

Bodies, features and visual awareness

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Chapter **7**

General summary and discussion

7.1 Overview of findings

Emotions can be transmitted in a myriad of ways, such as through the voice, the face, the body and even the eye gaze (Ekman & Friesen, 1967). Correctly interpreting these signals is undoubtedly crucial for navigating our social lives. Although much is known about the processing of facial expressions, the mechanisms underlying the perception of other sources of emotional information have lagged behind. In this thesis, we made special emphasis on one of these relevant other sources: body expressions. In five empirical chapters, the behavioral, physiological and neural correlates of body expression perception were investigated with various different approaches and perspectives. I hope this work has convinced you of the importance of investigating this evolutionary tool for social interactions and adaptive behavior.

7.1.1 Part I: neural correlates of combined face and body expression perception

Most research in affective science has been centered in elucidating the mechanisms underlying the perception of emotion from others, whether from facial expressions or bodily cues, to name a few. Common to this research is the focus on the isolated perception of each of these signals, without much interest in knowing what happens when you perceive them as an integrated whole. The ecological validity of studying the combined perception of different emotional signals is undeniable, as in the natural world we rarely perceive them in isolation. Some studies investigating behavioral and temporal signatures of combined face and body expression perception have already provided useful insights. However, much less is known about the neural correlates of emotional face-body combinations. **Chapter 2** shows the findings of a functional magnetic resonance study combining happy and fearful facial and body expressions to create both congruent and incongruent face-body compound stimuli. Our aims were two-fold: first, we examined the influence of task-irrelevant body expressions on the neural processing of the face; second, we investigated the effect of emotional ambiguity between the two, with emphasis on the role of the amygdala. The results showed that adding a body expression to a face increases the activity in several cortical areas including the prefrontal, motor and visual cortex. These findings are consistent with the notion of bodies as a social and adaptive source of information, triggering both emotional and action-

related processes. Furthermore, the study of emotionally ambiguous compounds revealed an enhancement of cortical activity and of amygdala functional connectivity for congruent as opposed to incongruent face-body compounds. We explained this ambiguity effect as resulting from a concurrent reciprocal inhibition in the amygdala that in turn causes a reduction of its modulatory influence over cortical areas. Taken together, these results show the relevance of using more ecologically valid stimuli for understanding emotional perception processes. In addition, this work pointed to the amygdala as a key area for integrating emotional signals from different sources and assessing their emotional congruence.

7.1.2 Part II: body expression perception beyond high-level semantic constructions

Another shortcoming of affective research has been the almost exclusive focus on investigating the behavioral and neurofunctional bases of body perception at the categorical level, either as a perceptual object or as a carrier of emotion. Although informative, this approach does not really tell us how a specific emotion is conveyed by a body posture or movement or what makes one emotion different from another. *Part II* goes beyond high-level body processing to further investigate the underlying mechanisms of body expression perception. Specifically, **Chapter 3** and **Chapter 4** investigate the contribution of several properties of body posture and movement, referred to as *midlevel body features*, in affective body perception. In both chapters, similar kinematic and postural features were computed from whole-body movements. In **Chapter 3**, these features were related to the emotional category of the stimuli as well as to subjective ratings of similar feature descriptors. The results of both the subjective (i.e., from participants' ratings) and objective (computed) features revealed that the affective information conveyed by body movements can be better discerned from postural than kinematic features. In addition, clearer distinctions between emotional categories were observed from subjective ratings than from objective body features.

In a further step to investigate the underlying mechanisms of body expression perception, **Chapter 4** shows the neural representation of these kinematic and postural body features with functional magnetic resonance imaging (fMRI) multivariate approaches. Of particular interest were limb angles and symmetry, two postural features that differentiated between fearful and other emotional movements. Interestingly, these features were not only represented in affective areas,

but also in action representation and motor preparation networks. This approach also provided insights into the functional role of body-selective areas. Both extrastriate body area (EBA) and fusiform body area (FBA) were sensitive to differences in body expressions based on postural features, which was not observed with regards to kinematic features. Yet, the data suggest that EBA and FBA may have different roles in body processing since they displayed a dissimilar stimuli representation (i.e., neural RDMs). Controversial findings were obtained from the posterior superior temporal sulcus (pSTS) since this area distinguished between fearful and other affective movements using limb contraction rather than kinematics. Taken together, these studies show the utility in using a feature-based approach not only to understand what makes and emotion different from another but also to further characterize the functions of the brain areas involved in their representation.

7.1.3 Part III: processing of emotional body expressions under different levels of perceptual awareness

Previous chapters have focused on the conscious perception of body expressions. There are times, however, when the emotional cues around us go unnoticed. These emotional signals can still be processed without conscious awareness and trigger behavioral, physiological and neural responses in the observer. Although there is ample scientific evidence supporting this (for a review see Tamietto & de Gelder, 2010), recently there has been much debate about the validity of such findings. These debates concern theoretical and methodological issues, one of which suggests that previous evidence of non-conscious emotional processing is confounded by the tasks used to assess awareness (Pessoa, 2005; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010; Wierzchoń, Pawlewicz, Asanowicz, Timmermans, & Cleeremans, 2014). In *Part III* we investigated the processing of body expressions under different levels of perceptual awareness using the continuous flash suppression paradigm. Instead of dichotomous measures (i.e., yes/no, seen/unseen), we employed a finer scale for measuring perceptual awareness to capture intermediate levels of perceptual awareness. In **Chapter 5**, we particularly explored the behavioral and physiological (pupillometry) correlates of angry, fearful and emotionally neutral body expressions under different levels of perceptual awareness. Behaviorally, we observed an increase in recognition sensitivity (d-prime) with

increased subjective stimuli awareness as well as no evidence of emotional discrimination in conditions of unawareness. Except during perceptual unawareness, recognition sensitivity was higher for fearful (vs neutral) than angry (vs neutral) bodies. These results were striking considering that angry bodies broke from suppression faster than neutral and fearful ones. We explained these findings based on the different types of threat conveyed by angry (direct) and fearful (indirect/ambiguous) bodies. Finally, we showed that affective expression and the time of breaking from suppression influenced pupil dilation and that pupillary responses may have different functions depending on the level of subjective perceptual awareness.

In **Chapter 6** we used a similar experimental design and a 7T MRI scanner to investigate the neural and physiological (heart rate) correlates of fearful body expressions under different levels of perceptual awareness. This study validated the behavioral findings of **Chapter 5** by showing increases in recognition sensitivity as a function of perceptual awareness as well as chance performance during perceptual unawareness. At the brain level, we observed a main effect of perceptual awareness in amygdala as well as in occipital, temporal, parietal and premotor regions. Activity increases with increased perceptual awareness were observed in extrastriate and fusiform body areas, inferior temporal gyrus, posterior superior temporal sulcus, inferior frontal gyrus, precuneus, intraparietal sulcus and amygdala. The opposite pattern was found in early visual areas. A further characterization of the relationship between the activity of these areas and perceptual awareness revealed that temporal areas were better described by a gradual model (i.e., gradual progression from unawareness to conscious perception) while a dichotomous model (i.e., ‘all-or-none’) was better suited for fronto-parietal regions. We interpreted these results as signifying different roles in conscious processing: while fronto-parietal regions may mediate stimuli entering into conscious perception, temporal regions may reflect subjective perception. We were also interested in the role of amygdala within our experimental design given its suggested role in non-conscious emotional processing. However, we did not find above-baseline activity in amygdala under conditions of unawareness. We argued that experimental choices, such as the task or the stimuli used, may have been the reason for these findings. Finally, the inspection of the physiological data revealed a slower heart rate for fearful than neutral bodies, in line with freezing behavior (Roelofs, 2017). Taken together, these studies provided a comprehensive take on the processing

of threatening body expressions in healthy participants at different levels of awareness and with converging evidence from behavioral, physiological and brain imaging measures. In addition, they stressed the crucial effects that experimental choices have on the study of perceptual awareness.

7.2 Combined perception of faces and bodies

Previous studies using behavioral, electroencephalography (EEG) and magnetoencephalography (MEG) measures have shown that body expressions influence the perception of facial expressions when presented as an integrated whole (Meeren, van Heijnsbergen, & de Gelder, 2005; Van den Stock, Righart, & de Gelder, 2007). When the emotional information conveyed by the body is similar to that of the face, faster and more accurate responses have been reported in emotional face recognition tasks. Conversely, when the body expression conflicted with that of the face, responses were slower and often inaccurate (Meeren et al., 2005; Van den Stock et al., 2007). Several explanations have been proposed to understand the nature of this congruence effect. Some accounts suggest that facial expressions are inherently ambiguous (Frijda, 1986) and, therefore, largely context dependent. Supporting this view, Avizier and colleagues (2008) reported that disgust faces (recognition rate of 65% in isolation) are just as likely to be categorized as angry when presented with an angry body than as disgust when presented with a congruent body (Aviezer et al., 2008). A similar finding was obtained by Van den Stock and colleagues (2007), who found that this incongruence effect was highest for the most ambiguous facial expressions (Van den Stock et al., 2007). These findings support the notion that ambiguous perceptions are more susceptible to perceptual malleability (Massaro & Egan, 1996).

Other accounts have pointed to the fact that there is a considerable overlap between the perceptual processing of facial and bodily expressions (e.g., configural processing) and their neurofunctional bases and time courses. For example, several EEG studies have shown that both bodies and faces elicit a positive (i.e., P1 component) and a negative (i.e., N1 component) deflection at occipito-temporal electrodes in approximately the same time window (Gluga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Minnebusch & Daum, 2009; Righart & de Gelder, 2006; Stekelenburg & de Gelder, 2004; Thierry et al., 2006; van Heijnsbergen, Meeren, Grezes, & de

Gelder, 2007). From these similar time courses and behavioral effects, it is not surprising to think that the integration of emotional information conveyed by the face and the body may occur during early stages of processing. Evidence for this was obtained by Meeren and colleagues (2005), who observed a marker for emotional face-body incongruence as early as 115ms post stimulus onset (Meeren et al., 2005).

Although some overlap between the neural correlates of facial and body expressions has been reported (e.g., partial overlap between face selective and body selective regions within the fusiform gyrus (Hadjikhani & de Gelder, 2003; Peelen & Downing, 2005), there is little research on the neural basis of combined faces and bodies or the emotional congruency effect between the two. EEG studies have already shown that neural processing varies depending on whether bodies are presented as headless bodies or with faces (Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Righart & de Gelder, 2006; Stekelenburg & de Gelder, 2004; Thierry et al., 2006). The investigation of combined perception of faces and bodies is therefore essential for an accurate understanding of social and affective processes. **Chapter 2** shows the findings of a functional magnetic resonance study where we combined happy and fearful facial and body expressions to create congruent and incongruent face-body compound stimuli. This provided the opportunity to investigate the brain correlates of combined facial and bodily expressions not only when these signals present similar information, but also when the unattended body cues conflict with those of the face.

Among other regions, the presentation of combined face and body expressions elicited higher activity in motor areas in comparison to isolated facial expressions (see **Figure 2** in **Chapter 2**). This is in agreement with previous literature showing that body expressions can trigger motor processes (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Huis In 't Veld, van Boxtel, & de Gelder, 2014a, 2014b; Pichon, de Gelder, & Grèzes, 2008). It also supports the notion that body expressions are essential for adaptive behavior by linking emotion and action (de Gelder, 2013). Importantly, these results add to the previous literature by showing motor-related activity even when the body was presented outside the focus of attention.

On a different note, the combination of face and body expressions gave different neural responses depending on whether the emotion conveyed by the unattended body was congruent

or not to that of the face. Several cortical areas showed sensitivity to emotional conflict, with higher activity for congruent as opposed to incongruent compounds in superior parietal lobule as well as in motor, anterior cingulate, dorsolateral prefrontal, orbitofrontal, primary and associative somatosensory cortices (see **Figure 2** in **Chapter 2**). Interestingly, no brain areas displayed higher activity for incongruent compounds. In **Chapter 2**, we argued that the reduction in cortical activity after the presentation of emotionally ambiguous information may occur due to a simultaneous reciprocal inhibition in subcortical areas that in turn downmodulates the activity of cortical regions. In view of these findings, we investigated the activity and modulatory role of the amygdala since this structure has previously been involved in the detection of emotional ambiguity (Kim et al., 2004; Whalen et al., 1998) as well as in the processing of facial and body expressions (de Gelder, de Borst, & Watson, 2015; Hadjikhani & de Gelder, 2003; Kim et al., 2004; Morris et al., 1996; Whalen et al., 1998). All the resulting areas from several psychophysiological interaction (PPI) analyses showed a positive correlation with the activity of the amygdala, with activity increases for congruent as opposed to incongruent compounds. One of these areas was the cingulate cortex, a region that also showed a higher activity for congruent compounds in the univariate analysis. These results not only support the role of the amygdala in face and body emotion perception, but also of its involvement in the signaling of conflicting emotional information between them.

It is important to note that the role of the amygdala in emotional ambiguity detection is not exclusive to the integration of facial and bodily cues, as it has also been reported in studies investigating emotional congruence between two faces (de Borst & de Gelder, 2016) or between face-voice pairs (Dolan, Morris, & de Gelder, 2001; Klasen, Kenworthy, Mathiak, Kircher, & Mathiak, 2011). Interestingly, both studies reported higher amygdala activity as well as higher cortical activity for unambiguous stimuli pairs as opposed to ambiguous ones. The combination of other types of emotional cues have also yielded similar results. For example, it has been reported a congruency effect between bodily expressions and the social context in which the bodies are shown (Kret & de Gelder, 2010; Kret & de Gelder, 2013). Therefore, it seems that the amygdala may have a general role in the integration and ambiguity detection of emotional information from different sources. Taken together, these results demonstrate the importance of investigating the

combination of different sources of emotional information, as this occurs regularly in the natural world.

Our study has several limitations that are important to consider. For example, no definite conclusions can be drawn about the nature of the modulatory role of the amygdala or the directionality of the PPI findings. In addition, many of the areas found in the univariate contrasts were not observed in the PPI analyses, and thus their increased activity for congruent as opposed to incongruent compounds may not have been related to amygdala modulations. The interpretation we reached in **Chapter 2** about a possible amygdala involvement was based on previous literature. Further research is thus needed to understand the neural correlates of emotional congruence between the face and the body and the role of the amygdala. These studies will need to take up on several challenges such as the difficulty of making facial and body stimuli comparable from the point of view of informational content (e.g., gender, identity, amount of motion). Furthermore, future studies will have to control for variations in attention that can occur depending on what emotion is being expressed by the face and body. For example, eye-tracking studies have shown that attention tends to be deployed to the head region during the perception of joy, while participants fixate more at the hands and arms during the perception of anger and fear (Fridin, Barliya, Schechtman, de Gelder, & Flash, 2009).

7.3 Lessons from a midlevel feature approach in the study of body expression perception

7.3.1 Methodological advances that made midlevel feature analysis possible

In the last decade we have witnessed interesting new orientations in methods as well as in theories that are directly relevant for understanding the mechanisms of communicating with the whole body (de Gelder & Poyo Solanas, 2021). On the methodological side, new developments have become available for tracking and analyzing naturalistic behaviors based on computer vision as well as machine and deep learning (e.g., OpenPose, Cao, Simon, Wei, & Sheikh, 2017; and DeepLabCut, Mathis et al., 2018). Such methods allow for descriptions of behavior that are more detailed and

more context sensitive than the classical abstract and conceptual emotion categories. They are also more precise than the methodologies employed in earlier studies linking verbal descriptions of body posture and movement to qualitative emotion categories (e.g., De Meijer, 1989; Wallbott, 1998).

In **Chapter 3** and **4** we made use of these new methodologies to investigate critical body features for affective perception. Particularly, we used a 2D pose estimation library (i.e., OpenPose, Cao et al., 2017) to obtain the location of the actor's main joints in a reliable manner to then compute relevant body features for emotional recognition. Other studies have previously related emotional perception to quantitative descriptions of posture (e.g., limb contraction) and movement (e.g., velocity) (for a review see Kleinsmith & Bianchi-Berthouze, 2012). In comparison to those studies, often employing point-light displays, static body images or dance sequences, the studies presented in **Chapter 3** and **4** used more naturalistic and dynamic stimuli that involved the whole-body rather than parts of it. Yet, a possible limitation of our approach may be that feature selection and definition did not follow a completely objective approach. For instance, our features were selected based on their importance in affective perception in previous studies rather than resulting from objective data-driven approaches. In this respect, other authors have employed principal component analysis (Santello, Flanders, & Soechting, 2002; Troje, 2002; Yacoob & Black, 1999), factor analysis (Ivanenko, Cappellini, Dominici, Poppele, & Lacquaniti, 2005; Ivanenko, Poppele, & Lacquaniti, 2004; Soechting, 1997; Tresch, Cheung, & d'Avella, 2006) or a blind-source separation algorithm (Roether, Omlor, Christensen, & Giese, 2009), partly solving the objectivity issue as well as reducing the inherent multidimensionality of moving body expressions. Nevertheless, it is noteworthy to mention that the definition of body features from perceptual experiments has shown to be in good agreement with those identified with data-driven approaches (Roether et al., 2009). In addition, it is yet to be known whether computational approaches (e.g., deep neural networks trained for emotional recognition from faces or bodies) can accurately reflect perceptual and brain processes.

7.3.2 Theoretical advances resulting from a midlevel feature approach

In parallel to methodological advances, new theoretical perspectives have been put forward that challenge the intuitive concept of emotions and the notion that emotions have a unique and discrete representation in the brain. As we saw at the beginning of this thesis, theories of human emotion and its neurofunctional basis are mostly based on experimental studies of facial expressions (Adolphs & Anderson, 2018; Barrett, 2017) that were later carried over to studies on body perception. These theories were initially based on hierarchical models in which emotion representation depended primarily on successful representation of the face as an object category. The coding of emotion would result from subsequent communication of face-selective areas with emotion areas and other networks (de Gelder & Poyo Solanas, 2021). According to this view, emotional recognition would thus require successful object categorization in object category areas (i.e., the fusiform face area and occipital face area in face processing; EBA and FBA in body processing). However, several studies showing the effect of contextual and emotional information on early visual object processing have challenged the hierarchical proposal. A clear example of this situation was discussed in **Chapter 2**, where it was reviewed that emotional incongruence between faces and bodies is signaled before category encoding takes place (Meeren et al., 2005) and that body posture biases facial expression processing, even when unattended (Meeren et al., 2005; Poyo Solanas et al., 2018; Van den Stock et al., 2007).

In view of these findings, other accounts have been proposed. The most accepted framework probably is the one by Haxby and Gobbini (2011), who suggested a model of distributed neural systems that considers the interaction of multiple contextual sources of information in ongoing face processing. In their model, facial expressions are not categorically represented but result from consecutive and cumulative stimulus evaluations that are context dependent (Haxby & Gobbini, 2011). These series of evaluations are represented as modulations of the core face network by activations in the extended network that can take place at early stages of face processing. Recently, we have proposed a new variant of Haxby and Gobbini's model in view of the findings reported in **Chapter 3** and **4**. In this model, called *radically distributed model*, face or body categorization would not be a necessary prerequisite for emotional expression coding. Instead, expression would be represented at the level between low-level physical coding and high-level symbolic representation:

the level of midlevel feature representation (de Gelder & Poyo Solanas, 2021). Interestingly, **Chapter 3** and **4** showed that certain kinematic and postural body features are characteristic of specific emotions and that these midlevel body features are related to several brain areas previously involved in emotional processing. A clear example was observed for the feature *limb contraction*, a feature with a central contribution in the perception of fearful body expressions. This feature was represented in areas previously involved in fear processing, spanning action observation, motor preparation, and affect coding regions, including the amygdala.

This new approach provides a new means to clarify the function of previously reported areas involved in body processing and their relation to emotion categories. It also provides the opportunity to understand the relation between the different regions involved in body (expression) perception. In this regard, we observed that the two body-selective areas, EBA and FBA, encode body features in a similar manner, with greater sensitivity to postural features than to kinematic ones. Yet, the stimuli representation in EBA was different to that of FBA. In **Chapter 4**, we argued that these findings may signify their different functions in body expression representation and that their different anatomical connections may be the basis of this functional difference (Zimmermann, Mars, De Lange, Toni, & Verhagen, 2018). The importance of a feature-based approach also becomes evident when trying to empirically dissociate the processing of body posture and motion, since these two types of information are closely linked and quickly integrated (Peelen, Wiggett, & Downing, 2006). Indeed, body motion can provide information about body form (Peelen et al., 2006). This debate pertains the functional specialization of pSTS and EBA. As previously mentioned, EBA is thought to be involved in the processing of body form cues (Peelen et al., 2006) while pSTS in the representation of biological motion (Grossman, Jardine, & Pyles, 2010), although not all evidence is consistent with this view (Jastorff & Orban, 2009; Jastorff, Popivanov, Vogels, Vanduffel, & Orban, 2012). A feature-based approach may help elucidate their respective functions as well as to investigate how the two separate existing pathways for the processing of body motion and posture (Giese & Poggio, 2003) represent emotional information at the mid-feature level.

7.3.3 Challenges of a midlevel feature approach

Although these developments represent a great step forward in the field of affective psychology and neuroscience, the biggest challenge yet to overcome is the development of a computational model that can guide affective body feature identification in an objective manner and within biologically plausible limits, just as it has been done for facial emotion recognition (Dailey, Cottrell, Padgett, & Adolphs, 2002; Fragopanagos & Taylor, 2005; Padgett & Cottrell, 1996). Given the link to action and intention (de Gelder, 2013), a biologically compatible model for body expressions would need to take into consideration not only the biological constraints of the visual system (Zhuang et al., 2021) but also environmental and survival functionalities of the organism (Mobbs, Headley, Ding, & Dayan, 2020). The development of such a model will also need large sets of ethnologically relevant stimuli involving quasi naturalistic conditions that can capture the relations between the organism and its ecological niche (de Gelder & Poyo Solanas, 2021; see also next section). This will also involve the integration of multimodal, contextual and cross-cultural factors (Poyo Solanas, Vaessen, & de Gelder, 2020).

Finally, another important issue is the lack of a common vocabulary in the description of features within and across fields. For example, in the field of face research, facial parts such as eyebrows, lips, etc. are often regarded as an intermediate feature level when in reality they constitute high-level object categories on their own (de Gelder & Poyo Solanas, 2021). In addition, feature descriptions are often based on subjective assessments or are very context-dependent, making cross-study comparisons a difficult task. Future theoretical and empirical work will need to develop common guidelines for the study and report of midlevel features processes.

7.3.4 The importance of naturalistic stimuli

Throughout this thesis, two types of information have been highlighted for their reported relevance in the perception of body movement: kinematics and postural information. In both **Chapter 3** and **Chapter 4**, several postural and kinematic features were defined and their relation to emotion perception analyzed. Interestingly, both chapters showed that postural body features constitute stronger candidates for differentiating distinct emotional body movements than kinematic

cues. These findings are in a way surprising when considering previous work reporting high performance in discriminating several types of social information from motion cues alone, such as sex (e.g., Barclay, Cutting, & Kozlowski, 1978) and identity (Richardson & Johnston, 2005), as well as action (Dittrich, 1993; Loula, Prasad, Harber, & Shiffrar, 2005) and emotion (Pollick, Paterson, Bruderlin, & Sanford, 2001; Sawada, Suda, & Ishii, 2003). This controversy comes into context when taking into account the type of stimuli used in these studies: point-light displays. The use of these stimuli has been certainly common because it allows the investigation of the role of motion cues while controlling for several confounds, including structural cues. This, and the findings showing that PLDs lead to equivalent or nearly equivalent performance in comparison to full-light or solid-body displays (e.g., Hill, Jinno, & Johnston, 2003; Runeson & Frykholm, 1983), led to the erroneous interpretation that postural information is less relevant than kinematic cues and even unnecessary for action, emotion and person perception.

This notion started to change with a series of studies investigating inversion effects using point-light displays. The initial belief was that the inversion of point-light-displays would impair performance on the task at stake on a greater extent than the inversion of full-light displays, the reasoning being that both stimuli portray kinematic information while form information is only present in full-light displays (Atkinson, Tunstall, & Dittrich, 2007). However, the inversion of point-light displays showed to disrupt identity recognition (Loula et al., 2005), sex judgements (Barclay et al., 1978) and emotional recognition (Dittrich, Troscianko, Lea, & Morgan, 1996) as well as to produce an attenuation or even the absence of neural activity (Grossman & Blake, 2001; Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004) in a similar manner to full-light displays.

Further support for the importance of form information comes from other studies. For instance, Atkinson et al. (2007) reported that even though kinematic information was sufficient for emotional recognition, disrupting form cues was seriously detrimental (Atkinson et al., 2007). Moreover, a brain-damaged patient with a deficit in perceiving moving stimuli was still able to identify actions from form information (McLeod, 1996). It has also been suggested that postural information is essential for the discrimination of emotion whereas kinematic information only provides additional cues used to resolve occasional ambiguities when, for example, different emotional movements share similar dynamic cues (Atkinson et al., 2007; Lange & Lappe, 2007; McLeod,

1996; Omlor & Giese, 2007). It has also been suggested that postural information may be particularly important in the discrimination of more complex stimuli such as emotional movements and complex actions (Casile & Giese, 2005; Giese & Poggio, 2003), in line with the results reported in **Chapter 3** and **4**. Taken together, these findings suggest a more relevant role of postural features than previously thought. They also highlight again the importance of the use of more ecological stimuli in the study of social and emotional behaviors, as previously argued when discussing **Chapter 2**.

7.3.5 Feature relevance

In the previous section we reviewed the literature on the relevance of postural and kinematic information and position ourselves within the notion of the importance of postural over kinematic features. However, it is important to note that postural and kinematic features may have different contributions in the attribution of affect depending on the specific emotion at stake (De Meijer, 1989; Wallbott, 1998). For example, in **Chapter 3** and **4** we saw that vertical movement was relevant in differentiating between fear and anger. Velocity, acceleration and shoulder ratio played a role in differentiating emotional from non-emotional body movements. Limb angles and limb contraction were relevant in differentiating fear from other expressive movements. Other studies have also reported the importance of postural and kinematic features in relation to specific emotions. For instance, postural features have shown to exert a stronger influence than kinematic ones in anger (Aronoff, Woike, & Hyman, 1992) and fear (Atkinson et al., 2007; Dittrich et al., 1996) than in happiness or sadness. While certain features may be essential for the attribution of a particular emotion, different emotions may share similar postural and kinematic features, but the contribution of these features may not be equally important (De Meijer, 1989). Indeed, certain body movements may present similar lower-level properties and still differ considerably in the high-level representations of emotion, action or intention (Jacob & Jeannerod, 2005; Roether et al., 2009; Wallbott, 1998). For instance, Wallbott (1998) pointed out that both disgust and pride are often portrayed with crossed arms over the chest but in disgust the head is bent forward while it is bent backward for pride (Wallbott, 1998). This overlapping feature representation could be important for understanding why certain emotions are often confused despite consisting of different body movements.

7.4 Methodological considerations when investigating non-conscious (emotional) processing

An intense debate still surrounds the theoretical and methodological question of how to best characterize perceptual awareness (Merikle, Smilek, & Eastwood, 2001; Snodgrass, Bernat, & Shevrin, 2004). On the theoretical side, there are several ways to think about perceptual awareness or visual experience that are outside the scope of this thesis (but see Seth & Bayne, 2022). On the methodological side, there are several implicit choices in the design of experiments that have a direct impact on what aspect of visual experience or perceptual awareness is being measured and how it can be interpreted (Windey & Cleeremans, 2015). One of these choices concerns the paradigm used to render stimuli invisible. In **Chapter 5 & 6**, the continuous flash suppression (CFS) was used, a technique thought to elicit a stronger, more stable and longer-lasting suppression of conscious visual perception than masking and binocular rivalry (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006; Yang, Brascamp, Kang, & Blake, 2014), especially in the investigation of body expressions. Yet, there are many unknowns about the use of this paradigm, one of them being the degree to which suppressed stimuli are actually being processed (Pessoa, 2005). It has been argued that CFS disrupts visual processing at an early stage, thus impeding higher cortical processing (Breitmeyer, 2015). This is in line with studies reporting a lower extent of processing under CFS in comparison to other suppression techniques (Fogelson, Kohler, Miller, Granger, & Tse, 2014; Izatt, Dubois, Faivre, & Koch, 2014; Peremen & Lamy, 2014). In fact, many behavioral and neuroimaging studies, including those in **Chapter 5 & 6**, have reported no evidence of high-level stimuli processing (e.g., emotion recognition) outside perceptual awareness (e.g., Cheng, Ding, Jiang, Tian, & Yan, 2019; Gelbard-Sagiv, Faivre, Mudrik, & Koch, 2016; Schlossmacher, Junghöfer, Straube, & Bruchmann, 2017), in contrast to positive findings often reported with other suppression techniques (e.g., Stienen & de Gelder, 2011; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Taken together, these findings have casted doubt on the suitability of CFS in the investigation of non-conscious processing (Schlossmacher et al., 2017).

However, CFS is not shielded from occasional breakthrough of stimuli information, either partially or completely. In fact, it is known that several physical stimulus parameters, such as the spatial frequency of the mask and the target stimuli (Stein, Seymour, Hebart, & Sterzer, 2014; Yang & Blake, 2012) or even their temporal frequency (Zhan, Engelen, & de Gelder, 2019), can influence suppression strength. In this regard, we chose a temporal frequency of 10Hz in **Chapter 5 & 6** because we wanted to investigate non-conscious processing but also processing at different levels of perceptual awareness and this frequency has shown weaker suppression compared to other frequencies (Zhan et al., 2019). Other aspects such as whether the target stimulus is being presented to the dominant or non-dominant eye (Yang, Blake, & McDonald, 2010) or the type of stimulus (e.g., affective stimuli: Gray, Adams, Hedger, Newton, & Garner, 2013; Stein et al., 2014; Yang, Zald, & Blake, 2007; Zhan et al., 2019) have shown to influence suppression duration. If that was not enough, a strong inter-subject variability in suppression strength has been reported across participants (Yamashiro et al., 2014). Taken together, the aforementioned findings call out for further investigation of the mechanisms underlying CFS with rigorous methodological comparisons.

Another methodological choice concerns the measurement of perceptual awareness. Some studies have employed verbal reports after the experiment (e.g., Whalen et al., 1998) while others have adopted a pre-defined objective threshold (e.g., 30ms target face presentation time; Dimberg, Thunberg, & Elmehed, 2000). Although widely used, these experimental choices may not provide a reliable measure of subjective experience during a task (Pessoa, Japee, Sturman, & Ungerleider, 2006; Tsuchiya & Adolphs, 2007). For example, adopting a universal objective threshold may not take into account different stimuli sensitivities across participants, biasing the results (Maxwell & Davidson, 2004; Pessoa et al., 2006; Pessoa, Japee, & Ungerleider, 2005). Relying on post-experimental reports may also overlook processes associated to the particular task (e.g., processes related to unattended items or specific stimuli features) (Tsuchiya & Adolphs, 2007). In an attempt to be more rigorous, other researchers have performed trial-by-trial evaluations. Typically, these studies characterized conscious perception using dichotomous tasks in which participants were asked to indicate whether they saw or did not see the target stimulus (e.g., Engelen, Zhan, Sack, & de Gelder, 2018). Recently, finer scales for the measurement of perceptual awareness have been developed, motivated by the notion that dichotomous tasks may not be able to capture weak

levels of perceptual awareness between a clear experience of the stimulus and perceptual unawareness (Lau & Passingham, 2007; Mazzi, Bagattini, & Savazzi, 2016; Overgaard, Fehd, Mouridsen, Bergholt, & Cleeremans, 2008). In **Chapter 5 & 6**, the use of one of these measures, the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004), indeed showed that intermediate states of perceptual awareness are possible. More importantly, the use of this scale resulted into a lack of behavioral and neural (e.g., amygdala) evidence of perceptual processing under perceptual unawareness, in line with other studies using PAS (e.g., Hesselmann, Darcy, Rothkirch, & Sterzer, 2018; Lähteenmäki, Hyönä, Koivisto, & Nummenmaa, 2015; Lamy, Alon, Carmel, & Shalev, 2015; Lamy, Carmel, & Peremen, 2017; Lohse & Overgaard, 2019; Peremen & Lamy, 2014; Ramsøy & Overgaard, 2004; Tagliabue, Mazzi, Bagattini, & Savazzi, 2016). These results suggest that further scrutiny in the differentiation between processes resulting from partial awareness from those reflecting non-conscious processing is necessary.

On a different but related topic, it has been argued that explicit reports of conscious experience may confound true correlates of consciousness with processes associated to metacognitive/introspective access (Tsuchiya, Wilke, Frässle, & Lamme, 2015). Same goes for indirect testing, where participants perform a forced-choice task about a particular stimuli feature (e.g., emotional categorization, gender), with or without explicit report of subjective visual experience. In this regard, several studies using no-report paradigms in combination with neuroimaging techniques (Lumer & Rees, 1999) or intracranial recordings (Noy et al., 2015) have reported no involvement of the dorsolateral prefrontal cortex in perceptual awareness, a region often found in studies with report requirements (e.g., Lumer, Friston, & Rees, 1998; Sterzer & Kleinschmidt, 2007). Although in **Chapter 6** we did not find involvement of the dorsal prefrontal cortex, an area located in the inferior frontal cortex was observed. The fact that no-report studies still found this area (Lumer & Rees, 1999; Noy et al., 2015) and that its causal role in conscious experience has been recently established with TMS (Weilhammer et al., 2021), made us conclude that this area may reflect perceptual awareness changes rather than cognitive processes related to participants' reports. Nevertheless, one could conclude that no-report paradigms constitute a relevant methodological solution for investigating the neural correlates of consciousness (Tsuchiya et al., 2015). However, no-

report paradigms are not exempt from confounds (Overgaard & Fazekas, 2016), as mentioned earlier. Both paradigms can provide complementary information in the study of perceptual awareness and conscious experience, yet critical comparisons between report and no-report paradigms are necessary.

In addition to report requirements, other task conditions or demands may influence experimental results. For example, while visual awareness does not appear to be modulated by attention when stimuli are presented foveally and in isolation (Koch & Tsuchiya, 2007), attentional modulations have been reported when introducing competing stimuli in the visual field (Desimone & Duncan, 1995). The presentation of emotional stimuli outside the center of attention has also given mixed results on non-conscious processing (Anderson, Christorf, Panitz, De Rosa, & Gabrieli, 2013; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001), with some authors ascribing this lack of result consistency to different attentional loads (Lavie, 1995; Pessoa, 2005; Pessoa, Kastner, & Ungerleider, 2002, 2003). The brain has indeed a limited capacity to process information and paying attention to a part of the visual field comes at the expense of another (Bundesen, 1990; Desimone, 1998; Desimone & Duncan, 1995). The fact that in **Chapter 5** and **6** we found no behavioral evidence of non-conscious body expression processing may have thus been related to the peripheral stimuli presentation. We also found no amygdala activation during perceptual unawareness, in disagreement with the notion of its automaticity, independent of attention (Anderson et al., 2013; Dolan, 2002; Öhman, 2002; Öhman, Flykt, & Esteves, 2001; Vuilleumier et al., 2001). However, other studies have also reported no evidence of amygdala involvement outside conscious awareness (Hoffmann, Lipka, Mothes-Lasch, Miltner, & Straube, 2012; Hoffmann, Mothes-Lasch, Miltner, & Straube, 2015; Pessoa et al., 2006; Phillips et al., 2004). Future research should further clarify the extent to which perceptual awareness and different attentional demands influence emotional processing.

Another key challenge in measuring subjective perceptual awareness is the criteria employed to assess whether a participant is aware or not of a stimulus. Two different approaches have divided researchers in this endeavor: those relying on subjective measures and those advocating for objective criteria (Snodgrass & Shevrin, 2006). Supporters of the objective criteria consider that perceptual unawareness occurs when participants show chance performance in a force-

choice task. However, the methodology employed to analyze the data resulting from these paradigms is equally important as it can lead to an overestimation of conscious processes. For example, the use of percent correct values alone to estimate chance performance can lead to the faulty conclusion that participants are unaware of the stimuli when they may still be able to detect them in a reliable manner (Green & Swets, 1966). To overcome this situation, many researchers have advocated for the use of signal detection theory (SDT) measures (Green & Swets, 1966; Tanner & Swets, 1954) as it allows the evaluation of subjective perceptual awareness in a response bias-free manner (Green & Swets, 1966). In this regard, no evidence of perceptual processing during perceptual awareness has been found in several studies controlling for different methodological confounds (Hedger, Adams, & Garner, 2015; Hedger, Gray, Garner, & Adams, 2016; Hoffmann et al., 2012; Hoffmann et al., 2015; Pessoa, 2005; Pessoa et al., 2005; Straube, Dietrich, Mothes-Lasch, Mentzel, & Miltner, 2010). On another note, this approach does not rule out the possibility that non-conscious processes may still be involved in objective above-chance level performance (Schlossmacher et al., 2017) or that objective unawareness may still have an impact on brain processing (e.g., **Chapter 6**; Wong, Bernat, Snodgrass, & Shevrin, 2004). Conversely, supporters of the subjective criteria consider that perceptual unawareness occurs when participants report not being perceptually aware of a stimulus, irrespective of their actual objective performance. This approach, however, suffers from possible biases in participants' responses (i.e., their standard for what should be counted as "seen" is different) (Eriksen, 1960; Kunimoto, Miller, & Pashler, 2001). In view of the above, a combination of both objective and subjective criteria has been suggested as the optimal solution for the study of perceptual awareness (Hedger et al., 2016; Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Wiens, 2006).

Taken together, it seems that every methodological choice has a direct impact on the outcome as well as on the interpretation of perceptual awareness findings. The selection of a specific paradigm (e.g., masking, binocular rivalry, continuous flash suppression), tasks demands (e.g., report/no-report, attention), assessment method (e.g., direct or indirect) or even the analysis procedures (e.g., SDT) can result in very different outcomes. Also, the fact that we do not know whether the same conscious versus non-conscious distinction can be applied to different stimuli adds another layer of complications. For example, face and body expressions have shown to be processed

differently under CFS (Zhan, Hortensius, & de Gelder, 2015). Body expressions of anger and fear have shown to be processed in a different manner despite both stimuli signaling threat (see **Chapter 5**). It has also been argued that low-level and high-level visual perception may have different relation to perceptual awareness, with high-level visual stimuli showing a dichotomous relationship while low-level visual stimuli a gradual one (Windey & Cleeremans, 2015). In **Chapter 5 & 6**, we also investigated this relationship between our body stimuli and perceptual awareness and saw that, despite being a high-level concept, emotional recognition presented a gradual relationship with perceptual awareness. Finally, study comparisons between patients and healthy participants should be performed with caution, as non-conscious processes may not always have the same neural basis across these populations. Perhaps, it may be safer to assume that, at present, different approaches may provide valuable contributions (Pessoa, 2005). Future research will not only require rigorous criteria and methodologies, but also a greater effort in the scrutiny and comparison of the different methodologies. This will only be possible if all methodological procedures are correctly and fully reported (e.g., in some studies, contrast specifications are missing (Jiang & He, 2006; Vizueta, Patrick, Jiang, Thomas, & He, 2012; Willenbockel, Lepore, Nguyen, Bouthillier, & Gosselin, 2012) as well as what aspect of consciousness is being characterized.

7.5 Fear has a special status

To conclude the discussion of this doctoral thesis, I would like to make a special mention to one very relevant emotion: fear. Fear is of vital importance for survival as it communicates the presence of a potential threat in our environment. It is therefore not surprising that the brain has evolved to have special mechanisms for the rapid detection and processing of this emotion. Indeed, previous research has associated fear with heightened vigilance and attention (Kret & de Gelder, 2013; Phelps, Ling, & Carrasco, 2006; Tamietto, Geminiani, Genero, & de Gelder, 2007) and increased visual processing (Borhani, Ladavas, Maier, Avenanti, & Bertini, 2015; van Heijnsbergen et al., 2007). The modulation of the motor system has also been reported after the observation of fearful body expressions (Borgomaneri, Gazzola, & Avenanti, 2012; Borgomaneri, Vitale, & Avenanti,

2015), evidencing their relevance in adaptive behavior. Across the five empirical chapters of this thesis, it also became clear to me that fearful body expressions hold a special status.

In **Chapter 2**, we saw that fearful body expressions, whether in incongruence with a concurrently presented facial expression or in isolation, cause the activation of several areas, including motor and executive regions. In addition, we saw that fearful bodies elicit a higher correlated activity between the amygdala and areas involved in emotional and social processing (anterior temporal lobe and PCC) (Wang et al., 2017), the monitoring and representation of bodily states (insula) (Critchley, 2005; Karnath, Baier, & Nägele, 2005) and scenes (SPL) (Haggard & Wolpert, 2005; Peelen & Downing, 2007) as well as in motor preparation (pre-SMA), regardless of the emotion conveyed by the face. Taken together, the different comparisons performed in **Chapter 2** have shown that fearful body expressions may indeed trigger adaptive motor preparation responses, even when presented outside the focus of attention and in emotional incongruence with the face.

As a further step in investigating the postural and kinematic characteristics of the body that convey a specific emotion, we defined several body features in **Chapter 3** and **4** and correlated them to emotional categories. Among the affective classes, only fearful body expressions were associated with specific body features. In particular, the features limb contraction and limb angles seemed to play a relevant role in the expression and perception of fear from body posture and movement (i.e., fearful bodies showed to be different from other expressions with respect to these features; **Chapter 3 & 4**). Interestingly, these features were represented in affective, action representation and motor preparation networks that have previously been associated with fearful expression perception (**Chapter 4**). These findings suggest that the display and detection of fear is imprinted in the brain already at the midlevel feature stage. Specific characteristics of fearful body expressions may not only be used for the understanding and recognition of the conveyed emotion, as they were coded in affective and action observation networks, but also for the preparation of adaptive behaviors, since they were also represented in motor cortices.

Privileged processing of fearful body expressions was also observed in **Chapter 5** and **6**. Although we did not find behavioral evidence of fearful body processing outside conscious awareness, we observed higher recognition sensitivity for fearful bodies at different levels of perceptual

awareness in comparison to angry bodies. However, fearful body expressions took longer to escape from suppression than angry body expressions. In **Chapter 5**, we argued that these findings may reflect the different nature of these threatening signals, both crucial for survival. While angry bodies convey information of a direct threat, the threat conveyed by fearful bodies is more ambiguous. This is maybe why fearful bodies need more attentional resources to disambiguate the threat (expressed as increased sensitivity) while angry bodies may not require such processes and instead trigger faster reactions (expressed as faster breaking from suppression). Taken together, these findings not only support the notion that bodies are relevant stimuli for adaptive behavior, but also provide evidence of the special status of fearful body expressions.

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