards the Islam. Generalized anxiety was measured with the STAI (Spielberger, 1983).

Relation with attitudes towards the Islam

We created a questionnaire measuring 'negative attitudes towards the Islam' consisting of 2 parts. The first part is an adapted version of Stephan et al.'s (2002) prejudice scale, measuring negative attitudes toward the homeless (twelve items, $\alpha = .85$), realistic threat (four items, $\alpha = .70$), symbolic threat (six items, $\alpha = .78$), and intergroup anxiety (six items, $\alpha = .91$). We changed "toward the homeless" into "toward women wearing a hijāb/niqāb". Furthermore, we measured frequency of negative contact (six items, $\alpha = .82$) to validate its relationship with intergroup anxiety (Stephan & Stephan, 1989). The second part is an adaptation of the modern racism prejudice questionnaire (Akrami, Ekehammar & Araya, 2000) measuring attitudes towards the Islam in general. The students who participated in the pilot experiment first filled out the questionnaire. Items with a corrected item-total correlation below .4 were removed. A few extra questions were added to measure how much the participant had been exposed to Muslims at school and in their neighbourhood. The students in Experiment 3 filled out this adapted version and based on these results we again made some improvements. The final version can be found in the supplementary materials and was used in Experiment 4. The total score of the negative attitudes towards the Islam-questionnaire did not correlate with the STAI. The two parts of the questionnaire correlated ($r = .81$, $p < .001$). Cronbach alpha was .93.

Results

Performance There were main effects of emotion [$F(3, 81) = 19.71$, $p < .001$, $\eta p2 = .42$] and face part [$F(3, 81) = 40.35$, $p < .001$, $\eta p2 = .60$]. Sadness was recognized worst ($p < .01$). Performance was best when the whole face was visible ($p < .001$). Emotion and face part interacted [$F(3, 81) = 13.16$, $p < .001$, $\eta p2 = .33$]. Fearful and angry faces were not recognized better from the whole face than from eyes ($p = .36$; $p = .18$) but happy and sad faces were ($t(27) = 4.024$, $p < .001$); ($t(27) = 4.892$, $p < .001$). There was an interaction between emotion * culture [$F(3, 81) = 3.56$, $p < .05$, $\eta p2 = .12$]. Happiness was recognized better in the in-group ($t(27) = 2.68$, $p < .05$); anger slightly better in the out-group ($t(27) = 1.96$, $p = .06$). There were interactions between emotion * face part [$F(3, 81) = 13.16$, $p < .001$, $\eta p2 = .33$] and between face part * culture [$F(3, 81) = 4.82$, $p < .05$, $\eta p2 = .15$]. As expected, emotions were recognized better when all face parts were visible than when only the eyes were visible (in-group ($t(27) = 5.264$, $p < .001$); out-group ($t(27) = 6.346$, $p < .001$). The difference between the whole face and the eyes only condition was larger in the out-group than in the in-group ($t(27) = 2.196$, $p < .05$). Importantly, there was an interaction between face part * emotion * culture [$F(3, 81) = 4.62$, $p < .005$, $\eta p2 = .15$]. Since we had clear expectations based on the prior experiments, we made three planned comparisons. Happiness and sadness were recognized better in women wearing a cap and scarf versus a niqāb ($t(27) = 2.607$, $p < .05$; ($t(27) = 1.899$, $p < .05$). Fearful women wearing a niqāb were recognized better than women with a cap and scarf ($t(27) = 1.92$, $p < .05$). See figure 4a.

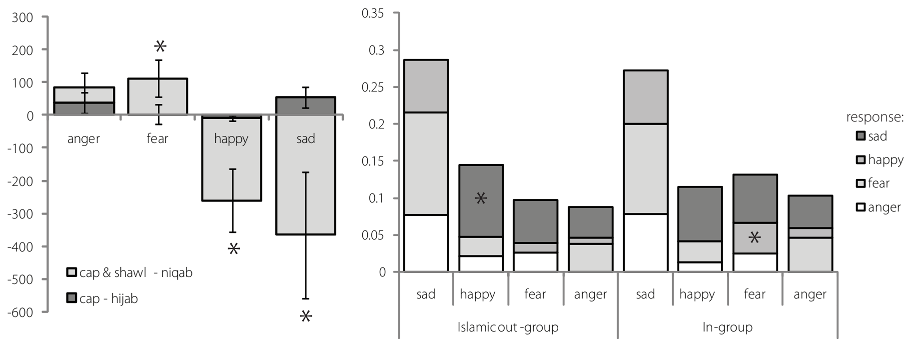
Individual differences in negative attitudes towards the Islam

Even though using shorter stimulus presentation increased task difficulty, few errors were made in the whole face conditions. For this reason we pooled the eyes only and the whole face conditions. Fearful in-group women were more often labeled as being happy than out-group women ($t(27) = 2.58$, $p < .05$); happy Muslim women were more often erroneously labeled as being sad than in-group women ($t(27) = 2.53$, $p < .05$). See Figure 4b. A median split revealed that students with positive attitudes towards the Islam more often labelled Muslim women as being sad when these women were angry ($t(26) = 2.21$, $p < .05$). There was a correlation between the score on the questionnaire and this specific confusion error ($r = .438$, $p < .05$). The difference score between this confusion error in the Islamic minus the Dutch condition also correlated with the questionnaire score ($r = .38$, $p < .05$). Similarly, fear was more often erroneously labelled as sad by those with positive attitudes ($t(26) = 2.01$, $p = .055$) and a correlation was observed between the score on the questionnaire and this specific error ($r = .376$ $p < .05$). Students with few Muslim friends (1 or 2 ($M = 2.75$, range 1-7)) more often misinterpreted a sad Muslim women as being angry ($t(26) = 2.58$, $p < .05$).

Discussion

Happiness was recognized better in women wearing a cap and scarf versus a niqāb. Fear was recognized best from niqābis. One could have predicted that participants with negative attitudes towards the Islam more often interpreted emotions negatively, irrespective of the emotion being shown. Such a response-bias, however, was not apparent. Two findings were observed. First, participants with positive attitudes towards the Islam more often labelled the out-group as being sad when they were actually angry or afraid. Second, participants with few Muslim friends more often misinterpreted a sad Muslim woman as being angry instead of sad.

Figure 4. Inverse efficiency scores in-group minus out-group headscarves and confusion matrix.



a) The graph shows difference scores of 'in-group minus out-group' for inverse efficiency scores. The upper part of the graph shows conditions where the out-group was better recognized; the lower part where the in-group was better recognized.

b) Confusion matrix. Fearful in-group women were more often labeled as being happy than out-group women; happy Muslim women were more often erroneously labeled as being sad than in-group women.

Table 2. Mean accuracy and reaction times.

	Anger				Fear				Happy				Sad			
	ACC		RT		ACC		RT		ACC		RT		ACC		RT	
Exp. 1																
Headdress:	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
None	90	9	1256	176	94	12	1272	208	99	5	855	197	91	1	1234	197
Eyes	86	18	1237	290	93	9	1185	255	84	20	1207	275	44	25	1510	272
Mouth	70	22	1356	257	43	30	1185	255	98	6	1013	273	88	15	1268	259
Exp. 2																
Headdress:	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Hijab	95	9	1068	178	88	14	1130	218	97	7	787	161	87	13	1164	250
Niqāb	91	10	1007	219	86	16	1141	232	84	15	925	244	49	22	1344	336
Burqa 80%	51	28	1070	238	80	18	1142	206	48	29	1063	328	18	20	1481	455
Burqa 90%	34	23	1219	402	57	24	1267	376	27	25	1163	450	17	20	1267	391
Pilot Exp.																
Headdress:	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Hijab	95	1	895	246	87	14	1213	327	99	6	735	214	80	23	1110	284
Cap	97	8	851	260	93	1	1136	291	98	6	745	220	76	18	1117	265
Niqāb	85	12	877	273	90	14	1094	244	66	22	1109	268	51	21	1297	355
Cap & scarf	87	12	917	250	87	15	1177	265	69	22	1064	280	59	24	1194	258
Exp. 3																
Headdress:	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Hijab	97	6	910	167	97	4	1166	217	97	4	774	146	84	13	1077	166
Cap	95	8	878	163	88	12	1135	229	96	5	786	157	80	13	1136	183
Niqāb	85	15	939	174	85	12	995	157	67	2	1104	198	49	22	1309	223
Cap & scarf	87	9	940	186	85	12	1030	187	63	26	1101	215	46	24	1354	306
Exp. 4																
Headdress:	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Hijab	93	6	842	175	88	13	1061	250	98	3	698	97	84	10	966	185
Cap	91	7	863	174	87	14	1040	194	98	4	686	96	80	10	962	185
Niqāb	89	8	846	183	87	11	985	199	72	20	927	213	56	18	1140	256
Cap & scarf	87	11	840	179	86	14	1019	217	78	18	892	199	62	17	1139	231

Mean (M) accuracy (ACC) and reaction times (RT) are followed by the standard deviation (SD).

General discussion

Everyday items like sunglasses, scarves, veils, caps, hats, helmets, medical masks etc lead to partial occlusions of the face, hampering identity and emotion recognition. In the West and the Islamic world alike, the headscarf is the subject of heated discussions. To our knowledge, the effects of wearing headdresses on emotion recognition are a matter of societal debate for which there is no scientific evidence yet available. Therefore, our aim was to investigate if headdresses influence emotion recognition and whether different types of headdresses influence emotion recognition differently.

In Experiment 1 we replicated earlier studies showing that emotions can be read from isolated face parts. The difference with these previous studies and the current study is that in this study, the face parts were presented in the context of a headscarf and not in isolation as is generally done. Angry and fearful faces were recognized equally well from the whole face as from the eyes when the rest of the face was covered by a niqāb. Sadness was recognized similarly from the whole face as from the mouth region. In Experiment 2 we explored the importance of the eye region in recognizing emotions from women wearing different headdresses (hijāb, niqāb, burqa) and show that recognizing sadness and happiness from the eyes was difficult. Although most emotions could be recognized in the niqāb condition, recognition in the burqa conditions was impaired; especially for sad expressions. However, recognition performance for the fear burqa conditions was still very high. Our results are consistent with the literature that stresses the importance of the eye region in emotional communication. We tend to often look immediately at the eye region of a face, and all the more so when the face is fearful (Yarbus, 1967). Visual cues provided by the eyes are particularly critical for the recognition of fear; other facial emotions can be recognized without looking at the eyes (Vuilleumier, 2005). Humans use the mouth but not the eyes for recognizing happiness and they use the eyes but not the mouth for the recognition of fearful expressions. Moreover, the wrinkles on the forehead and the mouth region are important in recognizing sadness and the intersection of the lower forehead and eyebrows when looking at an angry face (Smith et al., 2005). Our study adds to the existing literature on face part expression recognition since we provided a naturalistic cultural context in which these face parts were perceived.

In Experiment 3 and 4 the importance of seeing the whole face versus the eye region was further investigated. The hijāb and niqāb condition were directly compared with the conditions of a cap and cap and scarf covering the same face area. This allowed us to investigate whether fearful expressions are better associated with the Islam condition. The results show that a cap and scarf were more often associated with happiness than the niqāb. Moreover, happiness but also sadness was recognized better in women wearing a cap and scarf than a niqāb. Fear was recognized best in the niqāb condition. A smile is a strong cue in social communication and we routinely smile a lot to the people in our direct environment (Hess & Bourgois, 2009). It is therefore not surprising that this emotion was better recognized from women who can be counted to our in-group. Like happy faces, the display of sad expressions has long been linked to the inhibition of aggression and the elicitation of pro-social behaviour which may be particularly strong among members of the same social group (Miller & Eisenberg, 1988). Negative attitudes towards members of an ethnic out-group result in reduced facial mimicry and it has been suggested that empathy is bounded to a closed circle of similar others (Herrera, Bourgeois & Hess, 1998; Likowski et al., 2008). We would have predicted a direct relationship between negative attitudes towards the Islam and recognition performance of participants when observing fearful out-group (niqābis) minus in-group members (women wearing a cap and a scarf). However, it has been suggested that asking participants directly about their attitudes on a sensitive topic such as Islamic headscarves is not the best way to test attitudes. An important technique used by researchers to mitigate the effects of social desirability bias is indirect questioning. Indirect questioning is a projective technique that asks participants to answer structured questions from the perspective of another person or group (McConahay, 1981). Nevertheless, in the current study, we observed some correlations with the questionnaire. For example, participants with positive attitudes towards the Islam more often labelled a Muslim woman as being sad when she was angry or afraid. In contrast, students with few Muslim friends more often misinterpreted sad Muslim women as being angry. These results are somewhat in line with earlier studies showing better emotion recognition and increased empathic responses following greater exposure to the out-group (Dovidio et al., 1997; Elfenbein & Ambady, 2003; Stürmer, Snyder, & Omoto, 2005; for a meta-analysis, see Pettigrew & Tropp, 2006).

Our results are consistent with evidence on the role of these social factors in emotion perception (Macrae & Bodenhausen, 2000). For example, emotions are recognized better in the faces, bodies, and voices of in-group than in those of out-group members (Elfenbein & Ambady, 2002). Moreover, emotion recognition is typically faster for positive than negative emotions, but the reverse obtains when Caucasians judge Black targets (Hugenberg, 2005). Weisbuch and Ambady (2008) reported that negative automatic responses were activated in response to out-group expressions of joy and in-group expressions of fear. Subjects with prejudices tend to make anger judgments when the target is a black versus a white male (Hugenberg & Bodenhausen, 2003). As a consequence, both anger and fear may lead to better performance when displayed by out-group members rather than in-group members. In short, context (whether social, emotional or cultural) influences emotion perception and triggers automatic affective responses (Amodio et al., 2004; Devine et al., 2002; Fazio et al., 1995; Kret & de Gelder, 2010; Righart & de Gelder, 2006).

Our study differs from the literature on out-group and racial bias (Maddox, 2004) since the concept out-group is here purely defined by the visual context factors and not by facial features (for example a black versus a white man's face). Further research is needed to understand the perceptual mechanisms of these social factors of group membership. It would be interesting for example, to test the timing of these effects by using EEG. Analyzing event-related potentials in combination with measuring EMG responses from the zygomaticus major muscle (which we use when smiling) and the corrugator supercilii muscle (for frowning) following out-group versus in-group stimuli will provide more insight into unconscious socio-empathic responses.

There are some limitations to our study. Only two representative types of headdresses were included, whereas in real life there are many different ones. There are other important issues that we here ignored such as the texture and colour of the veil, the way it is draped around the head (the Turkish style giving more shade on the eye region than the Moroccan style for example), the heaviness and flexibility of the veil which may or may not allow perception of facial movement. Another limitation is the homogeneity of our participants: all were psychology students, all in their twenties. Of course, this is a very common problem in psychological research, but since students tend have quite left-sided political views, it would be interesting to investigate this further in people who voted "extreme" right. We expect to find even stronger effects in such a group, especially when compared with a group of Muslim participants.

To summarize, we show that a cultural context (i.e. headdress) can influence emotion perception from face parts. Emotional expressions can be recognized when only face parts are visible but performance is dependent on the specific context and emotion. Most importantly, fear was recognized better in the niqāb condition than in any other condition. Moreover, the performance in the niqāb condition reflected attitudes and experience with the Islam. The current study adds to the societal debate on whether women should be allowed to wear Islamic headscarves. It seems that the problem is not so much the headscarves themselves, but rather the negative associations and cultural biases people hold when being confronted with someone dissimilar to oneself.

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Appendix A

Pilot of Experiment 3

Method

Participants

Thirty-three new students (13 male; mean age: 19 years old, range 18-24 years old) participated. The four Muslim participants were excluded from analysis.

Procedure

Four different headdresses in greyscale were used; a hijab; a niqāb; a fleece cap; a fleece cap and knitted shawl. The latter two conditions represent the in-group (Dutch). Grey color of the headdresses was chosen since this colour is less lurid and more neutral than black. To make the stimuli more realistic, we cut out the headdresses from photographs and we specifically choose fabrics with visible texture. To evaluate recognition performance accounting for speed-accuracy tradeoffs and shifts in criterion, inverse efficiency scores (IES: mean reaction times divided by proportion correct responses) (Townsend & Ashby, 1983) were first computed and were analyzed in a 4*2*2 ANOVA (4 emotions, 2 face parts (eyes, whole face), 2 cultures (in-group, out-group (Islamic headscarves)). After the experiment, students filled out a questionnaire on 'negative attitudes towards the Islam'.

Results

A main effect was found for 'emotion' [$F(3, 84) = 24.02$, $p < .001$, $\eta p2 = .46$]. Pairwise comparisons revealed that sad faces were worst recognized ($p < .001$). Anger was better recognized than fear and happiness ($p < .00$). Face part and emotion interacted [$F(3, 84) = 12.28$, $p < .001$, $\eta p2 = .31$]. In general, expressions were more accurately recognized when more of the face was visible ($t(28) \geq 3.72$, $p < .001$), except for fear ($p = .85$). There was an interaction between emotion * face part * culture [$F(3, 84) = 8.84$, $p < .001$, $\eta p2 = .24$]. Anger was better recognized from women wearing a hijab versus women wearing a cap ($t(28) = 2.04$, $p < .05$). In contrast, fear was better recognized from women with caps than women with hijabs ($t(28) = 2.700$, $p < .05$). Sadness was recognized much better from women wearing a cap and a shawl than from women wearing a niqab ($t(28) = 2.39$, $p < .05$).

Discussion

In general, expressions were better recognized when more of the face was visible, except for fearful expressions. Anger was better recognized from women wearing a hijab versus women wearing a cap. In contrast, fear was better recognized from women with caps than women with hijabs. Sadness was recognized much better from women wearing a cap and a shawl than from women wearing a niqab. An open question is whether a cap and shawl are more often associated with happiness than the niqāb and the niqab more with negative emotions. We cannot answer this question since we have not presented these headdresses without the faces.

Appendix B

The means and standard deviations of the students who participated in Experiment 4 are indicated.

1. Are you male or female?

Male	**Female**
N = 6	N = 22

2. Date of birth

4-11-1988

3. What is your nationality?

Dutch

Different, namely........... All Dutch

4. What is your religious belief?

Christian	12
Islamic	2
Different, namely...........	14: no religion

5. Are you left or right-handed?

right	**left**
N = 25	N = 3

6. Do you carry glasses/contact lenses?

glasses	**contact lenses**	**none**
N = 1	N = 8	N = 19

7. Do you have complaints about your concentration or your memory? (eg difficulty in following the news or reading a book)

no	N = 27
yes: nature of the complaint...............	N = 1: minor concentration problems

8. How many children with an Islamic background did you have in class at elementary school? Please only fill in the number below.

2.36 (3.78)

9. How many children with an Islamic background you had in class in high school? Please only fill in the number below.

2.00 (2.23)

10. How was your experience with these students?

Positive							**Negative**
2.36 (1.22)	O	O	O	O	O	O	O

11. To what degree do you currently sort with people with an Islamic background?

Not at all							**Very much**
2.75 (1.90)	O	O	O	O	O	O	O

12. Below are some statements that are used by people to describe themselves. Read through each statement and color the dot to indicate how you generally feel. There are no right or wrong answers. Do not think too long, it is about your first impression. It is important to indicate how you generally feel.

My attitude towards women who wear Islamic clothing (headdresses, niqāb) is one of

	Strongly agree							Strongly disagree
approval	4.18 (1.79)	O	O	O	O	O	O	O
acceptance	5.11 (1.40)	O	O	O	O	O	O	O
disapproval	2.71 (1.70)	O	O	O	O	O	O	O
hostility	2.32 (1.49)	O	O	O	O	O	O	O
admiration	2.36 (1.52)	O	O	O	O	O	O	O
contempt	2.00 (1.39)	O	O	O	O	O	O	O
sympathy	3.54 (1.67)	O	O	O	O	O	O	O
antipathy	2.93 (1.70)	O	O	O	O	O	O	O
affection	2.54 (1.48)	O	O	O	O	O	O	O

13. In my opinion, women wearing Islamic clothing (headscarf, niqāb) are generally

	Strongly agree							Strongly disagree
Warm	4.43 (1.43)	O	O	O	O	O	O	O

14. Women wearing Islamic clothing (headscarf, niqāb) have too much .... on society

	Strongly agree							Strongly disagree
Political power	2.11 (1.23)	O	O	O	O	O	O	O
Influence	2.79 (1.55)	O	O	O	O	O	O	O

15. I see women who wear Islamic clothing (headscarf, niqāb) as a threat to society

Strongly agree **Strongly disagree**

2.04 (1.32)	O	O	O	O	O	O	O

16. I think that women who wear Islamic clothing (headscarf, niqāb) do not appreciate the values of women who do not wear Islamic clothing.

Strongly agree **Strongly disagree**

3.89 (1.85)	O	O	O	O	O	O	O

17. If I see a woman who wears Islamic clothing (headscarf, niqāb) on the street, I generally feel

	Strongly agree							Strongly disagree
Uncomfortable	2.11 (1.40)	O	O	O	O	O	O	O
Nervous	1.61 (.96)	O	O	O	O	O	O	O
Threatened	1.57 (.92)	O	O	O	O	O	O	O
insecure	1.57 (1.00)	O	O	O	O	O	O	O
not at ease	2.11 (1.32)	O	O	O	O	O	O	O
Anxious	1.61 (.96)	O	O	O	O	O	O	O

18. To what extent are you in the past offended by a woman who was wearing Islamic clothing (headscarf, niqāb)

Never							**Very often**
1.68 (1.22)	O	O	O	O	O	O	O

19. There are plenty of programs designed to create jobs for people with Islamic faith

Disagree					**Agree**
3.36 (.95)	O	O	O	O	O

20. The demand of people with Islamic faith for equal rights is easy to understand

Disagree					**Agree**
3.86 (1.04)	O	O	O	O	O

21. People with an Islamic belief are given too little attention in the media

Disagree					**Agree**
1.64 (.91)	O	O	O	O	O

22. People with Islamic faith are increasingly demanding in their fight for equal rights

Disagree					**Agree**
3.14 (1.30)	O	O	O	O	O

23. It is good to strive for a multicultural society in the Netherlands

Disagree					**Agree**
4.11 (1.10)	O	O	O	O	O

Chapter 12

Discussion

Context, gender and personality factors influencing the perception of facial and bodily expressions of emotion

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. Emotion research in the past has predominantly focused on facial expressions of emotion (de Gelder, 2006; 2009). Consequently, theories were derived from measuring emotions from pictures of emotional faces, measured in a homogeneous group of healthy psychology students. However, emotion perception is not just based on facial information alone (Hunt, 1941) and individual differences in responses are the rule rather than the exception (Canli et al., 2001; Hunton et al., 1996). In this final chapter, I will first present a summary of the studies described in this thesis. After that, the major results will be discussed in more detail, followed by an integration of the main findings and a schematic representation of emotion perception and corresponding behavior. This chapter is concluded with some general theoretical implications regarding studying human emotions.

Overview of findings

In *Chapter 2*, the neurofunctional network dedicated to processing facial and bodily expressions was systematically compared. Two fMRI experiments investigated whether areas involved in processing social signals were activated differently by threatening signals (fear and anger) from facial or bodily expressions. The major findings were threefold. First, the amygdala was more active for facial than for bodily expressions. Second, body stimuli triggered higher activation than face stimuli in a number of areas including the cuneus, fusiform gyrus, extrastriate body area, temporo-parietal junction, superior parietal lobule, primary somatosensory cortex, as well as the thalamus. Third, emotion-specific effects were found in the temporo-parietal junction and fusiform gyrus for bodies and faces alike whereas the extrastriate body area and superior temporal sulcus were more activated by threatening bodies.

Chapter 2 provided important similarities and differences in perceiving threat from dynamic faces and bodies. In *Chapter 3*, eye movements and EMG responses were measured to investigate how we look at facial and bodily expressions of emotion. Moreover, we investigated how participants observe emotionally ambiguous signals and whether ambiguity. To get more insight into this, emotionally (in)congruent face-body compounds were presented under different task instructions. Overall, participants looked longer at threatening than happy bodies and they spend more time observing the body when the face showed a non-threatening, happy expression. Participants' scan-path was longest in the presence of a happy face and/or body expression. Between 500-1000 ms, participants attended to the most emotionally informative parts: often the face, but also the hands.

In *Chapter 4*, we provided an overview of studies showing that emotion perception deficits are observed across different disorders. We concluded that future research should focus more on the similarities across these different disorders in order to make a broader model of disturbed emotion perception. The aim of the study presented in *Chapter 5* was to investigate how personality factors in a healthy population are associated with specific emotion regulation styles presumably linked with unique brain activity patterns. Type D (distressed) personality is defined as the simultaneous presence of both negative affectivity (e.g. worry, depression, irritability) and social inhibition (e.g., reticence and lack of self confidence). People with a Type D personality tend to experience negative emotions in different circumstances, while suppressing these emotions in social situations for fear of rejection or disapproval. The prevalence of Type D personality in the general population is 21%, and varies between 18 and 53% in cardiac patients. By using fMRI, the neural responses to threatening facial and bodily expressions were investigated in relation to negative affectivity and social inhibition. A negative correlation was observed between negative affectivity and activation of the amygdala, fusiform gyrus, insula and hippocampus while observing threatening versus neutral stimuli. Increased activation following threatening stimuli was observed in the left temporo-parietal junction and right extrastriate body area correlating with more social inhibition traits. Interestingly, threat related activity in the orbitofrontal cortex, superior temporal sulcus, inferior frontal gyrus (Brodmann area 45) and temporal pole correlated negatively with negative affectivity and positively with social inhibition. Follow-up experiments are required to investigate the specific timing of these activations further. For example, it is possible that people with a Type D personality first de-activate the "core emotion network" and subsequently over-activate a "cortical emotion network ". The role of the orbitofrontal cortex could be to connect the two networks via multiple feed-back and feed-forward connections. This is just a speculation. But what we can conclude is that while individuals with increased negative affectivity de-activated the core emotion system, socially inhibited people tended to over-activate a broad cortical network. Our findings demonstrate striking effects of personality traits on the neural coding of threatening signals.

Following the study in Chapter 5, the review in *Chapter 6* makes clear that emotion perception is not only influenced by personality factors, but is also a function of the gender of the observer and observed. Moreover, in *Chapter 7*, we provided further evidence that gender differences are indeed an important factor regulating our daily interactions. Brain areas involved in processing social signals were activated differently by threatening signals send from male and female facial and bodily expressions. Furthermore, activation patterns were different for male and female observers. Male participants paid more attention to the female face as was shown by increased amygdala activity. But a host of other areas showed selective sensitivity for male observers attending to male threatening bodily expressions (extrastriate body area, superior temporal sulcus, fusiform gyrus, pre-supplementary motor area, and premotor cortex). This study illustrates the importance of gender differences in affective communication.

In *Chapter 8*, the hypothesis was tested that violent offenders are impaired in recognizing emotions in the context of task irrelevant yet threatening cues. Direct and indirect emotion recognition tasks were given to a group of aggressive incarcerated offenders and control participants. On the direct tasks of matching either facial or bodily expressions of emotion, violent offenders performed similarly to controls. But in contrast to controls, dynamic fearful body expressions were often misinterpreted as angry. This bias toward interpreting emotions as angry expressions was clear in the indirect tasks. Violent offenders were impaired in recognizing a happy facial expression when the body showed a different, threatening expression. Moreover, they had great difficulty in categorizing the happy body expression of a target figure when it was presented in a violent scene. The results indeed indicate that one of the underpinnings of aggression and violent offences may be impaired recognition of emotional expressions, with a specific bias toward interpreting emotions as hostile angry expressions, especially when a threatening context was provided.

In *Chapter 9*, the influence of a social context on recognition of bodily expressions was investigated. Images of emotional body postures were briefly (100 ms) presented as part of social scenes showing either neutral or emotional group actions. In Experiment 1, fearful and happy bodies were presented in fearful, happy, neutral and scrambled contexts. In Experiment 2, we compared happy with angry body expressions. In Experiment 3 and 4, we blurred the facial expressions of all people in the scene. This way, we were able to ascribe possible scene effects to the presence of body expressions visible in the scene and we were able to measure the contribution of facial expressions to body expression recognition performance. In all experiments, we observed an effect of social scene context. Bodily expressions were better recognized when the actions in the scenes expressed an emotion congruent with the bodily expression of the target figure.

That the social context also influences looking patterns on bodily expressions of emotion was shown in *Chapter 10*. Participants' eye movements and EMG responses were recorded while passively viewing the above described body-scene compounds but this time with a duration of 4 seconds. Eye movement data showed that fixations were longer in response to angry versus happy body expressions situated in a neutral scene, thereby suggesting that attention is preferentially allocated to cues indicating potential threat in social situations. The fixation duration on happy bodies was influenced by the emotion depicted in the scene. There was no interaction between the emotion of the body and the emotion of the scene in the EMG data, but an angry scene increased the corrugator response and a happy scene the zygomaticus.

The eyes are the mirrors of the soul. In other words, a person's thoughts can be ascertained by looking in his or her eyes. This saying dates back to Cicero (106-43 B.C)[1]. If we indeed are able to recognize emotions perfectly by examining the eyes, context would be of little influence. Although we are often unaware of it, we frequently see just the eyes of someone (for example someone wearing a helmet, the mask of a physician or in the winter when we cover our faces as much as possible with a hat and scarf). In the Netherlands, there is an ongoing debate about the clothing (headscarves) that some Muslim women wear. These clothes are said to hamper communication, especially emotional communication. Until now, there is no scientific evidence for that. The goal of the study described in *Chapter 11* was to investigate whether recognition of the expression conveyed by the eyes is influenced by the surrounding visual information covering the rest of the face. In four experiments we tested whether emotions can be recognized from a face partly covered by a hijāb, a niqāb, a cap or a scarf. Fear was recognized best when the face was partly hidden by a niqāb, suggesting that a niqāb in combination with a fearful face, facilitated the fear response. Participants' performance was related to self-ratings of attitudes

[1] Ut imago est animi voltus sic indices oculi (The face is a picture of the mind as the eyes are its interpreter).

towards and experience with Islamic group members (such as the number of Muslims among their friends).

In summary, the studies about the neurofunctional basis of perceiving video clips of facial and bodily expressions of threat provided many new insights. First of all, the study described in chapter 2 offered the first direct comparison between dynamic facial and bodily expressions. Several similarities as well as differences between the neural basis of facial and bodily expression perception were revealed. By including additional measurements of personality type (chapter 5) and by taking into account the sex of the participant and that of the actor (chapter 7), we showed that these responses were not the same in each individual and depended on the sex of the actor. We found that male participants showed a clear motor preparation response in the brain when observing threatening body movements from other males. This result fits with the observation that aggressive offenders were impaired in recognizing threatening body movements and attended more to task irrelevant yet threatening body language than control participants (chapter 8).

Another dimension of research in this thesis is the role of context. In real life, parts of the face are often covered or occluded (for example by clothes or by other objects or people standing in the way between the observer and observed) (chapter 11). Most often we see a whole person (not just his face) and very often, other people are around. In this thesis, I showed that context influences how the information from the whole face or from the eye region is perceived and also how a social context influences emotion recognition of (chapter 9) and looking patterns on (chapter 10) bodily expressions. I will discuss the major findings in more detail below, starting with the role of the amygdala which is indisputably the mostly referred to brain area in the science of emotions.

The role of the amygdala revisited

The amygdala has been considered to be essential for recognizing fear in other people's facial expressions. Recent studies, including ours, shed partial doubt on this interpretation. Here we used movies of facial and bodily expressions instead of static photographs to investigate the putative threat selectivity of the amygdala using fMRI under more ecological conditions. At least five interesting observations regarding this brain area were done. The amygdala was found to respond:

1) …to dynamic facial and bodily expressions
2) …more to video clips of faces than of bodies
3) …equally to emotional as neutral videos
4) …less in participants with higher negative affect scores
5) … strong in male participants observing female faces

Let me start to discuss the, perhaps to the reader, most striking one: amygdala ACTIVITY WAS NOT SELECTIVE FOR THREAT. To put this result in perspective, most other studies that used dynamic facial expressions also did not find amygdala activity when contrasting emotional versus neutral faces but most did not capitalize this finding in their discussion (Grosbras & Paus, 2006; Kilts, Egan, Gideon, Ely, & Hoffman, 2003; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Puce et al., 2003; D. Simon, Craig, Miltner, & Rainville, 2006), although it has been discussed at great length in one study) (van der Gaag, Minderaa, & Keysers, 2007). This latter part of the sentence 'when contrasting emotional versus neutral faces' underscores the importance of using the correct contrast in fMRI, given that 'the correct contrast' exists at all.

In 2004, Sato and colleagues published an interesting paper in Cognitive Brain Research with the title "*Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study*"[2]. The facial expressions were dynamically morphed from static neutral to static fearful or happy expressions. Two types of control stimuli were used: 1) static fearful or happy faces, and 2) dynamic mosaic images. First, by contrasting these morphs (which are 50% neutral and 50% emotional) against a full blown emotional static picture (100% emotional), one risks showing brain areas that respond to movement or areas that respond more to neutral than to emotional expressions. Second, by contrasting against a scramble, one may reveal brain areas that are involved in processing social or biological stimuli, independent of emotion or worse, processing something with a form/shape versus something without (mosaic scramble). Nevertheless, the authors concluded that the amygdala was highly activated in response to dynamic fearful facial expressions relative to both control stimuli (Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). Would dynamic neutral faces have served as a better control condition?

The more complex stimuli become, the more difficult it is to find a suitable control condition. It is a challenge to make dynamic face stimuli that neutralize all emotional meaning and have dynamic properties comparable with those of dynamic emotional expressions. The presence of movement may be inherent to the specific emotion and a moving neutral face may be perceived as emotional (Wallbott & Ricci-Bitti, 1993). One possibility is to use the face of a person speaking with a neutral expression, such as the face of a reporter reading a news report. However, while emotional facial expressions contain complex motions involving multiple face parts, the movement in the faces of people speaking is mostly in the lower area of the face, such as the mouth and chin. Another difficulty is that a dynamic neutral face by itself has a strong social meaning and may be more ambiguous than a dynamic threatening face. We know that the amygdala is responsive to ambiguity. In monkeys, amygdala activity is larger when during social communication with unpredictable consequences as compared to physical aggression (Kling, Steklis, & Deutsch, 1979). This ambiguity may average out the amygdala's threat selectivity. In my research, Iincluded neutral facial expressions with as much facial movement as possible without losing the neutral content of the video, as control stimuli. But still, part of the results may be explained by the specific control condition that was used.

Another interesting observation which is described in chapter 2 is that the amygdala was more active for facial than bodily expressions, independent of emotion but especially for male observers watching female faces. This is consistent with earlier findings. Fischer et al (2004) reported an increased fMRI signal in the amygdala and adjacent anterior temporal regions in

[2] Most studies that came out after, justified the inclusion of dynamic faces by quoting the first part of this title.

men, but not in women, during exposure to faces of the opposite versus the same sex (Fischer et al., 2004). Moreover, amygdala activity in male observers was increased for viewing female faces with relatively large pupils, indicating an index of interest (Demos, Kelley, Ryan, Davis, & Whalen, 2008). Possibly, female faces provide more information to relevant males than male faces, whereas the distinction at the level of the face between male and female faces is less important for female observers.

Large differences between individuals existed in amygdala responsiveness following threatening stimuli. These differences may in part be accounted for by differences in personality type.Similar to the results of the study discussed in chapter 5, an earlier study also showed that participants with higher negative affect scores had lower amygdala responses following threat. To conclude, the amygdala response may be driven by neutral yet salient faces and fits with the notion that it encodes salience, being somewhat different from one individual to the other (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). In the next section, I will discuss these individual differences in more detail.

Individual differences

People differ in how they attend to, interpret, react to and cope with emotions. These differences are partly biologically defined but may have also been fueled by environmental factors. For example, criminal populations have often been confronted with violence during their life and were often raised in a violent environment (Cima, Smeets, & Jelicic, 2008; Driessen, Schroeder, Widmann, von Schonfeld, & Schneider, 2006; Heide & Solomon, 2006; Hosser, Raddatz, & Windzio, 2007; Kopp et al., 2009; Lindberg et al., 2009; Poythress, Skeem, & Lilienfeld, 2006). If we in daily life are surrounded by violence, we may be continuously looking out for danger, ready to quickly respond whenever we think someone is attacking us and this behavior may have been repetitively positively reinforced in the past.

Attentional biases can influence what information people are likely to focus upon and they have been observed in many disorders. For instance, patients with anxiety (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van, 2007), chronic pain (Schoth & Liossi) and eating disorders (Faunce, 2002) show increased attention to information representing their concerns (i.e. angry and painful facial expressions, and food, body shape, and weight related stimuli respectively). Besides differences in attention, people also differ in how they interpret emotions. For example, social phobia patients tend to interpret ambiguous social scenarios negatively even when a positive interpretation is available (Bar-Haim et al., 2007). Copello and Tata (1990) observed that offenders were more likely to interpret violent ambiguous sentences (e.g. "The painter drew the knife") in a threatening fashion, with the opposite being shown by a non-offender group (Copello & Tata, 1990). In our study with violent offenders, we also observed that they are guided towards threatening, yet task irrelevant cues when categorizing emotions. These attentional and interpretation biases as observed in a range of behavioral tasks are reflected in the individual brains' response to threat and even small differences in personality can account for large differences on the neural level.

We investigated the normal variance in negative affectivity and social inhibition scores in healthy participants and related the between-subject differences to between-subject differences in brain reactivity. This made clear that subclinical individual differences in negative affectivity, characterized by the tendency to worry and feel unhappy, etc., are related to differences in reactivity of the emotional brain. Moreover, the findings revealed that social inhibition may be marked by a sensitivity to over-mentalize and empathize when perceiving threat. Altogether, our study demonstrated that negative affectivity and social inhibition are differentially related to emotion-specific brain activation that may be relevant to both physical and mental health.

It is only in the last several years that the required technology, computational tools, and body of scientific research have become available to localize unique signatures (biomarkers) for specific emotional states in the brain and link these to individual differences in personality. These biomarkers may be used to make predictions about emotional states and health outcomes in new individuals. Moreover, recent years have shown a growing interest in studying the role of genetic variation in brain structure and function. Fueled by advances in molecular genetics and neuroimaging, the increasing number of studies in this area will potentially shed more light on the biological mechanisms involved in emotion. Identifying the gene-brain-behaviour markers that best capture emotional instability versus resilience is crucial to developing new tools and strategies for early intervention and prevention. But still, we need to take into account that the expression of certain genes only occurs given certain environmental factors and we should not underestimate the influence of the context in which emotions are perceived. In fact, emotions are ALWAYS perceived in context.

Emotions in context

Only recently affective neuroscience picked up an important factor that had already been studied for many years in the field of object recognition studies: context. In our everyday rich and complex surrounding world, objects are embedded in visual scenes. Because of repetitive co-occurrence of objects or because of co-occurrence of a given object in a specific contextual frame or schemata, our brains can generate expectations (Bar & Ullman, 1996; Biederman, Rabinowitz, Glass, & Stacy, 1974; Palmer, 1975). These expectations in terms of objects will not be the same when walking in a busy street or along a path in the country, so that object recognition can be facilitated (a car in the street) or perturbed (a telephone box in the country) by such expectations. Previous investigations have shown that facial expressions are influenced by context more than had been assumed before (Aviezer et al., 2009; Meeren, van Heijnsbergen, & de Gelder, 2005; Righart & de Gelder, 2006, 2008a, 2008b; Van den Stock & de Gelder, 2006; Van den Stock, Righart, & de Gelder, 2007). In fact, context can dramatically shift the emotional category recognized in basic facial expressions towards the emotion that is visible in the context. In chapter 11, we described how context can influence the emotion as observed in a woman's eyes. Participants judged the emotion differently depending on the type of headdress the woman wore. Recognizing fear from women with a niqab (Islamic headscarf) was easier than from women wearing a cap and a shawl (covering the exact same face region). Obviously, it was not just the clothing that served as a context, but the fact that the observed was most probably perceived as an out-group member. This is in line with previous research. For example, subjects with prejudices tend to make anger judgments when the target is a black versus a white male (Hugenberg & Bodenhausen, 2003). Moreover, emotion recognition is typically faster for positive than negative emotions, but the reverse obtains when Caucasians judge Black targets (Hugenberg, 2005). Weisbuch and Ambady (2008) reported that negative automatic responses were activated in response to out-group expressions of joy and in-group expressions of fear (Weisbuch & Ambady, 2008). Adams et al (2009) examined the neural correlates of the intra-cultural advantage of "reading the mind in the eyes[3]" using fMRI, revealing greater bilateral posterior superior temporal sulci recruitment during same- versus other-culture mental state decoding in native Japanese and white American participants (Adams et al., 2009). In short, stereotypes, negative attitudes towards an out-group, and in-group preferences can serve as a context in which we perceive another's emotion which is reflected in the brain. The study described in chapter 11 that an external cultural context that is not present in the facial features themselves can already influence the perception of otherwise identical emotional face parts.

The perception of another's emotion often occurs within a social group. During our life span, we are confronted more often with situations where people express similar (group) emotions. As a consequence, we are quicker and better in recognizing emotions in clear, non-ambiguous social situations. In chapter 9, we investigated the influence of a social context on the recognition of a single emotional body expression. The effects of congruency on emotional body perception were investigated using manipulated photographs containing a foreground figure that was either displaying the same or a different emotion than the people in the background. As expected, recognition of angry, fearful or happy expressions was better when they were situated in an emotionally congruent versus incongruent scene. There is a possibility that the congruency effect occurs at the response level. Especially in case of a more ambiguous stimulus, participants may increasingly attend to the context although it is not very likely because a presentation time of 100 ms is too short to make saccades from the fixation point and it was against the task instructions. We further investigated the influence of attention in chapter 10 by measuring fixation durations on the body and the scene over longer stimulus presentation durations. The finding that participants scanned the whole picture more when the body showed a happy versus angry expression is consistent with our previous findings as described in chapter 3. After 1500-2000 ms, the influence of an angry scene became visible, suggesting a cognitive mechanism in which the participant tried to understand how the person in the scene reacted to the threatening situation and possibly empathized with this person only after understanding the whole situation, as was reflected by the relatively late corrugator response. Importantly, the effects of incongruency between the body and the scene as observed in the manual responses under shorter presentation times were not observed in either looking patterns or EMG responses and thus reflect an earlier,

[3] Most studies that investigated the perception of emotions from the eye region used isolated eyes rather than providing a naturalistic context in which the eyes are often perceived (cats, hats, helmets, beards, masks etc).

more mandatory process. We elaborate on these findings and the timing of the effects in the next paragraph.

Given that in real life, we usually encounter a person with a head ánd a body which may or may not be both emotionally expressive, it is surprising that there is hardly any literature on how recognition of facial expressions are affected by emotional body contexts. Meeren et al (2005) used photographs of fearful and angry faces and bodies to create realistically looking face–body compound images, with either matched or mismatched emotional expressions. A short stimulus presentation time was used (200 ms), requiring observers to judge the faces on the basis of a "first impression" and to rely on global processing rather than on extensive analysis of separate facial features. The recognition of the emotion conveyed by the face was found to be systematically influenced by the emotion expressed by the body. Observers made better and faster decisions when faces were accompanied by a matching bodily expression than when the bodily expression did not match the facial expression. The EEG data showed an enlargement of the occipital P1-component as early as 115 ms after presentation onset for incongruent face-body combinations. This points to the existence of an ultra rapid neural mechanism sensitive to the degree of agreement between simultaneously presented facial and bodily emotional expressions, even when the latter are unattended (Meeren et al., 2005).

This thesis includes reports about experiments in which similar face-body compound stimuli were used in order to elaborate on the findings from Meeren et al (2005). Next to the emotions fear and anger, the emotion happiness was included. Fear and anger are both emotions with a negative valence and each is associated with evolutionary relevant threat situations. However, happiness is an emotion that we are exposed to much more often in daily life. Second, different presentation times (100 ms and 4000 ms) were used in order to gain more insight in the timing of the earlier described effects. Third, the influence of a congruent or incongruent facial expression on the categorization of bodily expressions was investigated. Fourth, these effects were measured in a student population and beyond; violent offenders and a matched control group. Fifth, EMG and eye movement patterns provided additional insight in the observed effects.

As one would expect, task instructions influenced looking patterns on emotionally (in) congruent face-body pairs. Participants attended more to the body when they were asked to do so and attended more to the face when they were instructed to ignore the bodily expression. Overall, participants attended more to threatening cues and when there was no threat, they scanned the whole picture in search of it, which is consistent with earlier studies (Green, Williams, & Davidson, 2003; Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009). Aviezer et al (2008) demonstrated that characteristic fixation patterns previously thought to be determined solely by the facial expression are systematically modulated by emotional context already at very early stages of visual processing (Aviezer et al., 2008). We also observed that a facial expression influenced looking patterns on the body, and a bodily expression influenced looking patterns on the face. However, a clear congruency effect was again not observed, suggesting that eye movements do not reflect a passive type of perception but represent active, goal-directed movements. The fact that we hardly see effects of face-body (in)congruence with this measurement, suggests that the earlier observed effects on the P1 that Meeren et al

(2005) obtained with much shorter presentation times (200 ms) reflect an automatic mandatory process which cannot be seen in fixation behavior because it occurs much earlier in processing time. This also illustrates the great influence of stimulus presentation durations on the perception and recognition of emotions. In real life, we can often observe emotions for longer durations. Moreover, they are never static.

Emotions are dynamic

In social contexts, facial and bodily expressions are dynamic in nature and vary rapidly in relation to situational requirements. Existing psychological evidence indicates that emotional processing is facilitated when expressions are dynamic rather than static. Dynamic stimuli are more ecologically valid than static images of faces and bodies: empirically, there is evidence that dynamic stimuli activate regions throughout the brain more strongly than static versions of the same stimuli (Kilts et al., 2003; Sato et al., 2004; Trautman et al., 2009).

Viewing dynamic emotional expressions as compared to static ones engages areas processing biological movements and emotion such as the superior temporal sulcus and the amygdala, but also areas involved in the production of these expressions, in particular the parietal and premotor cortex (Decety & Chaminade, 2003; Sato et al., 2004). Dynamic facial expressions induce more facial mimicry than static expressions (Sato et al., 2008). Dynamic stimuli also contain explicit movement information which elicits activity in movement sensitive areas like superior temporal sulcus, premotor areas and in the extrastriate body area, but also the amygdala and the lateral orbitofrontal cortex which play a role in the affective evaluation of stimuli. This is both the case for dynamical facial expressions (LaBar et al., 2003; Sato et al., 2004) and for bodily expressions alike (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008). When viewing dynamic emotional bodies, an important priority for the brain is to represent the perceived emotional action. This idea is in line with Adolphs et al. (2003)'s findings that patient B with extensive lesion of the ventral pathway, which includes the amygdala, is able to recognize emotions from a dynamic facial expression but not from a static one.

Adaptation to repeated presentation of the same static face or body may quickly occur. However, dynamic stimuli by their nature contain a greater range of images. They continuously change and may be more interesting and grab ones attention more easily. Given the selectivity of some face-responsive neurons to specific views and types of faces (Perrett et al., 1991), this greater range might activate a larger pool of neurons than static stimuli. Because dynamic stimuli provide more information than static ones, this possibly decreases ambiguity. Several studies have shown that the dynamic presentation of facial expressions improves recognition of the emotional content of the expressions (Harwood et al., 1999; Kozel et al., 1968). Studies of bodily expressions also reported better recognition rates for dynamic than static stimuli (Atkinson, Dittrich, Gemmell, & Young, 2004; de Meijer, 1989).

Numerous functionally distinct regions of cortex (e.g., V1, MT, the fusiform face area) can be easily identified in any normal human subject by the use of a functional localizer. Localizers that contrast brain signal when viewing faces or bodies versus objects are commonly used in fMRI studies of face and body processing. However, current protocols do not reliably show all regions of the core system for face and body processing in all subjects when conservative statistical thresholds are used (this problem was also apparent in the fMRI studies described in chapter 2 and chapter 7). Furthermore, arbitrary variations in the applied thresholds are associated with inconsistent estimates of the size of the regions of interest. It has been shown that the use of more natural dynamic facial images in localizers increases the likelihood of identifying face-selective regions of interest in individual subjects (Fox et al., 2009). Given the enhanced activations in body selective areas in studies that used dynamic bodies, this may apply for body localizers as well but this is still an open research question.

However, a critical note against the use of dynamic stimuli should be taken in mind. Dynamic stimuli are harder to control for low-level differences including luminance and contrast. Moreover, whereas a static picture shows the peak in the emotional moment, a dynamic stimulus contains a range of images with a less intense or arousing emotional content. Another drawback of dynamic stimuli is that they cannot be used in all experimental paradigms such as when one wants to investigate the unconscious perception of emotions by using a masking paradigm. For these reasons, I think we should not completely abandon the tradition of using still images in emotion research. But if the experimental design allows it, there is much evidence to advocate the usage of dynamic expressions.

Integration of main findings

In this thesis, I showed that emotions (whether from the eyes, the whole face or from the whole body) are best recognized in a context that has the same emotional valence. Intriguingly, measures of attention allocation, EEG activity, facial muscle activity and manual responses demonstrate distinct reaction patterns at different stages of processing. The fact that a reliable influence of context was obtained in implicit paradigms in which the bodies, faces, headscarves or social scenes were not task- relevant nor explicitly attended to, implies that the influence they exercise is rapid and automatic. We suggest that these patterns of reactivity subserve and contribute to the dynamic processes of person perception by constituting parts of the biological correlates of our propensity for social perception. This helps us to actively engage with others, to drive the allocation of attentional resources towards threatening cues and to inform higher-order cognitive functioning brain areas to provide essential information to help us to understand others and plan our own actions accordingly.

In the model on the next page (figure 1), I schematically represent and integrate the experimental findings that I observed in the emotional paradigms described in this thesis and combine these with other factors common in experiencing threatening situations. All factors from the different levels are interacting. An important issue concerns when and where in the perceptual system these interactions occur. In the model presented in figure 1, I overlaid these different levels with the corresponding brain areas which are printed in italics. Let me explain this model with the following situational example:

being confronted with a big guy pointing his knife at you[4]. In my view, there are two key factors that eventually define ones reaction: 1) the individual him/herself, 2) the type of stressor.

First, different people may react differently in this situation. *Level 1*. Most important factors underlying immediate behavioral outcomes are biological factors such as ones genetic make-up and current health status (of course including being physically capable of acting at all). *Level 2*. Next in the order of importance are the environmental factors specific to the individual including similar previous experiences and for example, how stressed one was just before the incident occured due to (un)related situational events. Ones biological sex may influence behavioral outcome. For example, the gender of the observer and observed combined, greatly influence brain activity (as seen in chapter 7). In chapters 5, 6 and 8, I stressed the importance of personality factors such as negative affectivity, social inhibition, anxiety and aggression which are responsible for attentional biases towards threat, avoidance, hyper-or hypo- sensitivity, rigidity and impulsivity. *Level 3*. At the third level, culture may prescribe stereotypical action patterns (i.e. men should be brave). Moreover, knowledge of how similar others felt and behaved in the same situation may influence ones final action plan. At least as important is ones current state of psychological wellbeing which is greatly influenced by hormonal levels, quality of sleep and many other factors.

On the side of the stressor, the context in which the stressor is perceived is of crucial importance. If we encounter a man with a knife at a carnival party, we may not feel scared at all because we are tuned to expect strange or supposedly frightening people there. Besides, everybody else around that person at the party seems not to care and is having a great time. But when the situation is more ambiguous, ones percept of the situation may become negatively biased when the observed is an out-group member. The same holds when being on unfamiliar ground. Other factors include the emotionality of the stressor including arousal, intensity and valence. I believe these factors are of influence on ones behavior at a very early level, and therefore fall under *Level 1* factors.

Level 2. Next are factors including the ambiguity of the stressor. In other words, how obvious or salient is the threat? Whether a threat is relevant depends on the situation of the individual. If, for example, the individual is protected by a thick glass wall, or if the threat is presented on a computer screen (I will come to this point in the next paragraph), cognitive processes quickly take over an initial reflex-like response. If, in the prescribed situation one may be carrying a big gun with him, he may feel better in control of the situation (active rather than passive protection). If, for some reason, one is daily confronted with guys carrying weapons and nothing serious ever happened before, ones familiarity with the situation may diminish the threat response

[4] The reason I choose this situation as an example is because it actually happened and I reacted very different than my boyfriend did. We were walking in the streets of the old city part of Bucharest. I was admiring the beautiful old houses and observing the people that looked all so different. But Jasper did not feel at ease. Out of nowhere, this big guy flipped open his stiletto right into our faces and demanded our money. He had this funny smile on his face and because of his strange accent I could not clearly understand him. But before I could fully psycho-analyze him and politely reply to his request, I found myself in a shop. Jasper immediately noticed the danger, grabbed my arm and pulled me into this shop. All I said was "Hey, they are playing Frans Bauer here!". Jasper was shaking…

(habituation and learning effect). *Level 3.* On this level, attitudes and expectations are carefully being weighed in order to decide which action one will take.

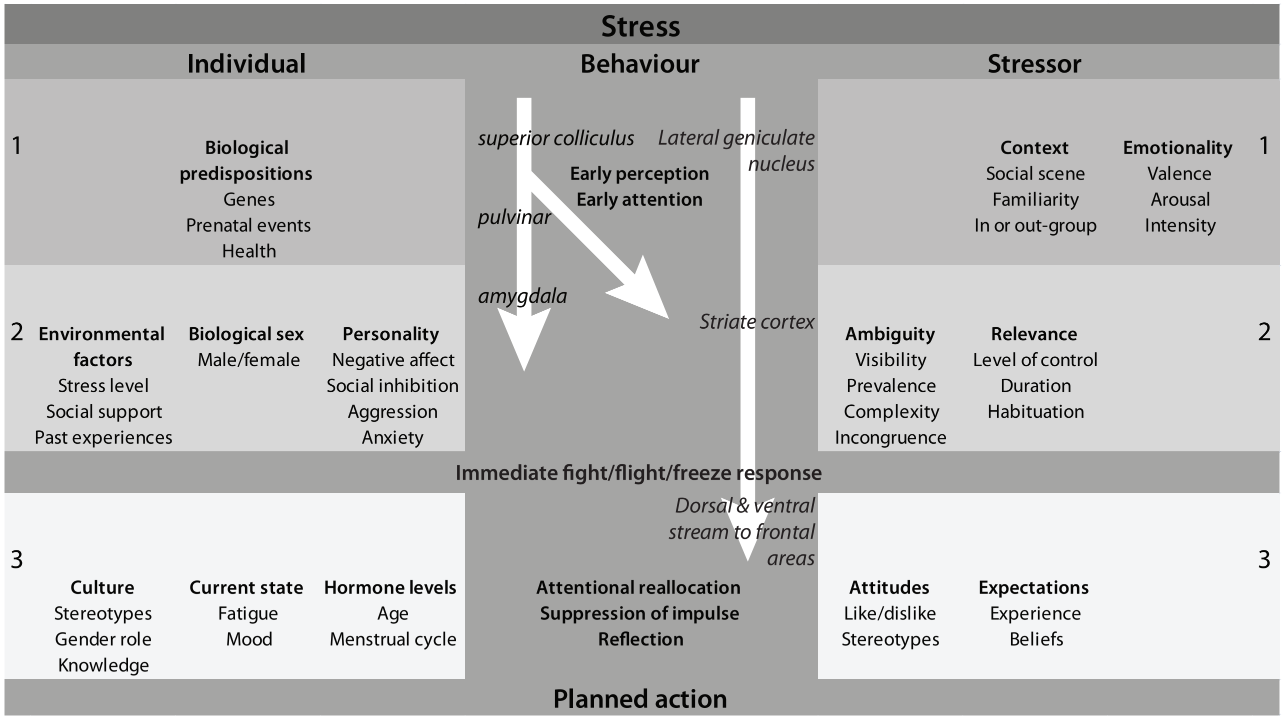
In short, the behavioral outcome of a stressful event on the individual level is dependent on multiple factors. These factors influence early perception which is guided by attentional resources towards the treat (orienting response). Thereafter, further processing takes place where attention is guided towards or away from the threat and initial impulses may be suppressed after which a full action plan is developed.

Ecological relevance and methodology

Simon (1990) argued that a study of cognition must explore both the mind and the environment in which the mind interacts. He likened this to two blades in a pair of scissors that cannot function unless both blades are present (Simon, 1990). This provides an important lesson for affective neuroscience as well (Zaki & Ochsner, 2009). Studies in this field frequently face criticism for overly artificial task environments and the presentation of un-naturalistic stimuli. Using simple stimuli in impoverished apparatuses offers clear advantages in terms of reducing the likelihood of confounding variables. Unfortunately, this gain in internal validity comes at the price of reducing external validity.

Measuring 'how humans perceive emotions' can be done in numerous ways and of course, this thesis provided just a snapshot. I presume that natural moving faces and bodies and naturalistic scenes provide a more valid stimulus basis for the examination of emotion perception than static pictures, morphs or animations. These more naturalistic stimuli should be further employed to probe the neural bases of perceiving social cues that better approximate those encountered by perceivers in the real world. I also presume that the use of a single method to test a hypothesis can result in a biased view of the phenomenon of interest. Similarly, models about human emotion perception that build exclusively on emotion perception studies that were conducted in a homogeneous group of healthy young adults may not be applicable to the whole population. Therefore, conducting experiments by combining different techniques, with their unique pros and cons, under different task instructions and by including a broad range of stimulus material in a wide-ranging group of individuals comes closest to measuring real emotions in real life situations.

Figure 1.



The processing of affective information has many attributes that make it special, such as speed, and relative independence from attention and awareness. A key question, therefore, is how this happens. One account involves a so-called sub-cortical pathway from the retina via the superior colliculus and pulvinar to the amygdala. At later, more "conscious" processing stages, cortical areas get involved in preparing an action plan. It has recently been suggested that the pulvinar works in a way that integrates cortical-subcortical processing, hence the oblique arrow in this model (Pessoa, 2010). In this model, I integrated different interacting factors affecting these processing roads at multiple stages. Thus, these stages should not be looked at as strictly separate, but as rather fluid levels which also provide feedback to the earlier levels. In fact, they may differ again from person to person and from situation to situation. Certain factors may be of greater weight in one individual versus the other.

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Nederlandse Samenvatting

Hoe context, man-vrouw verschillen en persoonlijkheidsfactoren de perceptie van gezichts- en lichaamsexpressies van emotie beïnvloeden

In het dagelijks leven worden we voortdurend geconfronteerd met andere mensen. Hoe ze zich gedragen en bewegen heeft een directe invloed op ons, of we ons daar nu bewust van zijn of juist niet. Onderzoek in het verleden heeft zich voornamelijk gericht op gezichtsexpressies. Als stimulusmateriaal werd en wordt veelal gebruik gemaakt van foto's. Uit deze eerdere onderzoeken zijn verscheidene theorieën gevormd over hoe wij als mens emoties verwerken. Een probleem hiermee is dat we iemands emotie vaak juist *niet* aan zijn gezichtsexpressie herkennen, maar dat iemands lichaamstaal of trilling in de stem ons veel meer vertelt over zijn of haar gemoedstoestand. Bovendien verschillen mensen onderling enorm in hoe ze emoties herkennen en ervaren. Echter, het overgrote deel van psychologisch onderzoek maakt vooral gebruik van gezonde psychologiestudenten wat natuurlijk een vrij homogene groep is en niet representatief voor de algehele bevolking. In dit proefschrift worden verschillende onderzoeken beschreven waarbij gebruik is gemaakt van meer naturalistische stimuli en tevens rekening is gehouden met individuele verschillen tussen mensen. De resultaten zijn hieronder kort samengevat.

De eerste studie die wordt besproken in hoofdstuk 2 beschrijft een systematische vergelijking tussen de hersengebieden die belangrijk zijn voor het verwerken van dynamische gezichtsexpressies en hersengebieden die verhoogd actief worden wanneer we een emotionele lichaamsexpressie waarnemen. In twee fMRI experimenten is onderzocht of deze hersengebieden verschillend reageerden op angstige of boze versus neutrale (niet emotionele) signalen. De resultaten laten zien dat de amygdala meer activiteit vertoonde voor de verwerking van gezichts- versus lichaamsexpressies van emotie. Lichaamstaal versus gezichtsexpressies zorgde voor verhoogde activatie in de cuneus, gyrus fusiformis, extrastriate body area, temporo-parietal junction, lobulus parietalis superior, de primaire somatosensorische cortex, evenals de thalamus. Emotie-specifieke effecten werden gevonden in de temporo-parietal junction en de gyrus fusiformis voor lichamen én gezichten, terwijl de extrastriate body area en de superior temporal sulcus veel meer en specifieker dreigende lichaamsbewegingen verwerkten.

In hoofdstuk 2 tonen we belangrijke overeenkomsten en verschillen tussen de verwerking van gezichts- en lichaamsexpressies op hersengebiednivo. In hoofdstuk 3 worden de oogbewegingen en electromyografische reacties (EMG responsen) van de zygomaticus major en corrugator supercilii van proefpersonen gemeten om zo te onderzoeken hoe er wordt gekeken naar gezichts- en lichaamsexpressies en of de waarnemers hun gezichtsuitdrukkingen aanpassen aan de emotie van de persoon die werd geobserveerd. Bovendien onderzochten we hoe er werd om gegaan met emotioneel ambigue signalen en of ambiguiteit van invloed is op ons empathisch reageren. We lieten proefpersonen foto's zien van mensen die een bepaalde emotie uitbeeldden. Echter, de gezichtsexpressie was gemanipuleerd, en was soms juist niet in overeenstemming met de emotie die het lichaam uitbeeldde (bijvoorbeeld een blij gezicht boven een dreigende lichaamshouding). In het algemeen keken proefpersonen langer naar dreigende dan naar blije lichaamsexpressies en keken ze langer naar het lichaam wanneer het gezicht een niet dreigende, blije uitdrukking had. Proefpersonen scanden een groter oppervlakte van de foto's en maakten meer saccades als het plaatje een blij gezicht en / of lichaam toonde, alsof ze op zoek waren naar een dreigende cue. Tussen de 500 en 1000 ms na aanvang van de stimulus presentatie keken proefpersonen vooral naar de meest emotioneel informatieve onderdelen: vaak het gezicht, maar bijvoorbeeld ook de handen.

In hoofdstuk 4 geven we een overzicht van studies waarin verschillende klinische populaties worden onderzocht in verschillende emotie-perceptie taken. In plaats van tekorten aan te tonen in één klinische populatie, zoals bijvoorbeeld is aangetoond bij schizofreniepatienten, zou toekomstig onderzoek zich meer kunnen richten op de gelijkenissen tussen deze verschillende aandoeningen. Er zijn sterke aanwijzingen voor genetische verwantschappen tussen verschillende stoornissen. Deze verwantschappen kunnen belangrijk inzicht verschaffen in tekorten waar het gaat om het herkennen van en het reageren op emoties, kenmerken die aanwezig zijn in verschillende stoornissen zoals bijvoorbeeld ook autisme.

Het doel van de studie gepresenteerd in hoofdstuk 5 is om te onderzoeken hoe persoonlijkheidsfactoren in een gezonde populatie zijn geassocieerd met specifieke emotie regulatie stijlen, gereflecteerd door unieke activatiepatronen in de hersenen. Type D (distressed) persoonlijkheid, een begrip uit de medische psychologie, is gedefinieerd als de gelijktijdige aanwezigheid van zowel negatieve affectiviteit (bv. piekeren, zwaarmoedigheid, prikkelbaarheid) en sociale inhibitie (bv. terughoudendheid en gebrek aan zelfvertrouwen). Mensen met een Type D persoonlijkheid hebben de neiging om in uiteenlopende omstandigheden negatieve emoties te ervaren, en tegelijkertijd deze emoties te onderdrukken in sociale situaties uit angst voor afwijzing of afkeuring. De prevalentie van Type D persoonlijkheid in de algemene populatie is 21%, en varieert tussen 18 en 53% in/bij hartpatiënten. In het eerder besproken fMRI paradigma wordt een mogelijk verband onderzocht tussen dit type persoonlijkheid en hersenactiviteit tijdens het waarnemen van dreigende of neutrale gezichts- en lichaamsexpressies. Een verband werd gevonden tussen negatieve affectiviteit en verminderde activering van de amygdala, fusiform gyrus, insula en de hippocampus bij het observeren van emotionele versus neutrale stimuli. Verhoogde activiteit werd onder andere gevonden in de linker temporo-parietal junction en in de rechter hersenhelft de extrastriate body area, die correleerden met meer sociale inhibitie eigenschappen. Het is met name interessant dat de orbitofrontale cortex, superior temporal sulcus, inferior frontal gyrus (Brodmann area 45) en temporal pole negatief correleerden met negatieve affectiviteit en juist positief met sociale inhibitie. Vervolgexperimenten zijn nodig om de specifieke timing van deze twee netwerken verder te onderzoeken. Het is bijvoorbeeld goed mogelijk dat mensen met een Type D persoonlijkheid eerst een de-activatie van het "core emotion network" laten zien, gevolgd door een over-activatie van het "cortical emotion network". Wat in ieder geval geconcludeerd kan worden is dat terwijl personen met een hoge negatieve affectiviteit het emotie netwerk minder activeren, sociaal geremde mensen een uitgebreid corticaal netwerk extra activeren. Onze bevindingen tonen opvallende effecten van persoonlijkheidskenmerken op de neurale codering van dreigende signalen.

Hoofdstuk 6 geeft een overzicht van de literatuur betreffende studies naar verschillen tussen mannen en vrouwen waar het gaat om de perceptie van emoties. In tegenstelling tot wat men vaak denkt, is het niet zo dat vrouwen emotioneler zijn dan mannen. Vrouwen uiten hun emoties meer, maar de literatuur suggereert ook dat mannen sterker reageren op negatieve emoties dan vrouwen. Hoewel de literatuur soms tegenstrijdigheden laat zien, zeker waar het hersenactiviteit betreft, blijkt het dat vrouwen vaak expressiever zijn dan mannen en dat het makkelijker is om een emotie te herkennen van een vrouw dan van een man. Echter, dit geldt met name voor bepaalde emoties zoals angst en blijdschap maar zeker niet voor woede. We kunnen concluderen dat de manier waarop we emoties waarnemen niet alleen beïnvloed wordt door persoonlijkheidsfactoren, maar ook een functie is van het geslacht van de waarnemer en dat van de waargenomene.

In hoofdstuk 7 laten we zien dat verschillende hersengebieden die betrokken zijn bij het verwerken van emoties meer of minder actief worden als het *geobserveerde* emotionele signaal van een man of een vrouw afkomstig is. Bovendien werd duidelijk dat ook het geslacht van de *proefpersoon* een grote rol speelt. Een aantal hersengebieden in de mannelijke proefpersonen reageerde sterk op mannelijke dreigende lichaamstaal (extrastriate body area, superior temporal sulcus, fusiform gyrus, het pre-supplementaire motorische gebied, en de premotorische cortex). Deze studie illustreert het belang van genderverschillen in de communicatie van emoties.

In hoofdstuk 8 wordt de hypothese getest dat agressieve en gewelddadige delinquenten problemen hebben met het herkennen van andermans emoties, met name wanneer deze worden waargenomen in de aanwezigheid van taak-irrelevante dreigende cues. Hun vermogen om emoties te herkennen werd getest door gebruikmaking van directe herkenningstaken en indirecte matchingtaken en werd vergeleken met controle proefpersonen. De delinquenten hadden geen problemen met het matchen van emotionele gezichts- of lichaamsexpressies. Maar in tegenstelling tot de controleproefpersonen interpreteerden ze angstige, dynamische lichaamstaal vaak als zijnde boos. Deze bias in de richting van negatieve emoties werd met name zichtbaar in de indirecte taken. De delinquenten waren slechter in het herkennen van een blij gezicht wanneer het lichaam een dreigende expressie toonde. Daarnaast hadden ze grote moeite met het identificeren van een blije lichaamsexpressie wanneer deze werd gepresenteerd in een gewelddadige scène (bijvoorbeeld met een groep vechtende mensen op de achtergrond). De resultaten laten zien dat een van de fundamenten van agressie en gewelddadige misdrijven een tekort zou kunnen zijn in het herkennen van andermans emoties en deze vooral als vijandig of boos interpreteren, met name in de aanwezigheid van een dreigende context.

In hoofdstuk 9 wordt de invloed van een sociale context op de herkenning van lichaamsexpressies onderzocht. Beelden van emotionele lichaamsposes werden kort (100 ms) gepresenteerd in scènes van neutrale ofwel emotionele groepsactiviteiten (bijvoorbeeld een groep sportende, feestende of vechtende mensen). In Experiment 1 werden angstige en blije lichaamsexpressies getoond in een angstige, blije of neutrale context. In Experiment 2 werden blije met boze lichaamsexpressies vergeleken. In Experiment 3 en 4 hadden we de kenmerken in de gezichten van alle mensen in de scène weggevaagd om mogelijke effecten van de scène toe te kunnen schrijven aan de aanwezigheid van emotionele lichaamstaal die zichtbaar was op de achtergrond. In alle vier de experimenten werd een duidelijk effect van de sociale context gevonden. Lichaamsexpressies werden beter herkend wanneer de mensen op de achtergrond dezelfde emotie lieten zien.

Dat de sociale context ook van invloed is op de fixaties van proefpersonen bij het kijken naar lichaamsexpressies van emotie wordt aangetoond in hoofdstuk 10. De oogbewegingen van proefpersonen en EMG responsen werden opgenomen, terwijl ze keken naar de hierboven beschreven lichaamsexpressies geplaatst en verschillende emotionele scènes. In dit experiment hoefden de proefpersonen geen taak uit te voeren en konden ze het plaatje gedurende vier seconden vrij observeren. De eyetracking data lieten zien dat fixaties langer duurden bij boze versus blije lichaamsuitdrukkingen in een neutrale scène. Dit geeft de indruk dat de aandacht bij voorkeur wordt toegewezen aan signalen die een potentiële dreiging vormen. Ook de lengte van fixaties op blije lichaamshoudingen werd beïnvloed door de emotie die zichtbaar was in de scène. Er was geen zichtbare interactie tussen de emotie van het lichaam en de emotie van de scène in de EMG-gegevens, maar een boze scène verhoogde de respons van de corrugator en een blije scène die van de zygomaticus.

Er wordt weleens gezegd dat de ogen de spiegels zijn van de ziel. Als we inderdaad in staat zijn om emoties perfect te herkennen door enkel naar de ogen te kijken, dan zou een eventuele context er weinig meer toe doen. Hoewel we ons er vaak niet bewust van zijn, zien we best vaak van iemand alleen de ogen (denk bijvoorbeeld aan iemand met een helm, aan het mondkapje van een arts of in de winter, wanneer we met een muts en sjaal ons gezicht zoveel mogelijk bedekken). In Nederland laait de discussie over de bedekkende kleding van sommige Islamitische vrouwen vaak hoog op. Wat als argument wordt aangevoerd is dat deze kleding de communicatie, en dan met name de emotionele communicatie, belemmert. Tot nu toe was daar geen enkel wetenschappelijk bewijs voor. In hoofdstuk 11 onderzoeken we dit vraagstuk door te testen in hoeverre wij emoties kunnen herkennen van iemand waarvan alleen de ogen zichtbaar zijn. Om precies te zijn: in vier experimenten werd getest of emoties kunnen worden herkend van een gezicht dat gedeeltelijk bedekt is met een hijab (hoofddoekje, met volledig gezicht zichtbaar), een niqaab (waarbij alleen de ogen zichtbaar zijn), een muts of een muts in combinatie met een sjaal die de helft van het gezicht bedekt. In de condities hijab en muts was precies evenveel informatie van het gezicht aanwezig. Dit gold ook voor de condities niqaab en muts-sjaal. Het meest opvallende resultaat van deze studie is dat de emotie angst het best werd herkend wanneer het gezicht deels verscholen ging achter een niqaab, veel meer dan wanneer evenveel van hetzelfde gezicht bedekt werd door een muts en een sjaal. Van een response bias was echter geen sprake. Het lijkt er dus op dat een niqab de angst respons vergemakkelijkt in het geval van een angstige gezichtsexpressie, wat mogelijk het gevolg is van negatieve associaties die Nederlanders hebben met de Islam. Uit deze studie bleek tevens dat de prestaties van proefpersonen afhingen van iemands attitude ten opzichte van de Islam en ook van het aantal Islamitische mensen die er in iemands nabije omgeving (bijvoorbeeld in de vriendenkring) zijn.

In dit proefschrift laat ik zien dat emoties (af te lezen uit iemands ogen, van het hele gezicht of van het hele lichaam) het beste worden herkend in een context die past bij de emotionele valentie van de geobserveerde persoon. Het feit dat een betrouwbare invloed van context werd verkregen in impliciete paradigma's, waarin de lichamen, gezichten, hoofddoekjes of sociale scènes niet direct relevant waren voor het uitvoeren van de taak, suggereert dat de invloed die zij uitoefenen al in een vroeg stadium van verwerking plaatsvindt. Deze interactie met context en diens vroege verwerking zorgt er voor dat we situaties snel en accuraat kunnen inschatten en onze eigen acties daar vlot op aanpassen. Maar hoe emoties precies verwerkt worden verschilt van persoon tot persoon en wordt mede bepaald door iemands persoonlijkheid of geslacht.

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