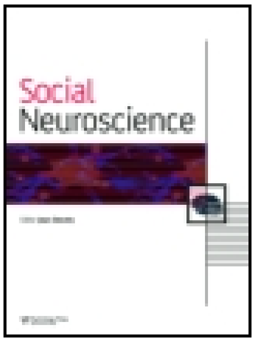

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REVIEW

Processing emotional body expressions: state-of-the-art

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ABSTRACT
Processing emotional body expressions has become recently an important topic in affective and social neuroscience along with the investigation of facial expressions. The objective of the study is to review the literature on emotional body expressions in order to discuss the current state of knowledge on this topic and identify directions for future research. The following electronic databases were searched: PsychINFO, Ebsco, ERIC, ProQuest, Sagepub, and SCOPUS using terms such as *"body," "bodily expression," "body perception," "emotions," "posture," "body recognition"* and combinations of them. The synthesis revealed several research questions that were addressed in neuroimaging, electrophysiological and behavioral studies. Among them, one important question targeted the neural mechanisms of emotional processing of body expressions to specific subsections regarding the time course for the integration of emotional signals from face and body, as well as the role of context in the perception of emotional signals. Processing bodily expression of emotion is similar to processing facial expressions, and the holistic processing is extended to the whole person. The current state-of-the-art in processing emotional body expressions may lead to a better understanding of the underlying neural mechanisms of social behavior. At the end of the review, suggestions for future research directions are presented.

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Body; emotion; body expression; perception

Background

Recognizing and decoding affective signals from faces, body postures, voices and other contextual information in our environment assure successful social interactions. Research in affective and social neuroscience has largely focused on the role of facial expressions and a combination of face and voice expressions in emotional communication to the detriment of bodily ones and their neural mechanisms.

As research progressed and focused on bodily expressions, it was found that, in certain circumstances, the human body can signal emotional states better than faces (de Gelder, 2009), and that the accuracy of identifying emotions in adults conveyed in body postures and movements is comparable to that of faces (Atkinson, Tunstell, & Dittrich, 2007; Zieber, Kangas, Hock, & Bhatt, 2014). Bodies have several advantages that facilitate emotional communication of information in comparison with faces, such as their larger size, which makes them visible at a greater distance and the fact that they allow the observation of emotional signals even when the person sits back (de Gelder, 2009). Research on bodily expressions allows neuroscientists to understand the importance of emotions as adaptive actions in social interactions (de Gelder & Hortensius, 2014).

The aim of this paper is to review the existing literature on the processing of emotional body expressions and highlight the evolution of research in affective and social neuroscience after 2009. In this respect, we first provided a summary of the most important findings until 2009 in order to have a clear image of the level of knowledge at that time, so that in the second part of the article we review the primary findings by 2014.

In 2010, de Gelder and colleagues reviewed the existing neurofunctional, behavioral and electrophysiological findings and identified the similarities and differences between bodily expression perception and facial perception. In 2009 there were only a few fMRI investigations that compared directly expressions of faces and bodies (de Gelder et al., 2010), and most of the studies used an indirect approach causing different results (Schwarzlose, Baker, & Kanwisher, 2005). In the literature until 2009, the concepts holistic and configural were used interchangeably in several studies on face perception. The question that arose was whether bodies were processed configurally, in a similar manner to faces. The results of the first research studies indicated that faces and bodies were not processed as an ensemble of features, but in a configural manner, as reflected in the inversion effect (Reed, Stone, Bozova, & Tanaka, 2003), while brain imaging studies emphasized

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the differences between face and body inversion effect (Meeren, Hadjikhani, Ahlfors, Hamalainen, & de Gelder, 2008). It was found that when assessed as the relative difference in latency and amplitude between a given stimulus and its upside-down presented counterpart, the electrophysiological inversion effect for bodies was of the same magnitude as that for faces (Stekelenburg & de Gelder, 2004). The study of the earliest onset of the electrophysiological inversion effect for face and body stimulus categories indicated that the cortical distribution was highly category specific (Meeren et al., 2008), demonstrating the differences in the time courses of activation in the common neural substrate in the fusiform gyrus (FG) and early cortical pathway for configural body and face perception (de Gelder et al., 2010). The extrastriate body area (EBA) is a distinct area in the occipitotemporal cortex that is activated more by neutral bodies and body parts than by faces (Downing, Jiang, Shuman, & Kanwisher, 2001). Studies that focused on the neurophysiology of body perception suggested that neurons that respond to static images of the entire body, corporal movements and body orientation can be found in the superior temporal sulcus (STS) (Barraclough, Xiao, Oram, & Perrett, 2006; Perrett et al., 1985). Therefore, bodily expressions of emotion activate cortical and subcortical motor areas, such as the putamen, caudate nucleus and the inferior frontal gyrus (IFG), which are not active for emotional faces (van de Riet, Grèzes, de Gelder, 2009). Furthermore, studies addressing the effects of emotional information on fearful body processing in the brain found an enhanced activation for these compared to instrumental bodies in the amygdala (AMG), FG (Hadjikhani & de Gelder, 2003) and the involvement of motor areas (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004).

Method

Search was conducted on the following electronic databases: PsychINFO, Ebsco, ERIC, ProQuest, Sagepub and SCOPUS. The electronic databases were searched using a combination of the following keywords and search terms: *"body," "bodily expression," "body perception," "emotions," "emotional body language," "posture" and "body recognition"*. The inclusion criteria for the present review included published peer-reviewed journal articles from January 2009 to December 2014. The exclusion criteria were: studies on children and the elderly, review articles, qualitative studies or mixed design, studies realized solely on facial expressions, without taking into consideration body expressions, and validating tools' studies (see Figure 1).

Results

After 2009, it would be inappropriate to sustain that the investigation of the neural networks involved in the

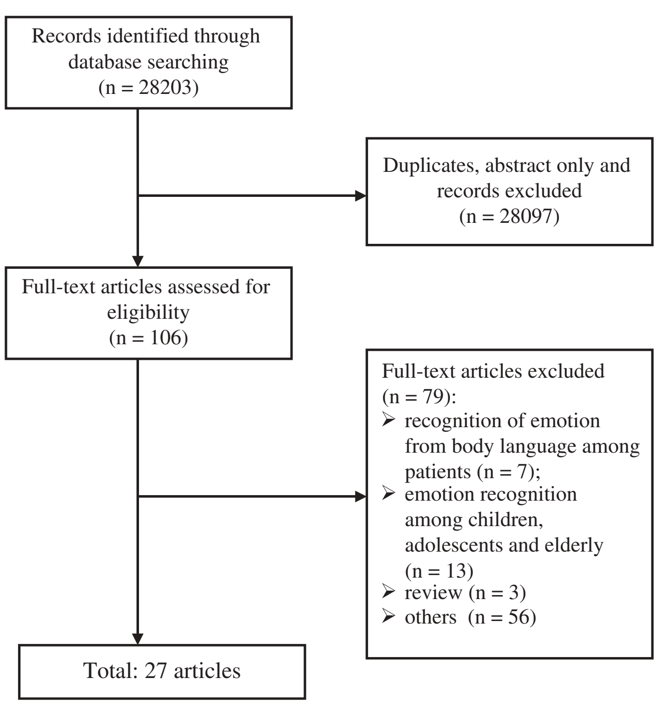

Figure 1. Study selection process.

perception of bodies and bodily expressions has not received much attention in social and affective neuroscience research due to the large number of studies that have addressed this topic. Most studies have included the analysis of facial expressions and body expressions, as both faces and bodies are important sources of emotional information (App, Reed, & McIntosh, 2012) and play an important role in social communication (Willis, Palermo, & Burke, 2011).

Main research questions addressed by the studies included in the review

Recent studies have used various techniques, such as transcranial magnetic stimulation (TMS) (Filmer & Monsell, 2013; Wold, Limanowski, Walter, & Blankenburg, 2014), functional magnetic resonance imaging (fMRI, see Table 1), electromyography, pupillometry and gaze measures (Kret, Stekelenburg, Roelofs, de Gelder, 2013), event-related potential (ERP) analysis (Gu, Mai, & Luo, 2013; Jessen & Kotz, 2011; see Table 2; Jessen, Obleser, & Kotz, 2012; Proverbio Calbi, Manfredi, Zani, 2014), magnetoencephalogram (MEG) and skin conductance response (SCR) (D'Hondt et al., 2010). We present below the main research questions addressed by the electrophysiological, neurofunctional and behavioral studies included in the current review.

Which are the neural mechanisms of emotion perception in body expressions?

Body postures have high social saliency (Filmer & Monsell, 2013) and besides facial expressions, gestures and even whole-body movements (Prochnow et al., 2013) people voluntarily or involuntarily use them to convey emotional states and intentions to others. In order to study the visual processing of emotions, neuroimaging studies have evolved from using static photographs with facial expressions as stimuli to the use of fully realistic dynamic stimuli, including gestures and body movements in video clips. Observing static emotional bodies in comparison with emotional faces found a greater neural activity in the left and right FG (van de Riet et al., 2009).

The question that arose was whether activation patterns of brain regions were the same when observing the dynamic facial expressions and gestures, taking into consideration the assumption that gestures might be processed in a more cognitive manner unlike facial expressions that primarily had an emotional meaning (Prochnow et al., 2013). In a recent fMRI study, Prochnow et al. (2013) found that inferior temporal gyrus (ITG) and IFG) were activated when observing dynamic facial expressions and gestures, unlike in other studies that found that in addition to IFG activation, the anterior medial prefrontal (Lotze et al., 2006) or paracingulate cortex (Gallagher & Frith, 2004) were also activated. The results obtained by Prochnow et al. (2013) suggested a right-hemisphere dominance for processing affective body expressions due to the intense activation of the right dorsal medial frontal cortex and the ITG.

In real-life social interactions the ability to understand others' intentions is essential for an optimal adaptation and success in different social situations. Previous kinematics studies have used biological motion to study human movement features. Recent studies continue to use it to investigate the neural basis of understanding everyday social interactions using whole-body point-light displays (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011). In addition, it was also used to study the processing of the visual cues by the body- and face-selective brain regions with point-light displays exhibiting either facial or bodily movements (Atkinson, Vuong, & Smithson, 2012).

Using an ERP analysis, Proverbio et al. (2014) investigated the neural mechanisms highlighting the human ability to understand emotional body language, with important consequences in inferring people's real intentions in social interactions. Stimulus materials were images of emotional body postures that were assigned to congruent versus incongruent condition. In the incongruent condition the verbal descriptions were incompatible with the emotional state displayed by the images. The results of this study outlined the activation of the right gyrus of the ventromedial orbitofrontal cortex, the bilateral uncus and the cingulat cortex, STS, FFA, EBA and the premotor cortex (PM). The recognition of incongruent body language took place 300 ms post-stimulus.

Recent studies found that the EBA is causally involved in non-facial body perception (Downing & Peelen, 2011), goal-directed actions (Wiggett & Downing, 2011), illusory body ownership (Limanowski, Lutti, & Blankenburg, 2014) and processing of haptic and visual information (Costantini, Urgesi, Galati, Romani, & Aglioti, 2011). Left EBA is involved in the processing of an own-body representation (Wold et al., 2014), while the STS responds to the observation of walking and grasping (Proverbio et al., 2014).

Which are the neural structures activated by threatening signals (anger and fear) from facial or bodily expressions?

In 2006, de Gelder argued that in emotion research, the most used emotions were angry, fearful, sad and happy

Table 1. Overview of fMRI studies.

Study	Objective	Subjects	Stimuli	Task	Results
Sinke et al. (2010)	The investigation of brain regions that process the differences in body language of two people interacting, even if the observer performs an irrelevant task	14 participants with a mean age of 23.6 years	Videos with a man who threatened a woman or teased her	Forced-choice color categorization task Emotion-naming task	When the subject was witness to a threat, the right amygdala was activated in both conditions (attention focused on the situation and when attention was directed toward an irrelevant task)
Kret et al. (2011a)	The investigation of brain areas involved in processing signals from threatening body and facial expressions	28 participants aged 18–32 years	Videos with facial and body expressions of fear, anger or neutral emotional state	Passive viewing	Amygdala was more active in the case of facial expressions than concerning the body expressions; a greater activation of bodily expressions was observed in: fusiform gyrus and extrastriate body area; extrastriate body area and superior temporal sulcus were more activated by threatening bodies
D'Hondt et al. (2010)	The determination of the stages of brain processing that are strictly related to the impact of emotions on the human body	18 students with a mean age of 25.9 years	Images selected from *International Affective Picture System*: 100 unpleasant images, 100 pleasant and 100 neutral	Internalizing of emotions in images; Assessment of images in terms of excitability and valence	There was a greater brain activity in the occipitotemporal component for emotional images compared to neutral images; the early effects of emotional arousal on early brain activity correlated with increased skin conductance
Kret et al. (2011b)	Studying the brain areas involved in the perception of facial and body expressions of emotion and implications of gender differences	28 participants aged 18–32 years	Videos with different facial and bodily emotions expressed by men and women	Passive viewing	Men paid more attention to women's faces; there was a selective sensitivity of men observers at menacing expressions of the same kind; amygdala was activated in observing facial expressions compared to bodily expressions, regardless of the emotion expressed
Atkinson, Vuong, & Smithson (2012)	The study of specific areas of the brain that processes the body movement and facial muscles	17 subjects aged between 21 and 39 years	2-second videos showing bright spots corresponding to facial and body movements	Judging the emotion expressed through body movement or face or color stimulus	Body movements had activated both areas of the extrastriate body area and only the right part of the fusiform area regardless of the respondents' task; facial movement had activated in a bilateral manner the fusiform facial area, and the right side of FFA during the evolution of emotions
Filmer and Monsell (2013)	Studying the role of the striatum in processing the emotional content of visual stimuli	29 students with a mean age of 21 years	Monochrome photos of the same person in eight different positions: aggressive, pleasant and neutral	Discrimination of categories: aggressive/pleasant	The discrimination of neutral image was affected when the brain that processed the stimulus was disrupted by transcranial magnetic stimulation; in the same condition, the discrimination of images with affective valence was less affected
Grèzes et al. (2013)	Investigating the manner in which "self-relevance" angry expressions affect processing	37 volunteers	Short videos with neutral or angry body expressions increasing in intensity	Passive viewing The task of maintaining attention	Perception of postures expressing anger triggered the activation of the amygdala, the fusiform gyrus, the cortex promoter and the superior temporal sulcus; this activation was independent of posture's orientation and was modulated by the intensity of the emotion expressed
Prochnow et al. (2013)	Exploring the brain processes involved in the observation and the discrimination of the evolution of emotional body expressions	15 subjects with a mean age of 22.3 years	Mute videos with gestures and faces that evolved from a neutral expression to one fully developed	Forced-choice valence categorization task	The right hemisphere was dominant in the processing of emotional expressions of the body. It was emphasized the brain circuitry and active areas in the identification and development of an expression's evolution
Wold et al. (2014)	Searching for evidence of the involvement of "extrastriate body area" (EBA) in the rubber hand illusion	19 participants aged between 21 and 42 years	A rubber hand	Reporting the location of their real hand and the intensity of illusion	Participants misjudged significantly their hand position during the rubber hand illusion compared to the false stimulation period following. EBA was necessary in multimodal integration.

Table 2. Overview of ERP studies.

Study	Objective	Subjects	Stimuli	Task	Results
Jessen and Kotz (2011)	Investigation of the multimodal processing of emotional facial and body expressions	23 participants aged between 19 and 32 years	Videos of postures/ facial expressions and audio recordings that expressed fear, anger or neutral emotional state divided into three conditions: audio, visual and audiovisual	Two forced-choice tasks: judging the emotion and the length of the stimulus	Visual information consisting of facial expression and body expression strongly influenced congruent auditory information processing; emotional stimuli were distinguished from the neutral after 100 ms
Jessen et al. (2012)	Investigation of the interaction processes in visual perception and auditory brain	24 participants with a mean age of 24.7 years	360 videos expressing anger, fear or neutral; images of actors in a neutral position	Forced-choice emotion classification	The human body + expressions of auditory stimuli were integrated efficiently and early in brain processing
Shields et al. (2012)	The study of emotions perception from facial and body expressions in congruent and incongruent situations	20 students	32 images: 16 images of face and body expressing the same emotion (congruent) and 16 images of face and body expressing different emotions	Forced-choice emotion categorization of the whole body	Greater accuracy and a faster response time for congruent images versus incongruent ones; In the incongruent condition, participants explored for more time the face than the body
Gu et al. (2013)	Testing integration time of emotional signals from the face and the body, with attention focused only on the face or only on the body	18 subjects aged between 19 and 25 years	60 images with faces of the selected combination of Chinese Affective Picture System Face and photos of bodies expressing joy and fear	Forced-choice emotion classification expressed on the face/on the body	Even if attention was focused on the face, threatening information provided by the body were rapidly extracted and processed among the first steps
Kret, Stekelenburg, Roelofs, de Gelder (2013)	Hypothesis: emotional expressions from the face and the body are processed similarly and their congruence leads to easier recognition	37 students, aged between 19 and 32 years	Six images of men with isolated facial expressions of sadness, joy and anger + body expressions related	Passive viewing and emotion categorization	The recognition of emotional facial expression or body expression is enhanced when it is presented with the congruent face/ body; regardless of context, people processed in a similar manner the body and facial expressions of emotions
Kret and Gelder (2013)	Testing the manner in which offenders perceive tangible expressions of other men	29 violent inmates, aged between 19 and 61 years	72 images expressing anger, fear, joy or sorrow, with a blurred face	Matching expression task	The postures of men expressing anger drew more attention than those of women; offenders had poorer results than the control group in recognizing the fear of bodily movements and interpreted it as anger
Kret, Roelofs, Stekelenburg, de Gelder (2013)	Examination of the perception of multiple simultaneous emotional signals (body + face)	37 participants aged 19–32 years	Experiment 1: images of faces/ bodies expressing different emotions in congruent/ incongruent condition Experiment 2: images in which body posture and background were congruent or incongruent	Passive viewing; Body expression categorization task	Participants were more focused on expressions of fear and anger, compared with neutral or happy expressions, whether the emotions were expressed in a facial or bodily manner, independent of the congruence body-background; Perception of emotional signals from the faces, bodies or background depends on the natural context, but when threatening indications were present, they attracted attention and caused congruent facial reactions
Proverbio et al. (2014)	The investigation of mechanisms underlying the ability to understand emotional body language	30 Italians aged between 18 and 29 years	280 images with emotional and verbal labels (140 congruent and 140 incongruent)	Forced-choice categorization (body expression congruent vs. incongruent with the emotional or mental state)	The body and face processing is very fast (300 ms) and involves the emotional side of the brain. The decision to act in a certain direction comes from the comparison between this output and verbal information.

expressions. After 2009, studies have also focused on the four basic emotions; however, the processing-threatening signals from facial and bodily expressions have been investigated using different methodological approaches (Jessen & Kotz, 2011; Kret, Pichon, Grezes, & de Gelder, 2011a, 2011b; Sinke, Sorger, Goebel, & de Gelder, 2010; Van den Stock, Vandenbulcke, Sinke, & de Gelger, 2014). During social interactions, emotional expressions are cues of others' emotional states that individuals attempt to correctly recognize in order to adjust their behavior, especially in situations when one's safety is under threat (Grèzes, Adenis, Pouga, Armony, 2013; Kret & de Gelder, 2013).

Many neurophysiological studies have focused on the perception of anger and fear, especially in terms of the differentiation between neural structures involved in the response to facial and bodily expressions, since bodily expressions, in contrast to facial expressions, imply action (de Gelder et al., 2010). Kret et al. (2011a) found a different neural activation involved in processing the threatening signals (fear and anger) from dynamic facial and bodily expressions. The AMG responded stronger to facial than to bodily expressions, whereas the cuneus, FG, EBA, temporoparietal junction (TPJ), superior parietal lobule (SPL), the thalamus and the primary somatosensory cortex responded stronger to bodily expressions. Recent fMRI studies have confirmed previous findings (Grosbras & Paus, 2006; Pichon, de Gelder, & Grezes, 2008), which showed that the perception of body expressions of anger activated the AMG, the FG, the STS and the PM (Grèzes et al., 2013; Kret et al., 2011a; Pichon, de Gelder, Grèzes, 2011; Van den Stock et al., 2011).

This neural network, associated with the ventromedial prefrontal cortex and the somatosensory cortices, which mediate emotional body signals, was suggested to play an important role in the behavioral reactions of an individual when the person is confronted with a social threat (Grèzes et al., 2013). In the activation of defensive behavior the areas involved are the PM and subcortical areas including the AMG, the hypothalamus (HYP) and the periaqueductal grey (PAG) (Pichon, de Gelder, & Grèzes, 2009), brain regions associated with rapid social adaptations (Grèzes,et al., 2013). The PM and subcortical areas including the AMG, the HYP and the PAG (Pichon et al., 2009), all of which are brain regions associated with rapid social adaptations (Grèzes et al., 2013), are all involved in the activation of defensive behavior. In contrast to previous studies that found a higher AMG activity in response to angry facial expressions displayed with direct gaze, Grèzes et al. (2013) suggested that AMG responded equally to both self- and other- directed anger. Future studies might explain this inconsistency. Van den Stock et al. (2014) reported that fearful bodies activated more the left and EBAs than neutral bodies, threatening scenes activated the putamen, a subcortical motor structure, and threatening bodies activated more STS and EBA (Kret et al., 2011a).

In our everyday social interactions, the perception of emotional states is multimodal. Similarly, researchers integrated in their experiments body language besides facial and vocal expressions. Jessen and Kotz (2011) investigated the multimodal perception of emotion expressions combining ERPs and time-frequency analysis. Participants were presented emotional stimuli (anger and fear) and nonemotional stimuli in three conditions: visually, auditorily and audiovisually. Results suggested a significant impact of visual information on early auditory processing and showed that anger and fear expressions were not distinct in the audiovisual condition. However, differences emerged in the auditory condition.

Recent research has investigated how different categories of participants react when confronted with fearful and anger facial and bodily expressions. Kret and de Gelder (2013) found that violent male offenders tend to incorrectly interpret fearful body movements by other males as expressing anger more often compared with the control group.

Also, violent offenders were impaired in recognizing happy signals (face or posture) when simultaneously presented as part of an aggressive posture or viewed against the background of a violent scene. Kret et al. (2013) showed that anxious individuals had amplified physiological responses to angry signals.

It has been demonstrated that the processing of fearful stimuli has a special status particularly in studies investigating the role of visual awareness in the perception of bodily expressions (Stienen & de Gelder, 2011; Stienen, Tanaka, & de Gelder, 2011). Regarding facial expressions, studies showed that visual discriminations of affective stimuli could be processed in the absence of visual awareness of the stimulus (Stienen & de Gelder, 2011). Stienen et al. (2011) showed similar findings for audiovisual integration between bodily expressions and affective prosody.

A neuroimaging study (D'Hondt et al., 2010), which corroborated observations of emotional processing of arousal state and autonomic activation, has indicated predominant activation of the right hemisphere in response to emotional stimuli.

Which is the time course for the integration of emotional signals from the face and the body?

In the domain of emotional perception, studies until 2009 that examined the integration of emotional signals from different sources focused mostly on voice and face, but recently researchers paid attention also to bodily expressions. An ERP study found that visual information consisting of facial and bodily expressions strongly influenced congruent auditory information processing and that emotional stimuli were distinguished from neutral stimuli after 100 ms (Jessen & Kotz, 2011). Gu et al. (2013) examined the time course of the integration of facial and bodily expressions also using the ERP technology. Participants were instructed to watch face-body compound stimuli and to focus their attention on facial expressions ignoring the body and then on bodily expressions ignoring the face. Results showed that the three-stage model of processing of facial expressions (Luo, Feng, He, Wang, & Luo, 2010) may be extended to processing bodily expressions (Gu et al., 2013). In the first stage of integration, the threatening information from the body was extracted quickly and automatically; in the second stage, the incongruent information was detected between facial expressions and the body expressions; and the third stage was modulated by the focused attention on the face and the body. Thus, when subjects' attention was focused on the face, it suggested more attention and also an elaboration of congruent emotional information extracted from face and body, and when the subjects' attention was focused on the body, a high degree of attention was suggested, along with an elaboration of threatening information from the body.

D'Hondt et al. (2010) used MEG data and SCR magnitude during the presentation of emotional and neutral images in order to determine the temporal stages of brain processing regarding the bodily impact of emotions. They found an arousal effect at 180 ms on the occipitotemporal component, which was significantly correlated with the subsequent impact of emotional arousal at the body level. Body responses to emotional stimuli occurred during the first 500 ms after the visual presentation (Rudrauf et al., 2009).

What is the role of context in the perception of emotional signals?

Studies have evolved from the use of static images, where the facial expressions influenced more the recognition of emotions (Lankes, Bernhaupt, & Tscheligi, 2010) compared to those that used dynamic visual stimuli and situational items. It was found that the processing of emotional expressions was influenced by contextual information (Buisine et al., 2014; Lankes & Bernhaupt, 2011; Lankes et al., 2010; Volkova et a., 2014). In the literature until 2009 studies examined the perception of facial expressions of emotion without taking into consideration the influences of body postures or social emotional contexts. A smile can be interpreted differently depending on the context of an aggressive or a fearful bodily posture as dominant, and, respectively, as an affiliative cue (Kret, Roelofs, Stekelenburg, de Gelder, 2013). However, the recognition of body expression is affected by the valence of the associated facial expression, including when judging the approachability of face-body composite images (Willis et al., 2011), and the influences of a social context (Kret & de Gelder, 2010; Kret et al., 2013). Moreover, the natural context influences the perception of emotional signals from faces, bodies and scenes (Kret, Roelofs, Stekelenburg, de Gelder, 2013; Kret, Stekelenburg, Roelofs, de Gelder, 2013; Van den Stock et al., 2014). Kret and de Gelder (2010) found that the congruence between the emotion expressed in action scenes and bodily expressions of the target figure determined a better recognition of bodily expressions. Furthermore, emotions conveyed by face and body influenced face identity matching (Van den Stock & de Gelder, 2014).

In a behavioral experiment following the scanning session, Van den Stock et al. (2014) presented participants with body-background compound stimuli and instructed them to categorize the emotion expressed by the body. The results showed that the interpretation of a neutral body posture is influenced by the emotional background information, like in a real- world situation when the perception of the emotional state of a man running depends on whether he is running in a race or he is running away from a fire. Fearful bodies are emotionally less ambiguous than neutral bodies and the emotional influence of the background scene was not present when the body posture expressed fear. This was explained by the authors as the perceptual bias effect. This effect implies (Van den Stock et al., 2014) that the more ambiguous the target stimulus, the more biased the perceptual response is in the direction of the scene, so that the emotional background effects are a function of the ambiguity of the body expression.

The perceptual mechanisms involved in body perception are similar to face processing?

Most researchers chose to use the term *"holistic"* more than the concept *"configural"* after 2009; however, it is not clear whether the two terms are similar or not (see Piepers & Robbins, 2012).

Among the main evidence that indicated the involvement of holistic facial processing, there are the composite face effect, considered to be a direct measure of holistic processing, and the face inversion effect, considered to be an indirect measure of holistic processing (Verfaillie, Huysegems, de Graef, & Van Belle, 2014; Willems et al., 2014). Stimuli used in a composite task were created by joining together complementary halves of two different faces (usually the top and bottom halves), and the task given to participants (in recognition of unfamiliar face version) was to identify whether a half (mostly the top) of the two faces sequentially presented was the same or not regardless of the other face half (mostly the bottom) (Willems et al., 2014). The composite facial effect appears when two identical top halves of a face are perceived as being different even when they are presented with different bottom parts. This composite face illusion disappears when the holistic processing is blocked by moving sideways (misalignment) both bottom halves. The face inversion effect refers to the fact that when faces and objects are turned upside down, they become difficult to recognize due to a failure of holistic processing of inverted faces (Rossion, 2013; Verfaillie et al., 2014).

Research that investigated the holistic processing of the body obtained different results depending on the direct or indirect measure of holistic processing. Processing holistic body was evidenced so far from the body inversion effect with the part-whole effect (Seitz, 2002) and heads (Minnesbusch, Suchan, Köster, & Daum, 2009; Robbins & Coltheart, 2012), but regarding a body composite effect the results are somewhat contradictory (Robbins & Coltheart, 2012; Soria-Bauser et al., 2011; Willems et al., 2014). Thus, even if imaging studies stated that faces and bodies were associated with different areas of the brain, Robbins and Coltheart (2012) and Willems et al. (2014) suggested that human bodies may also be holistically processed. By means of a delayed matching to the sample protocol and using a posture-based approach, Willems et al. (2014) provided evidence for both a horizontal and a vertical composite effect, indicating that body postures were holistically processed in the same manner like faces. Robbins and Coltheart (2012) reported the same results. In contradiction with these results, the study of Soria- Bauser et al. (2011), who used an identity-approach, investigated whether comparable composite effects could be observed for faces and bodies. The evidence is accumulating that body postures are holistically processed in the same manner like faces, but different approaches and differences in the experimental design are resulting in different findings.

Conclusions

In the last five years, neural mechanisms of the perception of bodily expressions have become the topic of intense research in the field of affective and social neuroscience, after decades of exclusive focus on facial expressions. The current review summarized the progress of knowledge and highlighted some of the important questions that have received attention and have been sufficiently investigated in the literature. Recent electrophysiological and imaging studies expanded the understanding of processing emotional body expressions, despite the questions that remained to be answered in future research studies. Owing to the technological evolution, the ability to combine different types of stimuli has been developed to be used in tasks in which participants were required to make forced-choice emotional classification. Some researchers have investigated the congruency effects using incongruent stimuli created to compare the differences between a congruent condition and an incongruent condition. Therefore, these studies supposed that participants categorized facial expressions that were presented together with emotionally congruent or incongruent body postures (Kret et al., 2013), images matching the face and body expression of the same emotion and incongruent combinations (e.g., sad face and happy body) (Shields, Engelhardt, Ietswaart, 2012) or verbal descriptions in a congruent or incongruent manner that immediately preceded pictures of emotional body postures (Proverbio et al., 2014). These recent investigations have shown that faces and bodies are processed as a single unit (Aviezer, Trope, & Todorov, 2012) and the processing of emotional body expressions is similar to the processing of facial expressions (Kret et al., 2013).

Emotions serve two general social functions: an affiliation function, when helping an individual or group, maintain cooperative relationships with others; and a social distancing function, when an individual or group competes with others for social status or power (Fischer & Manstead, 2008). Even if anger, fear and sadness have been enlisted as basic emotions, depending on societal and cultural contexts, they can be qualified as moral emotions (Moll, Zahn, Oliveira-Souza, Krueger, & Grafman, 2005). It is important to note that most researches have focused on processing threatening signals (anger and fear) from facial and bodily expressions, which is not surprising. Body posture and gestures are important channels through which we convey anger (Grèzes et al., 2013) and negotiate aggressive confrontations (Argyle, 1988). Beating or threatening are expressions through which one of the social function of anger (imposing change upon another person) is achieved (Fischer & Manstead, 2008). Bodies convey information not only on emotions and on intended or executed actions, but also on others' intentions (Iacoboni et al., 2005), and body motion is an integrated part of body expressions (de Gelder, de Borst, Watson, 2015; Perry, Troje, Bentin, 2010).

In conclusion, the current state-of-the-art in processing emotional body expressions may lead to a better understanding of the underlying neural mechanisms of social behavior. However, some answers to the questions addressed by the studies included in this review may not be categorical because of the limitations of research. The most important limitation is the lack of effect size calculation in most of the studies included in this review. Calculating and reporting standardized effect sizes, even in neuroimaging studies (Desmond & Glover, 2002), might facilitate future meta-analyses in which researchers compare effect sizes across the literature. Furthermore, the small sample size, which is another limitation of some studies, undermines the reliability of the results and decreases the statistical power of a neuroscience study (Button et al., 2013), like in any other field. Another limitation is that the tasks used in some experimental research are unnatural, whereas emotional expressions generally involve the whole body in action (de Gelder & Van den Stock, 2012). Outside the laboratory, in real human interactions, faces and bodies are normally seen together and bodies are not processed independently from the social interaction. Research evolved and investigated the neural mechanisms of individuals interacting; however currently, there is still a gap between the interaction scenario in which the participants passively observe a social interaction in the laboratory and a social interaction in real life.

Finally, this systematic review has several key limitations that should be acknowledged. The main limitation emerges from the process of the relevant articles' selection. We take into account the possibility that relevant neuroimaging studies were missed inadvertently or because we were not able to access them. Furthermore, we excluded the studies on children, which can likewise be highly informative about brain areas associated with theory of Mind (ToM) development and mentalizing processes.

Future directions

Future research may include the interdisciplinary area of neuroscience, social psychology, computer graphics and artificial intelligence by using immersive virtual environments (Bombari, Schmid Mast, Canadas, & Bachmann, 2015) with the aim of studying the neurological basis of information transferred in social interactions (de Gelder & Hortensius, 2014). Harnessing modern technology, haptic devices (Giannopoulos, Wang, Peer, Buss, & Slater, 2011) or new techniques such as motion capture within virtual environments (de Gelder & Hortensius, 2014), the perception of emotional body processing might be investigated in standardized conditions, similar to that in real-life conditions. Virtual reality stimuli can be moving robots and avatars with distinct personalities, which could be programmed to display distinct emotions and simulate real social situations, allowing participants to perceive the interaction with avatars as if they were human beings (de Borst & de Gelder, 2015). Further investigation is still needed in aspects such as the neurological basis of crowd perception and emotional reactions spreading within groups (de Gelder & Hortensius, 2014). Recently, Huis in 'T Veld and de Gelder (2015) investigated the neural basis of a crowd expressing fearful, happy or neutral emotions using realistic videos and found a lack of AMG activation, which has been previously found in the majority of studies on the perception of emotional body language. Neuroimaging studies could further investigate these discrepant findings.

Another line of research to take into account is that of nonconscious perception of bodily expressions in neurologically intact and neurotypical populations (see review by de Gelder et al., 2015). Stienen and de Gelder (2011) investigated the role of visual awareness in the perception of angry, happy and fearful bodily expressions in neurologically intact observers. The results showed that fearful expressions automatically capture the attention and activate fear responses. Advancing research, Candidi, Stienen, Aglioti, and de Gelder (2015) found that the right posterior Superior Temporal Sulcus (pSTS) plays an opposite role in the conscious visual perception of fearful emotional faces or bodies because its transient inhibition decreased the dominance of fearful faces' expressions and increased the perceptual dominance of fearful body postures. There is certainly a need for more studies on the neural correlates of conscious and nonconscious visual perception of emotions expressed by bodies and faces. In clinically blind patients with hemianopia, Tamietto et al. (2009) found that these patients guessed the bodily expressions presented in their blind field. Furthermore, Van den Stock et al. (2011) found a selective involvement of the right superior colliculus and bilateral pulvinar in nonconscious visual emotion body perception in a patient with unilateral destruction of the striate cortex. In addition, recent studies have investigated body recognition in a patient with cortical blindness over the entire visual field (Van den Stock, Tamietto, Hervais-Adelman, Pegna, & de Gelder, 2015), the recognition of emotional body expressions in people with frontotemporal dementia (bvFTD) (Van den Stock et al., 2015) and the role of insula in visual awareness for fearful bodies in parietal neglect (Tamietto et al., 2015).

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