

UNIVERSITA' DEGLI STUDI DI PARMA

Dottorato di ricerca in Neuroscienze.

Ciclo XXIX

**Neural mechanisms underpinning *Emotional Body Language*
comprehension: eye tracking and EEG studies.**

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INDEX

1. Introduction

1.1	The importance of <i>Emotional Body Language</i> – EBL	6
1.2	Models for EBL processing	11
1.3	Notes on <i>Embodied Simulation</i> mechanisms	12
1.4	Visual exploration mechanisms of emotional facial and bodily expressions	
1.4.1	Faces	14
1.4.2	Bodies	17
1.5	Time course of EBL processing: EEG studies	21

2. Study I:

Visual exploration mechanisms during the categorization of emotional facial and bodily expressions.

2.1	Materials and methods	27
2.1.1	Participants	27
2.1.2	Stimuli	28
2.1.3	Apparatus	31
2.1.4	Procedure	34
2.2	Eye movements analyses	36
2.3	Results	37
2.3.1	Faces	37
2.3.2	Bodies	39
2.3.3	Faces and bodies comparison	44
2.4	Behavioural analyses	45

2.5	Behavioural results	46
2.5.1	Faces	46
2.5.2	Bodies	46
2.6	Discussion	46
2.7	Conclusions	53

3. Study II:

“Embodied Body Language”: an electrical neuroimaging study with emotional faces and bodies.

3.1	Materials and methods	55
3.1.1	Participants	55
3.1.2	Stimuli and procedure	56
3.1.2.1	Stimuli validation	56
3.1.2.2	Final stimuli per ERP experiment	56
3.1.2.3	Procedure	57
3.1.3	EEG recording and preprocessing	59
3.2	EEG analyses	61
3.3	Behavioural analyses	65
3.4	Empathy Assessment: Interpersonal Reactivity Index	65
3.5	Results	65
3.5.1	Empathy Assessment: Interpersonal Reactivity Index	64
3.5.2	Behavioural results	66
3.5.3	Electrophysiological results	69
3.6	Discussion	84
3.7	General discussion and conclusions	90

4. <u>Conclusions</u>	93
5. <u>References</u>	97

1. INTRODUCTION

"Dispositions follow bodily characteristics and are not in themselves unaffected by bodily impulses. This is obvious in the case of drunkenness and illness; for it is evident that dispositions are changed considerably by bodily affections. Conversely, that the body suffers sympathetically with affections of the soul is evident in love, fear, grief and pleasure." (Physiognomics I, 805a 1–8)

1.1 The importance of *Emotional Body Language* – EBL

The field of Affective Neuroscience has been for a long time dominated by emotional facial expression studies. This is a curious circumstance given the relevance of bodies and body postures in expressing our emotional and mental states. It is, in fact, now well agreed that “emotional body language” (EBL) plays a fundamental part during social interactions (e.g. de Gelder, 2009; de Gelder et al., 2010; Van den Stock and de Gelder, 2014).

Yet, the roots of our awareness of the importance of the body in expressing our emotional states are ancient. We can think of the words in the pseudo-Aristotelian treatise of physiognomics, used to describe the interdependence between body and soul (see above). This reminds us of the ancient Greek culture characterized by the blooming of tragedy and comedy production, famous thus far, and by the tradition of pantomime and theatrical representations (de Gelder, 2016). This opens the theme regarding the *artistic power of body expressions*, as stated by Beatrice de Gelder in her last book “Emotions and the body” (2016), well known in numerous theatrical traditions all over the world.

Notwithstanding the fact that at the end of the seventeenth century, two of the most important theoreticians of emotions, Charles Darwin and William James, already focused their attention on

whole-body emotional expressions, only recently research on bodily expressions occupied a strategic position in the field (Darwin, 1872; James, 1890; de Gelder, 2016).

Body postures can be easily comprehended and imitated. Indeed, the *emotional mimicry* (i.e. the spontaneous tendency to synchronize our facial expressions with those of others) can be induced not only by facial expressions but also by bodily gestures and postures (Magnée et al., 2007; Tamietto et al., 2009). In addition, similarly to the Facial Action Coding System developed by Ekman and coworkers (FACS – Ekman and Friesen, 1978), it seems possible to build a coding system capable to measure the activation of muscular units engaged in bodily expressions' production (BACS - Huis in 't Veld et al., 2014; de Gelder & Hortensius, 2014).

Bearing in mind these first considerations, it is natural to think about the role of action during the experience of emotions. The strictly link between emotion and action was already highlighted by Nico Frijda in 1986 in his book "The Emotions". With his theory, the "*action-readiness theory of emotions*" (Frijda, 1986), he also states: "...*what we loosely call "emotions" are responses to events that are important to the individual.... First of all, those responses--"emotions"--are subjective experiences. Their core is the experience of pleasure or pain. That core is embedded in the outcome of appraisal, the awareness of situational meaning structure. ...Introspections produce a wealth of statements that refer to what I call "awareness of state of action readiness". Participants report impulses to approach or avoid, desires to shout and sing or move, and the urge to retaliate; or, on occasion, they report an absence of desire to do anything, or a lack of interest, or feelings of loss of control (Davitz, 1969; Frijda, 1986, 1987).*" (Frijda, 1988). In few words, the core of his theory regards these *states of readiness* for different kind of *actions*, each of which gives priority to a specific aim.

Moreover, we should also consider that facial and bodily expressions could have a different degree of specialization: some emotions could be better conveyed and recognized by facial expressions, some others by bodily postures, let's think about disgust and anger, respectively (de Gelder, 2012).

Finally, it has been recently demonstrated that isolated facial expressions could be perceived as ambiguous, in particular in contexts of high emotional intensity, leading an observer to a wrong discrimination between positive and negative emotions (Aviezer et al., 2012). Thus, a better interpretation of the emotional context can be given by the encoding of the emotional information conveyed by bodies.

Neuroimaging studies have demonstrated that visual processing of the human body is mainly underpinned by the extrastriate body area (EBA), found in the lateral occipitotemporal cortex (Downing et al., 2001; Peelen & Downing, 2007), and in the fusiform body area (FBA), located in the posterior fusiform gyrus (Peelen and Downing, 2005; Peelen & Downing, 2007; Taylor et al., 2007) and adjacent to the face-selective fusiform face area (FFA) (Kanwisher et al., 1997). Beyond these, other regions are engaged during the elaboration of EBL. For instance, de Gelder and coworkers (2004), investigating perception mechanisms of EBL using functional Magnetic Resonance Imaging (fMRI), found that during observation of fearful body expressions there was not only an involvement of emotion-related brain areas, but also of networks for action representation, suggesting a link between emotion and action. The discovery of Mirror Neurons, whose activity is modulated by both action execution and action observation, provided new insights into the role of motor-related areas in perception of EBL. The putative fronto-parietal human Mirror Mechanism (MM), comprehending inferior parietal lobule (IPL), inferior frontal gyrus (IFG), the premotor cortex (PMC) and the superior temporal sulcus (STS) (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004), could indeed provide the neurobiological basis for many emotional and social cognition skills (Gallese et al., 2004; de Gelder, 2006).

Urgesi and coworkers (2007a) subsequently demonstrated, with a Transcranial Magnetic Stimulation (TMS) study, the different role played by EBA and “mirror” regions during elaboration and comprehension of bodily actions. Applying Repetitive TMS in order to induce the inhibition of EBA and ventral PMC, respectively, they demonstrated that interference with EBA compromised the ability to discriminate bodily forms, while interference with ventral PMC impaired the ability to

discriminate bodily actions. Hence, the EBA has a crucial role in the processing and recognition of bodily morphological characteristics and so in the elaboration of their identity, while the ventral PMC, as part of the MM, has a role in the processing and recognition of bodily actions. Later on, these authors better clarified these findings demonstrating that the ventral PMC could have a role in the configural processing of the body, suggesting how this kind of processing could imply the mapping of the observed bodily postures representations on the sensorimotor representations of the observer (Urgesi et al., 2007a; Urgesi et al., 2007b).

More recently, Borgomaneri and colleagues carried out a series of TMS studies to investigate the specific role of the motor cortex during EBL perception. In order to test the hypothesis that motor reaction to emotional cues and motor resonance mechanisms are implemented in the motor cortex at different times (Borgomaneri et al., 2014), they recorded motor-evoked potentials (MEPs) caused by stimulation of primary motor cortex – M1 (left and right) at 150 and 300 ms after stimulus onset (i.e., the presentation of fearful, happy and neutral bodily expressions), while participants performed a categorization task. In regard to the earlier stage of processing (150 ms), results showed an increase of motor excitability of the left hemisphere in response to fearful body postures, and the inhibition of the excitability in the right hemisphere in response to both fearful and happy postures, in this latter case correlated with the visual recognition of bodily expressions. At 300 ms, they recorded an increase of motor excitability, comparable between the two hemispheres, and similar for all the three emotional categories (dynamic happy, fearful and neutral bodily postures). In accord with their hypothesis, these authors concluded by hypothesizing the presence of two distinct stages of motor cortex involvement during perception of EBL (Borgomaneri et al., 2014; Borgomaneri et al., 2015). At an early stage of processing an increased motor excitability in the left hemisphere is involved, while in the right hemisphere are carried out visual perceptual mechanisms. At a later stage of processing, instead, there is the implementation of motor resonance mechanisms in bilateral M1. Hence, the motor excitability *indexed the presence of body motion in the stimulus rather than its emotional content* (Borgomaneri et al., 2014). To better investigate the role of motor

cortex and motor reaction mechanisms in response to fearful body postures, they ran a single-pulse and paired-pulse TMS study exploring the motor excitability in bilateral M1 at the earlier time window in which fearful body postures and facial expressions exert a modulation of the occipito-temporal cortex (100-125 ms) (Borgomaneri et al., 2015). Their hypothesis was to find, before the two stages of motor cortex involvement already demonstrated, a fast suppression of motor reactions to EBL and, in particular, to fearful body postures. Using as stimuli happy, fearful and neutral body postures, they asked participants to categorize them. They ran three different experimental sessions (single-pulse; paired-pulse, *short intracortical inhibition*; paired-pulse, *intracortical facilitation*) to investigate not only the functional state of the corticospinal system (single-pulse session), but also the excitability of *intracortical facilitatory* and *inhibitory* circuits (paired-pulse sessions) in bilateral M1. They demonstrated the existence of a very fast modulation (100-125 ms) of left and right motor cortices when observing EBL, and fearful bodily expressions in particular. This mechanism, explicable in terms of a transient motor excitability reduction of bilateral M1 (suppression of *intracortical facilitation* circuit), would reflect a fast orienting response to emotionally relevant bodily postures, allowing *perception of and subsequent motor reactions to the emotional cues* and monitoring processes (Borgomaneri et al., 2015).

Considering together the results of the two studies (Borgomaneri et al., 2014; Borgomaneri et al., 2015), it emerges how the involvement of M1 during EBL processing could be explained by a three-stage model (Borgomaneri et al., 2015):

- 1) 100-125 ms: “negative bias” or transient reduction of motor excitability (cortical level), in response to fearful body postures in particular.
- 2) 150 ms: EBL starts to influence the corticospinal system; on the left hemisphere in terms of an increased excitability, while on the right in terms of involvement of perceptual mechanisms.
- 3) 300 ms: implementation of motor resonance processing.

1.2 Models for EBL processing

In the light of the first discoveries regarding EBL, Beatrice de Gelder elaborated a “two-system” model of emotion-behaviour connectivity (de Gelder, 2006): the first system, the *primary-reflex like network*, includes the superior colliculus, pulvinar, striatum and amygdala, and supports the rapid and automatic perception of EBL and the preparation of adaptive reflexes; the second network, the *visuomotor perception network* or *reflection-based network*, involving lateral occipital cortex, STS, intraparietal lobule, fusiform gyrus, amygdala and PMC, is, instead, devoted to deeply elaborate EBL and calculate behavioural consequences of an emotion deciding for the best answer to the stimulus. These two systems, reciprocally connected, are linked with a third system, the *body awareness system*, which involves the insula, somatosensory cortex, anterior cingulate cortex (ACC) and ventromedial prefrontal cortex. (de Gelder, 2006; de Gelder, 2016).

More recently, Amoruso and co-workers (Amoruso et al., 2011), focusing on the critical role of human body in expressing not only intentions but also goal-directed actions, proposed a functional neuroanatomic model for the processing of contextual goal-directed actions based on the capability of EBA and FBA to provide perceptual information, which are then integrated in a larger fronto-insular-temporal network. In particular, several frontal areas would update contextual information in relation to episodic memory, while temporal regions (e.g. parahippocampal cortex and amygdala) would index the value learning of target-context associations. In addition, the insular cortex would coordinate internal and external contexts with an interior motivational state.

1.3 Notes on *Embodied Simulation* mechanisms

The aim of this paragraph is to provide some fundamental information about the Embodied Simulation mechanism (ES), in our opinion capable to provide a valid frame of interpretation of EBL processing.

As previously affirmed, the MM could *provide the neurobiological basis for many emotional and social cognition skills* (Gallese et al., 2004; de Gelder, 2006), hence MM might constitute the substrate of the experiential comprehension of others allowing a direct simulation of the observed events (Gallese et al., 2004). This means that, for example, whenever we are looking at somebody executing an action, there is an activation of the same motor network that is involved when we perform the same action. Specifically, during the observation, the actual execution of the action is inhibited: “*action is not produced, is only simulated*” (Gallese, 2013). We could define it as an “*as if*” mechanism or as *action simulation* (Gallese, 2001): it matches action observation and action execution providing the same neural substrate. Since this simulation mechanism permits the observer to understand basic motor intentions and goals of others’ actions, it emerges how it could be considered a mechanism at the base of inter-subjectivity. Before extending this theory to the comprehension of sensations and emotions of others, Gallese introduced the concept of *shared manifold of intersubjectivity* (2001), positing that it is fundamental to recognize other individuals as similar to us. He suggested that it can be operationalized at three different levels (Gallese, 2001):

- 1) *Phenomenological or empathic level*: it is responsible for the *sense of similarity*; we can understand others’ actions, sensations and emotions because *we can share them with them*.
- 2) *Functional level*: simulation sequences or “as if” processes.
- 3) *Subpersonal level*: the outcome of activity of different mirror matching neural circuits.

Subsequently, it has been theorized that the same simulation mechanism could underpin also the comprehension of others’ emotions, sensations and pains through the activation of visceromotor centers (e.g. insula and anterior Cingulate Cortex).

Thus, the so-called *shared manifold* depends on the specific functional mechanism of ES (Gallese, 2003). These simulation mechanisms have been defined as *embodied* because, as stated by Gallese (2013): “...people reuse their own mental states or processes represented in bodily format to functionally attribute them to others.” (Gallese, 2003; Gallese & Sinigaglia, 2011).

In our opinion, as already stated for the comprehension of facial expressions, ES mechanisms, beside the activation of related visual areas, could subtend EBL comprehension in terms of motor, sensorimotor and visceromotor activations allowing a direct match between the emotional bodily posture observed and executed, hence allowing the correct interpretation of the emotion conveyed by bodily postures themselves.

1.4 Visual exploration mechanisms of emotional facial and bodily expressions.

Albeit one of the aim of the present dissertation is to demonstrate the relevance of bodies and bodily expressions in conveying emotional information, we have to first take into account the well-known mechanisms underpinning facial expressions processing as the basis from where to start.

1.4.1 Faces

Among the techniques employed to investigate how facial expressions are processed, the recording techniques of eye movements have been widely used to investigate how faces are visually explored, since the gaze pattern could be considered as an index of related perceptual and cognitive processes. By means of eye tracking techniques it is possible to evaluate the spatial distribution of the fixations, in order to define regions of interest, assuming that they represent the more informative cues in the stimulus. Moreover, it is also possible to measure the duration of the fixations, considered as an index of both the quantity of information located in a specific region of the stimulus, and of the time needed to elaborate it. Using these techniques, it is also possible to measure the modulation of pupil diameter due to affective and cognitive information processing (Partala & Saurakka et al., 2003). Indeed, pupil diameter can be considered as a reliable index of the individual's emotional state: previous studies demonstrated significant modulations in response to emotionally salient visual and auditory stimuli (e.g., Partala & Surakka, 2003; Bradley et al., 2008; Babiker et al., 2013).

In most cases, in order to obtain a clearer and more accurate gaze data elaboration, investigations about faces visual processing have been developed by means of the analysis of fixations on *Areas of Interests* (AOIs): specific regions or single features of faces. As a matter of fact, it has been extensively demonstrated that while looking at a facial stimulus, people tend to direct their attention (i.e. to make more and longer fixations) to the eyes, nose and mouth. Specifically, almost 70% of

fixations are directed to the eyes (Sullivan et al., 2007; Hsiao & Cottrell, 2008). Moreover, multiple evidences revealed how the upper region of a face is more salient for the comprehension of negative emotions (e.g. sadness and fear), while the lower half is more informative for the understanding of positive emotions and, particularly, of happiness, due to the presence of the smile (e.g. Eisenbarth & Alpers, 2011; Guo, 2012). In sum, considering Ekman's FACS (1978), it is possible to sustain that different facial affects could be expressed, and so perceived by others, through different facial features providing expression-specific information (Guo, 2012).

Bearing in mind previous studies, Guo (2012) noticed a methodological problem due to the use of stimuli displaying exaggerated facial expressions or conveying a peak of intensity, albeit during our social interactions we more often see less intense facial expressions. Considering previous behavioural results showing less accuracy in the interpretation of facial expressions when displayed in low-intensity (Herba et al. 2006; Gao & Maurer, 2010), they recorded eye movements while participants performed an emotion categorization task of facial expressions pertaining to six basic emotions (happiness, anger, sadness, fear, disgust and surprise), displayed at different emotional intensity. Their results showed that the performance was improved when participants saw stimuli of high emotional intensity, with shorter reaction times and less fixations to the face than when they saw low-intensity stimuli (the degree of the effect was dependent on the kind of expression). With their results they also confirmed the tendency to adopt a *holistic* viewing strategy (the tendency to integrate all the salient facial features in a single representations of the face) to explore and categorize facial expressions: “...we tend to scan all key facial features to reliably label expressions, and allocate most of the gaze at the eye region, followed by the nose and mouth regions” (Guo, 2012; Guo & Shaw, 2015).

In a more recent study, Guo and Shaw (2015) took into account the role of face's orientation and the effect that this could have on the perception of facial intensity, demonstrating how profile faces reduced the perceived intensity of facial expressions than when they were presented in a frontal

view. Also in this case, the distribution of fixations was independent of viewpoint and expression type, suggesting again the adoption of a holistic viewing strategy (Guo & Shaw, 2015).

It is worth noting that when scanning faces, there seems to be a bias toward the left side of the face, the so called “left-side bias”. It refers to the perceptual and attentional advantage for the left side of an observed face (i.e. *lateralization of perception*) (e.g., Gilbert & Bakan, 1973; Burt & Perrett, 1997) and, as a consequence, to the tendency of making more and longer fixations to the left side of the observed face (i.e., the half-face at the left visual field from the point of view of the observer) (e.g. Hsiao & Cottrell, 2008).

Mertens and colleagues, for example, demonstrated that, during a visual memory task, participants mainly fixated to the left than the right side, but only when they looked at faces, not when they looked at other objects, such as vases (Mertens et al., 1993). It has been argued that the left-side bias is due to the dominance of the right hemisphere in both face processing and facial expressions comprehension (e.g. Rossion et al., 2003). Other authors hypothesized that this bias is the result of the interaction between the hemispheric lateralization and a directional bias of visual scanning process, consolidated during the evolution (Vaid & Singh, 1989; Chokron, 2002).

It is noteworthy that only recently, researchers started to focus their attention to the investigation of gender differences. The face is a social and emotional stimulus, as such it is reasonable to expect significant differences in the way males and females scan this relevant stimulus considering the hypothesized different empathic capabilities between the two genders.

Recently, Vassallo and colleagues (2009), in view of the lack of eye-tracking studies conducted to investigate whether gender differences were dragged by a different way to orient the attention when looking at facial expressions, aimed to clarify “...*the role that visual scanning may play in the sex differences...*”. They recorded eye movements while participants (half of them males and half females) viewed pictures of facial expressions depicting one of the six basic emotions in order to perform a categorization task. The results showed that female were faster than male participants in identifying the correct emotions. The authors’ interpretation was that this was due to the different

visual scan-paths between males and females: males made more and longer fixations to less salient regions of the faces, such as the nose or the lower face.

Although different lines of research focused their attention on other related themes (e.g., age differences or differences between healthy individuals and patients), the aim of this paragraph was to make the reader familiar with the major findings regarding the visual mechanisms of face exploration in order to better understand the more recent findings about visual exploration mechanisms of bodies and emotional body postures, noticing in the next paragraph what are similarities and differences in their processing.

1.4.2 Bodies

As already stressed, bodies and body postures are capable to convey emotions, as they contribute, together with faces, to express mental and emotional states of human beings (e.g., Aviezer et al., 2008; 2012; Proverbio et al., 2014).

Nonetheless, very few studies have explored the pattern of eye movements implicated in the recognition of bodily postures (Tao & Sun, 2013). Among them, Tao and Sun in 2013 published a study aimed to investigate the *body inversion effect* through behavioural and eye tracking measures. The *body inversion effect* refers to a phenomenon first discovered for faces, the so-called *face inversion effect*, considered as a demonstration of the holistic processing of facial stimuli: presenting inverted faces, participants make worse performances in categorization tasks as indexed by longer reaction times and lower accuracy (e.g. Carey, 1992). Reed and coworkers more recently demonstrated the same effect for bodies suggesting that holistic processing could also be determinant for the recognition of human body postures (Reed et al., 2003). The aim of Tao and Sun was twofold: not only to investigate which was the most viewed region of the body postures but also whether a specific pattern of eye movements was responsible of the body inversion effect. In order to do so they employed as stimuli biomechanically possible and impossible body postures, both presented upright or inverted, during a recognition task (same-different task). From a

behavioural point of view, the effect was confirmed in terms of both accuracy and reaction times for biomechanically possible body postures, but only in terms of reaction times for biomechanically impossible body postures. Eye-movements results demonstrated that the body inversion effect influenced the duration of the first fixation: the first fixation was shorter to upright than to inverted biomechanically possible body postures, while there was no significant difference between upright and inverted biomechanically impossible body postures. The same results were obtained when considering the total number of fixations.

With respect to the most viewed region, the authors referred a significant difference among head, upper body and lower body: more fixations were directed both to the upper part of the body and to the head (upright or inverted).

In sum, their results suggested that upright body postures, as faces, are processed configurally (i.e. humans tend to adopt a holistic viewing strategy).

In the same year, Mariska Kret and colleagues (2013a), coordinated by Beatrice de Gelder, published an interesting and original study focused on the recognition of emotions from both faces and bodies, isolated or combined together as compound stimuli. The study was composed by three different experiments:

- 1) Categorization of isolated emotional faces and isolated emotional bodies (happy, angry and fearful).
- 2) Categorization of emotional facial expressions presented in compound stimuli with emotionally congruent or incongruent emotional body postures.
- 3) Categorization of emotions in bodily expressions presented together with congruent or incongruent emotional faces.

Among the techniques employed (electromyography and pupil size recording), the authors recorded also the eye movements of participants while performing these three different tasks.

Results of first experiment showed better accuracy in recognizing facial than bodily expressions, while gaze data demonstrated that participants looked longer at faces than at bodies, and at angry

and fearful stimuli than at happy ones. By means of the other two experiments the authors investigated the influence of body postures on facial expressions recognition and vice versa. The results of the second experiment showed better performances with happy faces, while performances with angry and fearful ones were better when presented with emotionally congruent bodily postures. Considering gaze data, the authors created two AOIs, face and body, showing how participants spent more time looking at face than to body; moreover, longer fixations were made to angry faces. In conclusion, results of the third experiment demonstrated a lower accuracy for happy than for angry and fearful bodily postures; happy bodies were better recognized when accompanied by congruent facial expressions. Contrary to the previous task, participants spent more time looking at the body than at the face. Gaze data also showed how participants made longer fixations to fearful than to angry or happy faces. It is worth noting that the time spent looking at faces depended mainly on the bodily expression: longer fixations were made when body postures expressed happiness. With regard to the observation of bodies, longer fixations were made to angry bodily postures. In sum, the authors concluded that angry and fearful faces and bodies attract more attention than happy expressions, suggesting a preferential way in focusing the attentional resources to potentially dangerous stimuli. In this regard, an interesting explanation is provided by the *motivated attention theory* (Lang et al., 1997; Bradley et al., 2003). Moreover, the recognition of facial and bodily expressions is enhanced when they are emotionally congruent, demonstrating how they could exert a reciprocal influence, in both directions (Kret et al., 2013a).

The same authors, to confirm previous behavioural results suggesting a better recognition of emotional bodily postures when presented in an emotionally congruent social context (Kret et al., 2010), measured physiological responses (electromyography, eye movement and pupil size recordings) to face-body-scene combinations. They aimed to investigate two questions:

- 1) *“How are face and body expressions processed when presented simultaneously?”*
- 2) *“How are body expressions processed when presented in a social emotional context?”*

In a first experiment they asked participants to freely explore images depicting face-body compound stimuli expressing congruent or incongruent emotions (anger, happiness, fear). Considering gaze data to the body, the kind of the emotion influenced how participant explored the body: they attended more to angry and fearful than to happy bodily postures. Testing the interaction with faces, results showed that longer fixations were made to bodies when they were incongruent with a happy facial expression. When looking at faces, a congruence effect emerged only when they were accompanied by angry than by happy or fearful bodies.

In a second experiment participants were asked to categorize the bodily emotion situated in a congruent or incongruent emotional context. Results showed that, when the context was neutral, participant made longer fixations to angry than to happy bodies.

In the last experiment, the task was the same as the second, but the presentation times of the stimuli were different, forcing participants to adopt faster recognition mechanisms. As previously demonstrated, accuracy was higher when bodily postures and context were emotionally congruent.

Taken together, these results showed that the perception of and the reactions to facial and bodily expressions are influenced by the surrounding natural context. In particular, confirming results of the previous study and in line with the *motivated attention theory* (Lang et al., 1997; Bradley et al., 2003), the attention and the reactions of the observers are captured when the emotional information conveyed by such stimuli is about threat and anger, both suggesting incoming dangerous situations (Kret et al., 2013b).

1.5 Time course of EBL processing: EEG studies.

Regarding the temporal dynamics of visual body processing, electrophysiological literature showed that the structural visual encoding of human bodies and body parts, as for faces, is indexed by a negative component (the N170) at occipitotemporal electrodes peaking in a range between 140 and 230 ms after stimulus presentation (e.g. Bentin et al., 1996; Stekelenburg and de Gelder, 2004; Meeren et al., 2005; Peelen & Downing, 2007).

Stekelenburg and de Gelder (2004), for example, conducted an electrophysiological investigation to study whether the body inversion effect, as a demonstration of the configural strategy of stimulus processing, was reflected in the N170, at that time thought to be specific for face structural encoding. They used as stimuli pictures of bodies (without head, fearful or neutral), faces (fearful or neutral) and objects, half of which were presented upright while the other half were presented inverted. Participants were asked to categorize each stimulus as upright or inverted. Results showed that the N170 was equally modulated by both inverted bodies and faces, as indexed by higher amplitude and longer latency. This, with a similar distribution on the scalp, suggested the possibility to consider the N170 component as an index of the early structural encoding of both faces and bodies. With regard to the influence exerted by the emotional content of the stimuli, results revealed a different pattern of amplitude modulation: while for faces there was an effect on the N170 and on other two early components (occipito-temporal P2 and fronto-central N2), fearful bodies modulated the *vertex positive potential* (VVP) on frontal sites and a sustained fronto-central potential at longer latency (Stekelenburg & de Gelder, 2004). Authors' opinion was that this difference was due to the absence of the head in the bodily postures, which made these stimuli harder to recognize and more ambiguous, requiring a prolonged attention to such stimuli for a correct elaboration. However, looking at the bodily stimuli employed by Stekelenburg and de Gelder, the first thing catching the eye is the difference between neutral and fearful bodily postures in terms of their implicit movement: while neutral bodily postures were almost static, fearful ones were on the contrary

dynamic. This implied the doubt that the emotional effect “*may have resulted from the difference in perceived implicit movement, instead of the presence of emotion per se.*”, as stated by van Heijnsbergen and colleagues (2007). Hence, they set up a new ERP study aiming to disentangle this possibility. They used as stimuli static images taken from dynamic videos showing actors executing an instrumental action, with or without fearful expression, and a scrambled version of the same stimuli, to verify if low-level properties could provoke differences in the amplitude of another early component, called P1, responsive to the physical characteristics of the stimulus. Results showed that both realistic and scrambled images elicited an occipito-temporal P1, while the N170 and the VVP emerged only in response to realistic images. In addition, P1 and VVP were modulated by the emotional content of realistic bodily postures, as indexed by faster latency in response to fearful bodily postures as compared to neutral ones. In conclusion, P1 and VVP, the positive counterpart of the N170, but not the N170, were sensitive to the expressed fear, indexing a rapid and preferential elaboration mechanism for fearful content conveyed by bodies, reasonable from an adaptive point of view (van Heijnsbergen et al., 2007).

To date, whether the N170/VPP and P1 are modulated in terms of latency and amplitude by the emotional content of bodily postures (not only fear-related), it has to be still clarified.

Recently, Bohrani and colleagues (2015) used as stimuli images depicting static bodily postures (without movement or emotional content), bodily postures with implicit movement, and bodily postures with both implicit movement and emotional content (happy or fearful). Their aim was to investigate whether the early stage of structural processing could be influenced by motion and emotion information conveyed by bodily postures. Furthermore, by means of the lateralized presentation of the stimuli (to the left or to the right with respect to the central fixation point), they explored also the different contribution of each hemisphere in bodily postures elaboration. Participants were asked to categorize each stimulus as non-emotional (static or neutral) or emotional (happy or fearful). Results showed that the stage of structural encoding of the stimulus, indexed by the N190, was modulated by both kinds of content. With regard to the lateralization

effect, it emerged that on the right hemisphere the N190 was modulated by both motor (higher amplitude in response to dynamic stimuli) and emotional information (higher amplitude in response to fearful bodily postures); on the other side the left hemisphere showed only motor modulation. Authors measured also an additional negative component, the Early Posterior Negativity – EPN, recorded at occipito-temporal sites around 150 ms, but better defined between 250 and 300 ms after stimulus onset, which is typically elicited by emotional negative stimuli and it is considered as an index of the attentional involvement caused by salient stimuli (Calvo & Beltran, 2014; Frühholz et al., 2011; Olofsson et al., 2008). It was of higher amplitude in response to fearful bodily postures on both the hemispheres, indexing an increased processing of motivational and adaptive relevant stimuli. Hence, these results are a first demonstration of how, during an early phase of bodily postures visual encoding, it is possible to distinguish between bodily postures conveying motor information and bodily postures expressing emotional information. In conclusion, the authors hypothesized that this information are rapidly extracted from visual stimuli and that they carry out a fast top-down modulation on neural processing mechanisms reflecting the structural encoding of such stimuli (Bohrani et al., 2015).

Concerning the stage of processing of semantic information conveyed by bodies, previous ERP studies investigated the time course and the neural correlates underlying elaboration of action's meanings, intentions and rules of execution by means of N400 modulation.

The N400, a negative component peaking around 400 ms after a meaningful stimulus onset, was first discovered by Kutas and Hillyard (1980), in response to semantically anomalous words at the end of a sentence, and from that time on, the characteristics of this component in the language field have been deeply investigated.

So far, two main views have been developed to explain the N400 effect: the *integration view* and the *lexical view* (Lau et al., 2008). The first one postulates that the N400 effect is elicited by a process of semantic integration of a target word with the context (combinatorial process), hence

N400 amplitude is higher in response to semantically inconsistent sentences because the integration process is harder than in congruent contexts. The *lexical view* assumes, instead, that the N400 effect reflects the preferential activation of representations stored in long-term memory and associated with a lexical item: anomalous sentences are more difficult because it is harder to recall from memory unpredictable words in context. Anterior and posterior temporal cortices, together with the inferior frontal cortex seem to constitute the *anatomical framework for semantic processing* (Lau et al., 2008). While posterior temporal cortices, with the Middle Temporal Gyrus, are hypothesized to be involved in storage of lexical representations, the anterior temporal cortex would sustain combinatorial operations and semantic integration processes with the context. Finally, the IFG seems to be the best candidate for semantic processing (Lau et al., 2008).

It is noteworthy that the N400 is not only sensitive to semantic and linguistic processing (e.g. Kutas & Federmeier 2000; Lau et al., 2008; Forgacs et al., 2015), but also to communicative gestures (e.g. Fabbri-Destro et al 2014; Proverbio et al., 2015), to perception of anomalous or incongruent images with context and expectations, or to violations of world-knowledge of the observer (e.g. Sitnikova et al., 2003; Reid & Striano, 2008; Proverbio & Riva, 2009; Proverbio et al., 2010; Proverbio et al., 2012).

Only recently, a study from Proverbio and colleagues (Proverbio et al., 2014) investigated the time course and the neural correlates underlying the comprehension of EBL, by analysing the electrocortical indexes recorded during an image categorization task. ERPs were recorded in 30 participants while viewing 280 full-body pictures of actors displaying a particular mood or emotional state, which could be congruent or incongruent with an immediately preceding verbal description. The results showed that incongruent images elicited an anteriorly distributed N400 (380-460 ms) reflecting the recognition of incongruent affective body language, starting as early as 300 ms post stimulus. The analysis of the inverse solution swLORETA applied to Incongruent minus Congruent difference wave in the time window corresponding to the anterior N400, showed the activation of the right rectal gyrus (BA11) of the ventromedial orbitofrontal cortex, the bilateral

uncus (limbic system) and the cingulate cortex (BA 23), the cortical areas underpinning face and body processing (STS, FFA and EBA) and PMC (BA6), which is involved in action comprehension and representation. Of note, these findings remind us of the three networks proposed by De Gelder (de Gelder, 2006) and are in accord with recent neuroimaging findings (de Gelder, 2009; Kana & Travers, 2012).

In this case, stimuli were full-body images: i.e. face was shown as a part of the whole body. Even though we usually perceive human bodies and faces as a whole, integrating them in a unified percept, they should be considered as two different categories of stimuli, since they are underpinned by neural networks that, although strictly linked, seem to be distinct (Peelen & Downing, 2007).

So far, a large amount of electrophysiological studies investigated the temporal characteristics and the neural correlates of face processing and of emotional facial expression comprehension (e.g. Balconi & Pozzoli, 2003; Batty & Taylor, 2003; Williams et al., 2006), while few of them explored the time course and the neural correlates of EBL (e.g. Proverbio et al., 2014; Bohrani et al., 2015), and even less investigated the characteristics of the integration process between affective information conveyed by both face and body (e.g. Meeren et al., 2005; Gu et al., 2013;).

With regard to the integration process between affective information conveyed by both face and body, Meeren and coworkers (Meeren et al., 2005) studied the influence of EBL on the perception of facial expressions by using as stimuli face-body compound images displaying the same or different emotional expressions. They analysed the early electrophysiological indexes recorded while participants attended to the face and performed an emotional expression categorization task. Behavioural results indicated an improvement in the task when face and body expressed the same emotion, while when there was an incongruence participants showed a bias in judging emotional facial expression toward the emotion displayed by the body, demonstrating that an integration of affective information took place. ERPs results, showing an higher amplitude of the occipital P1 component in response to incongruent stimuli, suggested that the integration process could happen very early.

In a more recent study, Gu and coworkers (Gu et al., 2013) investigated the same process adding a further question about the role of attention. ERPs were, indeed, recorded while participants observed face-body compound stimuli in two different experiments: in the first one they had to categorize the emotion expressed by the face, while in the second they had to categorize the bodily expression. Here too, results showed that the integration of emotional information conveyed by face and body starts early, and that the attention biased it only during later stage of processing.

These studies, however, focused their attention on the modulation due to the integration process of affective information conveyed by faces and bodies, of early ERP components, and did not explore which were the neural generators involved.

2. STUDY I

Visual exploration mechanisms during the categorization of emotional facial and bodily expressions.

In the light of the background exposed in the first chapter and considering the lack of previous eye-tracking studies focused on the visual mechanisms subtending visual exploration of bodies and EBL, the aims of the present study were manifold:

- 1) To investigate the patterns of visual exploration during the observation of facial and bodily expressions, clarifying the characteristics of the visual mechanisms during *Emotional Body Language* processing.
- 2) To investigate the influence of the gender of participants on these mechanisms.
- 3) To validate stimuli (facial and bodily expressions) to be used in a further EEG experiment.

2.1 Materials and methods

2.1.1 Participants

33 participants took part to this study (14 female), age range between 20 and 35 years ($M=24.2$, Standard Deviation – $SD = 4.04$), composed by two experiments.

During the first experiment we presented only bodies and the final sample was composed by 21 participants (11 females) ($M=23.7$, $SD = 3.3$); during the second experiment we presented only faces and the final sample was composed by 24 participants (11 females) ($M=24.9$, $SD = 4.5$).

All participants had normal or corrected to normal vision. Their handedness was assessed by the Edinburgh Inventory Questionnaire (Oldfield, 1971), reporting right-handedness in all participants. Ocular dominance of all participants was also assessed by a means of a practical test. The study has been conducted according to the principles expressed in the Declaration of Helsinki.

2.1.2 Stimuli

Stimulus materials were generated by taking ecological pictures of emotional faces and body postures. Eight semi-professional actors (4 males and 4 females), age range 23-34 years, were asked to display happiness, sadness or a neutral condition. Actors were asked to wear black clothes (t-shirt and trousers) without drawings or writings which could have been potential distractors.

We obtained 338 pictures of faces and bodies (172 (86 females, 84 males) and 166 (82 females, 84 males), respectively) (Fig. 1 e Fig. 2). Photographs were taken in a classroom while the actors stood in front of the camera in a black hall in light-controlled conditions. A set of standardized instructions was given to each actor indicating that they should spontaneously express happiness, sadness and a neutral condition, getting 51 neutral (26 females), 60 happy (31 females) and 61 sad faces (29 females), and 55 neutral (30 females), 53 happy (24 females) and 58 sad (28 females) bodies. The pictures were processed with Adobe Photoshop to remove the head from the body and to ensure homogenous grey background (R:128, G:128, B:128), faces size and bodies sizes.

Stimuli had the final dimension of 615 x 800 pixel for bodies (17 x 22 cm) and of 1024 x 768 pixel for faces (28 x 20 cm), in order to fit well with the screen resolution (1280 x 800 pixel).



Figure 1: example of face stimuli displaying sadness, happiness and a neutral condition, respectively.

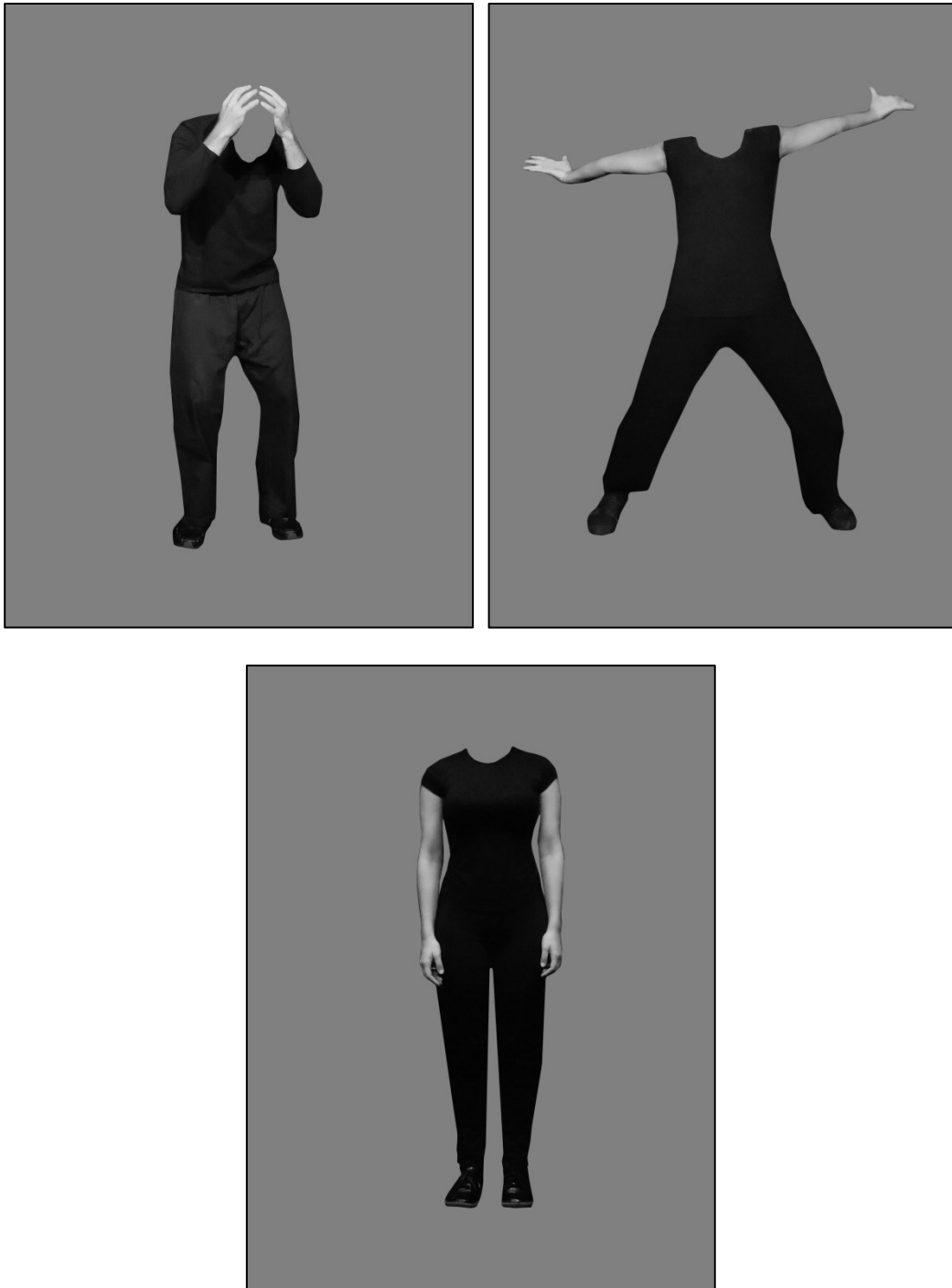


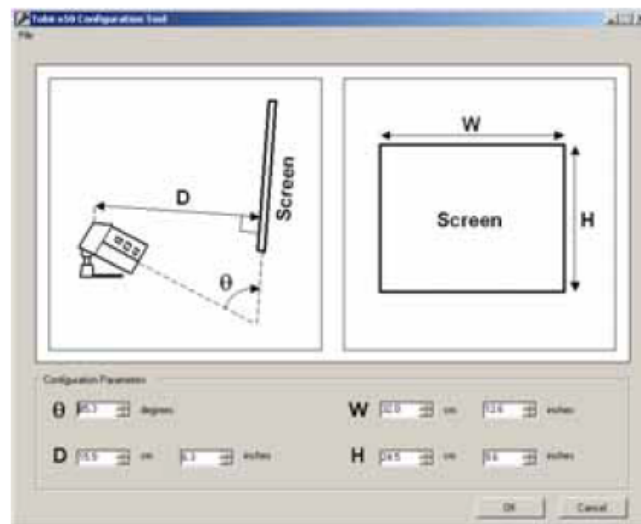
Figure 2: example of body stimuli displaying sadness, happiness and a neutral condition, respectively.

2.1.3 Apparatus

For eye movement recording, we used Tobii X50 with 50 Hz of sampling frequency and 0,5° of accuracy. During tracking it uses near infra-red light emitting diodes (NIR-LEDs) to generate lighting and reflection patterns in the eyes of the subject. (Tobii Technology AB, 2006).

ClearView 2.7.1 was used to collect number and duration of fixations and to manually created Areas of Interest (AOIs). For faces we based on the existing literature and on the inspection of the visual scan-path (e.g., Guo e Shaw, 2015; Guo, 2012; Eisenbarth & Alpers, 2011; Vassallo et al., 2009).

To make Tobii X50 properly work, some physical parameters of configuration needed to be defined; this was possible by filling geometrical information (screen dimension, angle between the camera axis of the eye tracker and the imaginary calibration plane, perpendicular distance from the calibration plane to the front edge of the Tobii X50) (Tobii Technology, 2006) in a specific tool of configuration (see Fig. 3).



Tobii x50 configuration tool

Figure 3: Tobii X50 Configuration tool.

We created six AOIs: *forehead*, *corrugator*, *eye left*, *eye right*, *nose* and *mouth*. To draw each AOI we adopted consistent criteria in order to guarantee similar AOI dimensions among participants, taking into account variations due to different facial expressions.

Specifically, the *eye* region included the eyes, eyelids, and eyebrows; the *corrugator* region included the glabella; the *forehead* region extended from the hairline to the brow ridge; the *nose* region included nasion, rhinion, naris and columella; the *mouth* region consisted of the main area of the mouth (from the philtrum to the middle of the chin) (Fig.4).

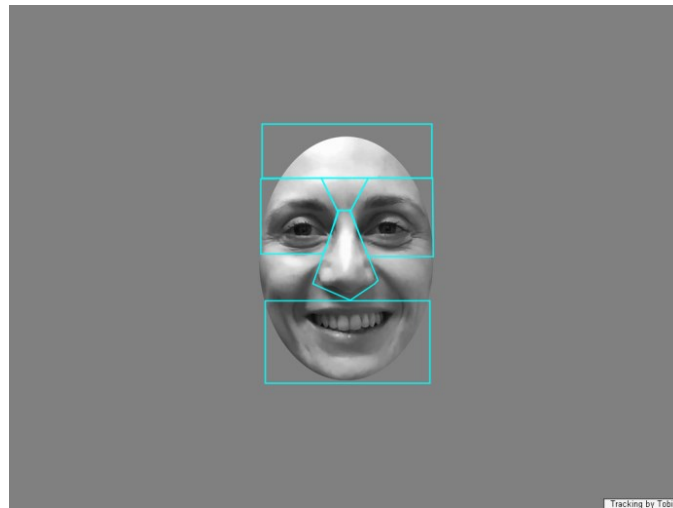


Figure 4: AOIs created for face stimuli.

To create the AOIs for bodies, because of the small number of previous studies, we adopted an explorative approach, following the inspection of the visual scan path and creating seven AOIs: *hand left*, *hand right*, *upper left*, *upper right*, *lower left*, *lower right* and *face*.

We also drew the AOI for the face region, although there was no head in our stimuli, in order to investigate if our participants needed in any case the information from the face to better comprehend the emotion expressed by the body.

We adopted consistent criteria in order to guarantee similar AOI dimensions among participants, taking into account variations due to the different bodily structures of the actors.

Specifically, the *hand* region included all the fingers and it extended to the wrist; the *upper* regions included neck, shoulders, chest, torso and arms; the *lower* regions included legs and feet (Fig. 5).

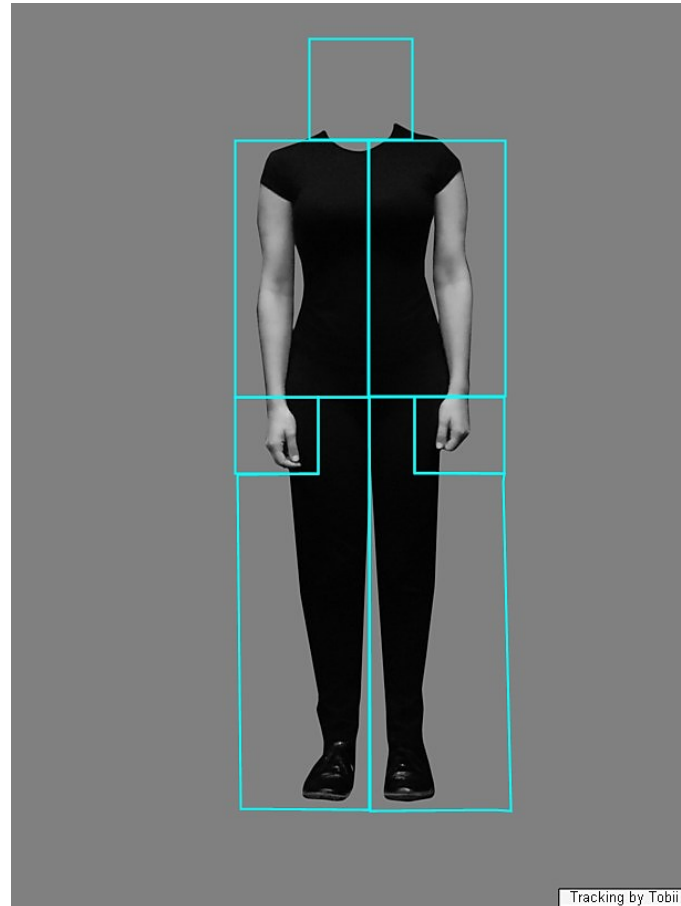


Figure 5: AOIs created for body stimuli.

To be more specific, the reader should know that with the terms *left* and *right* we refer to the left and right from the point of view of the observer (i.e. left and right visual field) and not to the left and right of the stimulus.

We used a double monitor configuration: one for the experimenter (20,5 cm X 33 cm) to control and evaluate the accuracy of the experimental procedure, and the other one (29,5 cm X 47 cm) for stimuli presentation to the participants, both connected with Tobii X50, and with screen resolution of 1280 x 800 pixel.

Participants were seated 60 cm from the monitor where Tobii X50 was placed. After that, we evaluated their correct position in front of the Tobii eye-tracker by means of the “track status meter”.

To calibrate eye movement signals, a small blue fixation point was displayed randomly at one of 5 positions across the monitor. This procedure is necessary for an accurate estimation of the participant’s gaze point (Tobii Technology, 2006).

A fixation was regarded as an eye position remaining within a 37-pixel area (calculated using the *degree to pixel fixation radius converter*, www.pitt.edu/~tol7/res/research/deg-to-pix/) for 100 ms or longer. In this way we modified the suggested parameters by Tobii Technology (2006) to define fixations when using as stimuli mainly images (fixations radius: 1.6°; duration: 200 ms). We based our choice on more recent literature recommending to adopt a spatial value between 0.7° and 1.3°, and a minimum duration value between 100 and 200 ms (Blignaut & Beelders, 2009; Blignaut, 2009; Manor & Gordon, 2003; Salvucci & Goldberg, 2000).

Blinks were defined as loss of ocular data for three or more sample in a sequence.

The number and duration of fixations reflects the time spent processing visual information at an AOI.

2.1.4 Procedure

For each experiment we created two different presentations (A and B for faces, C and D for bodies), in each of which stimuli were randomized. Hence, to each participant were shown two experimental sequences, one for each experiment (i.e. one for faces and one for bodies). The order of experiments’ presentation was counterbalanced among participants, and we did the same for the sequences within each experiment (A vs. B for faces, C vs. D for bodies).

Participants sat on a comfortable chair at a distance of 60 cm from the screen. They could wear glasses or contact lenses during the recording because they do not interfere with eye-tracking activity (Tobii Technology, 2006). In order to maintain light-controlled conditions and to help the

eye recording, the experiment was conducted in a dark room, with only one light on, coming from the back.

We recorded eye movements while participants carried out an emotion categorization task, paying attention to naturally explore each image avoiding eye blinks during stimulus presentation. They could blink during a 1 second grey background between each stimulus (*Inter Stimulus Interval*).

For each stimulus, presented for 3 seconds on the screen, they had to respond aloud as accurately and quickly as possible whether the expression was happy, sad or neutral. Besides these labels we added another one, “none of these”, in order to avoid that the choice for a particular option would have been due to the proposed form of answers (Frank & Stennet, 2001; Tracy et al, 2009).

Meanwhile, the experimenter wrote down the answers. These behavioural data were used to evaluate the emotional recognition accuracy of both facial and bodily expressions.

At the beginning of the sequence there was a black fixation cross of 2000 ms duration (Green et al., 2005; Horley et al., 2004) (see Fig. 6).

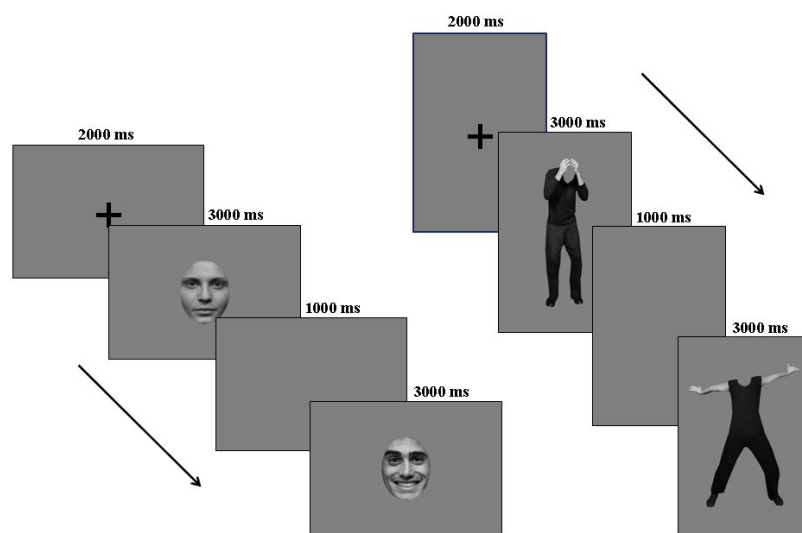


Figure 6: Experimental paradigm for the two experiments.

2.2 Eye movements analyses

In order to run the analyses on the visual scan path that participants adopted for each of the three emotional categories to be recognized, we analyzed fixation distribution at local facial and bodily regions for individual expressions using data only from accurate categorization trials.

Since sometimes the actors crossed their hands to display the requested emotion with their body, we decided to discard the related stimuli for the eye movements analyses in order not to confound any lateralization effects. As a consequence, the final number of body stimuli used for the analyses, for each category, was as follows: 43 *Sad*, 49 *Neutral*, 50 *Happy*.

Eye movement data recorded during the first stimulus presentation, were not included in the analyses to avoid influences of the initial fixation cross position (Guo, 2012; Kret et al., 2013a; 2013b).

We analyzed normalized data: number and duration of fixations directed at each feature was normalized to the total number and total duration of fixations of each trial for each participant. Different Repeated-measure ANOVA were conducted to analyze data including as WITHIN - Factors: Emotion (3 levels: Neutral, Happiness, Sadness) and AOI (6 for faces, 7 for bodies), and as BETWEEN- Factor the Gender of the participants (2 levels: Male or Female).

To compare total number and total duration of fixations between bodies and faces (obtained by the sum of number and duration, respectively, of all fixations made on the stimulus by each participant, and for each emotion), we considered as WITHIN – Factors: Emotion (3 levels: Neutral, Happiness, Sadness) and Stimulus (2 levels: Face or Body), and as BETWEEN – Factor the Gender of the participants (2 levels: Male or Female).

Multiple comparisons of the means were performed with Newman-Keuls test.

If data violated sphericity assumption, we reported Greenhouse-Geisser ($\epsilon < .75$) or Huynh-Feldt ($\epsilon > .75$) corrected values.

We performed Correlation analyses between total duration and total number of fixations within each emotion, for both faces and bodies. If data violated normality assumption, we ran Spearman's correlation analysis instead of Pearson's.

2.3 Results

2.3.1 Faces

Duration of fixations

The ANOVA revealed a significant main effect of AOI (Fig. 7) ($F_{(2,4,52,9)}=23.453$; $p = .000$): participants spent longer time viewing *eye left*, *eye right* and *nose*, not significantly different from each other ($M=24\%$, $SE=.03$; $M=28\%$ ms, $SE=.03$; $M=22\%$, $SE=.02$) but significantly different from the other AOIs (*mouth*, *corrugator*, *forehead*) ($p < .0004$).

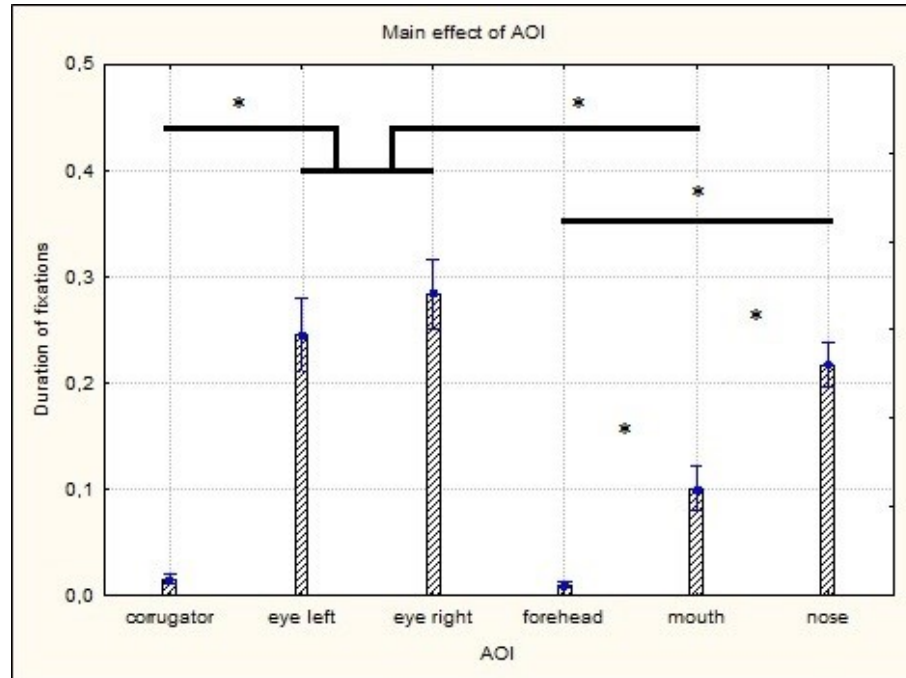


Figure 7: Faces – Duration of fixations. Main Effect of AOI

(please see longer durations to eye left, eye right and nose).

Please note that values on Y axis are expressed in percentages.

The asterisks indicate the main differences for the purposes of our discussion. Error bars are SE.

Number of fixations

More fixations were made to *eye left*, *eye right* and *nose*, as indicated by the significant main effect of AOI ($F_{(2.3, 50.8)} = 27.054$; $p = .000$); there was no significant difference in the number of fixations made among them ($M=25\%$, $SE=.03$; $M=27\%$, $SE=.03$; $M=23\%$, $SE=.02$) but only with the other AOIs ($p < .0002$) (Fig. 8).

The *mouth* AOI ($M=9\%$, $SE=.02$) was significantly different from all the other AOIs ($p < .04$).

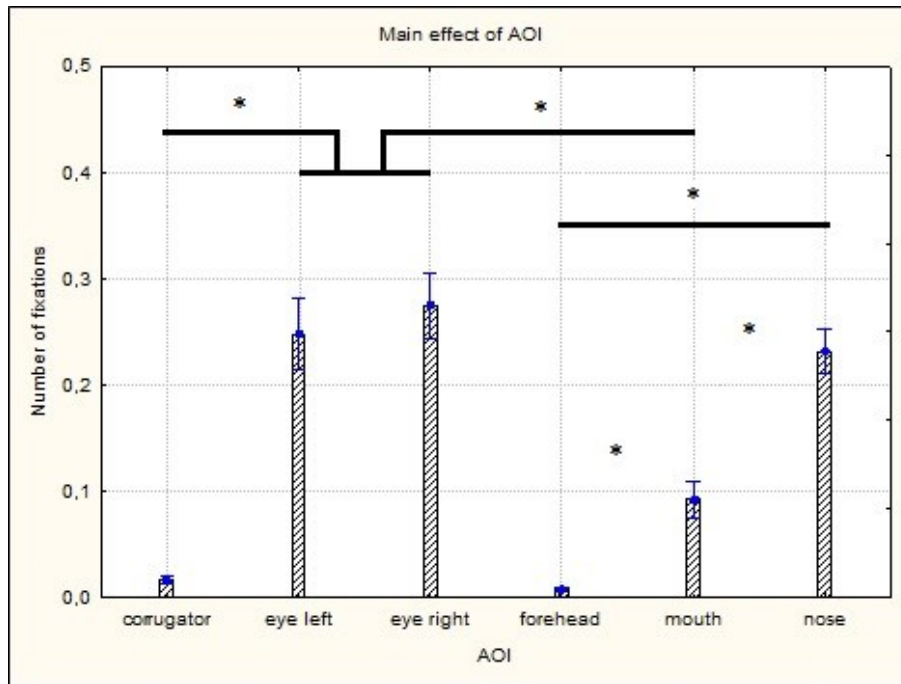


Figure 8: Faces – Number of fixations. Main Effect of AOI

(please see longer durations to *eye left*, *eye right* and *nose*).

Please note that values on Y axis are expressed in percentages.

The asterisks indicate the main differences for the purposes of our discussion. Error bars are SE.

Correlation between total duration and total number of fixations

The results showed a significant correlation for Neutral ($r = .41, p = .04$), for Happiness ($r = .41, p = .04$) and for Sadness ($r = .41, p = .04$): the longer the duration, the higher the number of fixations and vice versa.

2.3.2 Bodies

Duration of fixations

The ANOVA revealed a significant main effect of Emotion ($F_{(1.45, 27.5)} = 6.235; p = .01$): longer fixations were made to *Neutral* and *Sad* stimuli ($M = 13\%, SE = .006$; $M = 13\%, SE = .005$) followed by *Happy* ($M = 11\%, SE = .004$) stimuli, with a significant difference between *Happiness* and *Sadness*, and between *Happiness* and the *Neutral* condition ($p < .006$).

Participants made longer fixations to *upper left* ($M = 33\%, SE = .02$) and *upper right* ($M = 22\%, SE = .02$), as indicated by a significant main effect of AOI ($F_{(2.6, 50.2)} = 54.902; p = .000$).

The ANOVA also revealed a significant Emotion x AOI interaction (Fig. 9) ($F_{(3.5, 67)} = 6.021; p = .0006$): for all the emotional conditions, participants made, in this order, longer fixations to *upper left* and *upper right*.

The fixations' duration made to *happy upper left* ($M = 30\%, SE = .03$) was significantly different from *sad* ($M = 36\%, SE = .03$) ($p < .002$) and *neutral upper left* ($M = 35\%, SE = .03$) ($p < .002$). Considering, instead, fixations' duration for the *upper right*, there was a significant difference between *Sadness* ($M = 18\%, SE = .02$) and *Neutral* ($M = 24\%, SE = .03$) ($p < .0003$), and between *Sadness* and *Happiness* ($M = 24\%, SE = .02$) ($p < .0005$).

The comparisons within each emotion showed that there was a significant difference between *upper left* and *upper right* ($p < .002$) and they were significantly different from all the other AOIs (*face*, *lower left*, *lower right*, *hand left*, *hand right*) ($p < .006$).

Hand left in *Sadness* condition ($M=13\%$, $SE=.017$) was significantly different from *Neutral* ($M=8\%$, $SE=.01$) ($p < .006$) and *Happiness* ($M=7\%$, $SE=.02$) ($p < .002$).

Participants made shorter fixations to *face* ($M=4\%$, $SE=.008$) and there was a significant difference between *Neutral* and *Sadness* ($p < .007$).

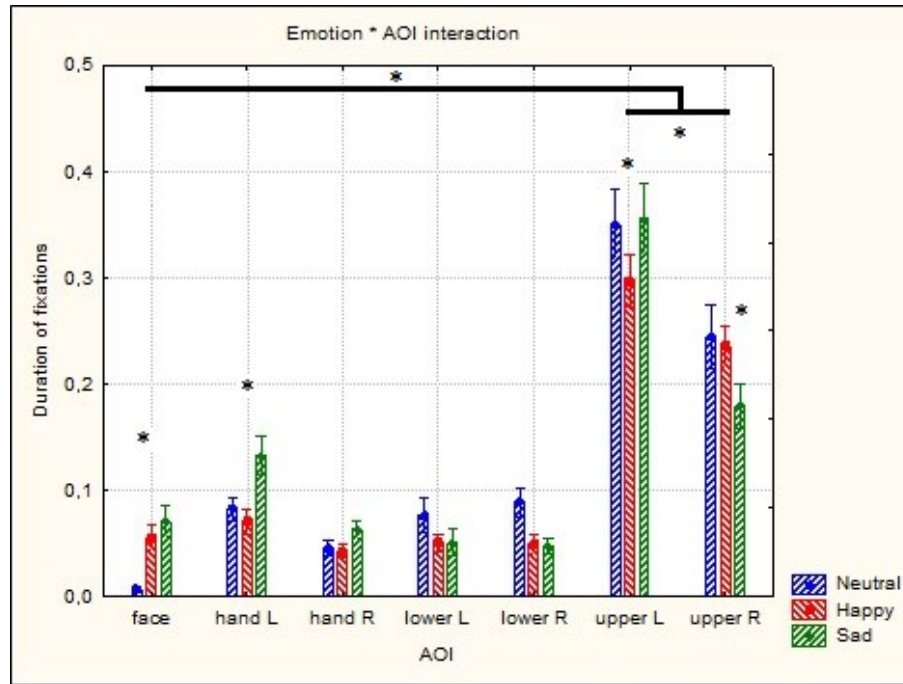


Figure 9: Bodies – Duration of fixations. Emotion * AOI Interaction.

Please note that values on Y axis are expressed in percentages.

The asterisks indicate the main differences for the purposes of our discussion. Error bars are SE.

Number of fixations

The ANOVA revealed a significant effect of Emotion ($F_{(2, 38)}=5.294$; $p = .009$): more fixations were made to *Neutral* ($M=13\%$, $SE=.004$) and to *Sad* ($M=13\%$, $SE=.004$) stimuli, and then to *Happy* ($M=11\%$, $SE=.004$) stimuli; *Happiness* was significantly different from both *Sadness* and *Neutral* condition ($p < .01$).

The ANOVA revealed also a significant main effect of Gender ($F_{(1,19)}=4.958$; $p = .04$): female made more fixations than male participants (Female: $M=13\%$, $SE=.004$; Male: $M=11\%$, $SE=.004$).

Participants made more fixations to *upper left* ($M=34\%$, $SE=.03$) and *upper right* ($M=23\%$, $SE=.02$); they were significantly different between each other ($p < .0002$), and from all the other AOIs (*face*, *lower left*, *lower right*, *hand left*, *hand right*) ($p < .0002$), as revealed by a significant main effect of AOI ($F_{(2, 38)}=48.542$; $p = .000$).

The ANOVA also revealed a significant Emotion x AOI interaction (Fig. 10) ($F_{(3.6, 69.2)}=5.061$; $p = .0017$).

Within each emotion, *upper left* and *upper right* were significantly different between each other ($p < .0007$) and from all the other AOIs ($p < .00005$).

Comparing the three emotional conditions, the number of fixations made to *upper left* was significantly different between *Happiness* ($M=30\%$, $SE=.03$) and *Neutral* ($M=36\%$, $SE=.03$) ($p < .007$) and between *Happiness* and *Sadness* ($M=35\%$, $SE=.03$) ($p < .02$); there was a significant difference in the number of fixations made to *upper right* between *Sadness* ($M=19\%$, $SE=.03$) and *Happiness* ($M=24\%$, $SE=.02$) ($p < .005$) and between *Sadness* and *Neutral* ($M=25\%$, $SE=.03$) ($p < .002$).

Considering *Hand left*, there was a significant difference among *Sadness* and both the other two conditions ($p < .008$): participants made more fixations to *Sadness* ($M=13\%$, $SE=.01$), than to *Neutral* ($M=8\%$, $SE=.01$) and to *Happiness* ($M=6\%$, $SE=.01$).

Participants made less fixations to *face* ($M=4\%$, $SE=.009$) and there was a significant difference between *Neutral* and *Sadness* ($p < .003$).

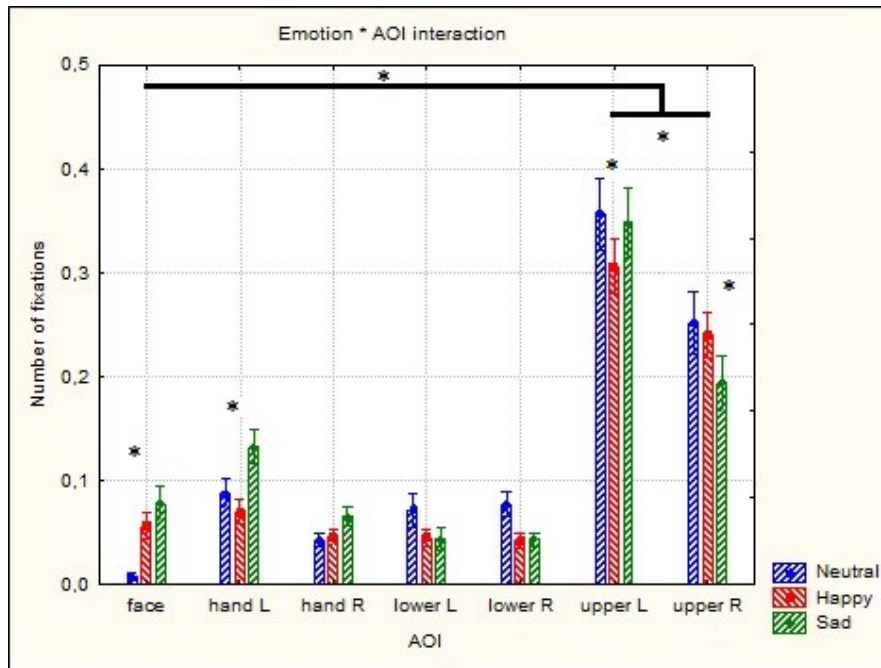


Figure 10: Bodies – Number of fixations. Emotion * AOI Interaction.

Please note that values on Y axis are expressed in percentages.

The asterisks indicate the main differences for the purposes of our discussion. Error bars are SE.

Correlation between total duration and total number of fixations

The results did not show any significant Correlation: *Neutral* ($r = -.03, p = .24$), *Happiness* ($r = .2, p = .36$) e *Sadness* ($r = -.24, p = .28$).

To verify if the absence of significant correlations was due to the data relative to the fixations made outside the AOIs (used to obtain the total duration and the total number of fixations), we compared the inside of the stimulus with its outside. In order to do so, we summed up the data regarding all the AOIs to create a macro-AOI *Inside*. We performed a Repeated-measure ANOVA including as WITHIN - Factors: Emotion (3 levels: Neutral, Happiness, Sadness) and stimulus Region (2 levels: Inside, Outside).

Duration of fixations

The ANOVA revealed a significant main effect of Emotion ($F_{(2,40)}=6.7491$; $p = .00298$): longer fixations were made to *Sad* stimuli ($M=1082$ ms, $SE=77.41$), then to *Happy* ($M=978$ ms, $SE=67.62$) and *Neutral* ($M=937$ ms, $SE=74.39$) stimuli.

Longer fixations were made to the *Inside* ($M= 1919.24$ ms, $SE= 136.07$) of the AOIs (*Outside*: $M= 78.73$ ms, $SE= 9.03$), as indicated by the significant main effect of Region ($F_{(1,20)}= 188.87$; $p < .001$).

The ANOVA results showed a significant Emotion x Region interaction (Fig.11) ($F_{(2,40)}= 160.780$; $p = .00001$): the duration of fixations made to *Outside* (*Sadness*: $M=22.5$ ms, $SE=5.02$; *Neutral*: $M=24.16$ ms, $SE=4.23$; *Happiness*: $M=189.5$ ms, $SE=21.15$) was significantly different from the duration of fixations made to the *Inside* of the AOIs (*Sadness*: $M=2141.5$ ms, $SE=155$; *Neutral*: $M=1849.66$ ms, $SE=147.5$; *Happiness*: $M=1766.6$ ms, $SE=131.31$), within each emotional condition ($p < .04$).

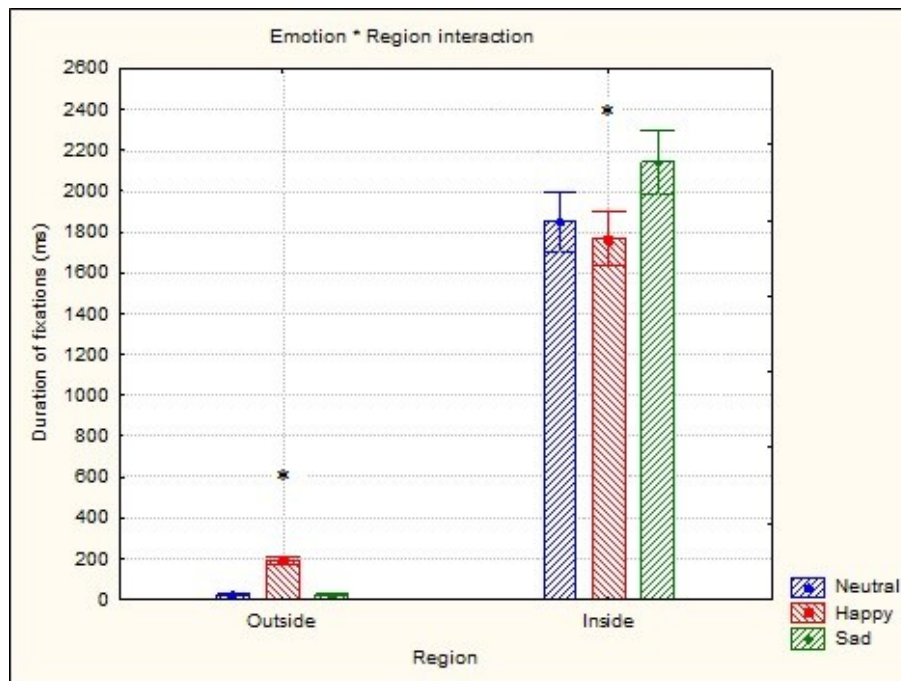


Figure 11: Bodies – Duration of fixations. Emotion * Region interaction.

The asterisks indicate the significant differences among emotions in each Region. Error bars are SE.

Number of fixations

The ANOVA revealed a significant main effect of Region ($F_{(1,20)}=570.82$; $p < .001$): participants made more fixations to the macro-AOI *Inside* ($M=6.77$, $SE=.28$) compared to the *Outside* ($M=.35$, $SE=.04$).

The results showed a significant Emotion x Region interaction ($F_{(2,40)}=15.806$; $p = .00001$). While for the *Outside* region there was a significant difference between *Happiness* and *Neutral* ($p < .003$), and between *Happiness* and *Sadness* ($p < .006$), for the *Inside* there was a significant difference among all the three emotional conditions ($p < .05$). The results confirmed that participants looked more at the AOIs than the *Outside*.

2.3.3 Faces and bodies comparison

Total duration of fixations

The ANOVA revealed a significant main effect of Emotion ($F_{(1.7, 32.6)}=5.8272$; $p = .0012$): participants made longer fixations to *Sad* stimuli ($M=2170.6$ ms, $SE=155.578$), then to *Neutral* ($M=2076.6$ ms, $SE=150.20$) and finally to *Happy* ($M=2044.25$ ms, $SE=156.67$) stimuli; Post-hoc tests revealed that *Sadness* was different from both the other two emotional conditions ($p < .02$).

The ANOVA also revealed a significant Stimulus x Emotion interaction (Fig.12) ($F_{(1.7, 33.3)}=4.4192$; $p = .0029$). While within bodies there was a significant difference between *Sadness* and *Neutral*, and between *Sadness* and *Happiness* (*Sadness*: $M=2329.33$ ms, $SE=158.94$; *Neutral*: $M=2184.6$ ms, $SE=133.72$; *Happiness*: $M=2098.124$ ms, $SE=146.67$) ($p < .005$), within faces post-hoc tests did not reveal any significant difference among the three emotional conditions (*Sadness*: $M=2011.82$ ms, $SE=175.231$; *Neutral*: $M=1968.52$ ms, $SE=188.16$; *Happiness*: $M=1990.38$ ms, $SE=181.84$).

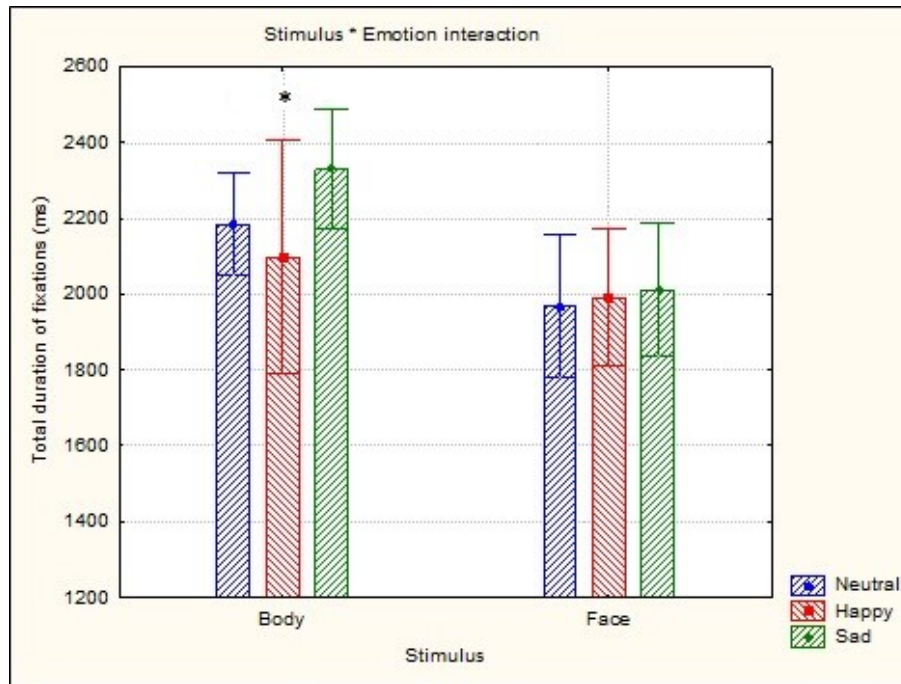


Figure 12: Face vs. Body comparison – Duration of fixations. Stimulus * Region interaction. The asterisk indicate the only significant difference among emotions for each Stimulus category. Error bars are SE.

Total number of fixations

The ANOVA revealed a significant Stimulus x Emotion interaction ($F_{(2,38)}=3.9762$; $p = .02704$), but post-hoc tests did not show any significant comparison.

2.4 Behavioral analyses

We analysed behavioural data in terms of accuracy in emotion recognition during the categorization task. We conducted a Repeated – Measure ANOVA including as WITHIN factor: Emotion (3 levels: Happiness, Sadness, Neutral), and as BETWEEN factor the Gender of participants (2 levels: Male or female). Scores were transformed as ArcSen values.

2.5 Behavioral results

2.5.1 Faces

The ANOVA revealed a significant main effect of Emotion ($F_{(1.35, 29.68)}=36.88$; $p=.000$): higher accuracy scores were obtained on *Happiness* ($M=97\%$, $SE=1.6$) then on *Neutral* ($M=83\%$, $SE=2.44$) and finally on *Sadness* ($M=64\%$, $SE=2.3$). Each emotional condition was different from the others ($p < .001$).

2.5.2 Bodies

Higher accuracy scores were obtained on *Neutral* ($M=77\%$, $SE=1.3$), then on *Happiness* ($M=76\%$, $SE=2$), and finally on *Sadness* ($M=56\%$, $SE=1.71$), which was different from both the other emotional conditions ($p < .0001$), as confirmed by the main significant effect of Emotion ($F_{(2,38)}=24.05$; $p=.00000$).

2.6 Discussion

The main aim of the present study was to investigate the patterns of visual exploration during the observation of facial and bodily expressions, clarifying the characteristics of the visual mechanisms during *Emotional Body Language* processing, in order to consider its importance for the recognition of emotions and intentions of others.

To this purpose we used as stimuli ecological pictures of facial and bodily expressions depicting sadness, happiness and an emotionally neutral condition. We recorded eye movements while participants performed an emotion categorization task.

Faces

Starting from behavioural results, it is worth to know how happy faces were better recognized than neutral and sad faces, with clear difficulties in correctly categorize sad faces. This result is in line with previous studies which used facial expressions categorization tasks demonstrating higher percentages of accuracy for happy than for sad faces (Calvo & Lundqvist, 2008; Calvo & Nummenmaa, 2009).

As shown in Fig. 13, eye gaze data showed that, in line with our hypothesis and with previous studies, participants made more and longer fixations to the eyes and the nose (e.g., Sullivan et al., 2007; Hsiao & Cottrell, 2008; Vassallo et al., 2009; Guo, 2012). Moreover, participants looked at the region of the mouth directing to it a number of fixations in-between eyes and nose on a side, and forehead and corrugator on the other. These results suggest how participants adopted a holistic viewing strategy, focusing their attention on the salient facial features (eyes, nose and then mouth) and integrating them in a whole representation of the face (Guo, 2012; Guo & Shaw., 2014) (see Fig. 13).

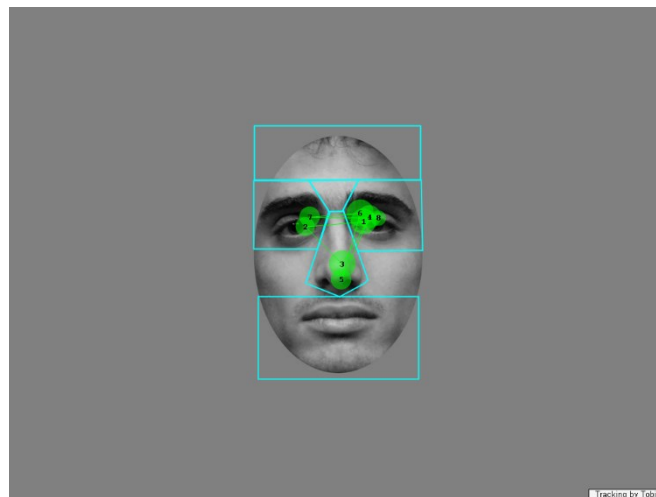


Figure 13: Example of visual scan-path of a single participant on a neutral facial expression. Please see fixations directed to eyes and nose.

Regarding the well-known left-side bias demonstrated by previous studies, which consists in a perceptual and attentional advantage for the left side of an observed face (see, Gilbert & Bakan,

1973; Burt & Perret, 1997) we did not find significant results. It should be added that the left-side bias has been assessed during face categorization tasks or during tasks requiring gender categorization, age and beauty judgment of faces (Burt & Perrett, 1997). This phenomenon is translated in more and longer fixations to the left side (from the observer point of view) of the observed face (Butler et al., 2005; Hsiao & Cottrell, 2008).

It has been argued that the left-side bias is related to the dominance of the right hemisphere in face perception, as suggested by both studies with patients with focal cerebral lesions and neuroimaging studies (see Rossion et al., 2003; Butler et al., 2005).

Other authors hypothesized that this bias is the result of the interaction between the hemispheric lateralization and a directional bias of visual scanning process, consolidated during the evolution. Such a phenomenon could also have been influenced by the preferential direction of reading, typical of different cultures (from left to right for English, and from right to left for Hebrew and Arabic languages), and capable of conditioning the direction of attention (Vaid & Singh, 1989; Chokron, 2002).

Our results did not show a significant difference in terms of number and duration of fixations between sadness and happiness, and we did not find a significant higher number of fixations to the mouth of happy stimuli, as previously demonstrated (e.g., Eisenbarth & Alpers, 2011).

In our opinion, this could be due to the presence of neutral stimuli which could have smoothed the effect.

Bodies

Considering accuracy data, participants better recognized neutral body postures, followed by happy and finally sad body postures. Specifically, happiness and sadness were confused with other emotions, as suggested by the higher number of “none of these” answers (see also Martinez et al., 2015).

The emotion displayed influenced also the number and duration of the fixations: participants made more and longer fixations to neutral and sad body postures than to happy ones.

The analyses on the AOIs revealed, in line with Tao & Sun' results (Tao & Sun, 2013), how participants directed their attention to the upper part of the body.

With respect to faces, with bodies we found an interesting left-side bias indexed by the significant difference between the left and the right upper part of the body. Moreover, the left upper part was different than all the other AOIs. It is worth nothing that, apart the upper parts of the body, the other focused region was the left hand (please remember that we are referring to the left from the observer's point of view) (Fig. 14).

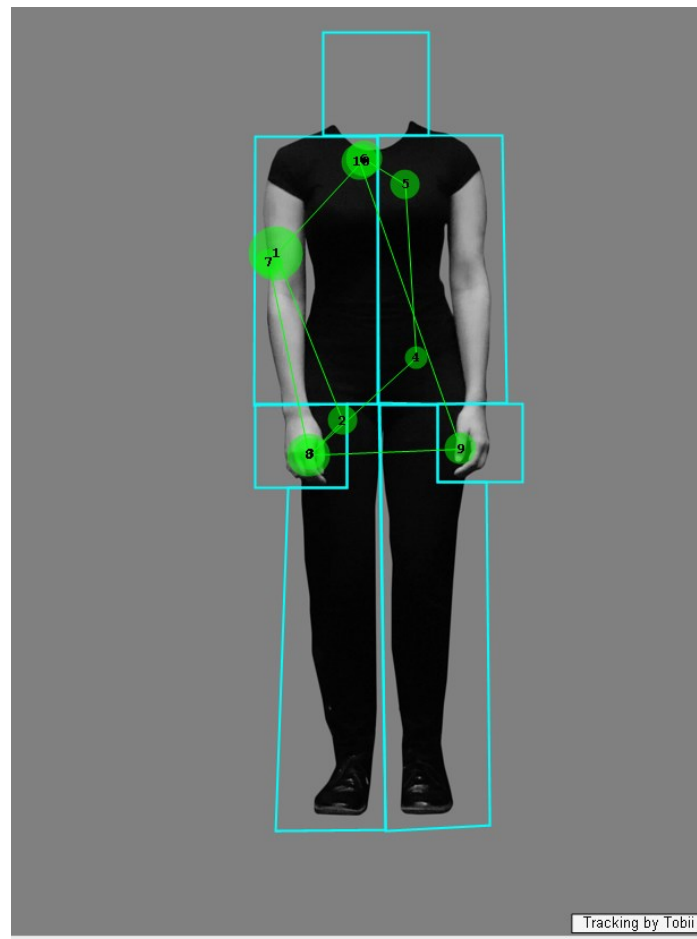


Figure 14: Example of visual scan-path of a single participant on a neutral body posture: please see fixations directed to the left upper part of the body and to the left hand.

Recently, Marzoli and colleagues hypothesized that the left-side bias could be observed also during bodies visual exploration. Bearing in mind that the left side of the visual field, from the observer's point of view, is more relevant than the right one, they argued that the attentional and perceptual advantage of left visual field could have an adaptive function from both a communicative and motor point of view, during a dyadic interaction: to direct the attention to the region where normally act the dominant hand of the other (Marzoli et al., 2014). Hence, our data, showing not only a left bias for the upper part of the body but also for the hand, could be explained by this hypothesis. It has also to be taken into account that all our participants were right-handed.

It is worth noting that more and longer fixations were made to the left hand of sad stimuli than the other two emotional conditions. In our opinion, this could be due to the configuration of our stimuli. As indexed by behavioral results, it has been difficult for our participants to recognize this emotion, as a consequence they tended to look for useful and salient information at the head/face, although it was absent: since our sad body postures were often characterized by the position of the hands near the face region, fixations were then made to the region of the head (Fig. 15). Indeed, during stimuli creation we did not ask the actors not to use their hands, in order not to prevent the natural representation of the bodily expressions (Martinez et al., 2014).

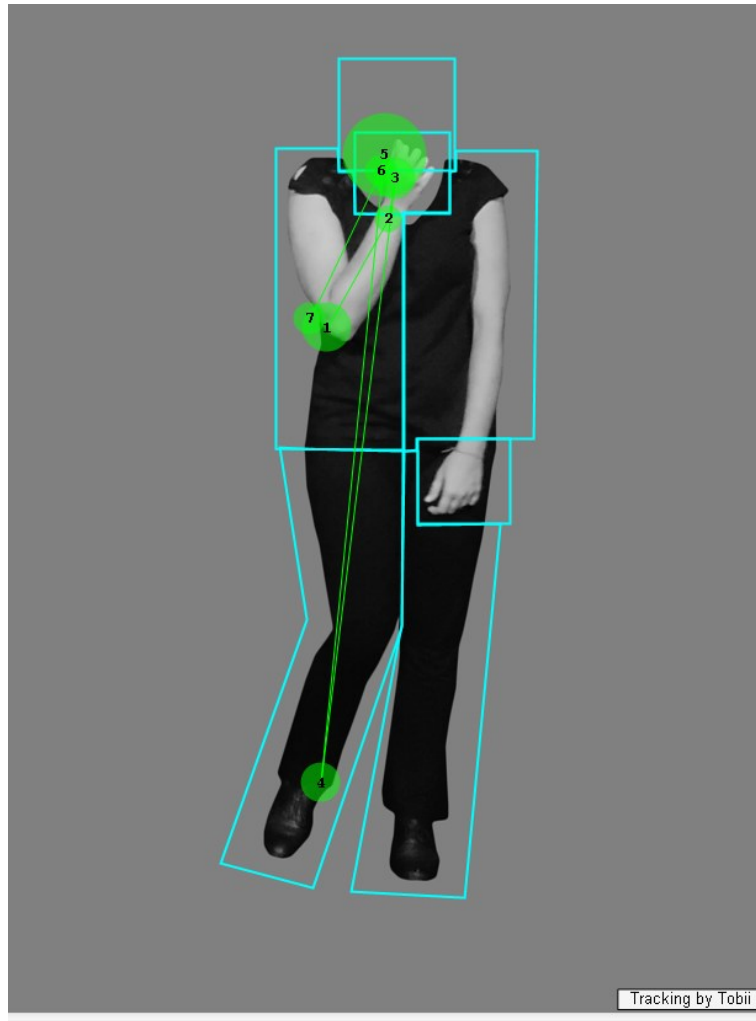


Figure 15: Example of a visual scan-path of a single participant on a sad stimulus: please see fixations on the hand, in proximity of the head region.

Leonards and Scott-Samuel (2005) argued that the left-side bias could take place specifically for socially relevant stimuli, and this idea could be confirmed by studies suggesting that the higher is the emotional load of both stimuli and task, the more emphasized could be the polarization to the left of the observed face (Thompson et al., 2009). In our opinion, this could explain our results indexing the presence of this left-bias only for bodies perception: the emotional and cognitive load of the two experiments (faces vs. bodies) was likely different and higher for bodies than faces.

Considering the differences in the visual scan-path among the three emotional conditions, it is worth to know that while participants made less and shorter fixation to the left upper part of happy stimuli than to sad and neutral ones, the opposite was true for the right upper part: participants made

less and shorter fixations to the right upper part of sad stimuli than to happy or neutral ones. In order to explain this emotional bias, we considered the “*valence model*”, which postulates that positive emotion could mainly activate the left hemisphere, while negative emotions would activate the right one (Davidson, 1992; 2003). In accord with this model, Cattaneo and colleagues recently published a study demonstrating that during a task of line bisection, the perception of happy faces, mainly activating the left hemisphere, provoked a preferential orientation to the contralateral right hemi-field (Cattaneo et al., 2015).

In the light of the similarities between faces and bodies, it is plausible that this bias, hypothesized for faces, could be also found for bodies. Hence, our emotional bias could be explained by the “*valence model*”.

The absence of significant correlations between total number and total duration of fixations for each emotion, could be explained by the variability of the visual exploration mechanisms among the participants (some of them explored the stimuli making few and long fixations, while other made many short fixations) and by the mutable dimension and configuration of the AOIs for the different emotional body postures. This was not true for the faces: albeit AOIs have been adjusted in accord to the face of each actor, they did not significantly differ among all the facial stimuli, as confirmed by the presence of significant correlations between total number and total duration of fixations for each emotion.

In order to find an explanation for the absence of significant correlations for bodies, we hypothesized that the reason was related to the fact that the total number and total duration of fixations were obtained by summing not only number and duration of fixations directed to each AOI but also fixations directed “outside” the AOIs. This is why we decided to run a new analysis comparing the “inside” of the stimulus with its “outside”. The results confirmed that participants looked more at the “inside” of stimulus, while the “outside” was explored differently according to the emotion: it was more explored in the happy condition. In our opinion, this significant effect could be due to the configuration of happy body postures, characterized by open arms.

These last results seem to suggest how participants implement a viewing strategy different than the clear holistic strategy employed for faces processing. In our opinion, this novel aspect should be further investigated by future studies.

Although we conducted a statistical comparison between total number and total duration of fixations made to faces and bodies, considering that our stimuli had different dimension and that we ran two different experiments (one only for faces and one only for bodies), our results should be considered with caution and as a first step for future studies more methodologically sound for this specific purpose.

2.7 Conclusions

In conclusion, the present study contributes to clarify the visual exploration mechanisms taking place during the recognition of emotional facial and bodily expressions. It confirms the presence of a holistic viewing strategy during face processing while revealing the occurrence of different mechanisms for body processing. Future studies should be conducted to better clarify this point, disentangling whether it can be generalized to all body postures or it is configuration and emotion-dependent.

The most interesting new result is the left-side bias arisen for bodies perception as indexed by the direction of attention to the left upper part and to the left hand of bodily postures. It could be explained by different theories linking this phenomenon to the dominance of the right hemisphere for face processing or to attentional and perceptual theories. Future studies should be conducted to confirm the presence of this bias and to clarify the underlying mechanisms. As a final point, the gender of participants exerted an influence only during the visual exploration of bodily postures, and only in terms of number of fixations.

Considering the few number of studies which explored the visual mechanisms of bodies exploration, these results could be considered as novel seeds to develop future studies in the field.

3. STUDY II

“Embodied Body Language”: an electrical neuroimaging study with emotional faces and bodies.

The aim of the present study was to investigate not only the time course, as previously mentioned studies did, but also the neural correlates underlying the integration of affective information conveyed by faces and bodies. To this purpose we used as stimuli ecological pictures of facial and bodily expressions, both depicting two basic emotions: sadness and happiness.

We used high-density EEG to record electrophysiological responses while participants performed an emotion categorization task by means of a Congruence-Incongruence paradigm (N400 paradigm), in two different sessions. In one session participants judged the emotional congruence between stimuli belonging to the same category (face-face or body-body), while in the other they judged the emotional congruence between different stimuli (face and body).

This was done in order to first clarify the time course of the affective integration within a category, elucidating the neural networks involved and looking at differences and similarities. Then, this permitted us to better investigate the integration mechanisms of affective information conveyed by both face and body, through the analysis of the second experimental session.

3.1 Materials and methods

3.1.1 Participants

Twenty-four young adult volunteers took part in the study: ten males, fourteen females; mean age 25.4 years (standard deviation, $SD = 3.42$); age range: 20-34 years. All participants had normal or corrected-to-normal visual acuity, no history of psychiatric or neurological impairments and were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield R., 1971).

Since data of four participants (three female) were excluded from EEG analyses because of too many artifacts, data from twenty volunteers (nine male, 11 female; mean age 25.5 years, $SD=3.48$; age range: 20-34 years) were included in the EEG analyses. All participants provided a written informed consent to participate in the study, which has been approved by the local ethical committee (Comitato Etico per Parma, Azienda Ospedaliero-Universitaria di Parma, Azienda Unità Sanitaria Locale di Parma, Università degli Studi di Parma) and has been conducted according to the principles expressed in the Declaration of Helsinki.

3.1.2 Stimuli and Procedure

3.1.2.1 Stimuli validation

To test the validity of the pictures (i.e. to ensure that they were easily comprehensible in terms of their intended emotions), we considered the behavioural results obtained in the previously described eye-tracking study. Specifically, we selected only pictures that were evaluated consistently by at least 80% of the first 15 participants to the eye-tracking study (seven male; mean age: 25.5 years; age range: 22-35 years) (please see Materials and Methods of Study I).

3.1.2.2 Final stimuli for ERP experiment

We selected 32 pictures (16 bodies and 16 faces), displaying four actors (two males and two females). The average percentage of correct recognition was 98% for emotional facial expressions and 95% for emotional body postures. For each actor we selected two different postures for each emotional condition (happiness and sadness). Hence, stimulus material comprehended eight happy (four male) and eight sad (four male) body postures, eight happy (four male) and eight sad (four male) facial expressions. By means of Adobe Photoshop CS6 software, pictures were placed at the centre of a homogenous grey background (R:128, G:128, B:128) reduced to a final dimension of 1280 x 1024 pixels. Stimuli were shown at the center of a 19-inches computer screen positioned at a distance of 57 cm from participants. All the pictures (faces and bodies) had the same

height of 4.70 cm, subtending 4.70° of visual angle, and different width to maintain proportions constant.

We created two different experimental sessions (“intra-category” and “cross-category” sessions): each session showed a two-picture sequence with a prime and a target stimulus in two different experimental conditions (Congruent and Incongruent conditions). Within the intra-category session, the prime and the target belonged to the same category (i.e., face-face or body-body), while in the cross-category session they pertained to different categories (i.e., face-body or body-face). In both sessions, in the Congruent condition the emotion displayed by the target was the same as the one expressed by the prime (happiness-happiness or sadness-sadness), while in the Incongruent condition the emotion displayed was different (happiness-sadness or sadness-happiness) (Fig. 16).

In sum, we had eight different conditions: face-face Congruent (FF-C), face-face Incongruent (FF-I), body-body Congruent (BB-C), body-body Incongruent (BB-I), face-body Congruent (FB-C), face-body Incongruent (FB-I), body-face Congruent (BF-C), body-face Incongruent (BF-I).

Each trial consisted of a white fixation cross (300 ms), followed by the prime, which was presented for 500 ms. After an inter-stimulus interval of 400 or 500 ms (Stimulus-onset asynchrony = 900 or 1000 ms), the target was shown for 1500 ms, followed by a green screen used as inter-trial interval with a duration of 1500 or 2000 ms (Fig. 16).

Each of the two sessions consisted of 320 trials, divided in two sequences of 160 randomized trials. Each picture was repeated 17-23 times per session, with the restriction that repetition of the same stimulus within a trial was avoided. Hence, we had 80 trials per condition with a total of 640 trials. Each sequence lasted about 12 minutes, with a rest period of five minutes between each sequence. The order of presentation of the two sessions was balanced among participants.

3.1.2.3 Procedure

The task consisted of responding as accurately and quickly as possible to the target judged to be emotionally congruent to the prime by pressing a response key with the index finger (of the

left or of the right hand) or judged to be incongruent by pressing a response key with the middle finger (of the left or right hand). The hand used was alternated during the recording session (to avoid possible biases due to the prolonged activation of the contralateral hemisphere). Hand order was counterbalanced across participants. At the beginning of each sequence, the participants were told which hand to use to indicate their responses. To keep the attentional level of participants high, errors, omissions and delay (more than 1400 ms after stimulus onset) were indicated through a short beep sound lasting 200 ms.

The experimental sessions were preceded by a training session including 16 randomized trials (eight intra-category and eight cross-category trials).

Stimuli delivery and response recording were controlled using E-prime 2.0 software.

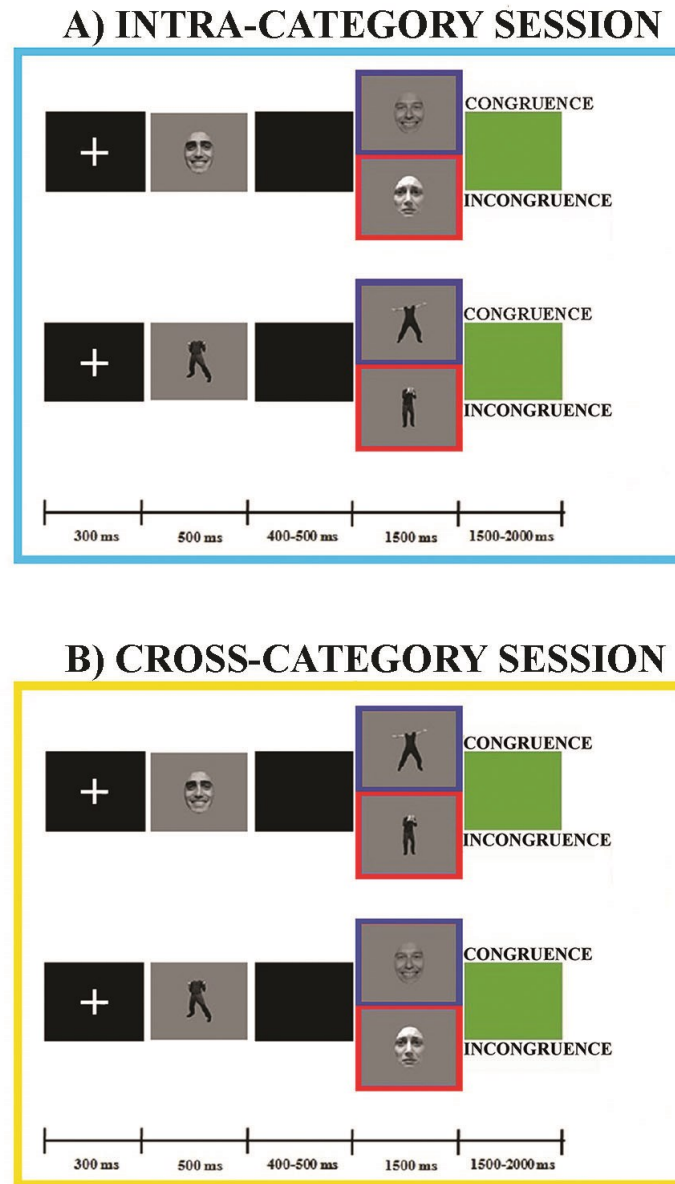


Figure 16: Examples of stimuli and experimental paradigm.

3.1.3 EEG Recording and Preprocessing

Continuous EEG was recorded using the 128-channels Geodesic EEG System (Electrical Geodesics Inc., Oregon) and the HydroCel Geodesic Sensor Net (GSN300) (Fig. 17), at a sampling rate of 500 Hz with the vertex as on-line reference; electrodes impedances were kept below 50 k Ω .

Continuous EEG recordings were band-pass filtered (1-30 Hz) and segmented in epochs lasting 1100 ms (from 100 ms before to 1000 ms after target onset), by means of NetStation software (Electrical Geodesics, Inc., Eugene, OR, USA). Trials with erroneous responses (omission and commission errors) were excluded from further analysis. For artefact detection and removal, the epoch-file of each participant was imported in EEGLAB toolbox (Delorme & Makeig, 2004).

The outermost belt of electrodes of the sensor net, more prone to show residual muscular artifacts, was excluded and the original template was reduced from 128 to 110 channels. Epoch-files were then analysed by means of Independent Component Analysis (ICA) (Delorme & Makeig, 2004), to exclude components bearing ocular (blink and saccades) and cardiac artefacts. A mean number of 8.1 ($SD = 1.9$) components were removed. The resulting epochs were further visually inspected to exclude remaining bad trials, and residual bad channels were interpolated using a spherical interpolation method as implemented in EEGLAB, and recalculated against the average reference.

The mean of accepted trials for intra-category conditions was: 71.2 ($SD = 3.4$) for FF-C and 70.2 ($SD = 5.4$) for FF-I, 69.9 ($SD = 5.4$) for BB-C and 69.9 ($SD = 3.7$) for BB-I. The mean of accepted trials for cross-category conditions was: 70.9 ($SD = 3.3$) for FB-C and 70.8 ($SD = 4$) for FB-I, 70.4 ($SD = 4.3$) for BF-C and 69.2 ($SD = 4.2$) for BF-I.

An ANOVA was performed in order to exclude differences in the number of accepted trials among conditions, which did not result significant ($F_{(7.133)} = 1.203$; $p = .305$).

Preprocessed data of each participant were subsequently imported and analyzed in Cartool software (version 3.55; <http://www.fbmlab.com/cartool-software/>).

To evaluate target-elicited ERPs, epochs from 100 ms before to 1000 ms after target onset were averaged across trials, separately for each participant and condition; these single-subject averages were then used to compute eight group-averaged ERPs, one for each experimental condition.

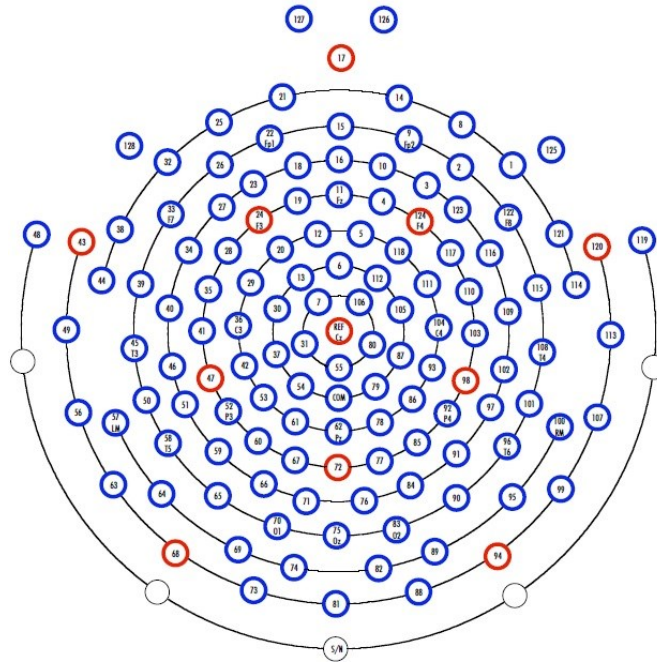


Figure 17: Hydrocel Geodesic Sensor Net – 128 channels.

3.2 EEG analyses

EEG data were subjected to two independent analysis procedures. The first one, a global ERP waveform analysis, was performed for completeness and as a preliminary step in determining the time course of ERP response modulations, to minimize the possibility of missed effects related to the pre-selection of specific electrodes and time periods used in canonical ERP waveform analysis.

The second one was a global scalp electric field analysis. We based the present study on this latter type of analysis, because it has three important advantages: 1) it is completely reference independent; 2) it allows the statistical assessment of the likely neurophysiological mechanisms (i.e., topographic and/or strength modulation) underpinning the observed effects (Murray et al., 2008); 3) it allows one to define time windows for source analysis in a more objective way, relying on the statistical proof that when the electric fields are different they are underpinned by different neural generators.

All the statistical analyses were conducted using Cartool software (Brunet et al., 2011)

1) Global ERP waveform analysis

The global ERP waveform analysis was conducted by means of point-wise paired t -tests computed on amplitudes of the single-subject ERP averages of the two compared conditions (see below “Compared conditions” section), at each electrode and time point. The statistical significance level was set at $p < .05$ and a 10 contiguous data points temporal criterion (20 ms at our 500 Hz sampling rate) for the persistence of significant effects was applied (Guthrie & Buchwald, 1991). Only differences over at least five contiguous electrodes within nine clusters (shown in the inset in Figs. 20, 22, 24, 26) reaching the statistical significance level were retained.

2) Global electric field analyses

Two statistical analyses were conducted on the global electric field: a) assessment of modulations in electric field strength, as measured by the instantaneous Global Field Power (GFP); b) assessment of modulations in electric field topography, measuring the global spatial dissimilarity index (DISS) (Lehmann & Skrandies, 1980)

Significant modulations in GFP and DISS between the experimental conditions were assessed by non-parametric statistical analyses based on point-wise randomization tests (Manly, 1991). Randomization provides a robust non-parametric method to test for differences in any variable without any assumption regarding data distribution, by comparing the observed data set with random shuffling of the same values over sufficiently large number of iterations (i.e., permutations); this method allows one to determine the probability that the data might be observed by chance. In the present study, the point-wise randomization tests ran 1000 permutations per data point and the significance level was set at $p < .05$, with an additional temporal stability acceptance criterion of 20 ms of consecutive significant difference (Guthrie & Buchwald, 1991).

These two analyses allowed a neurophysiological interpretation of the ERP modulations: indeed, differences in GFP without simultaneous topographic changes are indicative of amplitude modulation of statistically indistinguishable generators between experimental conditions. Conversely, topographic differences between conditions, with or without concomitant GFP

modulations, necessarily derive from changes in the configuration of the underlying active brain sources (Murray et al., 2008).

Changes in electric field strength were assessed by means of the statistical comparison of the GFP between compared conditions for each participant (Murray et al., 2008; Lehmann & Skrandies, 1980). GFP is the spatial standard deviation of the potentials at all electrodes at a given time point: it is calculated as the square root of the mean of the squared value recorded at each electrode (measured versus the average reference) and has higher values for stronger electric fields (Murray et al., 2008; Lehmann & Skrandies, 1980). Point-wise paired randomizations were conducted on the GFP of single-participants ERP averages between compared conditions at each time frame, with a significance level set at $p < .05$ and a temporal acceptance criterion of 20 ms of consecutive significant difference.

Significant periods of topographic modulation were identified using randomization statistics applied to DISS (Murray et al., 2008; Lehmann & Skrandies, 1980) between conditions, calculated for each time point and each participant data. DISS is a strength-independent index of configuration differences between two electric fields and it is calculated as the square root of the mean of the squared differences between the instantaneous voltage potentials (measured versus the average reference) across the electrodes montage, each of which is first scaled to unitary strength by dividing it by the instantaneous GFP. Point-wise paired randomizations were performed on the DISS data: this analysis is also known as “topographic analysis of variance” (TANOVA) (Murray et al., 2008). As above, 1000 permutations for each time point were performed and only effects with $p < .05$ and lasting for 20 ms or longer (Guthrie & Buchwald, 1991) were considered significant.

While GFP modulations indicate quantitative changes, DISS modulations between sessions reflect qualitative changes in the underlying generators configuration (Murray et al., 2008).

The results of the above topographic global scalp electric field analysis (TANOVA) defined time periods during which intracranial sources were estimated, using a distributed linear inverse solution based on a Local Auto-Regressive Average (LAURA) regularization approach (Grave De Peralta

Menendez et al., 2001). LAURA model reconstructs the brain electric activity in each point of a 3D grid of solution points, selecting the source configuration that better mimics the biophysical behavior of electric fields without *a priori* assumption on the number of dipoles in the brain. The solution space was calculated on a locally spherical head model with anatomical constraints (LSMAC) (Spinelli et al., 2000) and comprised 3001 solution points (voxels) homogeneously distributed within the brain structures of the Montreal Neurological Institute (MNI152) average brain. All solution points were labeled with their Talairach and Tournoux coordinates (Talairach & Tournoux, 1988) as well as their anatomical labels.

Intracranial source estimations for each participant and condition over time windows defined by the TANOVA were then statistically compared by means of a “voxel-wise parametric mapping analysis” (Michel et al., 2004). To do that, individual ERP data were averaged over time periods of significant topographic modulation, in order to generate a single data point per period for each participant and condition. LAURA source estimations for each solution point, normalized by their root mean square (RMS values), were then contrasted by means of paired *t* tests. Solution points with *p* values $< .05$ ($t_{(19)} > 2.09 / < -2.09$) were considered significant; in addition, a cluster threshold of at least 10 contiguous activated solution points was applied. Source analyses were performed using Cartool software (Brunet et al., 2011).

Since the main purpose of the present study was to investigate the temporal dynamics of the incongruence effect (N400), we performed global scalp electric field analysis (GFP and DISS) from 100 to 1.000 ms after the target onset.

Compared Conditions

Considering that our main interest was in the incongruence effect (N400), we compared Congruent and Incongruent conditions of each session: 1) FF-I vs. FF-C; 2) BB-I vs. BB-C; 3) FB-I vs. FB-C; 4) BF-C vs. BF-I.

3.3 Behavioral Analysis

Reaction times (RTs) that exceeded the mean value ± 2 *SD* were discarded. Accuracy data were converted to arcsen values. Both RTs and accuracy data were subjected to separate multifactorial repeated-measures ANOVAs with four within-subject factors (Target: face or body; Prime: face or body; Condition: congruence or incongruence; Response hand: left or right). Tukey post hoc tests were used to further explore significant interactions.

3.4 Empathy Assessment: Interpersonal Reactivity Index

After the EEG recording, the empathic ability of participants, were evaluated by means of Interpersonal Reactivity Index (IRI) (Davis 1980; 1983). It consists of 28 items answered on a 5-point Likert scale ranging from “Does not describe me well” to “Describes me very well”. The measure has four subscales, each made up of seven different items. These subscales are: 1) *Perspective Taking* (PT) – assessing the tendency to spontaneously adopt the psychological point of view of others; 2) *Fantasy* (FS) – assessing tendencies to transpose themselves imaginatively into the feelings and actions of fictitious characters in books, movies, and plays; 3) *Empathic Concern* (EC) – assessing "other-oriented" feelings of sympathy and concern for unfortunate others; 4) *Personal Distress* (PD) – assessing "self-oriented" feelings of personal anxiety and unease in tense interpersonal settings.

3.5 Results

3.5.1 Empathy Assessment: Interpersonal Reactivity Index

The mean PT score $\pm$ SD was 17.3 ± 5.4 ; the mean FS score $\pm$ SD was 17.4 ± 3.6 ; the mean EC score $\pm$ SD was 17.6 ± 4.7 ; the mean PD score $\pm$ SD was 10 ± 3.6 .

3.5.2 Behavioural Results

Accuracy

Analysis of accuracy data revealed a significant main effect of Target ($F_{(1,23)} = 12.066, p = .002$) indicating that participants were more accurate when the target was a face ($M=80.9, SE = 1.28$) than when it was a body ($M=78.8, SE = 1.13$). Participants were more accurate in response to Congruent ($M=80.5, SE = 1.1$) than to Incongruent pictures ($M=79.2, SE = 1.29$) as indicated by a significant main effect of Condition ($F_{(1,23)} = 6.7091, p = .016$). The ANOVA also revealed a significant Target x Hand interaction ($F_{(1,23)} = 5.3396, p = .03$) that was driven by more accuracy in responding to body-target with the right hand ($M=79.8, SE = 1.03$) than when participants responded with the left hand ($M=77.8, SE = 1.32$) (post hoc tests: $p = .03$). When participants responded to face-target there was no difference responding with right or left hand (post hoc tests: $p = .98$). The significant Condition x Hand interaction (Fig. 18) ($F_{(1,23)} = 7.5332, p = .01$) revealed that in the Congruent condition participants made less error when they responded with the right hand ($M=81.8, SE = 1.04$) than when with the left hand ($M=79.3, SE = 1.29$) (post hoc tests: $p = .0006$). In the Incongruent condition, instead, there was no difference due to response hand (post hoc tests: $p = .98$). In sum, when participants responded with the right hand there was a significant difference in accuracy data between Congruence and Incongruence (Congruence: $M=81.8, SE = 1.04$, Incongruence: $M=78.9, SE = 1.25$) (post hoc tests: $p = .008$), but not when they responded with the left hand (Congruence: $M=79.3, SE = 1.29$; Incongruence: $M=79.6, SE = 1.50$).

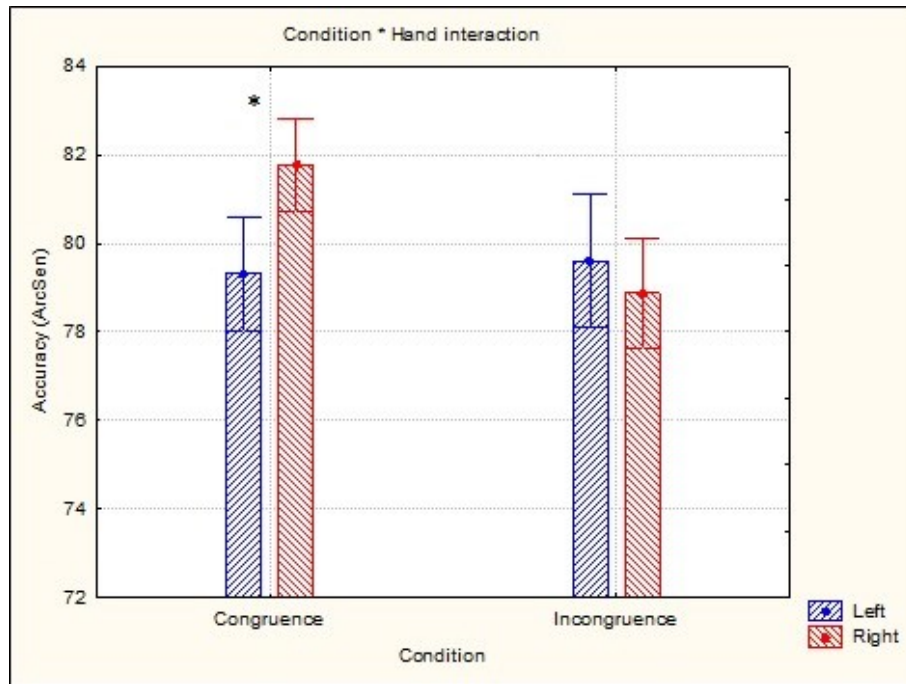


Figure 18: Accuracy. Condition * Hand interaction.

The asterisk indicate the only significant difference between left and right hand for each condition. Error bars are SE.

Reaction Times

Analysis of the reaction times (RTs) revealed a main effect of Target ($F_{(1,23)} = 25.841$, $p = .00004$) that was due to the responses to face-target ($M=702$ ms, $SE = 17.8$) being faster than those to body-target ($M=731$ ms, $SE = 17.6$). The significant main effect of Prime ($F_{(1,23)} = 11.591$, $p = .002$) was driven by faster responses when the prime was a face ($M=711$ ms, $SE = 17.6$) than when it was a body ($M=723$ ms, $SE = 17.5$). Participants were faster responding to Congruent ($M=687$ ms, $SE = 17$) than to Incongruent condition ($M=746$ ms, $SE = 18.9$) as revealed by a significant main effect of Condition ($F_{(1,23)} = 53.098$, $p = .000$). The significant Target x Condition interaction (Fig. 19) ($F_{(1,23)} = 18.406$, $p = .0002$) revealed faster responses to face and body target in the Congruent condition (Face: $M=666$ ms, $SE = 17.7$; Body: $M=708$ ms, $SE = 16.8$) than responses to face and body target in the Incongruent condition (Face: $M=739$ ms, $SE = 19$; Body: $M=754$ ms, $SE = 19.2$), with a significant difference among all conditions (post hoc tests: $p < .01$). The significant Prime x Condition interaction ($F_{(1,23)} = 12.457$, $p = .002$) indicated absence of significant

differences in RTs due to the prime (face or body) in the Incongruent condition (Face: $M=747$ ms, $SE = 19.3$; Body: $M=745$, $SE = 18.8$), while in the Congruent condition RTs were faster when the prime was a face ($M=675$ ms, $SE = 16.7$) than when it was a body ($M=700$ ms, $SE = 17.6$) (post hoc tests: $p < .0007$). The significant Prime x Hand interaction ($F_{(1,23)} = 5.4463$, $p = .03$) revealed faster responses to face than to body prime with the left hand (Face: $M=716.3$ ms, $SE = 20$; Body: $M=736$ ms, $SE = 19$), while there was any difference when participants responded with the right hand (Face: $M=706$ ms, $SE = 16.8$; Body: $M=709$ ms, $SE = 17$) (post hoc tests: $p < .0004$). The ANOVA also revealed a significant Condition x Hand interaction ($F_{(1,23)} = 11.549$, $p = .002$): in the Congruent condition right-hand responses ($M=669$ ms, $SE = 16.4$) were faster than left-hand responses ($M=706$ ms, $SE = 18.7$) (post hoc tests $< .0007$), while in the Incongruent condition there was any difference in RTs due to response-hand.

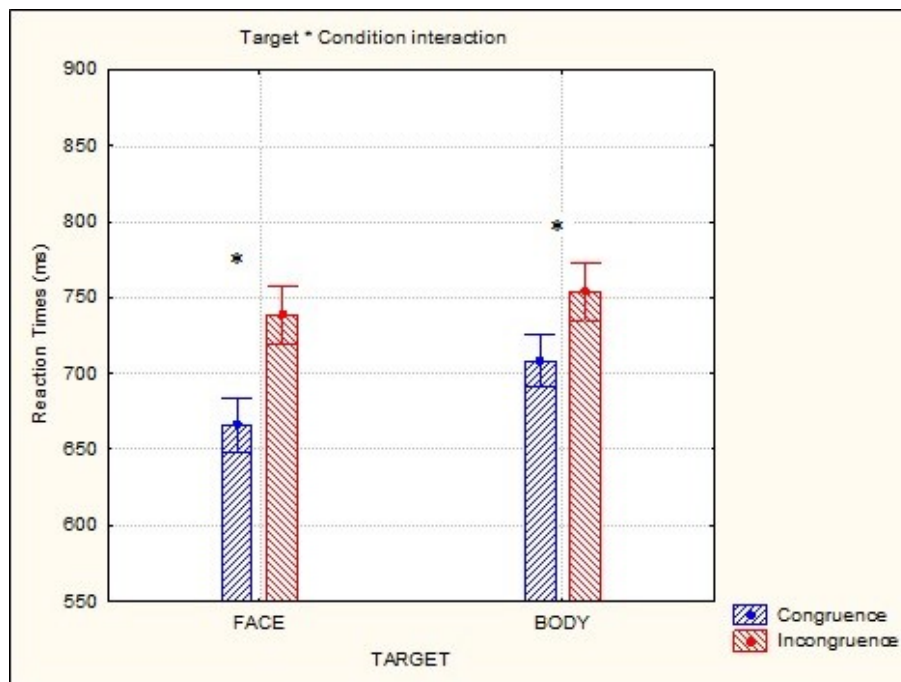


Figure 19: Reaction times. Target * Condition interaction.

The asterisks indicate the significant differences between Conditions for each stimulus category of Target. Error bars are SE.

3.5.3 Electrophysiological Results

FF-I vs. FF-C

The global amplitude analysis (see Fig. 20) revealed three periods of significant ERP modulation: 1) from 132 to 196 ms after target onset, in particular over central clusters of electrodes (right and midline location) from 132 to 168 ms, and over posterior clusters of electrodes, more sustained on a right location, during the whole time period; 2) from 200 to 250 ms after target onset, in particular over central clusters of electrodes, at a left and midline location, over left anterior cluster of electrodes, and over posterior clusters of electrodes, at a right and midline location 3) from 418 to 464 ms after target onset, in particular over central clusters of electrodes (at a left and midline location) from 418 to 444 ms, and over posterior clusters of electrodes, at a central and right location, during the whole time window. The GFP analysis (see Fig.20) showed one period of sustained difference between conditions, from 136 to 160 ms after target onset. The TANOVA (see Fig. 21) revealed one phase of significant topographic difference between conditions, from 424 to 496 ms after target onset.

In summary, GFP and DISS analyses revealed that, while the first period of amplitude modulation (132-196 ms after target onset) was characterized by strength difference between conditions, different cerebral generators underpinned only the third period (418-464 ms after target onset).

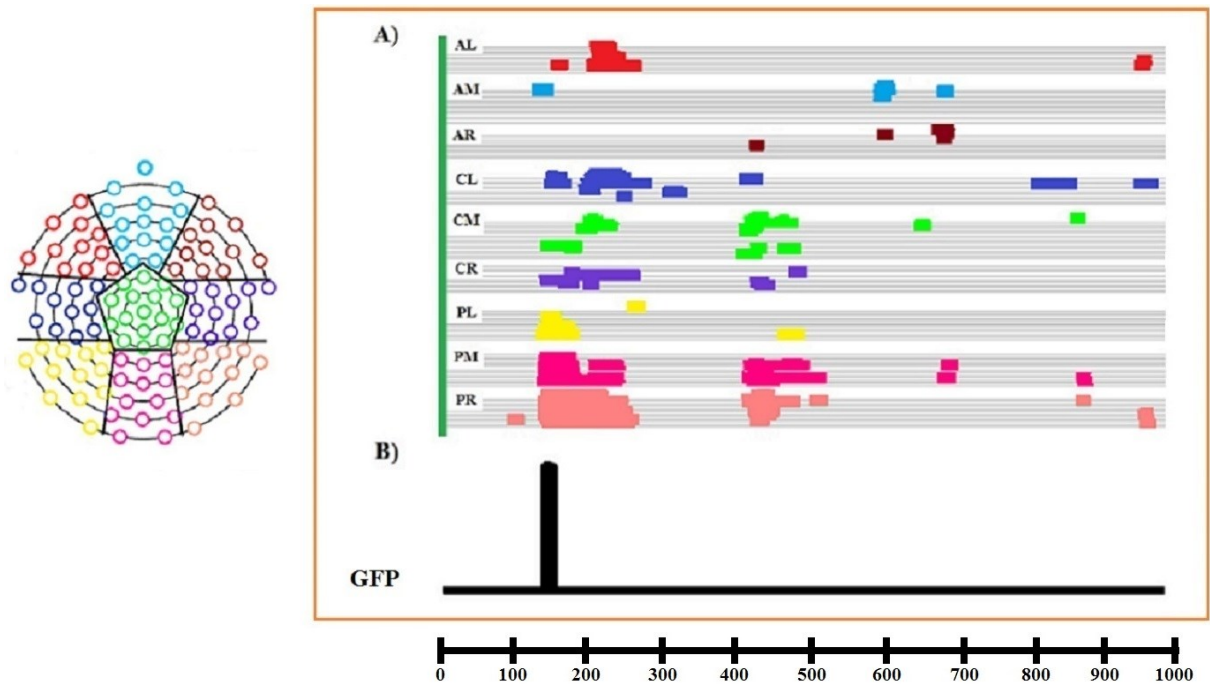


Figure 20: Electrophysiological results of FF-I and FF-C comparison: global ERP amplitude analysis and global electric field strength analysis. (A) Statistical analysis of global ERP amplitude. Periods of significant differences of ERP amplitude ($p < .05$; duration ≥ 20 ms) at each electrode and time point between FF-I and FF-C conditions are displayed as colored horizontal lines. Each horizontal line represents one scalp electrode. Different colors indicate different clusters of electrodes; the distribution of the clusters over the electrode montage is shown in the inset on the left side of the figure. AL: anterior left; AM: anterior midline; AR: anterior right. CL: central left; CM: central midline; CR: central right. PL: posterior left; PM: posterior midline; PR: posterior right. (B) Global scalp electric field analyses: statistical analysis of global electric field strength. Black areas indicate time intervals of significant differences ($p < .05$; duration ≥ 20 ms) of Global Field Power (GFP) between FF-I and FF-C conditions.

Source estimations

For the time period of different topography (424-496 ms after target onset) significant higher activity in FF-I as compared with FF-C (see Fig. 21C, in red; table 1) was found in different cerebral regions (table 1), including: the left middle temporal gyrus (MTG) extending toward the supramarginal gyrus (BAs 19, 37, 39, 40) and the right parietal sensorimotor cortices (BAs 5, 7,

40). Higher activity in FF-C (see Fig. 21C, in blue; table 1) was found in right middle and superior frontal gyri (BAs 8, 9, 46) and in right IFG and adjacent anterior insula (BAs 13, 46, 47).

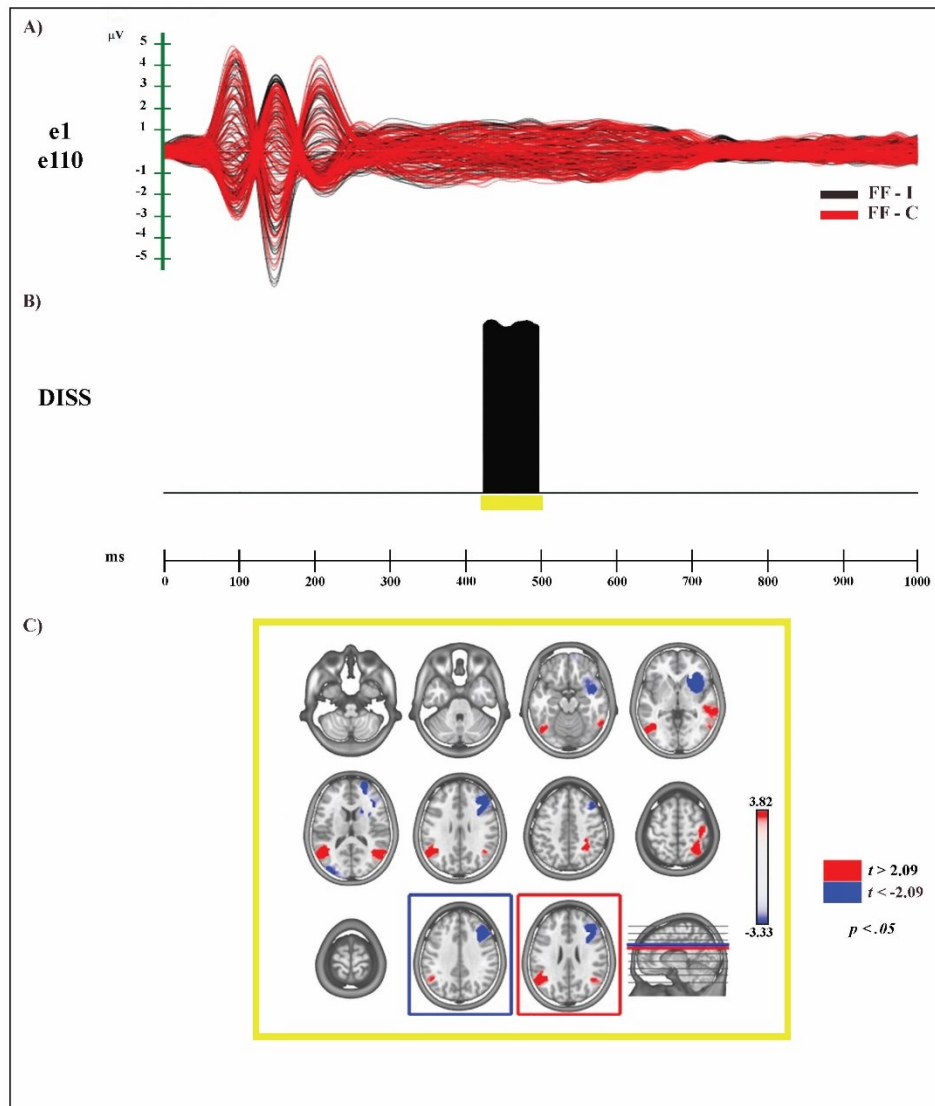


Figure 21: Electrophysiological results and statistical comparison of LAURA source estimations between FF-I and FF-C over significant TANOVA time intervals.

(A) Group-averaged ($n = 20$) event related potential (ERP) waveforms of the two experimental conditions (FF-C and FF-I), superimposed across the 110 recording channels (e1–e110). Black: FF-I; red: FF-C. (B) Global scalp electric field analyses: statistical analysis of global electric field topography (topographic analysis of variance, TANOVA). Black area indicate time interval of significant differences ($p < .05$; duration ≥ 20 ms) of global spatial dissimilarity index (DISS). (C) Significant TANOVA time interval (424–496 ms after target onset). All significant voxels are coloured ($t_{(19)} > 2.09 / < -2.09$, $p < .05$): positive t values

(red colour) indicate higher current source densities in FF-I than in FF-C; negative t values (blue colour) indicate higher current source densities in FF-C than in FF-I. LAURA solutions are rendered on MNI152 template brain (left hemisphere on the left side).

BB-I vs. BB-C

The global amplitude analysis (see Fig. 22) revealed three periods of significant ERP modulation: 1) from 138 to 274 ms after target onset, in particular over posterior clusters of electrodes from 166 to 228 ms, over anterior and central clusters of electrodes (in particular at a right location) from 240 to 274 ms after target onset, and over anterior and central clusters of electrodes (more sustained at a midline location) from 138 to 240 ms after target onset; 2) from 370 to 554 ms after target onset, in particular over central clusters of electrode from 370 to 440 ms (at a midline and left location), from 464 to 554 ms over anterior clusters of electrodes, and over posterior cluster of electrodes during the whole time period; 3) from 682 to 706 ms after target onset over anterior, central and posterior electrodes at a right location.

The GFP analysis (see Fig. 22) showed five period of sustained difference between conditions: 1) from 128 to 216 ms; 2) from 252 to 326 ms; 3) from 406 to 556 ms; 4) from 898 to 942 ms; 5) from 970 to 1000 ms after target onset.

The TANOVA (see Fig. 23) revealed three periods of significant topographic difference between conditions: 1) from 188 to 244 ms, yellow bar; 2) from 418 to 446 ms, orange bar; 3) from 676 to 702 ms after target onset, purple bar.

In sum, GFP and DISS analyses revealed that the first (138-274 ms) and the second (about 370-554 ms) periods of amplitude modulation were characterized by both strength and topographic differences between conditions. The fourth period (682 to 706 ms) was underpinned by different cerebral generators.

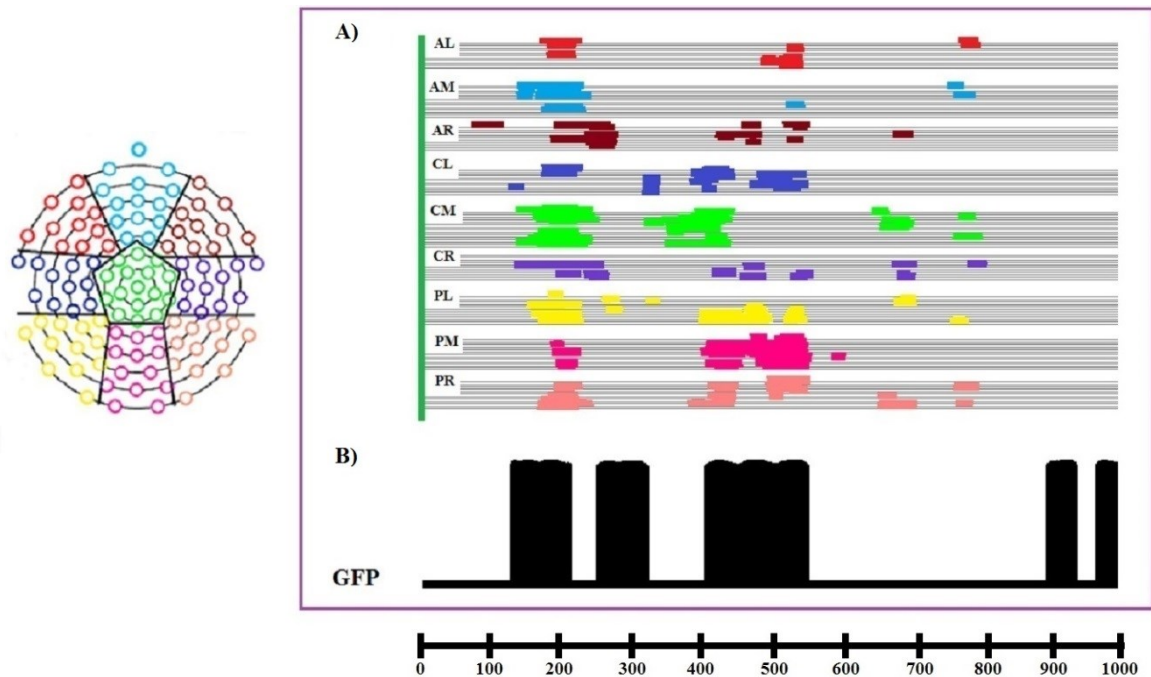


Figure 22: Electrophysiological results of BB-I and BB-C comparison: global ERP amplitude analysis and global electric field strength analysis. (A) Statistical analysis of global ERP amplitude. Periods of significant differences of ERP amplitude ($p < .05$; duration ≥ 20 ms) at each electrode and time point between BB-I and BB-C conditions are displayed as colored horizontal lines. Each horizontal line represents one scalp electrode. Different colours indicate different clusters of electrodes; the distribution of the clusters over the electrode montage is shown in the inset on the left side of the figure. AL: anterior left; AM: anterior midline; AR: anterior right. CL: central left; CM: central midline; CR: central right. PL: posterior left; PM: posterior midline; PR: posterior right. (B) Global scalp electric field analyses: statistical analysis of global electric field strength. Black areas indicate time intervals of significant differences ($p < .05$; duration ≥ 20 ms) of Global Field Power (GFP) between BB-I and BB-C conditions.

Source estimations

For the first time period of different topography (188-244 ms after target onset) significant higher activity in BB-I as compared with BB-C (see Fig. 23B, yellow bar; Fig. 23C, yellow outline, in red;

table 2) was found in different brain areas including: bilateral PMc and pre-supplementary motor area (pre-SMA) (BAs 6, 8) extending in ACC (BAs 24, 32) on the right hemisphere. In the same time period, higher activity in BB-C condition (see Fig. 23C, yellow outline, in blue; table 2) was found, among others, in left occipital cortex (BAs 17-19) and in bilateral parietal sensorimotor cortices (BA 5, 7).

In the second significant TANOVA period (418-446 ms after target onset) higher activity in BB-I (see Fig. 23B - orange bar; see Fig. 23C, orange outline, in red) was found in different cerebral regions (table 2), including left occipitotemporal areas for visual body processing, encompassing the MTG (BAs 18-22, 36, 37, 39, 42) and left premotor and motor cortices with the involvement of the IPL (BAs 4, 6, 40). Moreover, on the right hemisphere it is noteworthy the significant activation of somatosensory and parietal sensorimotor cortices (BAs 3-5, 7). In the same time period, higher activity in BB-C condition (see Fig. 23C, orange outline, in blue; table 2) was found in bilateral IFG (BAs 46, 47).

In the third period of topographic modulation (676-702 ms after target onset) significant higher activation in BB-I was found in left IFG (BAs 44, 45), (see Fig. 23B, purple bar; Fig. 23C, purple outline, in red; table 2), while higher activity in BB-C was found in right MTG (BAs 21, 39) and in medial frontal gyrus (BAs 10, 32), (see Fig. 23C, purple outline, in blue; table 2).

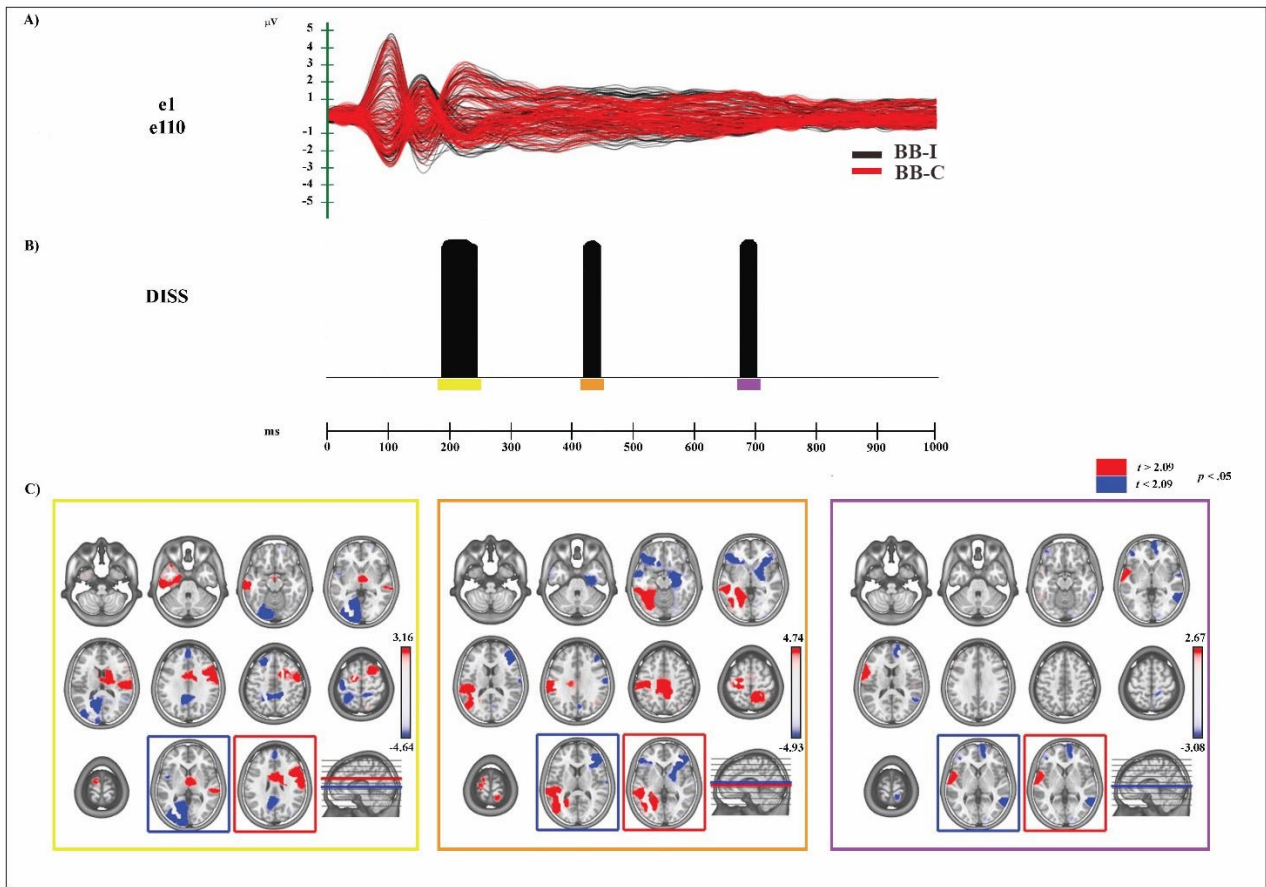


Figure 23: Electrophysiological results and statistical comparison of LAURA source estimations between BB-I and BB-C over significant TANOVA time intervals. (A) Group-averaged ($n = 20$) event related potential (ERP) waveforms of the two experimental conditions (BB-C and BB-I), superimposed across the 110 recording channels (e1–e110). Black: BB-I; red: BB-C. **(B)** Global scalp electric field analyses: statistical analysis of global electric field topography (topographic analysis of variance, TANOVA). Black areas indicate time intervals of significant differences ($p < .05$; duration ≥ 20 ms) of global spatial dissimilarity index (DISS). **(C)** Significant TANOVA time intervals. All significant voxels are coloured ($t_{(19)} > 2.09 / < -2.09$, $p < .05$): positive t values (red colour) indicate higher current source densities in BB-I than in BB-C; negative t values (blue colour) indicate higher current source densities in BB-C than in BB-I. LAURA solutions are rendered on MNI152 template brain (left hemisphere on the left side). Yellow outline: first significant TANOVA time interval (188-244 ms after target onset). Orange outline: second significant TANOVA time interval (418-446 ms after target onset). Purple outline: third significant TANOVA time interval (676-702 ms after target onset).

FB-I vs. FB-C

The global amplitude analysis (Fig. 24) revealed six periods of significant ERP modulation:

1) from 194 ms to 250 ms after target onset, in particular over central clusters of electrodes (more sustained at a midline location) from 194 ms to 226 ms, and over posterior clusters of electrodes (again, more sustained at a midline location) for the whole time period 2) from 372 ms to 456 ms after target onset over central clusters of electrodes at a right and midline location. 3) from 496 ms to 568 ms after target onset over anterior, central and posterior clusters of electrodes, in particular at a left location from 496 ms to 538 ms, and at a central and right location from 500 ms to 568 ms. 4) from 580 ms to 608 ms after target onset over posterior left cluster of electrodes, and over anterior and central clusters of electrodes (at a midline and right location). 5) from 626 ms to 716 ms after target onset, starting over posterior cluster of electrodes and then extending over the whole scalp. 6) from 726 ms to 786 ms after target onset, in particular over anterior and central cluster of electrodes (at a midline and left location) from 738 ms to 786 ms, and over central and posterior clusters of electrodes (more sustained at a right location) for the whole time period.

The analysis of the GFP (Fig. 24) showed two periods of sustained difference between conditions:

1) from 514 to 540 ms; 2) from 652 to 688 ms after target onset. The TANOVA (see Fig. 25) revealed four phases of significant topographic difference between conditions: 1) from 386 to 454 ms, green bar; 2) from 498 to 534 ms, yellow bar; 3) from 552 to 594 ms, yellow bar; 4) from 736 to 762 ms after target onset, red bar.

In summary, GFP and DISS analyses revealed that the second (370-456 ms), the fourth (between 580-608 ms) and the sixth (726-786 ms) periods of amplitude modulation were characterized by topographic differences between conditions. The fifth period (630-716 ms) of amplitude modulation was characterized only by strength modulation, while the third (496-568 ms) period of amplitude modulation was characterized by both strength and topographic differences between conditions.

Since the interval between the second and the third phases was shorter than the temporal acceptance criterion of consecutive 20 ms of significant difference, we estimated the intracranial sources of second and third phases together (from 498 to 594 ms).

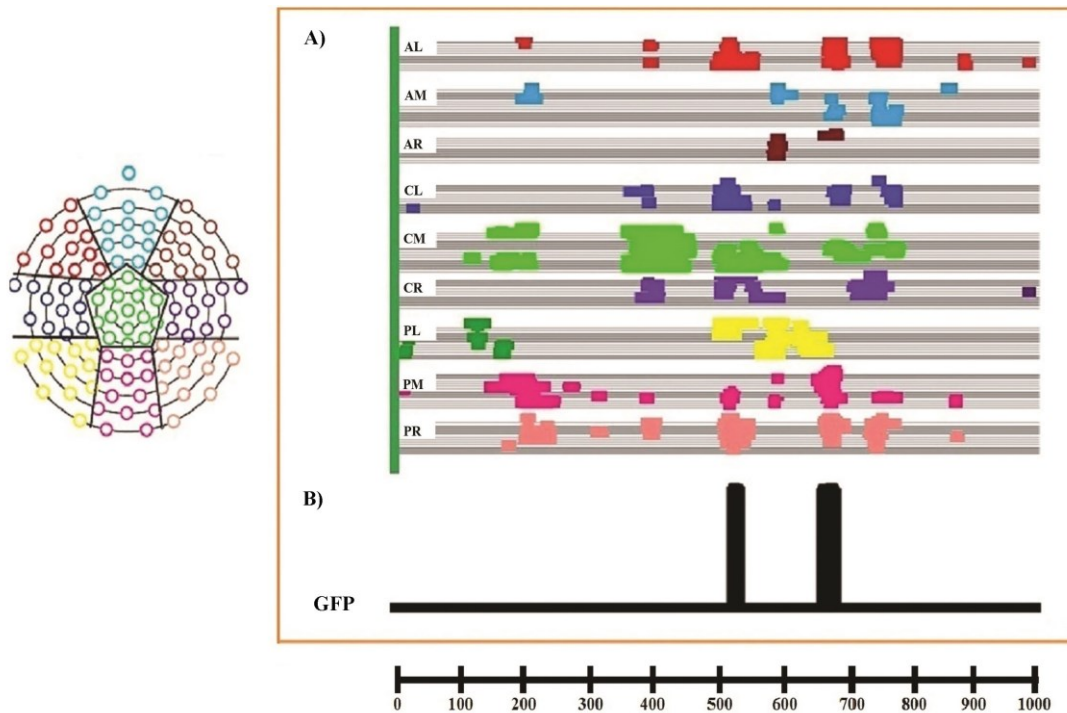


Figure 24: Electrophysiological results of FB-I and FB-C comparison: global ERP amplitude analysis and global electric field strength analysis. (A) Statistical analysis of global ERP amplitude. Periods of significant differences of ERP amplitude ($p < .05$; duration ≥ 20 ms) at each electrode and time point between FB-I and FB-C conditions are displayed as colored horizontal lines. Each horizontal line represents one scalp electrode. Different colours indicate different clusters of electrodes; the distribution of the clusters over the electrode montage is shown in the inset on the left side of the figure. AL: anterior left; AM: anterior midline; AR: anterior right. CL: central left; CM: central midline; CR: central right. PL: posterior left; PM: posterior midline; PR: posterior right. (B) Global scalp electric field analyses: statistical analysis of global electric field strength. Black areas indicate time intervals of significant differences ($p < .05$; duration ≥ 20 ms) of Global Field Power (GFP) between FB-I and FB-C conditions.

Source estimations

For the first time period of different topography (386-454 ms after target onset) significant higher activity in FB-I as compared with FB-C was found in left PMc extending toward IFG (BAs 6, 9) and left prefrontal cortex encompassing-ACC (BAs 8, 9 32), (Fig. 25B, green bar; Fig. 25C, green outline, in red; table 3). Higher activity in FB-C was found in right occipital cortex (BAs 18, 30), (Fig. 25C, green outline, in blue; table 3).

In the second significant TANOVA period (498-594 ms after target onset) higher activity in FB-I was found in different areas including: bilateral IFG (BAs 46, 47) and ACC (BAs 24, 32, 33), left PMc (BA 6) and right MTG and STS (BAs 21, 22), (see Fig. 25B – yellow bar; Fig. 25C, yellow outline, in red; table 3). Higher activity in FB-C was found, among others, in right somatosensory-related cortices and IPL (BAs 1, 3, 40) extending towards MTG and STS (BAs 22, 41, 42), (see Fig. 25C, yellow outline, in blue; table 3).

In the third significant TANOVA period (736-762 ms) higher activity in FB-I was found in a number of areas, including right occipito-temporal and parahippocampal regions (BA19-22, 35, 37, 41), IPL (BA 40), precentral and postcentral gyrus (BA 2, 6) and IFG (BAs 9, 44, 45), (Fig. 25B, red bar; Fig. 25C, red outline, in red; table 2). Higher activity in FB-C was found in left occipito-temporal and parahippocampal regions (BAs 20, 28, 35-37) and in left IPL (Bas 39, 40), (Fig. 25C, red outline, in blue; table 3).

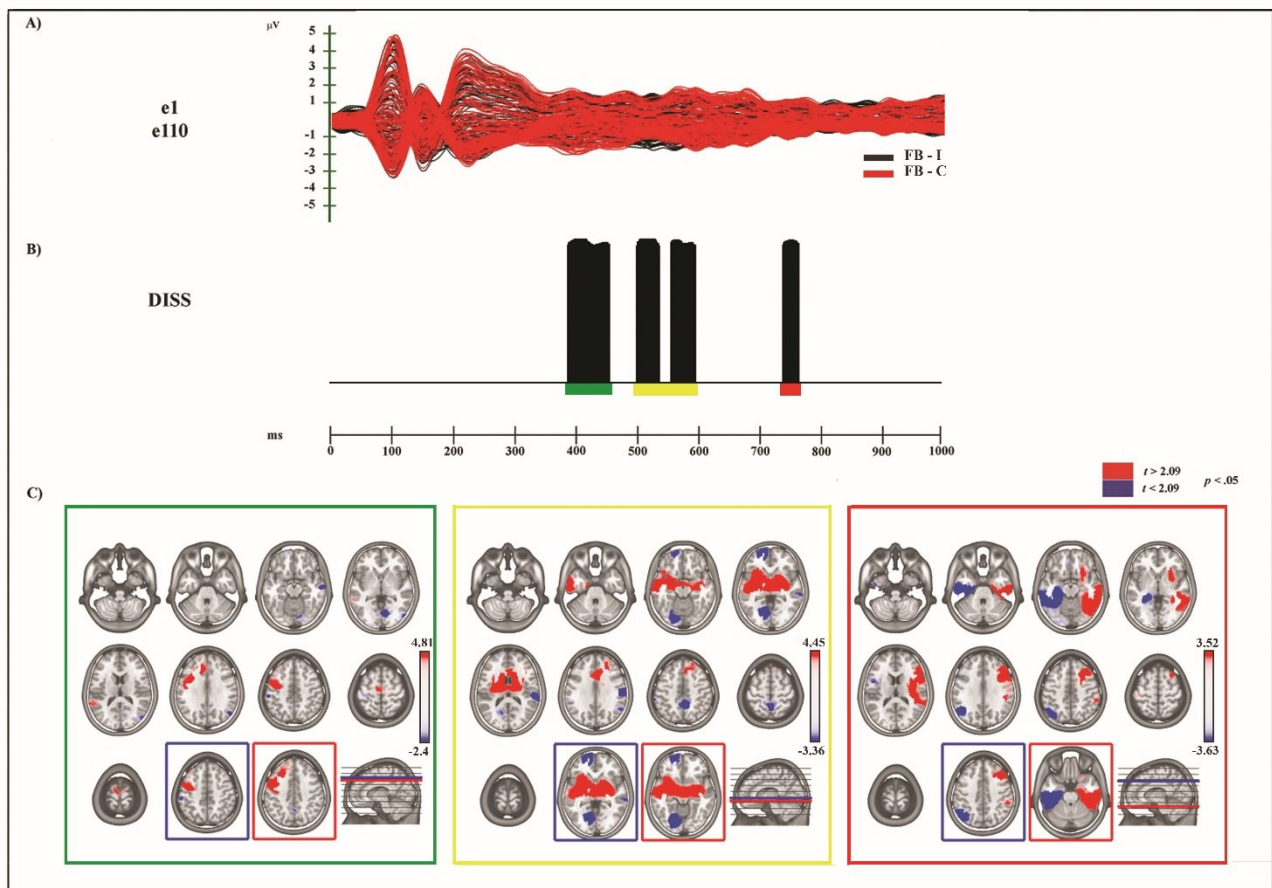


Figure 25: Electrophysiological results and statistical comparison of LAURA source estimations between FB-I and FB-C over significant TANOVA time intervals. (A) Group-averaged ($n = 20$) event related potential (ERP) waveforms of the two experimental conditions (FB-C and FB-I), superimposed across the 110 recording channels (e1–e110). Black: FB-I; red: FB-C. **(B)** Global scalp electric field analyses: statistical analysis of global electric field topography (topographic analysis of variance, TANOVA). Black areas indicate time intervals of significant differences ($p < .05$; duration ≥ 20 ms) of global spatial dissimilarity index (DISS). **(C)** Significant TANOVA time intervals. All significant voxels are colored ($t_{(19)} > 2.09 / < -2.09$, $p < .05$): positive t values (red colour) indicate higher current source densities in FB-I than in FB-C; negative t values (blue colour) indicate higher current source densities in FB-C than in FB-I. LAURA solutions are rendered on MNI152 template brain (left hemisphere on the left side). Green outline: first significant TANOVA time interval (386-454 ms after target onset). Yellow outline: second significant TANOVA time interval (498-594 ms after target onset). Red outline: third significant TANOVA time interval (736-762 ms after target onset).

BF-I vs. BF-C

The global amplitude analysis (Fig. 26) revealed three periods of significant ERP modulation: 1) from 54 to 102 ms after target onset over anterior clusters of electrodes (at a left and midline location); 2) from 332 to 374 ms after target onset, in particular over posterior clusters of electrodes (at a left and midline location) from 332 to 344 ms after target onset, and over central cluster of electrodes for the whole time period; 3) from 656 to 692 ms after target onset, in particular over left and right anterior clusters of electrodes from 656 to 676 ms after target onset, and over central and posterior cluster of electrodes (mainly at a midline location) for the whole time period.

The GFP analysis and the TANOVA did not show periods of sustained difference between conditions.

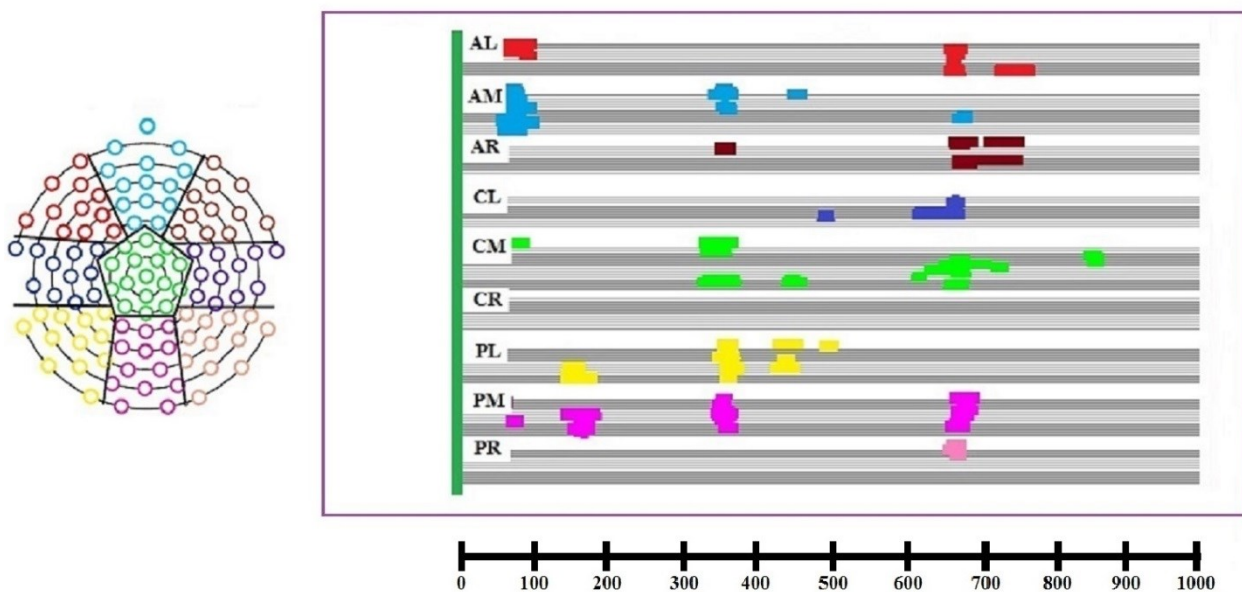


Figure 26: Electrophysiological results of BF-I and BF-C comparison: global ERP amplitude analysis.

Statistical analysis of global ERP amplitude. Periods of significant differences of ERP amplitude ($p < .05$; duration ≥ 20 ms) at each electrode and time point between BF-I and BF-C conditions are displayed as colored horizontal lines. Each horizontal line represents one scalp electrode. Different colours indicate different clusters of electrodes; the distribution of the clusters over the electrode montage is shown in the

inset on the left side of the figure. AL: anterior left; AM: anterior midline; AR: anterior right. CL: central left; CM: central midline; CR: central right. PL: posterior left; PM: posterior midline; PR: posterior right.

Table 1. Source localization of topographic maps: comparison between FF-I and FF-C condition. Significant results of the statistical comparisons of LAURA source estimations in significant TANOVA time periods are reported, with *t* and *p* values, Talairach and Tournoux coordinates (x,y,z) and anatomical labels of solution points with the local maximum different activities.

BA = Brodmann Area.

Condition	TANOVA time period	t value	p value	Talairach coordinates (x,y,z) mm	Brain region label
FF-I > FF-C	424-496 ms	3.82	.001	-48,-53,27	Left superior temporal gyrus, BA ¹ 39
		2.64	.01	48,-54,20	Right superior temporal gyrus, BA 39
		2.33	.03	33,-45,47	Right precuneus, BA 7
FF-C > FF-I		-3.33	.003	33,-19,30	Right middle frontal gyrus, BA 9
		-3.30	.003	33,18,2	Right insula

Table 2. Source localization of topographic maps: comparison between BB-I and BB-C condition. Significant results of the statistical comparisons of LAURA source estimations in significant TANOVA time periods are reported, with *t* and *p* values, Talairach and Tournoux coordinates (x,y,z) and anatomical labels of solution points with the local maximum different activities.

BA = Brodmann Area.

Condition	TANOVA time period	t value	p value	Talairach coordinates (x,y,z) mm	Brain region label
BB-I > BB-C	188-244 ms	3.16	.005	18,-2,24	Right caudate
		2.92	.008	48,-17,18	Right insula, BA ¹ 13
		2.83	.01	-63,-19,14	Left inferior temporal gyrus, BA 21
		2.52	.01	-18,0,59	Left middle frontal gyrus, BA6
BB-C > BB-I		-4.63	.0001	-33,-76,7	Left middle occipital gyrus, BA 19
		-2.86	.01	-11,-53,34	Left precuneus, BA 31
		-2.67	.01	-26,35,43	Left middle frontal gyrus, BA 8
		-2.47		11,-37,54	Right Paracentral lobule, BA 5
BB-I > BB-C	418-446 ms	4.74	.0001	-41, -32,5	Left superior temporal gyrus, BA 41
		3.84	.001	-56,-16,32	Left postcentral gyrus, BA 3
		3.25	.004	11,-45,54	Right precuneus, BA 7
		2.75	.01	-18,-31,39	Left posterior cingulate gyrus, BA31
BB-C > BB-I		-4.93	.00009	33,33,8	Right inferior frontal gyrus, BA 46
		-3.45	.002	33,-11,-15	Right parahippocampal gyrus BA
		-3.04	.002	-33,32,-4	Left inferior frontal gyrus, BA 47
BB-I > BB-C	676-702 ms	2.67	.01	-56,3,3	Left superior temporal gyrus, BA 22
BB-C > BB-I		-3.08	.006	56,-54,6	Right middle temporal gyrus, BA 39
		-2.55	.02	18,48,8	Right medial frontal gyrus, BA 10

Table 3. Source localization of topographic maps: comparison between FB-I and FB-C condition. Significant results of the statistical comparisons of LAURA source estimations in significant TANOVA time periods are reported, with *t* and *p* values, Talairach and Tournoux coordinates (x,y,z) and anatomical labels of solution points with the local maximum different activities.

BA = Brodmann Area.

Condition	TANOVA time period	t value	p value	Talairach coordinates (x,y,z) mm	Brain region label
FB-I > FB-C	386-454 ms	4.81	.0001	-41,-9,38	Left precentral gyrus, BA ¹ 6
		3.42	.0001	-18,27,29	Left medial frontal gyrus, BA 9
FB-C > FB-I		-2.39	.03	11,-70,-6	Right lingual gyrus, BA 18
FB-I > FB-C	498-594 ms	4.45	.0003	41,-11,-8	Right temporal sub-gyral, BA 21
		3.17	.005	-41,-11,-2	Left insula, BA 13
FB-C > FB-I		-3.36	.009	-11,-69,0	Right inferior frontal gyrus, BA 46
		-3.26	.004	63,-25,4	Right parahippocampal gyrus BA
		-3.20	.005	-11,62,-6	Left inferior frontal gyrus, BA 47
		-3.15	.005	3,-45,54	Right precuneus, BA 7
FB-I > FB-C	736-762 ms	3.52	.002	56,-19,-21	Right fusiform gyrus, BA 20
		3.20	.004	56,26,16	Right inferior frontal gyrus, BA 45
BB-C > FB-I		-3.63	.001	-56,-60,41	Left inferior parietal lobule, BA 40
		-3.52	.02	48,-34,-20	Left fusiform gyrus, BA 20

3.6 Discussion

The aim of the present study was to investigate the time course and the neural correlates of the integration of body and face emotion-related information. Specifically, we aimed to clarify similarities and differences between face and body emotional processing and to assess how the affective integration process of emotional faces and bodies is built up.

To this purpose we used as stimuli ecological pictures of facial and bodily expressions depicting sadness and happiness. We recorded electrophysiological indexes while participants judged the emotional congruence between stimuli belonging to the same category (face-face, body-body), or to different categories (face-body, body-face).

The N400 had higher amplitude in response to incongruent stimuli than to congruent ones in all comparisons, except for body-face condition, where we did not find significant difference between Congruence (BF-C) and Incongruence (BF-I).

For reasons of clarity, we will first discuss the results of each comparison, and then we will provide a general discussion.

FF-I vs FF-C

In accord with previous literature, our results showed higher N400 amplitude in response to FF-I than FF-C condition, as indexed by a significant period of amplitude modulation between about 420 and 460 ms after target onset. The global scalp electric field analysis revealed that this modulation was characterized by both strength and topographic differences between the two conditions. Significant higher activity in FF-I was found in bilateral MTG and STS extending toward IPL on the left hemisphere, with an involvement of parietal sensorimotor regions of the right hemisphere (Fig. 20 C). These results are in accord with the proposed Haxby model for face processing (Haxby et al., 2000; 2002), which suggests the contribution of the STS in the analysis of variable aspects of facial expressions (Narumoto et al., 2001; Britton et al. 2006; Sabatinelli et al., 2011). Although the involvement of the MTG is related to both emotional face perception and discrimination of

expressive faces (Batty & Taylor 2003; Sabatinelli et al., 2011), it is worth noting that in our study the bilateral MTG was engaged only in the incongruent condition, revealing its novel putative involvement in storage and interpretation of stimulus meaning, in line with the hypothesized integrative role for the N400 effect (Lau et al., 2008).

Of note, the activation of bilateral parietal sensorimotor regions, together with the STS, could index the involvement of the MM for emotion recognition during the processing of FF-I condition (Keisers et al., 2010). Possibly, the activation of sensorimotor representation is needed to solve the “conflict” created by the incongruence between prime and target-related emotional expressions. Specifically, it has been hypothesized that right sensorimotor cortices could contribute to the visual recognition of emotional facial expression: by means of an embodied simulation mechanism of *how one would feel if making the facial expression shown in the stimulus* (Adolphs et al., 2000) this cerebral region would provide the information needed to understand the meaning of the observed expression (see also Gallese, 2003; Atkinson and Adolphs, 2011; Sel et al., 2014).

In contrast, the activation of areas pertaining to the “extended system” of the neural network for face perception devoted to processing of changeable facial aspects (Haxby et al., 2000; 2002; Fairhall & Ishai 2007; Ishai, 2008), such as the inferior frontal cortex and the adjacent insula (Fig. 20C), emerged during the FF-C condition processing.

Taken together, these results suggest that on the one hand, the “extended system” of the neural network for face perception would be sufficient for the processing of emotion when the prime and the target convey congruent information. On the other hand, the access to the meaning storage system and the activation of sensorimotor representations are needed during the processing of the Incongruent condition, in order to solve the conflict between prime- and target-related affective information.

BB-I vs BB-C

So far, the investigation of body-related emotional information processing has been largely overlooked and the temporal dynamics of the hypothesized cerebral networks involved have to be still clarified. Our results showed three periods of amplitude modulations, corresponding to N200, N400 and Late Positivity (LP), reported in previous ERP literature.

The global amplitude analysis showed a first period of significant ERP modulation between BB-I and BB-C around 140-270 ms after the target onset, with a fronto-central negative component of higher amplitude in response to BB-C than BB-I condition (between 190-240 ms). Of note, a previous study reported a similar ERP modulation in response to semantically congruent actions (Proverbio et al. 2010), likely indexing their recognition. Our results further extend these previous findings, showing that this N200 modulation could also index the recognition of congruent emotions. During this period of amplitude modulation, the TANOVA suggested the involvement of different neural generators in the two conditions.

The source analysis showed in BB-C condition, higher activation, among others, in regions of the left ventral stream related to body processing (Downing et al., 2001; Peelen & Downing, 2007) and in bilateral precuneus and PCC, involved in processing of emotion-specific information from different stimulus type (e.g. Kim et al., 2015). Among activated areas, it is interesting to note the involvement of right parietal sensorimotor regions (Fig. 22C-yellow outline, in blue). Since the parietal cortex is also part of the MM, it could be involved in the processing of sensorimotor information conveyed by images of body postures expressing emotions, contributing to the comprehension of the emotional postures.

Among cerebral regions activated in BB-I condition, it is noteworthy the involvement of the right ACC, and of both bilateral pre-SMA and PMc (Fig. 22C-yellow outline, in red). The activation of ACC during the affective incongruence between prime and target, is in accord with its role in conflict monitoring and/or resolution (e.g. Botvinick et al., 2004), also in emotional tasks with a cognitively demanding component (Kerms et al., 2004; Muller et al., 2011).

Regarding bilateral PMc and pre-SMA, our results are consistent with previous evidence showing that during the observation of emotional body postures there is an activation of these brain areas (de Gelder et al., 2004).

Hence, these results suggest that the activation in both conditions of different regions pertaining to the MM (parietal sensorimotor cortices in the congruent vs. bilateral premotor regions in the incongruent condition) could contribute to the comprehension of the emotion conveyed by bodies.

In the second TANOVA significant time period (418-446 ms), corresponding to the N400 modulation, higher activity in BB-I emerged in left occipito-temporal regions of the ventral stream for body processing. Higher activity was also found, as for incongruent faces processing, in left MTG and STS (Fig. 22C, orange outline, in red). As already mentioned, MTG activation is consistent with evidence suggesting its role in storage and interpretation of stimulus meaning (Lau et al., 2008), and the STS activation likely underpins the analysis of movement and biological actions (Proverbio et al 2012; Iacoboni, 2005).

Of note, higher activation of left motor (M1) and premotor cortices together with the IPL, and of left primary (SI) and bilateral associative somatosensory and sensorimotor cortices emerged during BB-I condition (Fig. 22C, orange outline, in red).

Whereas M1 and PMc are considered part of the MM for action representation and comprehension, somatosensory-related cortices were shown to contribute to perceive others (e.g. Adolphs et al. 2000) and their actions (e.g. Valchev et al., 2016). Interestingly, it has been recently demonstrated a causal contribution of both SI and secondary somatosensory cortices to information processing in the MM (Valchev et al., 2016).

In BB-C condition we found higher activity in bilateral IFG and right limbic regions (Fig. 22C, orange outline, in blue). Their activation could be related to the processing of semantic aspects of bodies as in the “extended system” for faces (Haxby et al., 2000; 2002; Fairhall & Ishai 2007; Ishai 2008).

The last significant amplitude modulation between conditions, emerged between 676-702 ms, in a time window corresponding to the typical latency range of the LP, with higher amplitude in response to BB-C than BB-I, likely reflecting categorization and evaluation processes of the emotional content of congruent postures (e.g. Wu and Coulson, 2005). The TANOVA confirmed the overlapping of significant topographic difference between conditions, and the source analysis revealed the activation of the left IFG in BB-I and of mPFC in BB-C condition (Fig. 22C, purple outline, in red).

In sum, our findings are consistent with the model of emotion-behaviour connectivity for EBL comprehension proposed by de Gelder (2006), showing the activation of regions for the visuomotor perception of EBL. The major novel finding of our study is, indeed, the involvement of motor, premotor and somatosensory regions during the processing of the incongruent condition, especially in the N400 time window: these findings suggest that the resolution of the conflict between emotion-related information conveyed by the prime and the target requires the retrieving of sensorimotor representations associated with target emotional body postures.

FB-I vs FB-C

It is noteworthy that in this experimental condition (and in BF-I vs. BF-C too), FB-I contained a two levels conflict: a first level due to a perceptual incongruence (prime and target pertained to different stimulus categories) and a second level due to the emotional incongruence. Additionally, FB-C was characterized by the perceptual incongruence too. This lead us to consider the “cross-category” session more difficult than the other, as suggested also by behavioral results.

The global amplitude analysis showed a period of significant ERP modulation between about 370-450 ms after target onset, in a time window corresponding to the latency range of the P300 component, with higher amplitude in response to FB-C than FB-I condition, probably indexing the recognition process underpinned by cortical body- and face areas (Proverbio et al., 2014). The TANOVA confirmed the overlapping of significant topographic difference between conditions, and

the source analysis established the activation of right occipital regions in FB-C (Fig. 24C, green outline). The activation of left ACC in FB-I condition suggest its higher cognitively demanding component (Botvinick et al., 2004; Kerms et al., 2004; Muller et al., 2011). Interestingly, activation of left PMc and IFG emerged during FB-I condition (Fig. 24C, green outline, in red), likely indexing the involvement of MM for action representation and comprehension.

In the second significant TANOVA time period (498-594 ms), corresponding to the N400 modulation, higher activity in FB-I emerged in right MTG, STS and in bilateral ACC (Fig. 24C, yellow outline, in red). Of note, the activation of MTG and STS emerged also in the N400 time window of the other incongruent conditions (FF-I, BB-I).

The significant activation of bilateral IFG and PMc (Fig. 24C, yellow outline, in red) could represent the involvement of the MM for action comprehension, underpinning the processing of motor information conveyed by images of body postures expressing emotions.

The higher activation of somatosensory-related regions in FB-C condition could be explained by the presence of the perceptual incongruence between prime and target (face vs. body): likely, by means of an embodied simulation mechanism these regions would have provided the information needed to comprehend the meaning of the prime (facial expression) (Adolphs et al., 2000; Atkinson and Adolphs, 2011; Sel et al., 2014; see also FF-I vs. FF-C section). As a consequence, the involvement of the same mechanism/same regions during target perception (bodily expression) was needed to link the two emotional information and to solve the task.

The last significant amplitude modulation between conditions, emerged between 736-762 ms, in a time window corresponding to the latency range of the LP, with higher amplitude in response to FB-C than FB-I, likely reflecting categorization and evaluation processes of the emotional content of congruent postures (e.g. Wu and Coulson, 2005), as for BB-C condition. The TANOVA confirmed the overlapping of significant topographic difference between conditions, and the source analysis revealed a common activation of temporal and parahippocampal regions. The significant

activation in FB-I condition of right IFG, PMc and ACC could index the higher effort required to solve its double level conflict and to make a correct evaluation.

In sum, our findings suggest that the affective integration process of emotional faces and bodies is built up through a MM for action and emotion comprehension, which is different according to the emotional congruence/incongruence condition: in the presence of both perceptual and emotional conflict (FB-I) it involves a more action-related simulation mechanism, requiring also the access to the meaning storage system; when the conflict is only at a perceptual level (same emotion condition, FB-C) the simulation mechanism seems to be more somatosensory-related.

BF-I vs BF-C

Although the global amplitude analysis revealed three periods of amplitude modulation, the global scalp electric field analyses revealed that this modulation was characterized neither by strength nor by topographic differences between conditions. This lead us to hypothesize that emotional body postures were not effective as prime stimuli in creating a clear emotional context whereby participants could make judgment of congruence on a following emotional facial expression. Future studies with larger experimental samples will be needed to further assess this condition.

3.7 General discussion and conclusions

The present results contribute to clarify similarities and differences between face and body emotional processing, supporting previous findings regarding both emotional facial expression and EBL comprehension mechanisms (e.g. Adolphs et al., 2000; Keisers al., 2010; de Gelder, 2006; Proverbio et al., 2014).

Regarding “intra-category” session results, we show that in the presence of emotional incongruence between prime and target, during the N400 time window, both the access to the meaning storage system (likely represented by the MTG) and the activation of an embodied simulation mechanism (MM) are necessary to solve the conflict between prime- and target- related affective information.

Specifically, while the perception of incongruent facial expressions activates somatosensory-related representations, incongruent emotional body postures also require the activation of motor and premotor representations, exemplifying a tighter link between emotion and action (see Gallese and Caruana 2016).

When prime- and target- related emotional information are congruent, similarly to what happens during the processing of congruent facial expressions, there is an involvement of inferior frontal and limbic regions also during congruent body postures perception, suggesting the presence of an “extended system” devoted to the elaboration of semantic aspects of body postures and EBL.

The analyses of “cross-category” session allowed us for the first time to assess how the affective integration process of emotional faces and bodies is built up. While FB-I vs. FB-C comparison revealed a significant modulation of the N400, likely indexing the presence of a semantic/affective integration mechanism, the BF-I vs. BF-C comparison did not show any significant results, suggesting that emotional body postures are not effective in creating a clear emotional context whereby participants could make judgment of congruence on a following emotional facial expression. Future studies are needed to clarify if this depends on the emotional body postures we used as stimuli, possibly selecting other emotions (e.g. fear and anger) which could be more powerful.

Our findings during the N400 time window of FB-I vs. FB-C comparison, suggest that faces are able to build a clear affective context as prime stimuli, so that the affective integration process takes place (making possible a judgement of congruence) by both accessing the meaning storage system and activating a MM for action and emotion comprehension. It is worth noting that the MM seems to play a pivotal role also during the congruent condition, when the same affective information should be integrated between stimuli pertaining to different categories. Specifically, it is mainly action-related during FB-I, and more somatosensory-related during FB-C condition.

In conclusion, these results shed new light on EBL comprehension mechanisms clarifying commonalities and differences with well-known facial expressions processing. Future studies are

needed to better assess the capability of emotional body postures to build semantic and emotional contexts whereby obtain enough adaptive information in absence of other emotional cues (e.g. facial expressions).

4. Conclusions

The main aim of this dissertation was to shed new light on the importance of EBL in conveying and expressing our emotional and mental states.

In the light of the lack of previous studies investigating visual and neural mechanisms underpinning EBL comprehension, we adopted a step-by-step approach using as stimuli both emotional facial and bodily expressions, in order “*to look into face research to learn how to make progress on body perception*” (de Gelder, 2016).

The aim of the first study was to investigate the pattern of visual exploration during the observation of happy, sad and neutral facial and bodily expressions during an emotion categorization task. With regard to faces, our results confirmed what has been already demonstrated in the related literature: looking at the eyes and the nose, our participants adopted a configural viewing strategy (e.g. Guo, 2012; Gue & Shaw, 2015).

Considering bodies, our main novel result is the presence of the *left-side bias*, already established for faces, and mainly related with the dominance of the right hemisphere for both face and emotions processing (e.g. Mertens et al., 1993; Rossion, 2003; Hsiao & Cottrell, 2008). The reader should consider two main points about it:

- The left bias was significant when looking at the upper part of the body and at the hands (*upper left* and *hand left* were more viewed than *upper right* and *hand right*).
- Bodily postures, for their intrinsic nature, are action-related.

Hence, in our hypothesis this bias could also be explained by the tendency of our participants, all right handed, to implicitly pay their attention to the region where normally acts the dominant hand of the other (Marzoli et al., 2014).

To the best of our knowledge, this is the first demonstration of the presence of the *left-side bias* during bodies observation.

Moreover, our results suggest an emotional effect explicable in terms of the *valence model* (e.g. Davidson 1992; 2003; Cattaneo et al., 2015), where indexing is accomplished by a different lateralization of the visual attention to the upper part of the body (the most viewed by our participants) according to the displayed emotion (to the left for sad stimuli and to the right for happy stimuli).

Although previous studies hypothesized that humans tend to explore bodies adopting a configural viewing strategy (Tao & Sun, 2013), our results are not so clear about it, suggesting that our participants likely implemented a different strategy based on the spatial relation among the different parts of the body.

The aim of the second study was to investigate the time course and neural correlates of EBL processing by means of a Congruence-Incongruence (N400) paradigm, in order to assess how the integration process of emotional faces and bodies is built up. To this purpose we used as stimuli ecological pictures of facial and bodily expressions depicting sadness and happiness. We recorded electrophysiological indexes while participants judged the emotional congruence between stimuli belonging to the same category (face-face, body-body), or to different category (face-body, body-face).

The most interesting result concerns the involvement of embodied simulation (ES) mechanisms to solve the emotional conflict between prime and target. Furthermore, the contribution of ES mechanisms is specific, (i.e. different for emotional facial and bodily expressions processing), as it is characterized by different neural activations according to the nature of the stimulus. More precisely, while the perception of incongruent facial expressions would activate somatosensory-related representations, incongruent emotional body postures would require also the activation of motor and premotor representations, showing a tighter link between emotion and action (see Gallese and Caruana 2016).

In parallel, the results obtained when prime- and target- related information were congruent, suggest, similarly to what happens during face processing, the presence of an “extended system” devoted to the elaboration of semantic aspects of body postures and EBL, and underpinned by inferior frontal and limbic regions.

The analyses of “cross-category” session allow us to assess the capability of both faces and bodies to create a clear emotional context whereby participants could make judgement of congruence on the following emotional stimulus belonging to a different category. Contrary to our initial hypothesis, emotional bodily postures were not able to create a clear affective context as prime stimuli.

Future studies are needed to better assess the capability of emotional body postures to build semantic and emotional contexts whereby obtain enough adaptive information in absence of other emotional cues (e.g. facial expressions). In our opinion, bearing in mind previous findings in the field, the choice of more arousing bodily expressions (e.g. anger or fear) could provide different results.

Faces, instead, being able to create a stable emotional context, made possible a judgement of congruence carrying out the affective integration process by accessing the meaning storage system and activating the MM for action and emotion comprehension, indexing, also in this case, the involvement of ES mechanisms.

In sum, our findings substantiate the biological model for body and EBL processing proposed by Beatrice de Gelder (de Gelder, 2006; de Gelder, 2016), specifically stressing the involvement of motor and sensorimotor regions belonging to the MM, whose activation is an index of the role of ES mechanisms, *allowing a direct match between the emotional bodily posture observed and executed, thus allowing the correct interpretation of the emotion conveyed by bodily postures themselves.*

Here we focus our conclusions on the N400 time-window, but it should also be taken into account what happened in earlier time window, as indexed by a significant modulation of the N2 (BB-I vs.

BB-C comparison), which showed the activation of both bilateral pre-SMA and PMc in the Incongruent condition.

Considering previous studies (Borgomaneri et al., 2014; Borgomaneri et al., 2015), it would be interesting to run a TMS experiment to further investigate the role of these regions during an early stage (190-240 ms) of EBL processing. Thus, future studies could integrate the ideal “model” of the time course of EBL processing, which is nowadays emerging thanks to the first twenty years of research in this field.

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