SCUOLA DI DOTTORATO
UNIVERSITÀ DEGLI STUDI DI MILANO-BICOCCA

Department of Psychology

PhD program in Psychology, Linguistics and Cognitive Neuroscience

Cycle: XXX

Curriculum in: Mind, Brain and Behaviour

Investigating face and body perception

Surname: Bossi Name: Francesco

Registration number: 719746

Tutor: Prof. Paola Ricciardelli

Co-tutor: Prof. Marcello Gallucci

Coordinator: Prof. Maria Teresa Guasti

ACADEMIC YEAR 2016/2017

CONTENTS TABLE

CONTENTS TABLE 1

Preface 5

Summary 6

CHAPTER 1: SOCIAL COGNITION

1. Social cognition 9

1.1. Social cognitive neuroscience 11

1.2. Second person neuroscience 15

2. Neural bases of face and body perception 20

3. Theoretical models of face and body perception 24

4. Emotional expressions 31

5. Approach and avoidance 39

6. Aim and topics of the thesis 41

CHAPTER 2: EXCLUDE THE EMO: How social exclusion modulates social information processing: a behavioural dissociation between facial expressions and gaze direction

1. Introduction 45

1.1. What is social exclusion? 45

1.2. Social exclusion and affective state 46

1.3. Social exclusion and social information processing 49

1.4 Aim of the study 51

2. EXPERIMENT 1 53

2.1. Methods 53

2.1.1. Participants 53

2.1.2. Materials and procedure 54

2.2. Results 57

2.2.1. Power Analysis 57

2.2.2. Main analyses 59

2.2.3. Analyses with Empathy Quotient 62

2.2.4. Analyses with participants' Gender 64

2.2.5. Analyses on PANAS 66

3. EXPERIMENT 2 67

3.1. Methods 68

3.1.1. Participants 68

3.1.2. Materials and procedure 69

3.2. Results 70

3.2.1. Main analyses 70

3.2.2. Analyses with Empathy Quotient 74

3.2.3. Analyses with participants' Gender 74

3.2.4. Analyses of between-subjects variables 76

4. GENERAL DISCUSSION 79

5. Appendix 85

CHAPTER 3: THE BODY-INVERSION EFFECT. A meta-analytic review

1. Introduction 91

1.1. Face and body perception 91

1.1.1. Configural processing in faces and bodies 92

1.1.2. Neural bases of face and body perception 97

1.2. Manipulation of body perception 100

1.2.1. Importance of the head 100

1.2.2. Lessons from the body composite effect 103

1.2.3. The importance of clothes 104

1.2.4. Clinical studies 105

1.3. Meta-analysis on the Body Inversion Effect 107

2. Methods 108

2.1. Literature search methodology 108

2.2. Selection criteria 108

2.3. Meta-analytic methods 110

2.4. Meta-regression 112

3. Results 113

3.1. Meta-analysis – overall effect 113

3.2. Trim and fill method 113

3.3. Meta-regression – moderators 115

4. Discussion 117

CHAPTER 4: NEURAL OSCILLATIONS INVOLVED IN FACE- AND BODY-INVERSION EFFECTS. Theta- and Gamma- band activity discriminates face, body and object perception

1. Introduction 125

2. Methods 129

2.1. Participants 129

2.2. Stimuli 129

2.3. Procedure 130

2.4. EEG data recording and analysis 131

2.5. Statistical analyses 134

3. Results 137

3.1. ERP analysis 137

3.2. Induced activity 139

4. Discussion 141

CHAPTER 5: INVERSION AND EMOTIONAL EXPRESSIONS BOTH AFFECT VISUAL PROCESSING OF FACES AND BODIES, BUT INDEPENDENTLY. An ERP study

1. Introduction 148
2. Methods 154
  2.1. Participants 154
  2.2. Stimuli 154
  2.3. Procedure 155
  2.4. EEG data recording and analysis 156
  2.5. Statistical analyses 159
3. Results 160
  3.1. Experiment 1 – Accuracy 160
  3.2. Experiment 1 – P1 component 164
  3.3. Experiment 1 – N170 component 166
  3.4. Experiment 1 – P2 component 169
  3.5. Experiment 2 – N170 component 172
4. Discussion 174
  4.1. Hypothesis 1 174
  4.2. Hypothesis 2 178
  4.3. Hypothesis 3 179
  4.4. Hypothesis 4 181
  4.5. Hypothesis 5 183
  4.6. Conclusions 186
5. Appendix 188

Final remarks 190
References 193

Preface

During our everyday interactions, we communicate with other people through verbal and non-verbal cues. Human face and body convey the most important non-verbal cues for social interactions. Face and body provide numerous cues essential for recognition of other people's identity, gender, age, intentions and emotional state. All faces and bodies are symmetrical and share a common 3D structure (i.e., two eyes above the nose, above the mouth; legs connected to the lower part of the torso, arms to the upper part and head on top), but humans are able to easily indentify hundreds of different people, just relying on facial and bodily information. Therefore, our cognitive system has developed to process this information in a very fast and efficient way.

Face and body processing have been widely studied and several cognitive and neuroanatomical models of these processes have been put forward. Despite many critical differences, all these models recognized different stages of processing from early coarse stimulus encoding (mainly related to neural activity in occipital visual cortices) to higher-level processes aimed to identify invariant (e.g., identity) and changeable features (e.g., gaze, emotional expressions), related to activity in a broad neural network including temporal, parietal and frontal areas. It was demonstrated that these processes involve configural processing, i.e., processing of the configuration of features composing the stimulus, in addition to processing of single features. Moreover, emotional expressions seem to influence the encoding of these stimuli. Processing of emotional expressions occurs at very early latencies (about 100 ms post-stimulus onset) and seems to involve the activation of a subcortical pathway. The studies presented in this thesis were aimed to investigate the visual perception of faces and bodies, and whether and how it can be modulated.

In the literature, these processes were investigated by means of several electrophysiological and imaging techniques. Electroencephalography (EEG) is a technique that allows studying psychophysiological activity related to particular processes with very high temporal definition. This technique was used in some of the studies presented in this thesis to investigate the psychophysiological processes involved in face and body perception, since it allows studying the different stages of perceptual processing in details.

Summary

The first Chapter is aimed to present the theoretical background in which this thesis was conceived. The first section presents a general discussion and a brief historical evolution of the definition of *social cognition*. It also presents two fundamental accounts of social cognition, which are *social cognitive neuroscience* and *second person neuroscience*. The second and third sections present the neural bases of face and body perception (discussing the most relevant neuroimaging studies in this field) and the cognitive and neuroanatomical theoretical models for these processes. The fourth and fifth sections focus more in depth on the literature concerning two specific topics of face and body processing, and their neural bases: perception of emotional expressions and of approach-avoidance orientation. Both these topics were further investigated in the studies presented in this thesis.

The second Chapter presents a first study (composed of two experiments), aimed to investigate how the perception of social cues can be modulated by social exclusion, and the process investigated is the perception of two different, but interacting, facial cues: emotional expression and gaze direction. In this study, we found that the identification of gaze direction was specifically impaired by social exclusion, while no impairment was found for emotional expression recognition. The results of this study brought important insights concerning the relevance of gaze as a signal of potential re-inclusion, and how the impaired processing of gaze direction may reiterate social exclusion.

The third Chapter presents a meta-analytic review on the *body-inversion effect*, a manipulation aimed to demonstrate configural processing of bodies. The literature available on configural processing of both faces and bodies is presented in this Chapter, together with open debates and controversies. The following meta-analysis was aimed to investigate consistency and size of this effect, fundamental in studying structural encoding of body shapes.

In the fourth Chapter, a study on the neural oscillations involved in face and body inversion effects is presented. Neural oscillations in theta and gamma bands were measured by means of the EEG since they are a very influential measure to investigate the psychophysiological activity involved in different processes. The results of this study showed that configural processing of faces and bodies involve different perceptual mechanisms.

In the fifth Chapter, a study investigating the influence of inversion and emotional expression on the visual encoding of faces and bodies is presented. The neural correlates of these processes were investigated by means of event-related potentials (ERPs). Both inversion and emotional expressions were shown to influence the processing of these stimuli, during different stages and through different perceptual mechanisms, but results revealed that these two manipulations were not interacting. Therefore, configural information and emotional expressions seem to be processed through independent and non-interacting perceptual processes.

CHAPTER 1

SOCIAL COGNITION

Introduction

The work presented in this thesis was aimed to investigate in depth specific aspects of social cognition and social cognitive neuroscience. But, before discussing the specific areas of interest of this work, it is necessary to define what social cognition is, and then narrow the discussion to specific subfields of the literature.

1. Social cognition

What is social cognition? An unambiguous definition is not so easy to find. Social cognition was often defined as "a subfield of social psychology focused on the role of cognition in human social behaviour." (Carlston, 2013), even though this construal immediately sounds reductive.

It was defined as a field or subfield already in the first Handbook of Social Cognition, by editors Robert Wyer and Thomas Srull (1984). However, as time passed by, experts tended to define social cognition as an *approach* rather than a field of research. The definition of social cognition as an approach grew as it became a much broader endeavour, embracing apparently divergent fields, unified more by a common point of view than overlapping research interests. A similar conclusion was expressed by Devine, Hamilton, and Ostrom (1994): they hypothesized that "social cognition could not really be considered a content area because that implied a limited range of applicability, which was belied by the broad range of topics already being addressed by the approach." Also Wyer and Srull (1994) explained in the second edition of their manual that social cognition's influence had extended beyond its own borders "to many other subareas (health psychology, clinical psychology, personality, etc.)," as well as to some "totally different disciplines (political science, marketing and consumer behaviour, organizational behaviour, etc.)". Therefore, the opinion that “social cognition is not a content area, but rather is an approach to understanding social psychology.” (Sherman, Judd, & Park, 1989) has widely grown over time.

Nevertheless, considering social cognition as an approach does not preclude from considering it also as a content field. There is still a significant core of research that represents the central focus of the field. One of the earliest definitions of social cognition was “how people think about people” (Wegner & Vallacher, 1977). The typical oversimplified description of social cognition was: Harry meets Sally; Harry forms an impression of Sally; Harry departs and retains memories of Sally. This stereotypical event, however, captures little of the richness of the situation that it describes, but it was probably the simplest description of what was the original core focus of social cognition.

During the years, this core focus has become much wider than what pioneers of social cognition could have ever imagined. It was recognized that impression formation is a more complex social process than described above. At the same time, the information processing model (a key component of the social cognition approach) expanded our comprehension of different aspects of impression formation. As a matter of fact, the information processing model, and the field more in general, extended in order to embrace a variety of different concepts from social psychology, such as motivation and affect, that were not always taken into account in early social cognition. And to conclude, the definition of cognition itself has expanded over the years.

In today’s social cognition, Harry’s memories of Sally include visual images, affective material, and relationship schemas that are not only explicitly stored in memory and retrieved but also represented implicitly in the recesses of perceivers’ minds. Today, what was called “impression formation” is no longer a single process, but rather various stages of information processing. The core of the social cognition field is now the expanded and improved understanding of impression formation, along with various other related processes and phenomena. When thoroughly elaborated, the social cognitive event “Harry meets Sally” is actually very complex and multifaceted, and it apparently touches almost every aspect of human social behaviour.

As regards the expanding definition of cognition, today it includes also subconscious goals, automatic processes, and implicit memories. It is now assumed to comprise many processes that once would have been excluded. Habits are cognitive, and so are simple associations, including those once classified as classical and even operant conditioning, as well as moods, emotions and motivation. The effects of undetected stimuli are cognitive, as the subconscious mechanisms by which these influence behaviour and memory.

To define social cognition, it is thus necessary to recognize its dual nature (Carlston, 2013): a subfield of psychology that examines all of the countless cognitive complexities, mental representations, and processes implicated when “Harry meets or thinks about Sally”; and, at the same time, as an approach to study Harry, Sally, the pair of them, or the groups, cultures, and societies to which they belong.

The research presented in this thesis is more specifically focused on social cognitive neuroscience, the fruitful interface between social cognition and neuroscience. Two of the main theoretical accounts which contributed in creating a common framework in the study of social cognitive neuroscience will be briefly presented below: the *social cognitive neuroscience* account (which named the field itself) and the *second person neuroscience* account.

1.1. Social cognitive neuroscience

Social cognitive neuroscience (Lieberman, 2007; Lieberman, Gaunt, Gilbert, & Trope, 2002; Ochsner & Lieberman, 2001) was defined as a promising and rapidly growing interdisciplinary field combining the tools of cognitive neuroscience (such as neuroimaging, neurophysiology and neuropsychology) with questions and theories from various social sciences including social psychology, but also economics and political science.

In two extensive reviews (Lieberman, 2007; Lieberman et al., 2002) some of the most eminent authors in this field examined four broad areas of research within social cognitive neuroscience in order to highlight common processing systems: understanding others (in terms of representing their minds or experiencing their mental states), understanding oneself (recognizing one self and reflecting on the self), controlling oneself (intentional and unintentional self-regulation), and the processes that occur at the interface of self and others (imitation, the interaction between self and social understanding, attitudes and prejudice, social connection and rejection, and social decision-making). In this last field, some topics are of particular interest for the work presented in this thesis, as social rejection (on which we will focus in the next Chapter), emotion recognition and face processing (on which we will focus later in this Chapter).

By reviewing these fields, the authors highlighted two core processing distinctions that can be neurocognitively identified across all of these domains. The first is the more classic distinction between *automatic* vs. *controlled* processes, originally proposed by cognitive psychology (Schneider & Shiffrin, 1977). Consistent with the notion that these two categories of processes are supported by distinct systems (Smith & DeCoster, 1999), distinct neurocognitive systems have been hypothesized to support these two forms of social cognition (Fig. 1.1).

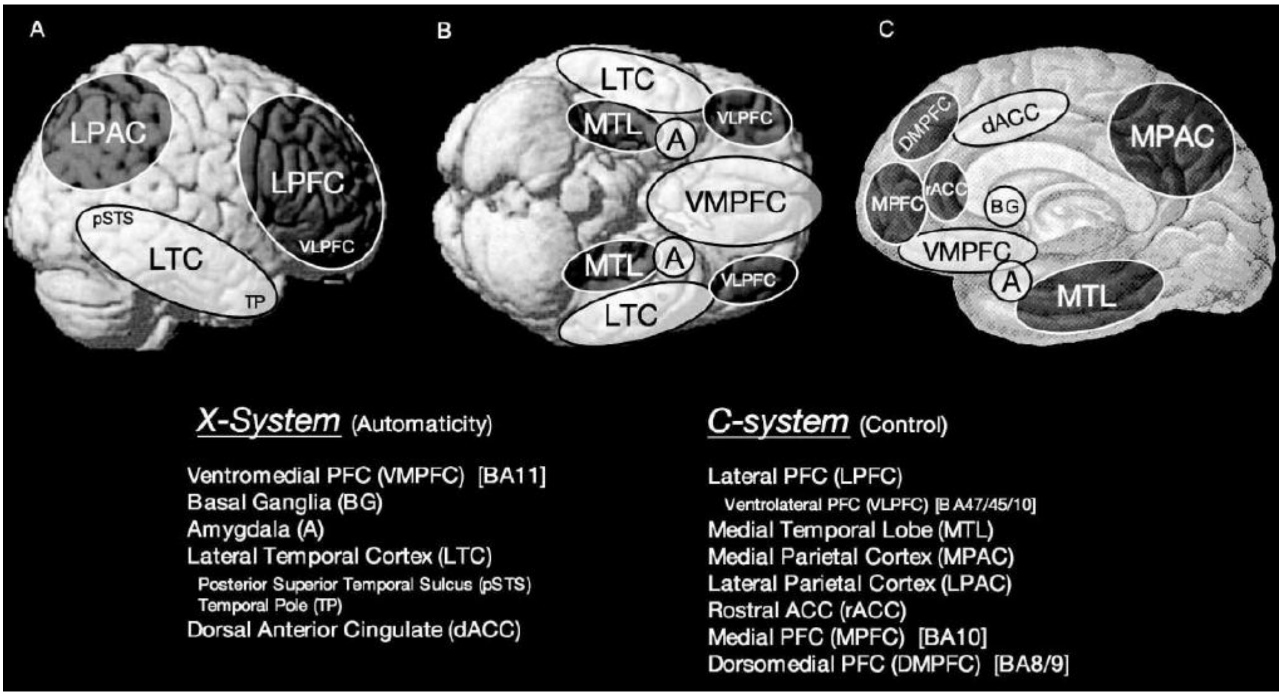


Fig. 1.1: Hypothesized neural correlates of the C-system (dark shade) supporting reflective social cognition (controlled processing) and the X-system (light shade) supporting reflexive social cognition (automatic processing) displayed from (A) lateral, (B) ventral, and (C) medial views (adapted from Lieberman, 2007)

What they defined as the X-system, named for the “x” in “reflexive” (Lieberman et al., 2002; Satpute & Lieberman, 2006), corresponds to an automatic social cognition system: it is fast, spontaneous, typically sensory, unaffected by cognitive load, facilitated by high arousal, phylogenetically older, represents common cases, and is characterised by parallel processing and non-reflective consciousness. The neural regions associated with the X-system (Fig 1.1) are the amygdala, basal ganglia, ventromedial prefrontal cortex (VMPFC), lateral temporal cortex (LTC), and dorsal anterior cingulate cortex (dACC). On the other hand, the C-system, named for the “c” in reflective, corresponds to a controlled social cognition system: it is slow, intentional, typically linguistic, altered by cognitive load, impaired by high arousal, phylogenetically newer, represents exceptions and abstract concepts, and is characterised by serial processing and reflective consciousness. The neural regions associated with the C-system are lateral prefrontal cortex (LPFC), medial prefrontal cortex (MPFC), lateral parietal cortex (LPC), medial parietal cortex (MPC), medial temporal lobe (MTL), and rostral anterior cingulate cortex (rACC).

Alternatively, these authors also proposed a second distinction in processes involved in social cognition (Lieberman, 2007), which is data-driven, i.e., a discrimination found in several studies investigating topics across numerous domains of social cognitive neuroscience, not deriving from a specific theory of social sciences. The differentiation they propose is between *internally-focused processes*, that focus on one's own or another's mental interior state (e.g., thoughts, feelings, experience), and *externally-focused processes*, that focus on one's own or another's visible features and actions, which are perceived through sensory modalities and are experienced as part of the material world. This distinction emerges from investigations in social cognitive neuroscience.

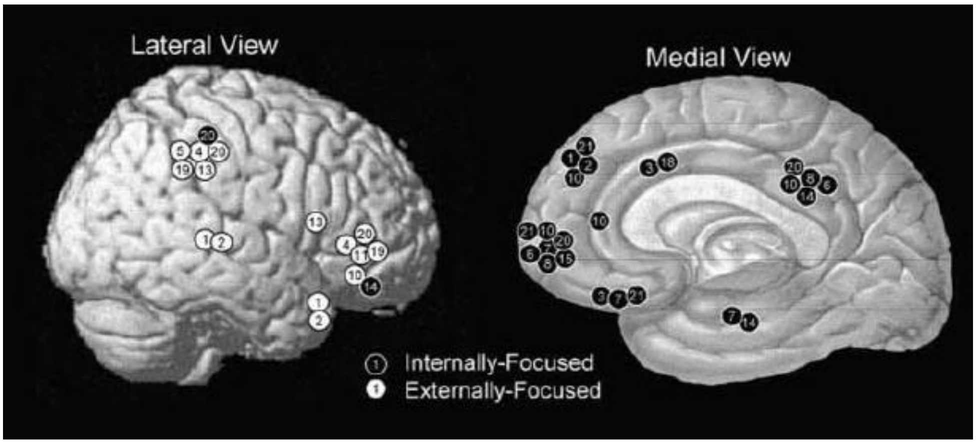


Fig. 1.2: Neural correlates of *internally-focused* (small circles with white text on a black background) and *externally-focused processes* (black text on a white background) from multiple domains of social cognition (adapted from Lieberman, 2007). Each circle represents a study in which an internally- or externally-focused process was found to be correlated with neural activity over that region. Small circles are placed schematically within a region and are not meant to indicate a precise location within a region.

As regards this distinction, a clear division seems to be present between the neural correlates of tasks that focus attention on interior psychological worlds and tasks that focus attention on the exterior social world and the physical social agents in it. Externally-focused processes are associated with a lateral fronto-temporo-parietal network, whereas internally-focused processes are associated with a medial fronto-parietal network (Fig 1.2).

On the one hand, the externally-focused network is more active during social-cognitive tasks that focus attention on the external, physical, and most often visual characteristics of other individuals, oneself, or the interaction of the two. On the other hand, the internally-focused network is more activated by social-cognitive tasks that focus attention on the internal, mental, emotional, and experiential characteristics of other individuals or oneself.

It is important to highlight that this categorization is not a distinction between self- and other-focused cognition: it is orthogonal to and cuts across self and other processing. Consequently, this distinction refers to two ways that self and other can each be processed.

Considering this theoretical framework, in this thesis we will focus particularly on externally-focused processes (i.e., visual processing of social stimuli as faces and bodies, in Study 2 and 3) or on the interaction between internally- and externally-focused processes (i.e., the influence of social exclusion on the perception of specific facial features, in Study 1). Alternatively, if we consider the previous “classical” distinction between automatic and controlled processes, these researches are focused on processes involved in the X-system (Study 2 and 3) or on the interaction between C- and X-systems (Study 1).

1.2. Second person neuroscience

The theoretical account of second person neuroscience (Schilbach, 2010; Schilbach et al., 2013) assumes the premise that social cognition is fundamentally different when we are in interaction with others rather than merely observing them.

In discussing their point of view, the authors consider two neuroanatomically distinct large-scale networks that have obtained central relevance as the neural substrates of social cognition: the so-called *mirror neuron system* (Rizzolatti & Sinigaglia, 2010) and the *mentalizing network* (Frith & Frith, 2010).

The former is thought to include areas of inferior frontal cortex (IFC) (in particular the ventrolateral premotor cortex – VLPMC) and inferior parietal cortex (IPC) (Rizzolatti & Sinigaglia 2010). Individual nodes of this network are known to become active during both the execution and observation of goal-directed actions in monkeys and humans (Rizzolatti & Craighero, 2004). They suggested that its functional relevance for cognition results from a “mirror mechanism” that allows individuals to understand the actions of another individual by giving the observer a “first-person grasp” of the motor goals and intentions of the other. These are the bases of the simulationist account of social cognition, also called *first-person social cognition* by the authors.

The latter is a network of brain regions recruited by tasks which tap “the ability to read the desires, intentions, and beliefs of other people” (Frith & Frith, 2008). In line with meta-analyses of functional neuroimaging studies which have investigated mentalizing, medial prefrontal cortex (MPFC) and the posterior cingulate cortex (PCC) were identified as the most important nodes of this network, sometimes also referred to as the “cortical midline structures” (Northoff & Bermpohl, 2004; Schilbach, Bzdok, et al., 2012). The study of this mentalizing network has provided important evidence for the so-called “Theory Theory” account of social cognition, believed to give an inferential, reflective, and what was called by the authors “a *third-person grasp*” of others’ mental states (Frith & Frith, 2008, 2010).

Both these accounts are, in fact, committed to *spectator theories of knowledge*. They have focused on the use of “isolation paradigms” (Becchio, Sartori, & Castiello, 2010), in which participants are required to merely observe others or think about their mental states rather than participate in social interaction with them.

As opposed to these two accounts, Schilbach and colleagues (2013) proposed an approach to the investigation of social cognition focused on *second-person engagements* in order to “help social neuroscience to really go social”. These authors based their work on classical theories, drawing upon Gestalt theory and phenomenology: before recent social cognition research, there was already an important body of theory and research proposing that, when relating to one another, people are not engaged in a tortuous process of inferences and theorizing about one another, but immediately experience the other as a subject (Heider & Simmel, 1944; Runeson & Frykholm, 1983; Schultz, 1972). Their approach to social knowing was based on interaction and emotional engagements between people, rather than mere observation. This *second-person approach* already produced results in neuroimaging and psychophysiological studies, finding profound differences in neural processing related to the reciprocity of social interaction.

This approach makes explicit reference to the *enactive account* of cognition, which stresses that cognition is achieved by an animal's active exploration of and coupling with its environment (De Jaegher, 2009; Di Paolo & De Jaegher, 2012). According to this approach, an individual adopts a "second-person perspective" in which interaction with the other can be considered as essential or even constitutive for social cognition, rather than simply observing others and relying on a "first- (or third-) person grasp" of their mental states (as in previous approaches).

The central claims of the second person neuroscience account are that social cognition is fundamentally different when we are *emotionally engaged* with someone as compared to adopting an attitude of detachment, and when we are in *interaction* with someone as compared to merely observing him/her (Fig 1.3).

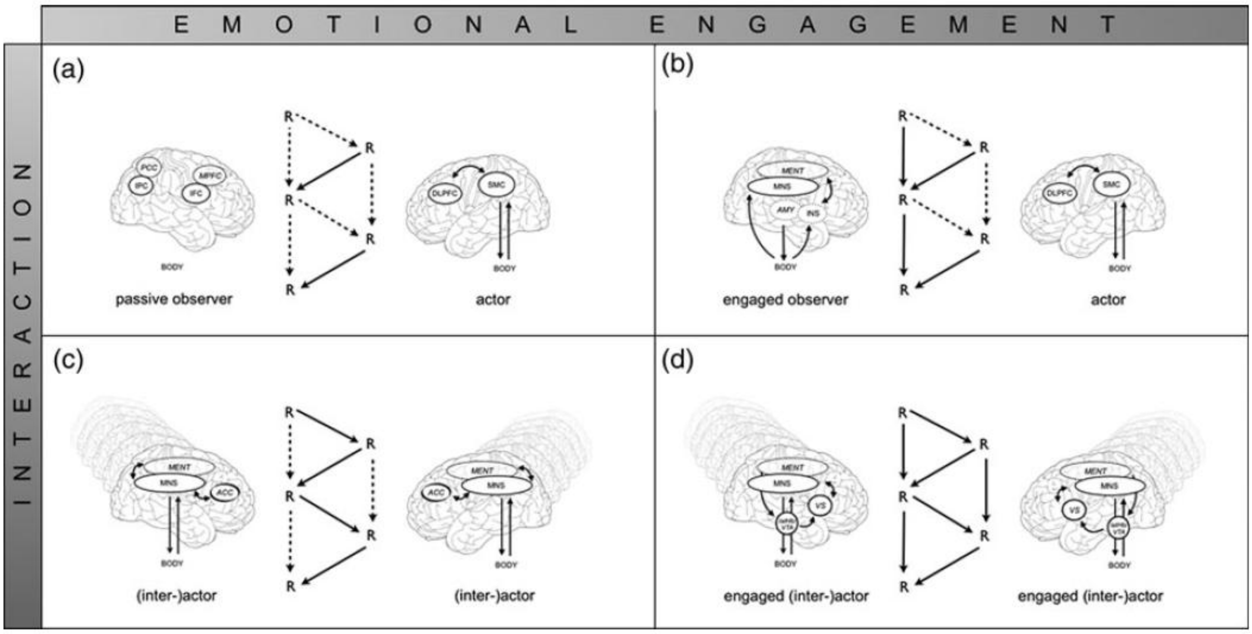


Fig. 1.3: Schematic depiction of interaction contingencies for situations of (A) no social interaction and no emotional engagement, (B) no social interaction, but emotional engagement, (C) social interaction, but no emotional engagement, and (D) social interaction and emotional engagement. Dotted lines indicate the absence or relatively decreased influence of actions on oneself (vertical arrows) or the other (oblique arrows), temporal sequence is shown from top to bottom (adapted from Schilbach et al., 2013). For abbreviations: see body text.

The authors argue that a “second-person grasp” of other minds is first closely related to feelings of engagement with and emotional responses to the other. According to their point of view, awareness of other minds fundamentally depends on emotional engagement and responsiveness to another person’s states or actions, in contrast with a detached observer’s attitude, which does not include such responding (Reddy, 2003, 2008; Rietveld, 2008). The authors indicate that affective responses relying upon proprioceptive afferences from the body and action-based processes are likely to be closely linked and to interact in complex ways. For example, it would seem plausible that emotional responses could facilitate more cognitive ways of understanding minds, whereas the absence of such responses could make this a more effortful process. Processes involving emotional engagement (see Schilbach et al., 2013 for an extensive review) typically elicited greater activation of subcortical structures as bilateral amygdala (AMY in Fig 1.3) and insula (INS), compared to tasks requiring a detached attitude.

Secondly, the authors see social interaction as a key feature of “grasping” other minds. Social interactions are characterized by intricate reciprocal relations with the perception of socially relevant information prompting reactions, which are themselves processed and reacted to. Being in interaction with someone additionally depends on the perception of the environment in terms of the resources assumed collectively by both interactors rather than those held by each individual alone (Costall, 1995; Marsh, Richardson, & Schmidt, 2009; Richardson, Marsh, & Baron, 2007; Schilbach, Eickhoff, Cieslik, Kuzmanovic, & Vogeley, 2012). In social interaction, rather than exercising one’s own reflective capacities we exercise our own practical know-how in dealing with others as interactors. Schilbach et al. (2013) highlighted three aspects of social interaction that are important for research in social cognitive neuroscience. (i) interaction involves different roles for the interactors. At the simplest level, one can be an “initiator” or a “responder” in an interaction, i.e., the same action can be performed in an attempt to initiate an interaction or as a response to someone else’s action. (ii) shared intentions and motivations are created as new within an interaction, with relevant consequences for the performance of joint actions and for the progress of the interaction itself. (iii) interaction always involves experience, suggesting that social phenomena must be understood, at both the psychological and the neural level, within the context of the past interactions and must involve developmental trajectories. Social interactions (in comparison to analogous tasks not involving social interaction) elicited greater activation of the anterior cingulated cortex (ACC) and, if also a high level of emotional engagement is involved, other subcortical structures as the ventral striatum (VS), the ventral tegmental area (VTA), and the lateral habenula complex (LatHb).

The second person neuroscience approach is therefore extremely relevant to comprehend today’s studies in the field of social cognitive neurosciences, since it has brought a new perspective and theoretical framework to study social cognition. However, no direct interaction was used as a manipulation in the studies that will be presented in this thesis, even though a bogus social interaction was used to induce social exclusion in Study 1. Nevertheless, this approach could bring important insights considering the implications of these studies and it definitely represents a potential development of this research.

After a general discussion about what social cognition is and the presentation of the most outstanding accounts, a more specific theoretical framework ought to be introduced. The studies in this thesis focused on a specific subfield of social cognitive neuroscience, which is the visual perception of faces and bodies. Consequently, in the next Paragraphs the neural bases of these processes (Paragraph 2) and the main theoretical models and frameworks in which they are outlined (Paragraph 3) will be presented and discussed.

2. Neural bases of face and body perception

Human faces are a socially special stimulus and a very broad field of research has been focusing on the study of face processing (see Rossion & Gauthier, 2002 for a review). Faces provide numerous cues relevant for social communication and interaction, essential for recognition of other people’s identity, gender, age, intentions and emotional state. All faces are symmetrical and share a common 3D structure (i.e., two eyes above the nose, above the mouth), but humans are able to easily indentify hundreds of different faces (McKone & Yovel, 2009). Thanks to the fascination for this extraordinary ability, researchers in the field of social cognitive neuroscience have examined in depth the neural bases of face processing. We will present below only results of studies in the field of neuroimaging, obtained mainly using functional magnetic resonance imaging (fMRI) methodology. Psychophysiological correlates of face and body perception will be presented in Chapter 3.

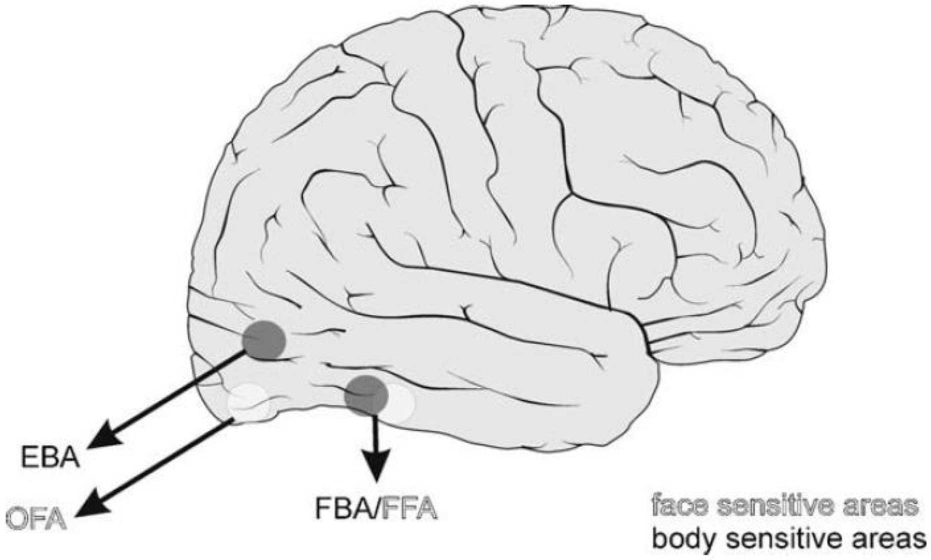


Fig. 1.4: Schematic representation of the location of face sensitive (light shade) as well as body sensitive (dark shade) neural areas (adapted from Minnebusch & Daum, 2009).

Thanks to fMRI studies, a region in the fusiform gyrus was identified, the *fusiform face area* (FFA), which is activated more strongly by passive viewing of faces compared to passive viewing of objects (Fig. 1.4) (Haxby, Hoffman, & Gobbini, 2000; Kanwisher & Yovel, 2006). Bilateral FFA activation correlated with correct face identification, with the highest correlations in the right hemisphere (Haxby et al., 1999; Kanwisher, McDermott, & Chun, 1997; Rossion et al., 2000), suggesting preferential lateralization of face processing over the right FFA. As well as FFA, also the *superior temporal sulcus* (STS) and the inferior and middle occipital gyri showed significantly greater activation during face processing in the same studies, also showing a right hemispheric dominance. The inferior occipital face-sensitive area was named *occipital face area* (OFA; Gauthier et al., 2000) and seems to be sensitive to invariant features of face stimuli, while the STS appears to process dynamic aspects of faces (e.g., expression, gaze).

It was clearly proven that the FFA is specifically involved in face perception and identification (Kanwisher & Yovel, 2006; Kanwisher, McDermott, & Chun, 1997), even if its precise functional role remains to be fully explored and understood. According to an alternative view (the so-called “expertise hypothesis”, Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) the FFA activation may reflect expertise in processing a certain category of visual stimuli. The FFA might thus be activated by any stimulus which the subject perceives as distinct specimen rather than as generic example of a category, independently of the nature of this category (e.g., humans, birds, dogs, objects, etc.). Faces may activate this cortical region because all people are experts in face perception since birth. We will not discuss in depth the expertise hypothesis, since it is not the purpose of this Chapter and it is still debated in literature (Gauthier & Bukach, 2007; McKone & Robbins, 2007; Robbins & McKone, 2007).

Even though body processing was not studied as extensively as face processing, also bodies represent a category of special social stimuli (de Gelder, 2009). As a matter of fact, bodies share important communicative features with faces, i.e., they contribute to recognition of identity, gender, age, intentions and emotional state. As faces, all bodies are symmetric and share a specific 3D structure (i.e., legs connected to the lower part of the torso, arms to the upper part and head on top).

As face perception, also perception of human bodies has been associated with specific cortical areas (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Downing, Jiang, Shuman, & Kanwisher, 2001; Downing & Peelen, 2016; Peelen & Downing, 2017, 2007; Schwarzlose, 2005). The *extrastriate body area* (EBA) (Fig. 1.4) shows greater activation during perception of human bodies and body parts compared to objects or faces (Downing, Jiang, Shuman, & Kanwisher, 2001). The EBA seems to be part of a specialized system for the identification of a stimulus as a human body. EBA activation is also generalized to line drawings, stick figures and silhouettes, indicating that the EBA might have an abstract body representation (Downing, Jiang, Shuman, & Kanwisher, 2001). Moreover, EBA seems to be insensitive to familiarity of bodies, suggesting that this area may be involved in body detection but not identification (Hodzic, Muckli, Singer, & Stirn, 2009). It is interesting to know that EBA activation could be modulated by the presence or absence of a face (Minnebusch, Suchan, & Daum, 2009), but this topic will be discussed more in depth in Chapter 3.

From the anatomical point of view, EBA is located at the posterior end of the inferior temporal sulcus (Fig. 1.4) and overlaps with the visual motion selective and object-form selective areas (Downing, Wiggett, & Peelen, 2007; Peelen & Downing, 2007a). Overlapping activation in this region might reflect a common neuronal system engaged in body, object, and motion perception. A few studies using multi-voxel pattern analysis (MVPA) with fMRI data were performed to investigate whether this overlap reflected a common neural system or processing mechanisms related to this region could differentiate between categories. MVPA is a method aimed to decode the information that is represented in the subject’s brain at a particular time-point. Instead of focusing on individual voxels, MVPA uses pattern-classification algorithms (from machine learning) to determine the information that is represented in a given pattern of activity (Norman et al., 2006). These studies indicated functional independence in overlapping extrastriate cortical regions (Downing, Wiggett, & Peelen, 2007; Peelen & Downing, 2007a, 2007b; Peelen, Wiggett, & Downing, 2006). Using this method, Downing and colleagues (2007) showed that the form of a human body, visual motion and object form elicited independent patterns of fMRI activation.

Furthermore, a second area sensitive to vision of human body form was identified, the *fusiform body area* (FBA) (Peelen & Downing, 2005; Schwarzlose, 2005) (Fig. 1.4). The FBA is located in the posterior fusiform gyrus and responds to the form of the whole body rather than body parts (Taylor, Wiggett, & Downing, 2007), thus showing a specific and separate function from EBA. Moreover, the FBA may distinguish between familiar and unfamiliar bodies (Hodzic, Kaas, Muckli, Stirn, & Singer, 2009).

Therefore, faces and human bodies seem to be processed in adjacent and partially overlapping but distinct networks within the fusiform gyrus (Peelen & Downing, 2005, 2007b; Schwarzlose, 2005), i.e., face- and body-selective activations can be dissociated both anatomically and functionally.

After having discovered selective activation for faces and bodies in these neural areas, some brilliant experts managed to systematize neural networks in neurocognitive models, thus giving a precise theoretical framework to face and body perception.

3. Theoretical models of face and body perception

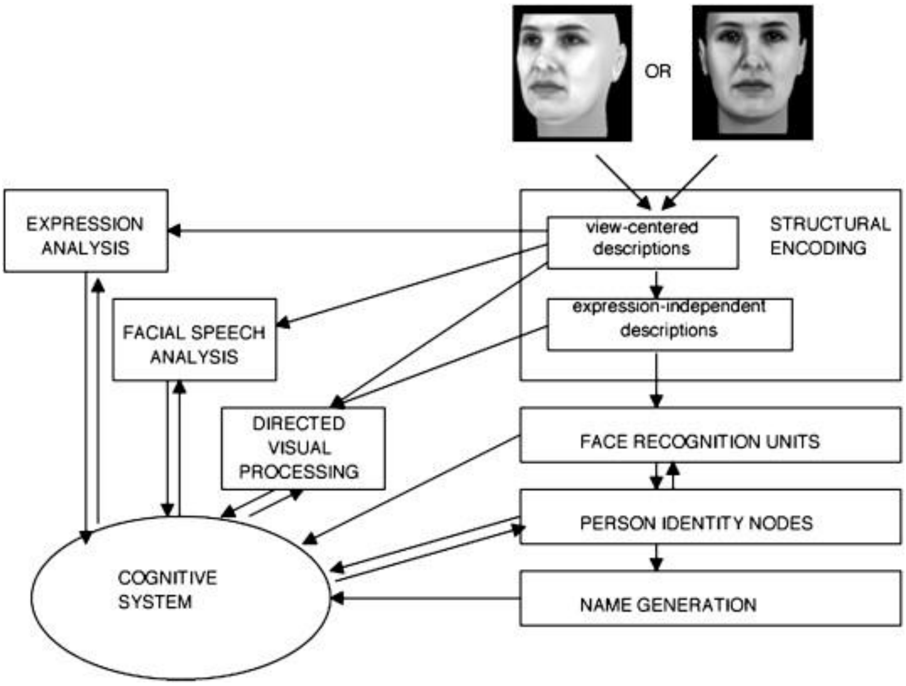


Fig. 1.5: Face perception model by Bruce & Young (1986)

The first box-and-arrows cognitive model of face processing was suggested by Bruce & Young (1986) (Fig. 1.5). According to this model, the perceptual image of a face is analysed through view-centred descriptions (for mainly featural processing) and then transformed in view- and expressions-independent description. The processing occurring during these first modules is named *structural encoding*. After structural encoding, information is passed to two functionally separate pathways, i.e., (i) one pathway (left of the picture) for changeable features recognition, composed of independent modules specialized in processing emotional expression, facial speech and directed visual processing; (ii) a second pathway (low-right of the picture) is aimed to identity recognition and is composed of serial modules specialized in face recognition, identity processing and name generation. The authors hypothesized complete functional independence between the two pathways, since they are aimed to process different information. This independence was corroborated by studies on prosopagnosic patients, which found a double dissociation between identity recognition and emotional expression identification in face processing (Bruyer et al., 1983; Kurucz & Feldmar, 1979).

Burton, Bruce, & Johnston (1990) proposed a revision of Bruce & Young's model: these authors extended this cognitive functional model using an interactive activation implementation. We will not present Burton et al.'s model in detail since it goes beyond the purpose of this Chapter.

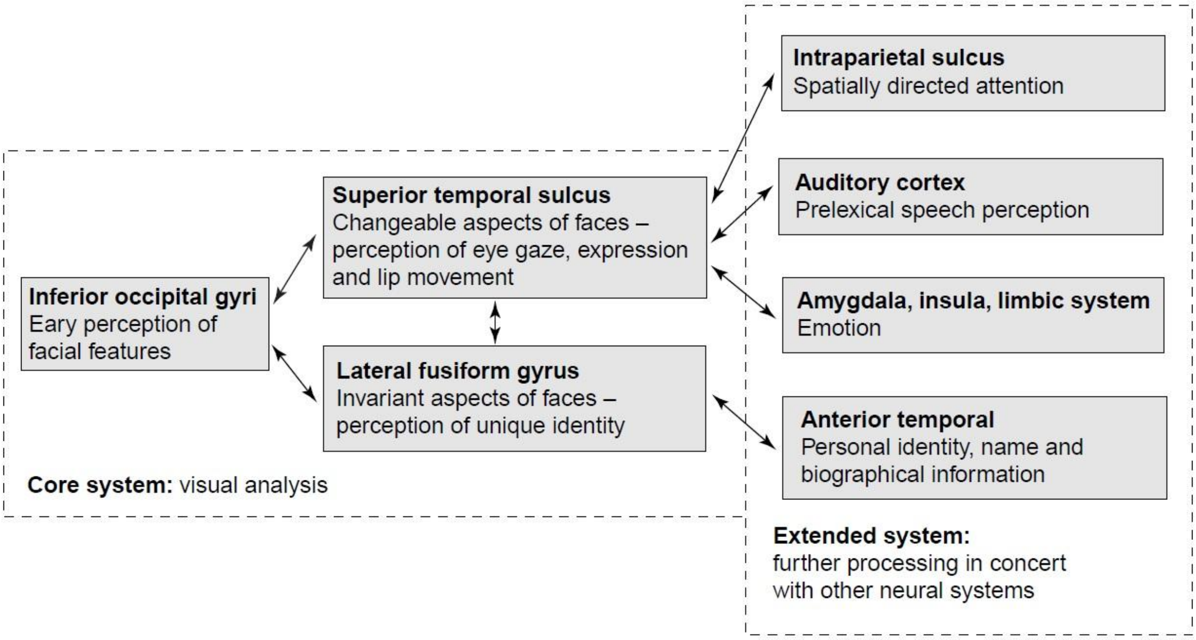


Fig. 1.6: Face processing model by Haxby et al. (2000)

Some years later, a hierarchical neuroanatomical model for face processing (Fig. 1.6) was developed by Haxby, Hoffman, & Gobbini (2000), originating from Bruce & Young's (1986) model. This model identified neural bases of the different modules involved in face processing according to Bruce & Young. This model is divided in a *core system* and an *extended system*. The core system is specialized in visual face analysis and includes three cortical areas: inferior occipital gyri (IOG) (corresponding to the region later named OFA) are assumed to be the bases of Bruce & Young's structural encoding and are dedicated to the extraction of early perceptual facial features. Two independent circuits originate from this area, processing separate information: (i) on the one hand, IOG is connected to STS, which processes changeable and dynamic aspects of faces, i.e., eye gaze, facial expressions and lip movements. This information is strongly involved in socio-emotional processing of faces (Haxby, Hoffman, & Gobbini, 2002), and it is independent from identity recognition. It corresponds to the first pathway in Bruce & Young's model; (ii) on the other hand, IOG showed strong connections with FFA, designated to process invariant aspects of faces. The processing occurring in this area is aimed to recognize the facial identity, thus it corresponds to the first pathway in Bruce & Young's model. It is important to underline that, in Haxby et al.'s model, IOG, FFA and STS have *reciprocal* connections. Therefore structural encoding, processing of changeable and invariant aspects can interact with each other. This property will be further discussed in Chapter 5.

Instead, the extended system comes into play if additional information is extracted from faces. It is composed of several cortical and subcortical areas, which can process information received from the core system. The extended system is multimodal, therefore it can be accessed by both faces and other stimuli. FFA is connected to the anterior temporal lobe, where person identity, name and biographical information are stored. Furthermore, STS is connected to the intraparietal sulcus (IPS; specialized in spatial attention deployment, particularly in respect to gaze direction), to the auditory cortex (processing pre-lexical speech information, in particular prosody) and to the limbic system, insula and amygdala (specialized in emotional information processing).

O’Toole and colleagues revised Haxby et al.’s model (O’Toole, Roark, & Abdi, 2002; Roark, Barrett, Spence, Abdi, & O’Toole, 2003), proving the interaction between the two processing pathways (against the independence hypothesis of Bruce & Young). In particular, these authors studied the contribution of dynamic information to recognition of identity. They proved that dynamic information contribute to identity recognition in non-optimal conditions, e.g., poor visibility, low resolution, or long distance (O’Toole et al., 2002). FFA and STS would thus be both involved in a network aimed to recognize identity, by using both static and dynamic facial information.

With regard to body shape processing, three models of body perception have been put forward so far (see Minnebusch & Daum, 2009 for a review). The first model was suggested by Taylor et al. (2007) and is based on similarities between face and body processing, focusing on EBA and FBA. The second model hypothesizes that visual processing of body shapes involves an extensive fronto-temporo-parietal network (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007; Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Candidi, Ionta, & Aglioti, 2007). The third model proposed a segregation between a *body-detection network* and a *body-identification network* (Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009).

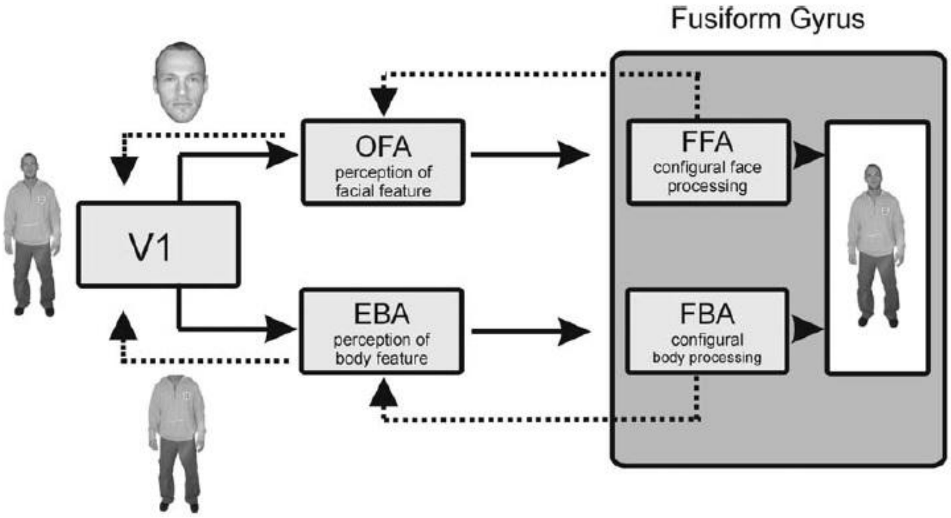


Fig. 1.7: Body perception model by Taylor et al., 2007 (adapted from Minnebusch & Daum, 2009)

Taylor and colleagues (2007) highlighted the fact that two cortical regions seem to be specialized in the perception of human bodies (FBA and EBA) and body parts (EBA only) (Peelen & Downing, 2007b). Taylor et al. have emphasized the parallels of face and body processing considering the similar functional neuroanatomy in the face-sensitive OFA and the body-sensitive EBA, and in the FFA and the FBA (Fig. 1.7). Varying the amount of body information gradually from single fingers to the whole body form, EBA activation remained approximately constant while FBA showed a clear increase when whole torsos were presented. The EBA thus seems to be involved in the basic analysis of body features (analogous to OFA in face processing), while FBA (analogous to FFA) seems to be implicated in processing the configuration of body parts (Taylor et al., 2007). Functional connectivity between face-specific regions was analysed (Fairhall & Ishai, 2007) and the results confirmed this hypothesis, while functional connectivity between EBA and FBA still needs to be explored.

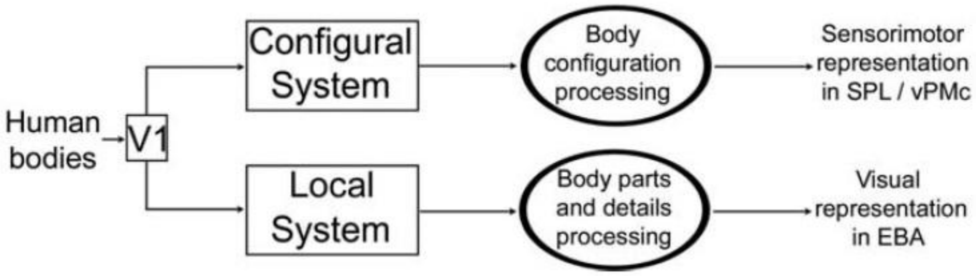


Fig. 1.8: Body perception model by Urgesi et al., 2007

Urgesi, Calvo-Merino, Haggard, & Aglioti (2007) have suggested that the human brain includes two dissociable and independent pathways, specialized for processing human bodies (Fig. 1.8): one pathway processes the whole body in a configural way and involves dorsal stream brain areas and the mapping of observed postures onto the observer’s sensorimotor representation through a mirror mechanism (Rizzolatti & Craighero, 2004). This sensorimotor representation seems to be generated in the superior parietal lobe (SPL) and in the ventral premotor cortex (VPMC). These authors found no Body Inversion Effect (marker of configural processing) after disrupting the activity of SPL and VPMC through repetitive transcranial magnetic stimulation (rTMS). Configural processing of bodies, thus, depends on sensorimotor representations rather than visual representations in the extrastriate visual cortex, which seems to be involved in local body processing. The second pathway processes local features of the body, such as body parts and body form, and is associated with the EBA. Studies on patients with focal lesions in the EBA and ventral premotor cortex (Moro et al., 2008) provide evidence for this model. These authors reported a double dissociation between deficits in body form perception (defined “body form agnosia” and associated with lesions including EBA) and deficits in action perception (defined “body action agnosia” and associated with lesions including VPMC), producing thus important evidence for a dissociation of these two types of perception.

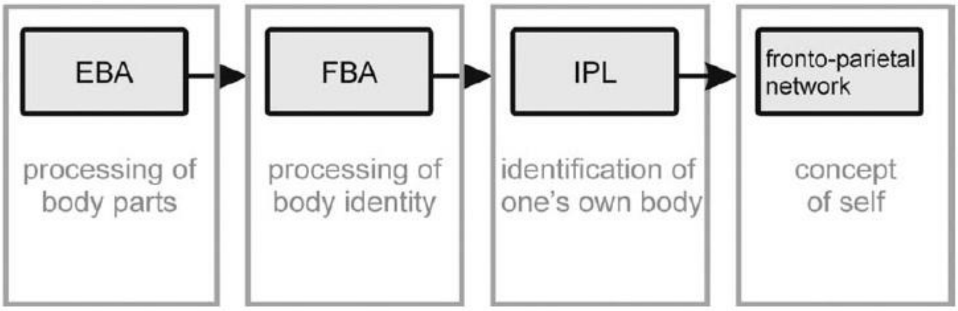


Fig. 1.9: Body perception model by Hodzic et al. (2009a, 2009b) (adapted from Minnebusch & Daum, 2009)

A study by Hodzic, Kaas, Muckli, Stirn, & Singer (2009) found the existence of a third region (beside the previously reported EBA and FBA) in the inferior parietal lobe (IPL) that might be sensitive to the perception of human bodies (Fig. 1.9). This region seems to be involved in the identification of both body parts and whole bodies (Hodzic, Muckli, et al., 2009). Therefore, these authors proposed the existence of distinct (but strictly connected) networks for body detection (the *body-detection network*, including bilateral EBA, right FBA and right IPL) and for body identification (the *body-identification network*, involving areas in the inferior frontal gyrus, the cingulate gyrus, the post-central sulcus, IPL and FBA). The right IPL seems to be critical to perceive one's own body together with the right inferior parietal sulcus, the left posterior orbital gyrus and the lateral occipital gyrus (Hodzic, Kaas, et al., 2009). Moreover, a fronto-parietal network might encode an abstract concept of self.

After having discussed the main theoretical frameworks of face and body perception, we will briefly present below the literature concerning two specific topics in the field of face and body processing: perception of emotional expressions and of approach-avoidance orientation. Both these topics are further investigated in the studies presented in this thesis.

4. Emotional expressions

In social cognition, faces are the most important and most studied stimuli to communicate emotions to other members of the species. Emotional facial expressions are particularly salient stimuli and, in humans, are immediate indicators of affective dispositions in other people. The most famous cross-cultural study in the emotional expression field (Ekman & Friesen, 1971) proved that the facial expression of six basic emotions is universal. They are expressed and recognized by the same facial patterns in many different cultures. The six basic emotions are happiness, sadness, anger, fear, disgust and surprise. These emotions were recognized with comparable accuracy by very different cultures: western individuals and inhabitants of New Guinea.

Emotional expressions recognition may rely on disparate strategies (Adolphs, 2002a, 2002b). For example, recognition of fear from a facial expression may occur by linking the perceptual properties of the facial stimulus to various knowledge-based processes. These include the knowledge of the concept of fear, its lexical label “fear”, the perception of the emotional fear response (or a representation of it) that the stimulus may trigger in the observer, and also knowledge about the motor representations of facial movements necessary to produce the expression shown in the stimulus.

Considering the massive emotional significance of facial expression, numerous recent functional imaging, lesion, and single-cell recording studies have used emotional faces to identify neural substrates of emotional processing. These studies have found that brain areas generally involved in the processing of emotional information are also activated during the processing of facial emotion (Adolphs, 2003). A rapid evaluation of the emotional and motivational significance of facial expression appears to be mediated by the amygdala and orbitofrontal cortex, while structures such as the anterior cingulate, prefrontal cortex and somatosensory areas seem to be linked to the conscious representation of emotional facial expression for the strategic control of thought and action (Damasio et al., 2000; Fusar-Poli et al., 2009; Gorno-Tempini et al., 2001; Kesler-West et al., 2001; Lane, Fink, Chau, & Dolan, 1997; Streit et al., 1999), as well as to the production of concomitant feeling states (Adolphs, 2003).

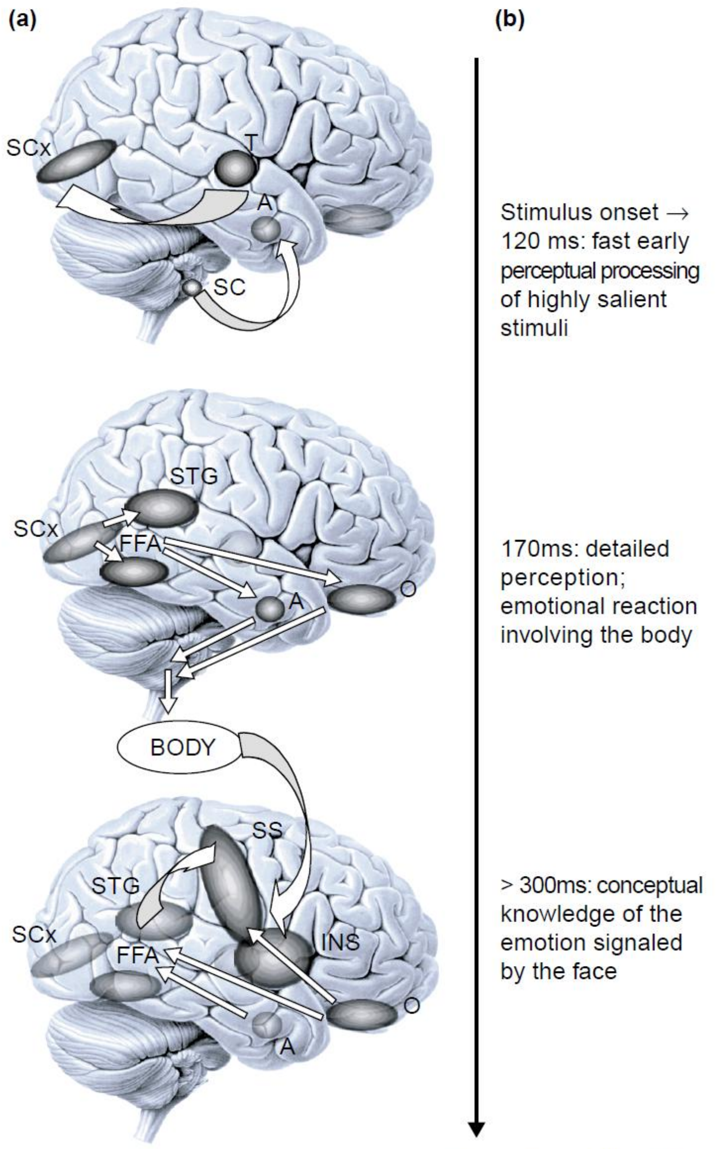
Further separation of neural networks has been demonstrated for processing specific facial emotions (most of the following neural regions are highlighted in Fig. 1.10). The amygdala has often been linked with processing of fearful faces (Adolphs, Tranel, Damasio, & Damasio, 1994; Morris et al., 1996; Morris, Ohman, & Dolan, 1998; Vuilleumier, Armony, Driver, & Dolan, 2001; Whalen et al., 2001) and sad faces (Blair, Morris, Frith, Perrett, & Dolan, 1999; F. Schneider, Habel, Kessler, Salloum, & Posse, 2000), while the cingulate sulcus seems to be activated by happy faces (Kesler-West et al., 2001; Phillips et al., 1998) and the orbitofrontal regions by angry faces (but not exclusively, as we will discuss later) (Blair et al., 1999). Disgust seems to activate preferentially basal ganglia and insula (Adolphs, Tranel, & Damasio, 2003; Calder, Keane, Manes, Antoun, & Young, 2000; Phillips et al., 1997, 1998). Most of the above studies offer evidence of a dissociation as well as an overlapping of the cerebral structures involved in processing different facial emotions. Therefore, it is important to examine further findings related to some of these structures.

The amygdala takes part in recognition of emotional signals through at least two classes of input mechanisms: a subcortical route via the superior colliculus and the pulvinar (in the thalamus), and a cortical route via the visual neocortex. Structures in the subcortical route are activated both when normal individuals are shown subliminal facial expressions of fear (J. S. Morris, Ohman, & Dolan, 1999), and when individuals with blindsight, due to striate cortex damage, show to discriminate emotional facial expressions (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Morris, de Gelder, Weiskrantz, & Dolan, 2001; Tamietto et al., 2009). Lesion studies have consistently found a deficit in recognition of emotional facial expressions following bilateral amygdala damage, typically disproportionate for fear (Adolphs, Tranel, Damasio, & Damasio, 1995; Anderson & Phelps, 2000; Calder, 1996; Calder, Lawrence, & Young, 2001), but sometimes involving multiple negative emotions, including fear, anger, disgust, and sadness (Adolphs, 1999; Adolphs et al., 1999; Schmolck & Squire, 2001).

Nevertheless, such activation seems to depend on passive or implicit processing of the emotion: perceptual processing of facial expressions of fear can activate the amygdala, whereas asking participants to label the emotion can instead result in deactivation (Hariri, Bookheimer, & Mazziotta, 2000). The reduction of amygdala activity in response to emotional expressions, when the demand for explicit emotion recognition is increased, is quite commonly observed (Critchley et al., 2000) and may be mediated by the amygdala's inhibition by frontal cortex.

Also the orbitofrontal cortex seems to play a major role in emotional expression processing. Damage to the orbitofrontal cortex, especially in the right hemisphere, may result in a generalized impairment of emotions recognition from the face and the voice (Hornak, Rolls, & Wade, 1996). These findings are consistent with the increased activation found in right orbitofrontal cortex during fearful faces processing (compared to neutral faces) (Vuilleumier et al., 2001). Opposite to amygdala's activation in response to passive viewing of emotional faces or gender judgements, orbitofrontal regions may be activated when subjects are engaged in a cognitive task requiring explicit identification of the emotion (Nakamura et al., 1999; Narumoto et al., 2000). The orbitofrontal cortex, like the amygdala, can exhibit extremely rapid responses to emotionally salient stimuli, therefore these structures can modulate early aspects of perceptual processing via top-down influences (Kawasaki et al., 2001). The earliest activity that discriminates between emotional facial expressions is seen in midline occipital cortex as early as 80 ms to 110 ms (Pizzagalli, Regard, & Lehmann, 1999), while responses encoding fine-grained, subordinate, information sufficient to distinguish different emotional expressions only appear at around 170 ms (Shlomo Bentin, Allison, Puce, Perez, & McCarthy, 1996; Sugase, Yamane, Ueno, & Kawano, 1999). These findings suggest the possibility that responses to emotional stimuli in visual cortices may be modulated by feedback, perhaps from structures such as the amygdala and orbitofrontal cortex.

Moreover, it was demonstrated that right somatosensory cortices play a critical role in facial expression processing in an investigation of the association between lesion location and facial emotion recognition (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). The interpretation of these findings is based on the literature related to the mirror neuron system (Gallese, 2003; Iacoboni, 2009; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). This interpretation posits that viewing facial expressions of emotion may trigger an emotional response in the perceiver that mirrors the emotion shown in the stimulus (Wild, Erb, & Bartels, 2001), and that representing this emotional response in somatosensory cortices in turn provides information about the emotion. This idea, that knowledge of other people's emotions may rely on simulating the observed emotion, is consistent with several other findings in humans and monkeys (Rizzolatti & Sinigaglia, 2010).



Current Opinion in Neurobiology

Fig. 1.10: Processing of emotional facial expressions as a function of time.

(A) Structures involved in emotion recognition at various time points. A: amygdala; FFA: fusiform face area; INS: insula; O: orbitofrontal cortex; SC: superior colliculus; SCx: striate cortex; SS: somatosensory cortex; STG: superior temporal gyrus; T: thalamus.

(B) Time course of emotion recognition, from the onset of the stimulus at the top, through perception to final recognition of the emotion at the bottom (adapted from Adolphs, 2002a).

Starting from these findings, Adolphs (2002a, 2002b) developed a very elegant model to describe recognition of emotional facial expressions (Fig. 1.10).

1. Upon presentation of an emotionally meaningful stimulus, an individual might envision a first, feed-forward flow of information processing. Initial perception of the face modulates activity in subcortical structures as well as in early visual cortices. The subcortical structures implicated include the superior colliculus and the pulvinar, structures probably specialized for very fast, automatic, and coarse processing of the stimulus. Information from the pulvinar, in turn, feeds into early processing within the amygdala. Cortical structures would include V1, V2, and other early visual cortices, via input from the lateral geniculate nucleus of the thalamus. This early visual processing would extract perceptual information from faces and, after about 80-120 ms in humans, would coarsely categorize the stimulus as expressing an emotion or not, on the basis of the structural properties of the image. The early visual processing may be relatively specialized to extract information about highly salient stimuli and may likely be fairly automatic and obligatory.
2. After this early visual processing stage, regions more anterior and including visual association cortices (FFA, STS) would construct more detailed perceptual representations that depend more on processing the configuration of the face. Separate representations are constructed that make explicit information useful for recognizing identity or recognizing emotion (Haxby et al., 2000). During this fine-grained encoding, posterior temporal cortices and cortex in the fusiform gyrus construct a detailed structural representation of the face, by about 170 ms post-stimulus onset. Contribution of dynamic information to create a representation of the face through temporal areas may occur at this stage of processing.

3. In a third processing stage, late feed-back processes from the orbitofrontal cortex and the amygdala to visual cortices may contribute to produce a conceptual representation of the emotion signalled by the face. This processing stage seems to occur after 300 ms post-stimulus onset. During this stage, also somatosensory-related cortices in the right hemisphere seem to participate in representing aspects of the body state that define an emotion.

Importantly, there would be feed-back influences from the amygdala at multiple temporal scales. Amygdala and orbitofrontal cortices serve to link a perceptual representation of the facial expression to three strategies for producing conceptual knowledge of the emotion: First, they may modulate *perceptual representations* via feed-back. This mechanism might contribute, in particular, to fine-tuning the categorization of the facial expression and to the allocation of attention to particular features. Second, the amygdala and orbitofrontal cortices may trigger *associated knowledge*, via projections to other regions of neocortex and to the hippocampal formation. This mechanism might contribute especially to retrieval of conceptual knowledge about the emotion. Third, they may generate an *emotional response* in the subject, via connections to motor structures, hypothalamus, and brainstem nuclei, where components of an emotional response to the facial expression can be activated. This mechanism might contribute to the generation of knowledge about another person’s emotional state, via the process of simulation, and would draw on somatosensory related cortices in the right hemisphere for representing the emotional changes in the perceiver.

As already mentioned, body shape perception was studied less extensively than face perception in social cognition, and the same goes for emotional expressions of body postures. However, in the last years the *emotional body language* (EBL) found new interest in social cognitive neuroscience and an increasing number of studies were performed to investigate this aspect (see de Gelder, de Borst, & Watson, 2015; de Gelder, 2006; de Gelder, 2009; Minnebusch & Daum, 2009 for extensive reviews).

A first hypothesis in modelling the perception of EBL posited that a single system might be responsible for the perception and production of EBL, and this system may be part of the *mirror-neuron network* (Gallese, Keysers, & Rizzolatti, 2004; Gallese, 2003). According to this hypothesis, perception of emotion is based on the same motor representation which is associated with emotion expression, similar to action understanding and execution. Whereas this was already hypothesized for facial expressions (see above), this theory is even more valid for emotions expressed by body postures or body movements. We would use our own body for the perception of other people and for understanding their emotions and intentions (Gallese, Keysers, & Rizzolatti, 2004). Therefore, the mirror-neuron system seems to play an important role in the perception of both facial and bodily emotional expressions: increased activation were observed in the amygdala, insula, fusiform gyrus and STS while processing EBL (Gallese, Keysers, & Rizzolatti, 2004; Grèzes, Pichon, & de Gelder, 2007; Hadjikhani & De Gelder, 2003), with higher activation for dynamic (compared to static) body expressions in motion-sensitive areas as STS and the premotor cortex (Grèzes et al., 2007).

After analysing the available literature, de Gelder et al. (2006, 2015) postulated a two-system theory of EBL (Fig. 1.11), not very different from Adolphs' model (2002a, 2002b) for the perception of facial expression. This model consists of two separate emotional circuits cooperating with each other: a rapid and non-conscious automatic system including predominately subcortical structures (superior colliculus, pulvinar, striatum, basolateral amygdala) and a cortical system (visual cortices - IOG, the fusiform gyrus and STS - together with frontoparietal motor system and connections between the amygdala and the dorsolateral prefrontal and ventromedial prefrontal cortex) with bidirectional connections to the first system. The second system processes EBL in more detail and predicts behavioural consequences of an emotion by decoding emotional stimuli in combination with past experience, memory and conceptual knowledge. These two systems are connected to a third system, aimed to process body awareness of EBL in relation to body representation (ventromedial prefrontal cortex, anterior cingulated cortex, somatosensory cortex and insula).

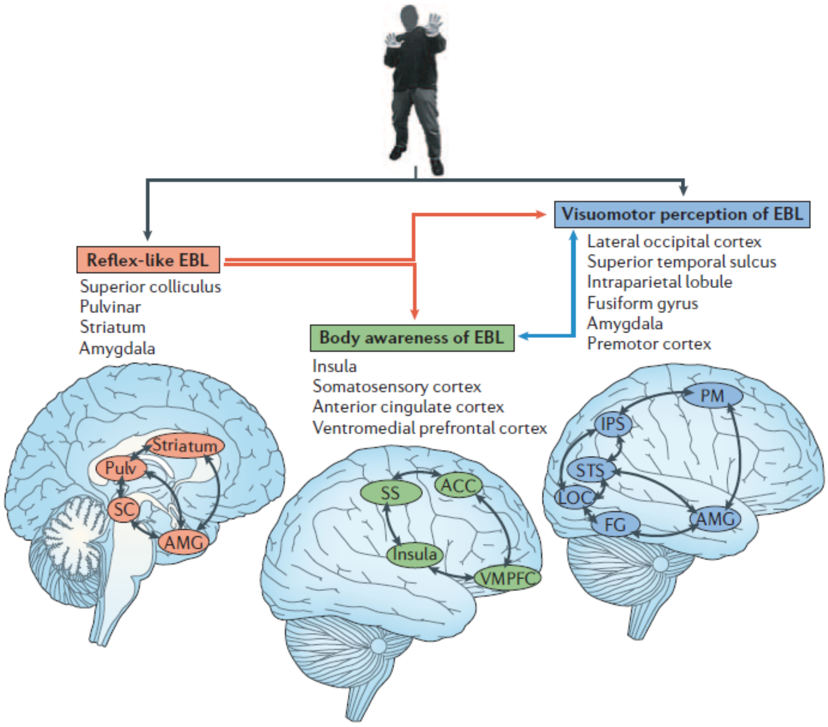


Fig. 1.11: The three interrelated brain networks involved in emotional body language processing according to de Gelder et al. (2006, 2015).

(1) Reflex-like emotional body language (EBL) (orange) involves the superior colliculus (SC), pulvinar (Pulv), striatum and amygdala (AMG).

(2) Body awareness of EBL (green) involves the insula, somatosensory cortex (SS), anterior cingulate cortex (ACC) and ventromedial prefrontal cortex (VMPFC).

(3) Visuomotor perception of EBL (blue) involves the lateral occipital complex (LOC), superior temporal sulcus (STS), intraparietal sulcus (IPS), fusiform gyrus (FG), amygdala (AMG) and premotor cortex (PM).

Visual information from EBL enters in parallel via a subcortical (red) and a cortical (blue) input system. Feed-forward connections from the subcortical to the cortical system and body awareness system are shown in red, reciprocal interactions between cortical system and body awareness system are shown in blue (adapted from de Gelder, 2006)

A brief citation has to be done for Schindler, Van Gool, & de Gelder's (2008) model. They proposed a biologically inspired, hierarchical model of the recognition of emotion expressed by body postures. According to this computational model, discriminations between neutral expressions and the six basic emotions (anger, disgust, fear, happiness, sadness and surprise) can be achieved by input based on static views of body postures, with emotional body language being based on low-level form processing. This computational model seems to bring evidence corroborating de Gelder's model.

5. Approach and avoidance

Approach and avoidance are investigated in association with emotional response, in terms of "behavioural states" (Adolphs 2002a, b). The tendency to approach or avoid an individual may be related to threat (e.g., angry or fearful expressions) or not (e.g., happy or sad expressions). This tendency may be conveyed by different social cues, i.e., facial expression, gaze direction, body posture, vocal prosody, etc.

The investigation of these behavioural tendencies was carried out in the framework of *appraisal theories of emotions* (Frijda, 1986; Lazarus, 1991; Scherer, Schorr, Johnstone, 2001; Scherer, 1992; Scherer, Scherer, & Ekman, 1984). Appraisal theories of emotions hypothesize that emotional responses are generated by appraisals (evaluations, interpretations, explanations) of a stimulus/event. Different appraisals may lead to different specific reactions in different people. With regard to evaluation of social stimuli (e.g., facial expressions), appraisal theories suggest that the face expresses cognitive processes involved both in the orienting of attention (primarily gaze direction) and in the evaluation of emotion-eliciting events. This relationship implies an interaction effect between perceived gaze direction and perceived facial expression in inferring emotions from the face. Thus, gaze direction plays a key role in interpreting emotional expressions, since it becomes part of the overall constellation of facially expressive cues that constitute what we perceive as a facial expression. Many studies have evaluated these theories, especially testing their validity regarding the appraisal of facial expressions (Adams & Kleck, 2003, 2005; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007) and in the updating process in working memory (Artuso & Palladino, 2015; Artuso, Palladino, & Ricciardelli, 2012).

By investigating this behavioural tendency in the framework of appraisal theories, Adams & Kleck developed their *shared signal hypothesis* (Adams & Kleck, 2003, 2005; Adams, Ambady, Macrae, & Kleck, 2006). They postulated that all social cues expressing the tendency to approach or avoid an individual were processed as a whole, in an overall appraisal of the social stimulus (in their case, a face) (Adams & Kleck, 2005). According to their theory, when gaze direction matches the underlying behavioural intent (approach-avoidance) communicated by an emotional expression, the appraisal of that emotion would be enhanced. They proved their theory by performing a series of experiments in which happy and angry (approach-oriented), fearful and sad expressions (avoidance-oriented) were combined with direct (approach-oriented) and diverted (avoidance-oriented) gaze direction. The results of these experiments demonstrated that emotion recognition was faster when emotional expression and gaze direction showed congruent behavioural tendency (Adams & Kleck, 2003). The same result was found also by using trait attributions to neutral faces, blended expressions of fear and anger, different emotional intensity (Adams & Kleck, 2005), and also moving faces visually going near to or far from the participant (Adams, Ambady, Macrae, & Kleck, 2006).

From the neurocognitive point of view, these authors investigated the neural bases of this “shared” appraisal of facial expressions and gaze directions in an fMRI study (Adams, Gordon, Baird, Ambady, & Kleck, 2003). They demonstrated that the amygdala seems to be sensitive to “ambiguous threat”: it showed greater activation while processing approach-oriented expression (anger) with avoidance-oriented gaze direction (diverted) and vice versa. In other words, the amygdala showed to be sensitive to incongruence in the binding between facial expressions and gaze direction. Once again, the amygdala is proven to represent a crucial structure in the appraisal of social stimuli conveying emotions.

This hypothesis was also corroborated by studies using eye-tracking (Rigato, Menon, Farroni, & Johnson, 2013), which showed sensitivity to the gaze-expression congruence for both the approach- and avoidance-oriented emotions in adult participants, and also using EEG: these studies found that gaze-expression congruence increased the amplitude of N170 (an occipitotemporal component linked to structural encoding of faces) (Akechi et al., 2010) or P2 (an occipitotemporal component linked to higher-level conceptual encoding of stimuli) (Rigato, Farroni, & Johnson, 2009) and even later (Klucharev & Sams, 2004) ERP components. We will present and discuss these ERP components more extensively in Chapter 3 and 5.

In a recent study, Paulus & Wentura (2015) proposed that emotions cannot be considered as universally approach- or avoidance-oriented. On the contrary, approach and avoidance reactions to emotional expressions would be triggered by their appraisal based on the specific context. As a matter of fact, they demonstrated that negative emotional expressions (anger, fear, sadness) elicited avoidance reactions if contrasted with expressions of happiness, whereas, if contrasted with a different negative emotional expression, anger and sadness triggered approach reactions and fear activated avoidance reactions. Therefore, these authors concluded that different behavioural reactions may be triggered if the valence (positive/negative connotation) of the 2 emotions presented in a task differ or are the same. Approach and avoidance are not always basic behavioural states, but actually they could be triggered by a more complex appraisal of the emotional cues in the face. This appraisal would be aimed to extract the social message conveyed by facial expression, depending thus also on the context in which they are located.

6. Aim and topics of the thesis

As we saw, social cognition is an extremely broad field of study, sometimes even considered as an approach to studying different fields of knowledge (Carlston, 2013). Therefore, it is necessary to narrow the field of research on specific topics in order to increase our knowledge, always keeping an eye on the big picture of the theoretical framework we discussed.

Investigations carried out in this thesis were aimed in two different directions within the field of social cognition. On the one hand, the first study (composed of two experiments, presented in Chapter 2) was aimed to investigate the influence of social exclusion, a manipulation pertaining the internally-focused system according to Lieberman’s (2007) model, on the perception of two different, but interacting, facial cues: emotional expression and gaze direction. The perception of these cues is clearly supported by the externally-focused system. These features were chosen considering (i) the critical importance of emotional expressions in social cognition, as widely discussed above, (ii) the relevance of gaze as a signal of social inclusion or exclusion (that will be discussed in the next Chapter) and (iii) the interaction between these two features in the appraisal of facial expressions. The identification of gaze direction was specifically impaired by social exclusion, while no impairment was found for emotional expression recognition. The results of this study brought important insights concerning the relevance of gaze as a signal of potential re-inclusion, and how the impaired processing of gaze direction may reiterate social exclusion.

On the other hand, research was carried out in a different direction, investigating and comparing the encoding of faces and bodies. This was done by performing (i) a meta-analytic review on the body inversion effect (in Chapter 3), aimed to investigate consistency and size of this effect, fundamental in studying structural encoding of body shapes; (ii) a study on the neural oscillations involved in face and body inversion effects (in Chapter 4). Neural oscillations were measured by means of the electroencephalographer (EEG) and showed that configural processing of faces and bodies involve different perceptual mechanisms; (iii) a study investigating the influence of inversion and emotional expression on the visual encoding of faces and bodies, and how these two manipulations may interact (in Chapter 5). The neural correlates of these processes were investigated by means of event-related potentials (ERPs). Both inversion and emotional expressions were shown to influence the processing of these stimuli, during different stages and through different perceptual mechanisms, but a systematic study in which inversion and four different emotional expressions were manipulated in both faces and bodies was never performed. These studies were aimed to shed new light on how faces and bodies are perceived, how they convey emotional information, pointing out similarities and differences between these two stimulus categories.

CHAPTER 2

EXCLUDE THE EMO:

How social exclusion modulates social information processing:

a behavioural dissociation between facial expressions and gaze direction

1. Introduction

This Section presents the state of the art in the literature about social exclusion, with a specific focus on the topics addressed in the study. It will start with a generic presentation and definition of what social exclusion is and its effects on cognitive processing. Then the discussion will narrow to the effects of social exclusion on affective state and social information processing. After this literature review, the study will be presented.

1.1. What is social exclusion?

Everyone has experienced social exclusion in different measures. Being excluded, ostracised, or even simply ignored is part of everybody's life. Thus, everyone knows how painful, crippling, and confusing this experience can be. This pain arises because being excluded is a threat to our need to belong (Baumeister & Leary, 1995), one of the most fundamental human needs.

In psychological terms, social exclusion is defined as being ignored and excluded by someone (Williams, 2007). Despite subtle definition differences, the terms "ostracism" and "social exclusion" will be used as synonyms in this thesis. In addition to our personal experience, we know from many studies that social exclusion has specific impacts on our behaviour, cognitive abilities, emotional feelings, and especially our motivation, defined as fundamental needs (see Baumeister, Brewer, Tice, & Twenge, 2007 for a complete review).

From the behavioural point of view, ostracism does appear to have a very strong effect on aggressiveness, as shown in different studies (Chow, Tiedens, & Govan, 2008; Riva, Romero Lauro, DeWall, Chester, & Bushman, 2014; Twenge, Baumeister, & Tice, 2001). This reflects the effect of the anger experienced during ostracism: Chow and colleagues (2008) showed in their studies that self-reported anger is the strongest mediator between experienced social exclusion and anti-social behaviours (especially for unfair social exclusion).

The effects of social exclusion on cognitive performance are very well known: ostracism can cause a significant decrease in different cognitive skills as a consequence of the experienced threat to individuals' need to belong (Baumeister et al., 2007), also defined as a "defensive state of cognitive deconstruction" (Twenge, Catanese, & Baumeister, 2003). This effect was clearly shown by worse performance in IQ tests (Baumeister, Twenge, & Nuss, 2002), time interval estimations, proverbs explanations, simple reaction times tasks (Twenge et al., 2003), and purely cognitive tasks such as the antisaccade task (Jamieson, Harkins, & Williams, 2010). This last study also shows an important effect of re-inclusion, which will be discussed later. The ostracism effect on cognitive performance is also supported by psychophysiological evidence: Otten & Jonas (Otten & Jonas, 2013) measured the electrophysiological responses to a Go/No-go task performed after social inclusion/exclusion. In No-go trials, excluded participants showed specific ERP patterns: larger amplitude of N2 and smaller amplitude of P3 components, reflecting an increased ability to detect response conflicts and decreased inhibition of predominant (unwanted) responses, respectively. Inhibition and self-regulation are indeed some of the cognitive features affected by ostracism and threat to the need to belong: socially excluded participants were shown to lose self-control on different measures, as demonstrated by impulsive eating, reduced persistence on a frustrating task, less tendency to show a healthful but unpleasant behaviour, and impaired performance on an attention control (dichotic listening) task (Baumeister, DeWall, Ciarocco, & Twenge, 2005).

1.2. Social exclusion and affective state

If the effect of ostracism on cognition is often referred to as "cognitive deconstruction", its effect on emotional feelings is often defined as "emotional (or affective) numbness". Despite the fact that on an intuitive ground it is easy to think that the dominant reaction to ostracism could be immediate emotional distress, in fact the most common response was emotional insensitivity (Baumeister et al., 2007; DeWall & Baumeister, 2006), which often led to a lack of empathy and prosocial behaviour (Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007). In addition to cognitive performance, Twenge *et al.* (2003) also studied the influence of social exclusion on emotions, by using both explicit measures and an implicit emotion task (word guessing). Although clear differences in explicit measures were not found, the study showed that excluded participants tended to report fewer emotional words in the implicit emotion task, displaying a deficiency in emotional information processing.

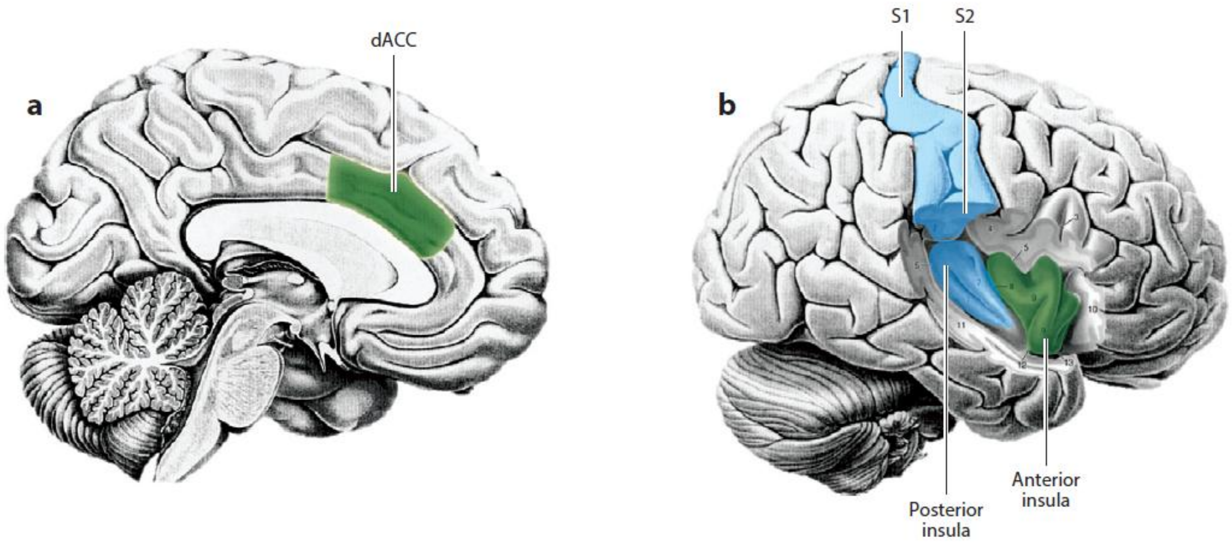


Fig. 2.1: Cortical neural regions associated with the affective and sensory components of pain.

The neural regions associated with the affective component of pain (in green) include the dorsal anterior cingulate cortex (dACC) (a) and the anterior insula (b).

The neural regions associated with the sensory component of pain (in blue) include the posterior insula, primary somatosensory cortex (S1), and secondary somatosensory cortex (S2) (b) (adapted from Eisenberger, 2015)

This effect of emotional numbness has often been related to the effect of physical numbness generated by ostracism: as a form of induced analgesia, social exclusion reduces sensitivity to physical pain, increasing both an individual’s threshold for and tolerance to it (DeWall &

Baumeister, 2006). Therefore, a very fruitful line of research has been devoted to studying the overlap between physical and social pain (induced by social exclusion), the so-called *pain overlap theory* (see Eisenberger, 2015 for a complete review) (Fig. 2.1). On the one hand, several fMRI studies found that there is a strong overlap between neural areas active during experiences of physical and social pain, especially the dorsal anterior cingulated cortex (dACC) and the anterior insula (Eisenberger & Cole, 2012; Eisenberger & Lieberman, 2004; Eisenberger, Lieberman, & Williams, 2003; Macdonald & Leary, 2005; Slavich, Way, Eisenberger, & Taylor, 2010; Way, Taylor, & Eisenberger, 2009), supported by studies using behavioural or self-report data (Eisenberger, Jarcho, Lieberman, & Naliboff, 2006; Riva, Wirth, & Williams, 2011). On the other hand, some recent studies, specifically focused on psychological features of painful experience, have set a boundary condition to pain overlap theory (Riva & Andrighetto, 2012; Riva, Williams, & Gallucci, 2014), stressing specific characteristics of physical and social pain that are not overlapping. Nevertheless, the debate on pain overlap theory boundaries is still open, and it’s not the purpose of this work going deeply into it.

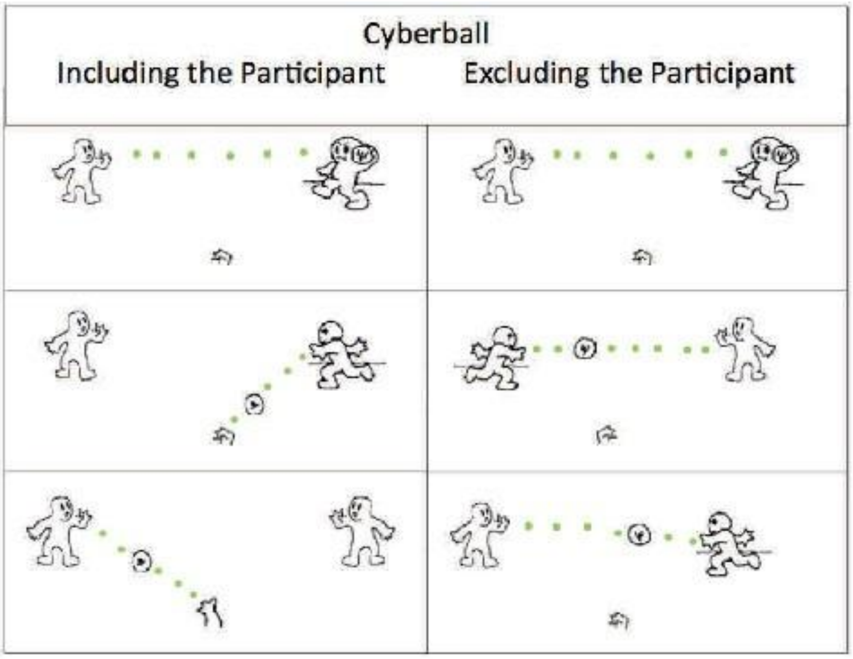


Fig. 2.2: A display showing the typical dynamic passages during a session of the Cyberball game (adapted from Williams & Jarvis, 2006)

In order to explain in a more specific and accurate way how social exclusion manipulations work, we present Cyberball (Williams, Cheung, & Choi, 2000; Williams & Jarvis, 2006) (Fig. 2.2). Cyberball is a manipulation-inducing method of mild social exclusion that is very broadly used since it is fast (lasting approximately 3 min) and easy to administer. It has shown very consistent effects, recently collected in a comprehensive meta-analysis (Hartgerink, van Beest, Wicherts, & Williams, 2015). Cyberball indeed showed its efficacy in many different experimental contexts (Carter‐Sowell, Chen, & Williams, 2008; Gonsalkorale & Williams, 2007; van Beest & Williams, 2006; Zadro, Williams, & Richardson, 2004) and in different populations: children (Zadro et al., 2013), adolescents (Ruggieri, Bendixen, Gabriel, & Alsaker, 2013a), bullying victims (Ruggieri, Bendixen, Gabriel, & Alsaker, 2013b), alcohol-dependent individuals (Maurage et al., 2012), and individuals affected by borderline personality disorder (Staebler et al., 2011). It is a simple ball-tossing game in which the participant is led to believe that he or she is playing online with other people. The participant can be included, receiving one-third of the passes from the other characters, or excluded, receiving only two passes in the beginning of the game and none thereafter.

1.3. Social exclusion and social information processing

Many studies have investigated the consequences of social exclusion on experienced emotions and feelings, but only a few have examined in depth how emotional and social information is processed by an individual who has experienced ostracism. It is well known that social information is usually processed in a specific way, as shown by the activation of selective brain regions or networks (see previous Chapter). In addition, since ostracism is primarily a social phenomenon, one may reasonably expect that it affects social information processing, assuming an interaction between the two systems described by Lieberman (2007) and presented in the previous Chapter.

The best-known effect of ostracism on social information processing is the so-called "tuning to positivity" (DeWall et al., 2011; DeWall, Maner, & Rouby, 2009). In their 2009 study, DeWall and colleagues revealed that socially excluded participants showed an enhanced selective attention to social signals of acceptance, in particular, smiling faces. This effect was tested on several tasks including visual search, eye-tracking, and visual cueing. In the 2011 study (DeWall et al., 2011), they extended these results by showing that social exclusion increased non-conscious positive affect. This process was revealed to be automatic and unconscious. In fact, it was detected only in tasks that required an implicit processing of emotional information (spontaneous recall of more positive memories, higher weight to positive emotions in words judgement and words completion) but was not shown in explicit emotional tasks (overestimation of explicit distress and underestimation of implicit positivity in an imagined situation of social exclusion). Interestingly, this "tuning to positivity" effect was not found in excluded participants with depressive symptoms or low self-esteem (*ibidem*). Therefore, the automatic emotion regulation and enhanced selective attention, both tuned to make positive emotions and acceptance-related signals more accessible, were described as protective mechanisms related to positive mental health.

Other studies have explored the importance of re-inclusion after experiencing social exclusion: since ostracism threatens people's fundamental need to belong (Baumeister et al., 2007; Baumeister & Leary, 1995), looking for any possible signal of social inclusion may become a priority for these individuals. Socially excluded people are more accurate in discerning real from fake smiles (Bernstein, Young, Brown, Sacco, & Claypool, 2008), manifesting higher accuracy in detecting re-inclusive signals. In another experiment, socially excluded participants showed worse performance on a cognitive task, but when they knew they could have a chance of being re-included, they performed even better than included participants (Jamieson et al., 2010). This effect was explained as higher motivation to increase their own inclusionary status by demonstrating their worth on the cognitive task. In addition, excluded people tend to recall social events more accurately (Gardner, Pickett, & Brewer, 2000) and show higher motivation to create social binding with new partners (Maner, DeWall, Baumeister, & Schaller, 2007). These effects were again explained as a consequence of the threatened need to belong. To close the loop, individuals with a greater need to belong tend to be more attentive to and accurate in decoding social cues (Pickett, 2004)

Considering the existing work in the literature, it is clear that some effects of social exclusion on social information processing exist, but they still need to be explored in depth. We know that social exclusion improves the processing of re-inclusive signals, but many questions concerning the interaction of these two processes are still unanswered.

The study we are going to present is aimed to explore more in depth some specific features of the interaction between these processes.

1.4 Aim of the study

We decided to investigate social information processing (after social inclusion/exclusion) using faces. Facial processing was broadly studied (see Chapter 1) and robust literature described how faces are perceived through very elegant models (Adolphs, 2002b; Haxby et al., 2000). More specifically, this study was based on appraisal theories of emotions (see Chapter 1, Paragraph 5) and, starting from the shared signal hypothesis (Adams & Kleck, 2005), it was aimed to investigate the processing of emotional expressions and gaze direction (and their combination) after social inclusion/exclusion.

Many research questions could be extrapolated from this context. For instance, a scared face looking away from us is a socially relevant stimulus that may warn us about an approaching danger, even if it is not related to exclusion or inclusion. Other combinations of facial expression and gaze direction may have different meanings to included and excluded participants. What is the role of important personal differences, such as participants' empathy and gender, in these processes? The aim of this study is to answer these questions about how social information processing is affected by social exclusion.

Therefore, we decided to study the processing of faces with different emotional expressions and gaze directions after social exclusion or inclusion. The processing of these stimuli was tested in two different tasks, asking alternatively explicit processing of one out of the two features: emotional expression recognition or gaze direction recognition. By doing so, we aimed to explore if there were any differences in explicitly and implicitly processed features (i.e., emotion and gaze direction, respectively, during emotion recognition, or vice-versa during gaze direction recognition).

Several hypotheses can be made: since it is known that social exclusion can impair cognitive abilities (Twenge et al., 2003) or enhance social information processing (DeWall et al., 2009), we expected that (i) social exclusion could enhance or impair some or all facial features processing, and (ii) this enhancement/impairment was moderated by participants' empathy. In the literature (Twenge et al., 2007), in fact, the effects of social exclusion on prosocial behaviour were shown to be mediated by participants' empathy. Therefore, it is reasonable to expect that this construct may be a moderator of the effects of social exclusion on social information processing. Finally, we expected that (iii) this enhancement/impairment was dependent on participants' gender, as differences between males and females in social information processing have been widely reported (Pavlova, 2016), and the effects of social exclusion have been shown to change depending on participants' gender (Williams & Sommer, 1997).

2. EXPERIMENT 1

To test these hypotheses, Experiment 1 was conducted. The participants were required to (i) fill in the Empathy Quotient questionnaire (Baron-cohen & Wheelwright, 2004) to record a validated measure of empathy, (ii) take part in the Cyberball procedure (one half of the participants excluded, one half included), (iii) fill in the Positive And Negative Affect Scale (PANAS) (Watson, Clark, & Tellegen, 1988) as a self-report measure of positive and negative emotions felt after social exclusion/inclusion, and (iv) take part in a behavioural task in which they were asked to recognize emotional expressions or gaze direction from displayed faces.

2.1. Methods

2.1.1. Participants

A total of 62 participants were recruited mostly among psychology undergraduate students at the University of Milan – Bicocca. Two participants were excluded from the analyses since one could not understand the instructions for the tasks, and one already knew the bogus nature of the Cyberball paradigm (and thus could not be considered a naïve participant). The remaining 60 participants (30 males and 30 females, mean age = 24.9 yr, std dev = 3.79) were included in the analyses. In both Experiment 1 and Experiment 2, participants received course credits for their participation in the study. Both experiments were conducted with the approval from the local Ethical Committee of the University of Milan – Bicocca and in accordance with the ethical standards established in the 1964 Declaration of Helsinki. All participants had normal or corrected-to-normal vision. None of the 60 remaining participants knew about the Cyberball procedure before taking part in the experiment.

2.1.2. Materials and procedure

The experiment was carried out in a dimly illuminated room. After reading and signing the informed consent, participants were seated approximately 60 cm away from a 19-inch LCD monitor (resolution: 1024 × 768 pixels; refresh rate: 60 Hz) interfaced with a personal computer with an Intel® Core™ i7-3517U 1.90 GHz processor (see Fig. 2.3).

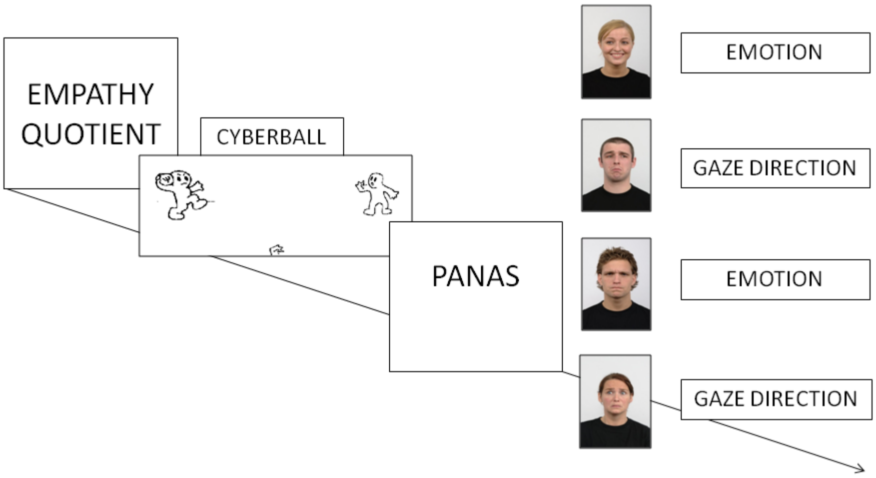


Fig. 2.3: Experimental procedure for Experiment 1.

To begin with, participants filled in a computerized version of the Empathy Quotient (EQ) questionnaire (Baron-cohen & Wheelwright, 2004), presented using E-Prime® 2.0 (W. Schneider, Eschman, & Zuccolotto, 2007) software. This questionnaire consisted of 60 statements: 40 questions assessing participants' empathy and 20 filler questions. Participants were asked to respond to each statement choosing among four possible answers ("Strongly agree", "Slightly agree", "Slightly disagree", "Strongly disagree") using their mouse. The rough scores and category scores were recorded (according to the authors' cut-offs, explained in the Results section).

After completing the EQ questionnaire, participants took part in the Cyberball procedure (Williams & Jarvis, 2006). The Cyberball game was presented using Inquisit® 4 (Draine, 2014) software. Half of the participants were included during this procedure, receiving one-third of the passes; the other half were excluded, receiving only two passes in the beginning of the game and none thereafter. The number of male and female participants was balanced in each condition (inclusion: 15 males, 15 females, exclusion: 15 males, 15 females).

Then, participants filled in the PANAS questionnaire (Watson et al., 1988) to assess participants' felt positive and negative emotions just after the Cyberball game. The questionnaire was presented in computerized form using E-Prime® 2.0 (W. Schneider et al., 2007) software. A list of 20 adjectives (10 positive and 10 negative, in mixed order) was presented to participants, and they were asked to indicate to what extent they were feeling the emotion described by the adjective at that precise time.

After the PANAS questionnaire, participants began the experimental task. This was performed using E-Prime® 2.0 (W. Schneider et al., 2007) software. The stimuli used in this task were 96 pictures of Caucasian faces taken from the Radboud Faces Database (RaFD) (Langner et al., 2010). The faces were chosen using 8 different identities (4 male actors and 4 female actresses; 4 identities were used only during the training phases): for every identity, 12 pictures were chosen, representing 4 different emotions (happiness, sadness, anger and fear) combined with 3 different gaze directions (direct, left and right). These pictures were presented in a size of 25 x 30 cm (681 x 1024 pixels) and subtended a visual angle of 23° x 26.6°.

The experimental task was divided in 4 alternating blocks in order to avoid learning effects. Depending on the block, participants were asked to perform 2 different tasks: during the first and third blocks, they were asked to identify facial expressions, and during the second and fourth blocks, they were asked to identify gaze direction. Participants could respond by pressing different keys on the keyboard: during the emotion recognition task they pressed key "Q" for happiness, key "D" for sadness, key “K” for anger and key “P” for fear; during the gaze direction recognition task they pressed key “C” for left, the spacebar for direct and key “M” for right. The keys were marked using adhesive labels representing emoticons (for keys “Q”, “D”, “K”, “P”) or arrows (for keys “C”, “M”, and the spacebar). The association between every key and every emotion/gaze direction was reported in the experimental instructions and by the experimenter him- or herself before the beginning of the experiment. Participants were asked to respond as accurately and quickly as possible. The instructions were shown at the beginning of each block and repeated after every training phase.

Every trial was composed of the presentation of the face (selected in random order) for 1 s, followed by a black screen for maximum of 5 s. Participants could respond during both the presentation of the face and the black screen. If participants had not answered 5 s after the black screen was shown, the trial was considered unanswered, and the following trial was presented. A grey screen lasting 1 s followed every response, before the presentation of the following stimulus.

Every block was composed of 12 training trials and 64 test trials. During the test phase, every stimulus with a direct gaze was presented twice in order to balance the doubled number of stimuli with averted gazes (left and right). After every training phase, participants were given feedback reporting how many trials were answered correctly out of 12. The identity of the stimuli varied across the training phases (one different identity for each training phase), while the 4 identities presented during the test phase were the same across all blocks.

After completing the experimental tasks, participants were debriefed about the experiment (especially about the bogus nature of the Cyberball game) and the experimenter answered their questions.

The entire experiment lasted approximately 25 min. Participants were free to interrupt the experiment in any moment and to take a brief pause between different blocks.

2.2. Results

Statistical analyses were performed using RStudio software (version 1.0.44, (RStudio Inc., 2016)), based on R software (version 3.3.2, (R Core Team, 2016)). Plots were created using the open-source package “ggplot2” (Wickham, 2009). Power analyses were performed using the open-source package “pwr” (Champely, 2016). Mixed Effect Linear Model analyses were run using the open-source packages “lme4” (Bates, Maechler, Bolker, & Walker, 2014) and “lmerTest”(Kuznetsova, Brockhoff, & Christensen, 2015). Post hoc comparisons were performed using the open-source package “lsmeans”(Lenth, 2016). R^2 computations were performed using the open-source package “MuMIn” (Barton, 2016).

2.2.1. Power Analysis

First, a power analysis was performed before collecting data in order to determine how many participants were needed to find reliable results. The power analysis was performed for general linear models, considering f^2 as a measure of effect size. f^2 is a measure of effect size based on R^2, as shown in Formula 1, and is considered to be the most reliable effect size measure in Mixed Effects Models (Selya, Rose, Dierker, Hedeker, & Mermelstein, 2012), which will be used in further analyses. f^2 is typically used as a measure of effect size with continuous dependent variables. In fact, we have also used it (as a function of R^2 changes) for effects computed on participants’ accuracy (binomial) because there is no literature related to other effect size measures in mixed effects models.

$$f^2 = \frac{R^2}{1 - R^2}$$

Formula 1: Formula used in order to calculate f^2 effect size from R^2.

To determine the strength of the effect size, we based our decision on a meta-analysis assessing the effects of the Cyberball procedure (Hartgerink et al., 2015), which found a large effect (d > 1.4) of social exclusion. We decided to consider a medium-large effect of social exclusion in our power analysis, in order to be conservative: $f^2 = 0.3$ is suggested as a medium-large effect size (Jacob Cohen, 1988). Other parameters were set in the analysis: numerator degrees of freedom were set to 1, since we were mainly interested in the main effect of Exclusion and in the interaction effect of Exclusion * Task[1] (both effects have 1 degree of freedom); Alpha (Type I error probability) was set to 0.05; and the power of the test (1 - Type II error probability) was set to 0.95. This power analysis led to the result of 43.33 degrees of freedom for the denominator, suggesting that testing 44 participants would give a reliable result. We decided to test 60 participants in order to be conservative and to find even more reliable results.

All of the following analyses were performed using (Linear or Generalized Linear) Mixed Effects Models (LMM or GLMM). Since the most appropriate use of these models is under debate (e.g., 75,76), it is important to specify the decisional pipeline we followed to create the models. First, all of the fixed effects that allowed the model to converge were included. This inclusion typically meant keeping a full factorial model for LMM, but not for GLMM. The same criterion was used to decide whether to include the random effects. In addition, we included only random effects that presented a correlation $|r| < .80$ with other random effects in order to avoid overfitting.

---

[1] As a matter of fact, Exclusion * Task is a between-within subjects effect. We decided to keep $f^2 = 0.3$ in this effect as well in order to be conservative: if exclusion and task factor are not correlated, the power remains 0.95; if they are correlated, the power increases.

Whenever we needed to choose between two random effects that fit the previous criteria but would not allow the model to converge if taken together, we performed two Likelihood Ratio Tests (LRTs) with a null model and chose the model with the best resulting LRT. The significance of each effect was estimated using the Satterthwaite approximation for degrees of freedom in LMMs and performing LRTs with corresponding null models in GLMMs.

2.2.2. Main analyses

The first main analysis for this experiment was a GLMM using the following as independent factors:

- Exclusion (Cyberball manipulation; between subjects; 2 levels: included, excluded),
- Task (experimental task; within subjects; 2 levels: emotion, gaze direction),
- Direction (gaze direction in stimuli; within subjects; 2 levels: direct, averted),
- Emotion (emotion expressed by the stimuli; within subjects; 4 levels: happiness, sadness, anger, fear)

Participants' Accuracy (binomial: 0-1) was used as the dependent variable. The distribution used in the GLMMs was binomial. Included fixed effects are listed in Table 1, while included random effects are listed in Table 2. All tables are available in the Appendix. The R^2 calculations of the model were as follows: Marginal R^2 (considering only the variance explained by fixed effects) = 0.24 and Conditional R^2 (considering also the variance explained by random effects) = 0.34 (Nakagawa & Schielzeth, 2013).

The statistically significant fixed effects were as follows: Emotion: χ^2 (3) = 195.95, p < .001; Direction: χ^2 (1) = 39.331, p < .001; Task: χ^2 (1) = 443.16, p < .001; Emotion * Task: χ^2 (3) =

72.795, p < .001; Direction * Task: χ^2 (1) = 5.109, p = .024; and Exclusion * Task: χ^2 (1) = 6.3085, p = .012.

The last effect (Exclusion * Task; Fig. 2.4) is the most interesting one according to our hypotheses, since it is the only statistically significant effect involving an interaction with the manipulation of social exclusion. We then probed this interaction effect with Simple Effect, in order to understand how social exclusion influenced different experimental tasks. A Simple Effect analysis is analogous to post hoc multiple comparisons but is only used to test an interaction effect. In this analysis, the difference between two (or more) groups (in our case, included and excluded participants) is tested under two (or more) conditions (i.e., the two experimental tasks) (Cohen, Cohen, West, & Aiken, 2013). In this way, we found a statistically significant difference between included and excluded participants in the gaze direction identification task (included mean = 0.982; excluded mean = 0.973; *z* = 2.227; p = .026), but not in the emotion recognition task (included mean = 0.900; excluded mean = 0.902; *z* = 0.410; p = 0.682).

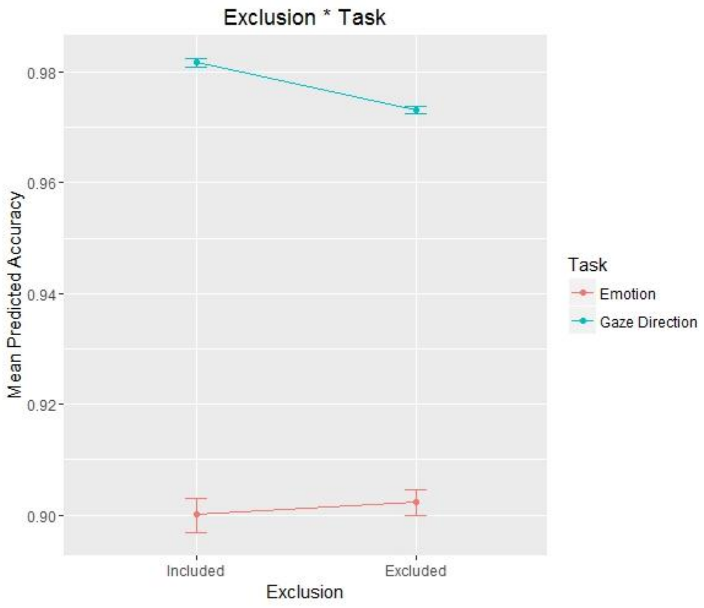


Fig. 2.4: Plot representing the effects of social exclusion in different tasks on participants' Accuracy in Experiment 1. In this and following plots dots represent the mean value and error bars represent 95% confidence intervals.

The second main analysis for this experiment was a LMM using the same independent variables of the previous model and participants' response times (RTs; continuous) as the dependent variable. Trials containing errors (Accuracy = 0) and outliers were removed from this analysis. To identify outliers, we compared the same model performed on 2 different datasets, where trials exceeding the average ± 2 or 3 standard deviations for each participant were removed. Since the results did not differ on a significant level between the two models, we kept 3 standard deviations as a cut-off. RTs were logarithm-transformed in order to obtain a normal distribution of the residuals. Fixed effects included interactions across all levels among the four independent variables in a full factorial model. Included random effects are listed in Table 3. The R^2 calculations of the model were as follows: Marginal $R^2 = 0.42$; Conditional $R^2 = 0.58$.

The statistically significant fixed effects were as follows: Direction: F (1, 57.9) = 7.4, p = .009; Emotion: F (3, 57.8) = 118.8, p < .001; Task: F (1, 13875.2) = 12691.4, p < .001; Direction * Emotion: F (3, 13858.4) = 3.7, p = .011; Direction * Task: F (1, 13885.1) = 5.5, p = .019; Emotion * Task: F (3, 13894) = 234.5, p < .001; Exclusion * Task: F (1, 13875.2) = 11.2, p < .001; and Exclusion * Task * Direction: F (1, 13885.1) = 6.5, p = .011.

The last two effects (Exclusion * Task and Exclusion * Task * Direction) were the only statistically significant effects containing an interaction with the manipulation of social exclusion. We then probed these interaction effects with Simple Effect. In Exclusion * Task interaction, we found that excluded participants were slower than included ones (excluded mean = 939 ms; included mean = 865 ms; t (59.54) = -1.969; p = .0536), approaching a statistically significant difference during the emotion recognition task, while there was no significant difference during the gaze direction identification task (excluded mean = 577 ms; included mean = 548 ms; t (59.18) = -1.257; p = .2136). The Simple Effect probing the Exclusion * Task * Direction interaction showed that the trend of exclusion found in the emotion recognition task was mainly carried by stimuli with direct gaze (included mean = 853 ms; excluded mean = 927 ms; t (61.25) = -2.126; p = .0375). All other comparisons between included and excluded participants across Task and Gaze direction were not significant.

2.2.3. Analyses with Empathy Quotient

Then, four different analyses were performed in order to understand the role of the Empathy Quotient score as a moderator of the previous effects, maintaining the previous independent variables. Two analyses were performed on participants' Accuracy (using the structure of the first main analysis) and two on participants' RTs (using the structure of the second). The first one used the Empathy Quotient score (centred on the overall mean) as a moderator in a GLMM but did not show any significant interaction effects, including the EQ score. The second analysis used the Empathy Quotient categories as a 4-level moderator in a GLMM, as defined by Baron-Cohen's cut-offs (Baron-Cohen, 2004): "Low" category: EQ < 32; "Medium": 33 < EQ < 52; "Over the mean": 53 < EQ < 63; and "Very High": 64 < EQ < 80. The only statistically significant effect in the interaction with EQ categories was EQ categories * Task (χ^2 (2) = 8.24, p = .016), which was irrelevant for our hypotheses.

The third analysis used the EQ score as moderator and RTs (log-transformed) as the dependent variable in a LMM. Fixed effects included interactions across all levels among the five independent variables in a full factorial model. Included random effects are listed in Table 4.

The most relevant effect was the significant main effect of the EQ score (Fig. 2.5): t (73) = -2.674, p = .009. This effect showed that participants with higher EQ scores responded more quickly. Another significant effect was the EQ score * Task: F (1, 13848.5) = 26.5, p < .001. This effect shows that the slope of the previous effect was more negative in the emotion recognition task, but we are not going into further detail since it did not interact with social exclusion.

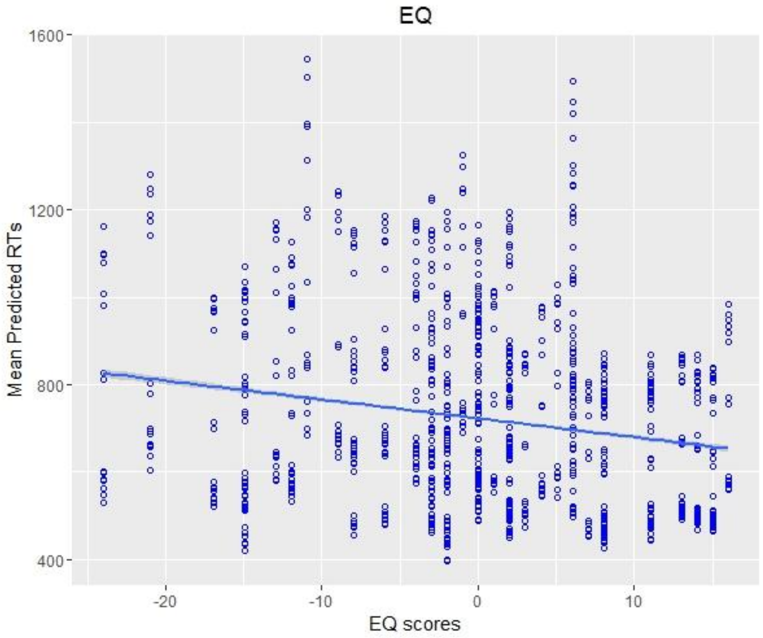


Fig. 2.5: Scatterplot representing participants' Empathy Quotient scores (centered of the overall mean) on X-axis and trials predicted RTs on the Y-axis in Experiment 1. Data are fitted by a regression line plotted using the General Linear Model method. Shaded area represents Standard Error.

Similar to the analyses on Accuracy, the last analysis on RTs included the Empathy Quotient categories as a 4-level moderator in a LMM. Fixed effects included interactions across all levels among the five independent variables in a full factorial model. Included random effects are listed in Table 5.

Significant main effects and interactions including the EQ category scores were as follows: EQ category: F (2, 54) = 3.9, p = .026; EQ category * Task: F (2, 13831) = 35.5, p < .001; EQ category * Emotion * Task: F (6, 13830.3) = 2.3, p = .031; and EQ category * Exclusion * Task: F (2, 13831) = 24.8, p < .001. This last effect (EQ category * Exclusion * Task; Fig. 2.6) was revealed to be the most interesting, since it included the interaction EQ category * Exclusion. Post hoc tests were then performed on this effect. Comparisons of different EQ category scores indicated that in the emotion recognition task, excluded participants who scored "Low" (mean = 931 ms) or "Medium" (mean = 983 ms) in the EQ category were significantly slower than those who performed "Over the mean" (mean = 738 ms; "Low" comparison: t (55.55) = 2.378, p = .021;

"Medium" comparison: t (55.51) = 3.378, p = .001). Furthermore, in comparing included and excluded participants, we found that during the emotion recognition task, included participants in the "Medium" category showed significantly faster RTs than excluded participants (included mean = 884 ms; excluded mean = 983 ms; t (55.55) = -2.158; p = .035).

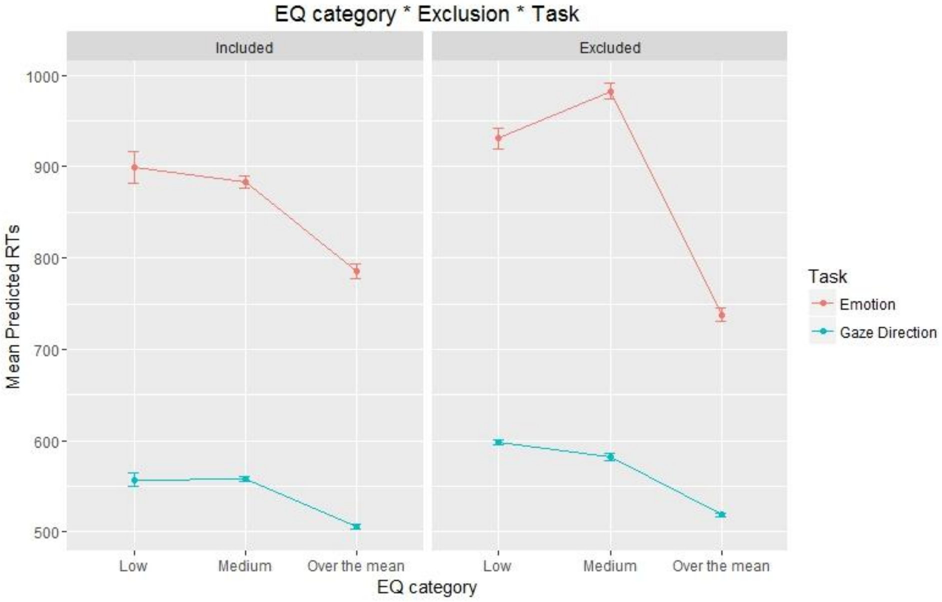


Fig. 2.6: Plot representing the differences between Empathy Quotient categories in different tasks on participants' Response Times in Experiment 1, divided by social inclusion or exclusion of participants.

2.2.4. Analyses with participants' Gender

To understand the role of gender differences as a moderator of the effects of social exclusion, we performed two analyses including participants' Gender as a moderator: a GLMM on Accuracy and a LMM on RTs.

The first analysis maintained all the previous independent variables and added Gender as moderator. Participants' Accuracy was the dependent variable. Included fixed effects are listed in Table 6, while included random effects are listed in Table 7.

The statistically significant effects including Gender were as follows: main effect of Gender: χ^2 (11) = 54.494, p < .001; Gender * Task: χ^2 (1) = 31.944, p < .001; Gender * Exclusion: χ^2 (1) =

3.591, p = .058 [p-value close to the level of significance]. This last effect (Gender * Exclusion; Fig. 2.7) is the most interesting according to our hypotheses and was probed with a Simple Effect: male excluded participants were shown to be significantly less accurate than included male participants (excluded mean = 0.925; included mean = 0.939; z = -2.488; p = .013), while excluded female participants were not significantly more accurate than included female participants (excluded mean = 0.951; included mean = 0.943; z = 0.14; p = .89).

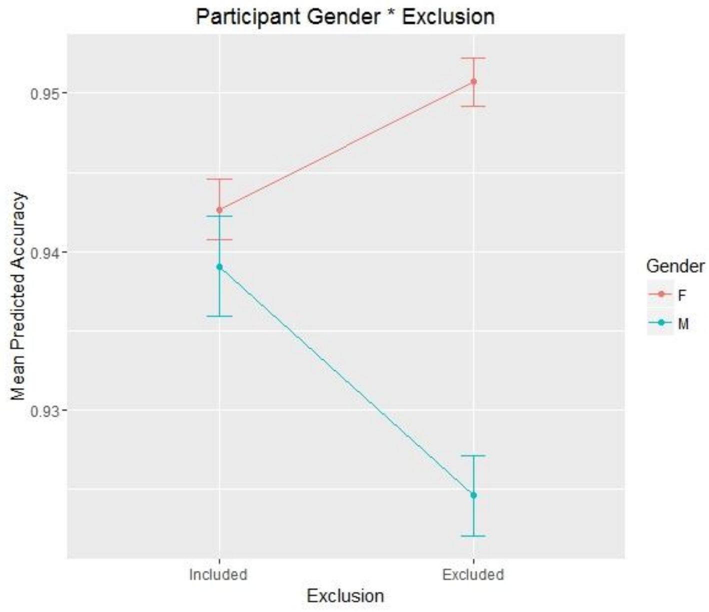


Fig. 2.7: Plot representing the effects of social exclusion in different participants' gender on participants' Accuracy in Experiment 1.

The second analysis was a LMM maintaining the four previous independent variables and adding Gender as a moderator. The dependent variable was log-transformed RTs. In this model, outliers over 2 std dev from the mean were removed, since this model showed a higher proportion of explained variance (conditional $R^2_{2\ st\ dev} = .582$, conditional $R^2_{3\ st\ dev} = 0.576$) and reduced the level of noise in the dataset (i.e., the F values of some effects were shown to be higher when outliers over 2 std dev were excluded) compared to the model excluding outliers over 3 std dev from the mean. Fixed effects included interactions across all levels among the five independent variables in a full factorial model. Included random effects are listed in Table 8.

The only statistically significant effect containing an interaction with Gender was Gender * Emotion * Exclusion: F (3, 13533.9) = 4.25, p = .005.

2.2.5. Analyses on PANAS

Two independent samples t-tests were performed in order to determine if there were any significant differences in PANAS scores between included and excluded participants. In both t-tests, the independent dummy variable was Exclusion, while the dependent variable in one case was Positive Affect score (obtained by summing all positive items in the PANAS), and the dependent variable in the other case was Negative Affect score (all negative items summed). These tests revealed no significant differences in any model examined: Positive Affect: t (58) = -0.459, p = .648; Negative Affect: t (58) = -0.848, p = .4. Additionally, social exclusion appeared to have no influence on participants' positive or negative affect.

3. EXPERIMENT 2

In Experiment 1, we found that excluded participants were less accurate in gaze direction identification and slightly slower in emotion recognition when compared to included participants. Moreover, this effect on response times was found to be moderated by participants' Empathy scores: only during the emotion recognition task, the participants who were excluded and scored in the "Over the mean" Empathy category were shown to be faster than those who were excluded and in lower Empathy categories. Finally, excluded male participants were shown to be less accurate than included male participants. All of these effects were considered particularly interesting, taking into account the reciprocal influence of gaze direction in reading emotional expressions and vice-versa (Adams & Kleck, 2005), the importance of empathy in ostracism-related phenomena (Twenge et al., 2007), and the gender-specific features of social cognition (Pavlova, 2016), which will be discussed later.

To replicate these effects in a more controlled experimental design, we ran Experiment 2. Specifically, since in Experiment 1 we did not find any effect of exclusion on the PANAS questionnaire (experienced emotions), which in previous studies was often used as a manipulation check for the Cyberball manipulation (DeWall et al., 2011; Twenge et al., 2001, 2003), we included another measure that has been shown to be strongly associated with social exclusion effects (Eisenberger et al., 2003; Jamieson et al., 2010; van Beest & Williams, 2006): the Need Threat Scale (Williams, 2009).

A methodological issue we had to face was that the order of blocks was not varied between participants, despite the fact that we alternated the two experimental tasks in four different blocks to avoid learning effects. This issue could be a potential confound in the interpretation of the results; therefore we decided to present the four experimental blocks in reverse order to half of the participants (balanced for social exclusion and gender) in Experiment 2. Thus, half of them performed the experiment in the order emotion – gaze – emotion – gaze and the other half in the order gaze – emotion – gaze – emotion.

Moreover, we were concerned about the duration of the Cyberball manipulation. If the PANAS and further questionnaires were administered just after the Cyberball game as a manipulation check, we could not be sure of the lasting effects of social exclusion until the end of the experimental tasks. For this reason, we decided to present the questionnaires (Need Threat Scale and PANAS post-manipulation) after the experimental tasks to half of the participants (balanced by exclusion, gender and experimental tasks order). The other half filled in the questionnaires just after the Cyberball manipulation, as in Experiment 1. In this way, we tested for any possible differences in the questionnaires' scores related to the presentation order (before or after the experimental tasks).

3.1. Methods

3.1.1. Participants

In total, 51 participants were recruited based on the criteria described in Experiment 1. None of them participated in the previous experiment. The sample size was smaller than that of Experiment 1, since the power analysis performed for Experiment 1 showed that 44 participants were sufficient to show reliable results, which was confirmed by the effect sizes. Six participants were excluded from the analyses since three could not understand the instructions for the tasks, two already knew about the bogus nature of the Cyberball paradigm (and thus could not be considered naïve participants), and one was an outlier for age (47 years). A total of 45 remaining participants (22 males and 23 females, mean age = 22.9 yrs, std dev = 2.66) were included in the analyses.

3.1.2. Materials and procedure

The materials and experimental procedure were the same as in Experiment 1, except the Need Threat Scale (NTS) questionnaire (Williams, 2009) was administered just after the Cyberball manipulation and before the PANAS questionnaire (Fig. 2.8), since the NTS questionnaire is more sensitive than the PANAS and can more accurately discriminate differences between included and excluded participants.

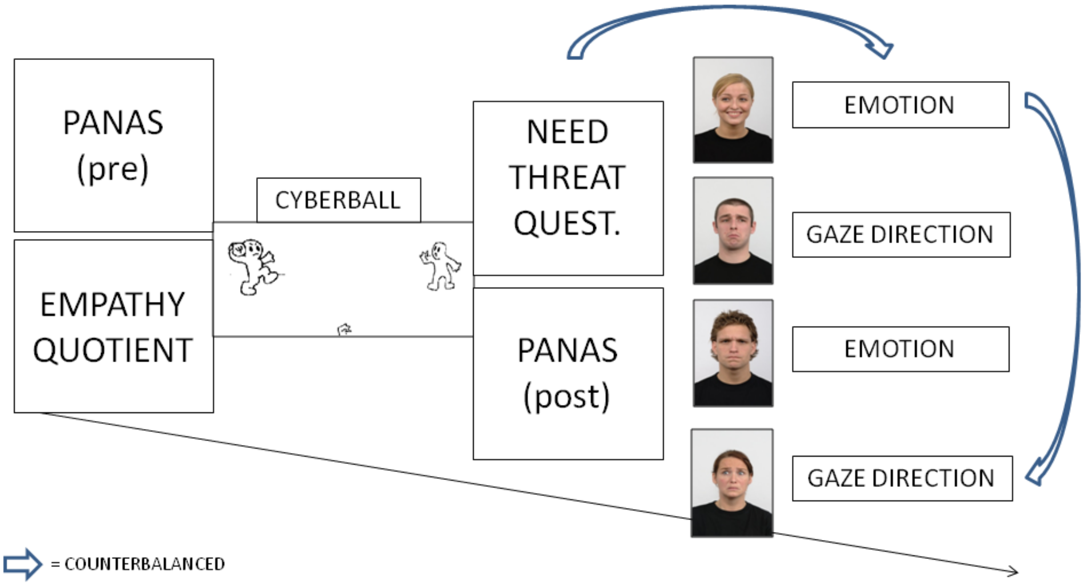


Fig.2.8: Experimental procedure for Experiment 2. Arrows represent counterbalanced order (across participants) of (i) questionnaires (Need Threat Scale and PANAS post-manipulation) and experimental tasks; and (ii) different experimental tasks.

The NTS questionnaire, as a matter of fact, is widely used in the literature to measure the effects of social exclusion as a threat to fundamental needs (Eisenberger et al., 2003; Gonsalkorale & Williams, 2007; Williams et al., 2000). The questionnaire was presented in computerised form on E-Prime® 2.0 software (Schneider et al., 2007). We decided to use it in the version presented by Zadro et al. (2004): 12 statements were presented in random order, 3 for each fundamental need (Belonging, Self-esteem, Meaningful existence, Control). Participants were asked to specify a score from 1 (Absolutely false) to 5 (Absolutely true) for each item. The aggregate score for each fundamental need was then computed by summing the scores of the three related items. Three further questions were included as manipulation checks, as in Zadro et al (*ibidem*): “What percent of the throws were thrown to you?” (1 = 0%, 5 = 100%), “To what extent were you included by the other participants during the game?” (1 = None, 5 = Completely), “During the Cyberball game I felt…” (1 = Rejected, 5 = Accepted). Furthermore, we also decided to include the PANAS questionnaire before the Empathy Quotient questionnaire. In this way, we had a measure of experienced emotion both before and after the Cyberball manipulation. In this way, we could obtain a more sensitive measure of participants’ emotional experience by computing the difference between scores before and after the ostracism manipulation. Moreover, the NTS questionnaire could not also be used before the manipulation in the same way, since it was specifically concerning the Cyberball game, and thus could not be presented more than once.

The entire experiment lasted approximately 28 min.

3.2. Results

All analyses were performed in the same order and with the same structure (independent variables, moderators, type of models, decisional pipeline for factor inclusion) as in Experiment 1. All differences from previous analyses are noted.

3.2.1. Main analyses

The first main analysis was a GLMM on Accuracy. Included fixed effects are listed in Table 9, while included random effects are listed in Table 10. The R^2 calculations of the model were as follows: Marginal $R^2 = 0.21$; Conditional $R^2 = 0.27$.

The statistically significant fixed effects were as follows: Emotion: χ^2 (3) = 114.9, p < .001; Direction: χ^2 (1) = 12.782, p < .001; Task: χ^2 (1) = 260.53, p < .001; Exclusion * Task: χ^2 (2) = 14.638, p < .001; Emotion * Task: χ^2 (3) = 49.099, p < .001.

The only significant interaction with the social exclusion manipulation was the 2-way interaction Exclusion * Task (Fig. 2.9). As in Experiment 1, we probed this interaction with Simple Effect in order to determine how social exclusion influenced participants' Accuracy in the different tasks. In the gaze direction identification task, included participants responded more accurately than excluded participants (included mean = 0.986; excluded mean = 0.969; *z* = -2.985; p = .003), while included and excluded participants showed no significant differences in the emotion recognition task (included mean = 0.909; excluded mean = 0.916; *z* = 0.374; p = .709).

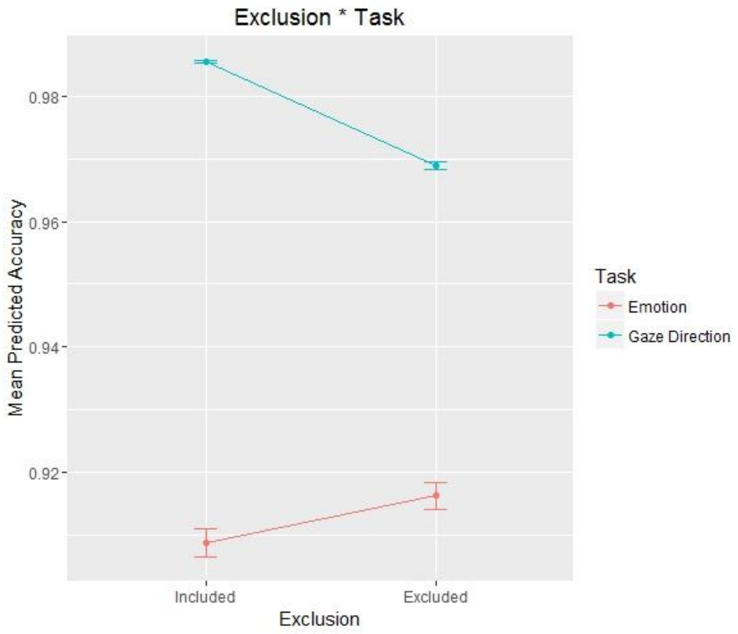


Fig.2.9: Plot representing the effects of social exclusion in different tasks on participants' Accuracy in Experiment 2.

The second main analysis was a LMM using participants' RTs (continuous) as dependent variable. Trials with Accuracy = 0 and outliers were removed from this analysis. To identify outliers, we performed the same procedure used in the previous experiment. Since the results differed (some effects changed in a significant way) between the models when keeping 2 *vs.* 3 std dev from the mean, we kept 2 standard deviations as a cut-off in order to be more conservative. RTs were logarithm-transformed in order to obtain a normal distribution of the residuals. Fixed effects included interactions across all levels among the four independent variables in a full factorial model. Included random effects are listed in Table 11. The R^2 calculations of the model were as follows: Marginal $R^2 = 0.34$; Conditional $R^2 = 0.62$.

The statistically significant fixed effects were as follows: Emotion: F (3, 10289.7) = 117, p < .001; Task: F (1, 10289.9) = 8624.8, p < .001; Direction * Emotion: F (3, 10293) = 5.5, p < .001; Direction * Task: F (1, 10294.3) = 23.1, p < .001; Emotion * Task: F (3, 10289.6) = 140, p < .001; Exclusion * Task: F (1, 10289.9) = 62.9, p <.001; and Exclusion * Task * Emotion: F (3, 10289.6) = 3.8, p = .010.

The last two effects (Exclusion * Task and Exclusion * Task * Emotion; Fig. 2.10) are the only statistically significant effects involving an interaction with the manipulation of social exclusion. We then probed these interaction effects with Simple Effect, but the multiple comparisons revealed no significant differences.

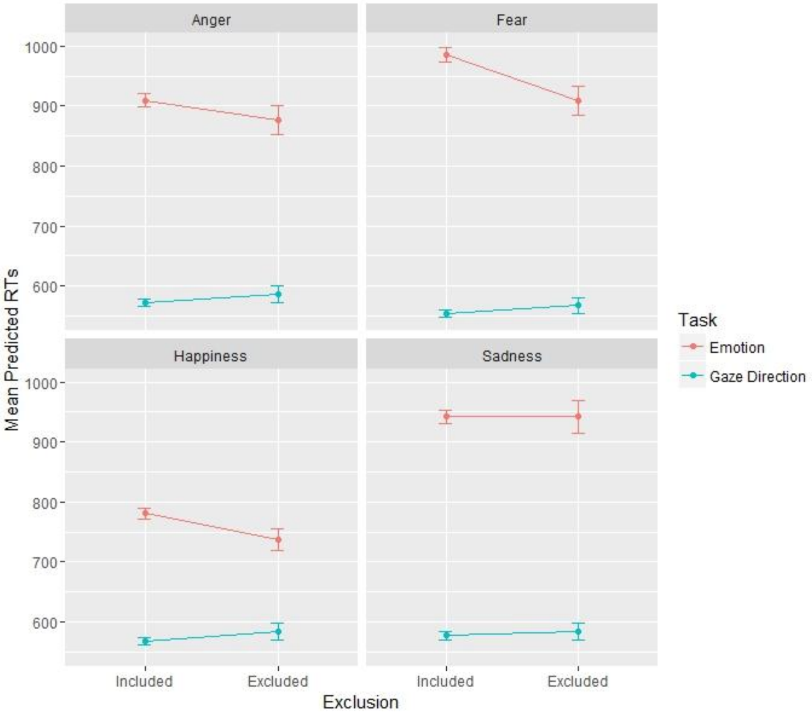


Fig.2.10: Plot representing the effects of social exclusion in different tasks on participants' Response Times in Experiment 2, divided by emotions expressed by stimuli.

A Simple Effect analysis on the 3-way interaction Exclusion * Task * Emotion (Fig. 2.10) revealed very interesting trends, although no significant differences between included and excluded participants were found (all p-values > .07). To explore these trends more in depth, four different models were created, one for each emotion. All of these models were analogous to the main one: LMMs, with Intercept | Subject and Direction | Subject as random effects, same independent and dependent variables, except for Emotion, as only one emotion was considered in each model. These models revealed a significant effect of Exclusion * Task for all emotions (Happiness: F (1, 2687.01) = 24.7, p < .001; Anger: F (1, 2454.08) = 13.73, p < .001; Fear: F (1, 2453.59) = 35.83, p < .001), except for Sadness, which did not show this effect as statistically significant (F (1, 2458.36) = 1.91, p = .167). Simple Effect analysis on these effects did not show any significant comparisons between included and excluded participants (all p-values > .09).

3.2.2. Analyses with Empathy Quotient

Four different analyses, analogous to those carried out in Experiment 1, were performed in order to understand the role of the Empathy Quotient score as a moderator of the previous effects. Two analyses were performed on participants' Accuracy and two on participants' RTs. The two analyses on Accuracy were two GLMMs that used the Empathy Quotient score (centred on the overall mean) and the Empathy Quotient categories (as defined before) as moderators. None of these models showed any significant interaction effects including EQ * Exclusion.

The third and fourth analyses considered RTs a dependent variable in two LMMs using the Empathy Quotient score (centred on the overall mean) and the Empathy Quotient categories as moderators. Despite the fact that the third model did not include any significant interactions including EQ * Exclusion, the fourth model showed an interaction effect including these factors: EQ category * Exclusion * Emotion * Task. This model included as fixed effects interactions across all levels among the five independent variables in a full factorial model, while included random effects are listed in Table 12. Post hoc comparisons (Tukey correction) did not show any significant comparisons between included and excluded participants on any level of Emotion, Task, or EQ category considered. Nevertheless, this effect shows that the previous 3-way interaction (Exclusion * Task * Emotion) was moderated by participants' empathy scores; however, too many levels were involved in the interaction, which prevented us from exploring this effect further.

3.2.3. Analyses with participants' Gender

As in Experiment 1, two analyses were performed in order to understand the role of participants' Gender as a moderator of the previous effects.

The first analysis is a GLMM using participants' Accuracy as the dependent variable and Gender as a moderator. Included fixed effects are listed in Table 13, while included random effects are listed in Table 14.

The statistically significant fixed effects including Gender were as follows: main effect of Gender: χ^2 (10) = 22.064, p = 0.015; Gender * Exclusion: χ^2 (1) = 9.5551, p = .002. The main effect of Gender showed that female participants (mean = 0.951) were generally more accurate than male participants (mean = 0.939). The interaction effect Gender * Exclusion (Fig. 2.11a) was also the most interesting for our hypotheses, since it confirmed the trend we found in Experiment 1. This effect was probed with a Simple Effect: excluded male participants were shown to be significantly less accurate than included male participants (excluded mean = 0.925; included mean = 0.952; z = -3.574; p < .001), while excluded female participants were not significantly more accurate than included female participants (excluded mean = 0.962; included mean = 0.943; z = 0.785; p = .432). Furthermore, this Simple Effect analysis showed that included female and male participants did not differ from each other in a significant way (z = -1.561, p = .119), while excluded females showed significantly higher Accuracy than excluded males (z = 2.819, p = .005).

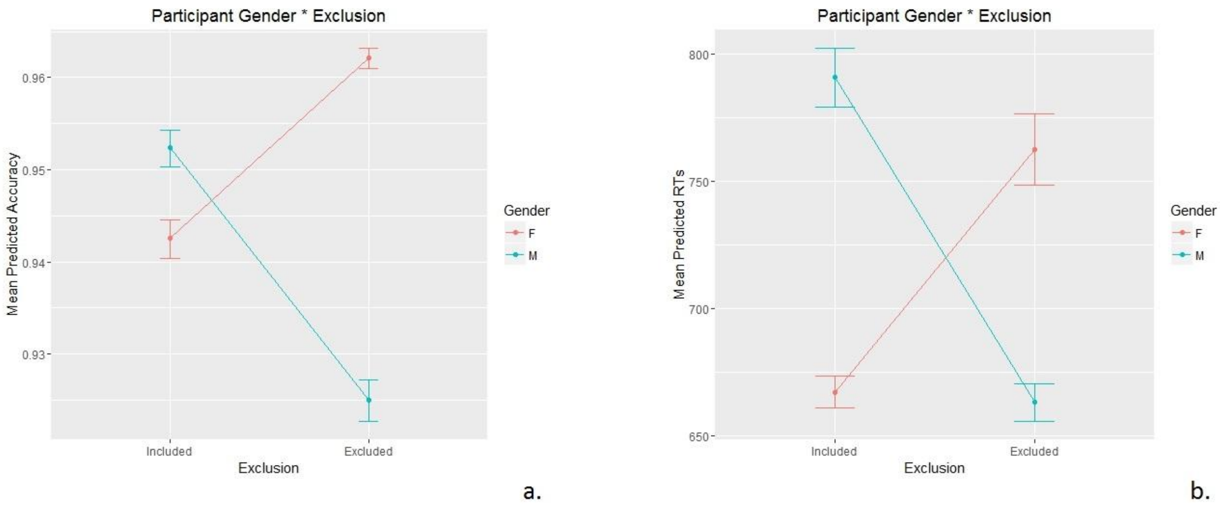


Fig.2.11: A.: Plot representing the effects of social exclusion in different participants' gender on participants' Accuracy in Experiment 2. B.: Plot representing the effects of social exclusion in different participants' gender on participants' Response Times in Experiment 2.

The second analysis performed using Gender as a moderator was a LMM using log-transformed RTs as dependent variable. As in the first experiment, outliers over 2 std dev from the mean were removed. Fixed effects included interactions across all levels among the five independent variables in a full factorial model. Included random effects are listed in Table 15.

The significant fixed effects involving the Gender were as follows: Gender * Task: F (1, 41) = 5.807, p = .021; Gender * Exclusion: F (1, 41) = 4.215, p = .046.

This second interaction effect, which was interesting as it involved social exclusion effect (Fig. 2.11b), was probed with a Simple Effect and showed that excluded male participants were slightly faster than included male participants, showing a trend towards statistical significance (excluded mean = 663 ms; included mean = 791 ms; t = -1.902; p = .064), while excluded female participants were not significantly slower than included female participants (excluded mean = 763 ms; included mean = 667 ms; t = 0.995; p = .326).

3.2.4. Analyses of between-subjects variables

The first analysis of between-subjects variables was performed on PANAS questionnaire scores. For each participant, two scores of PANAS Positive Difference and PANAS Negative Difference were computed, subtracting the scores obtained before the Cyberball game from those obtained after. Then, two independent samples t-tests were performed in order to find any significant differences between included and excluded participants on these two scores. Neither showed any statistically significant differences: PANAS Negative Difference: Excluded mean = 2.14, Included mean = 0.54, t (43) = -1.070, p = .291; and PANAS Positive Difference: Excluded mean = -4.81, Included mean = -3.67, t (43) = 0.711, p = .481. Given these findings, we can conclude that social exclusion did not influence PANAS scores.

The second analysis was aimed to test whether there were any significant differences between included and excluded participants in the Need Threat Scale (NTS) questionnaire. Four different scales (one for each fundamental need) were created for each participant by summing the scores of the related items. Four independent samples t-tests were performed in order to find any significant differences in these scales. All of these tests found significantly lower scores for excluded participants: Belongingness: Excluded mean = 4.38, Included mean = 7.92, t (43) = 6.158, p < .001; Control: Excluded mean = 4.67, Included mean = 7.46, t (43) = 5.488, p < .001; Meaningful Existence: Excluded mean = 6.81, Included mean = 9.71, t (43) = 4.249, p < .001; Self-esteem: Excluded mean = 7.52, Included mean = 9.63, t (43) = 2.844, p = .006.

The third analysis was aimed to study the differences in manipulation checks that were used between included and excluded participants. Three independent samples t-tests were performed on the scores obtained by participants in each of the three questions used as manipulation checks. Excluded participants obtained significantly lower scores in all these tests: Accepted: Excluded mean = 1.48, Included mean = 2.67, t (43) = 4.207, p < .001; Included: Excluded mean = 1.05, Included mean = 2.42, t (43) = 6.035, p < .001; and Percentage of throws received: Excluded mean = 1.52, Included mean = 2.25, t (43) = 5.107, p < .001.

The fourth between-subjects analysis was aimed to check if the Cyberball manipulation effects lasted until the end of the experiment. To do so, we looked for any possible differences in NTS scores and manipulation checks due to the order of questionnaires and experimental task presentation. If no differences in the questionnaires between these two groups were found, then we could assume that the manipulation effects lasted until the end of the experiment. Therefore, seven independent samples t-tests were performed on the four NTS scales and on the three manipulation checks, with order of questionnaires as the grouping factor. None of these tests revealed significant differences in any scores due to the order of questionnaires: Belonging: t (43) = 0.73, p = .469; Control: t (43) = 1.627, p = .111; Meaningful Existence: t (43) = 0.61, p = .545; Self-esteem: t (43)

= 1.533, p = .133; Accepted: t (43) = 0.985, p = .330; Included: t (43) = -0.679, p = .501; and Percentage of received throws: t (43) = -1.598, p = .117.

4. GENERAL DISCUSSION

The aim of this study was to explore how social exclusion manipulation can influence social information processing. To this end, two experiments were carried out, in which participants were asked to identify two of the most relevant and interacting features studied in social cognition (Adams & Kleck, 2005), i.e., facial expression and gaze direction (which varied across all stimuli). Participants were asked to perform these experimental tasks after being socially included or excluded by means of the Cyberball paradigm (Williams & Jarvis, 2006). To replicate the results found in Experiment 1 in a more robust experimental design and to be confident about the effectiveness of the Cyberball manipulation, Experiment 2 was designed. This experiment replicated the most important part of the results obtained in Experiment 1, thus corroborating them.

We found a significant Exclusion * Task interaction in both experiments, both on participants' Accuracy and RTs: results on Accuracy showed that socially excluded participants were less accurate in the gaze direction recognition task, while they did not show any significant differences in the emotion recognition task. By contrast, the results on RTs showed no differences between included and excluded participants in any of the two tasks, thus confirming some influence of social exclusion on social information processing, as hypothesized. This finding is in line with the results of studies by DeWall and colleagues (DeWall et al., 2011, 2009), which showed an increase in selective attention to signals of social acceptance after social exclusion (due to the threatened need to belong), leading to faster identification of smiling faces and longer fixations on them during eye-tracking tasks. Considering that faces can potentially show signals of re-inclusion (or further threat) through a combination of emotional expressions and gaze direction (Wirth, Sacco, Hugenberg, & Williams, 2010), one could have expected higher deployment of attentional resources in processing these cues after social exclusion. In contrast, no enhancement was found, but lower accuracy for excluded participants was detected. This result is consistent with the "deconstructed state"

(Baumeister et al., 2007) found by Twenge et al. (Twenge et al., 2003). In this study, these authors found effects of cognitive deconstruction (lower performance in cognitive tasks) and emotional numbness (deficiency in emotional information processing) in socially excluded people. According to our results, these phenomena seem to extend to a "social cognition impairment", specifically affecting the processing of gaze direction, the main feature that communicates where the other person is attending to (Driver et al., 1999; Ricciardelli, Bricolo, Aglioti, & Chelazzi, 2002) and possible social re-inclusion (Wirth et al., 2010). This "social cognition impairment" is a new effect and, to the best of our knowledge, it has not been reported before. It shows that excluded people enter into the deconstructed state induced by ostracism, which impairs their ability to deploy their own attentional resources in processing potentially re-inclusive cues. Therefore, the numbness induced by ostracism does not only concern cognitive and emotion-related abilities. Exclusion seems to elicit an effect linked to refusal. That is, ostracized people experience more difficulties in processing signals concerning other people's attention. This refusal effect could be due to threatening people's need to belong (Baumeister & Leary, 1995). In other words, if people were excluded, they did not belong to that group; thus, they did not pay attention and process potentially re-inclusive signals from the faces they saw.

Our results did not show an overall impairment in both tasks, but we did find a specific decline in gaze direction judgement, which suggests a dissociation between the two tasks, implying the involvement of different processes. As stated before, gaze direction plays a key role in interpreting the meaning of expressions, since it becomes part of the configuration of different cues that constitute what is perceived as a facial expression (Adams & Kleck, 2005). The gaze is a fundamental feature in the appraisal of emotional expressions because it conveys their meaning (Artuso et al., 2012; Sander et al., 2007). Its fundamental role in conveying the meaning of the facial expression to the observer is most likely the reason why gaze direction recognition is specifically impaired by social exclusion ("social cognition impairment"), thus damaging its crucial processing. Some recent work has shed new light on the effects of ostracism on the perception of gaze direction (Lyyra, Wirth, & Hietanen, 2017), showing that this social feature is clearly involved in the processes affected by social exclusion.

It is important to acknowledge that this specific effect on gaze direction recognition is small (~ 1-2% on participants' Accuracy) but extremely consistent. It was coherent between Experiment 1 and 2, both in direction and in effect size. Moreover, the variance in participants' Accuracy in gaze direction recognition was very low: the variance pooled across experiments was 0.0003 for included participants and 0.0008[2] for excluded ones. Therefore, we can conclude that the social exclusion manipulation generates an apparently small, but very consistent, effect. In addition, gaze-related effects (e.g., gaze cueing) are very small (i.e., differences typically smaller than 100 ms) but extremely constant in direction and size (Carraro et al., 2016; Frischen, Bayliss, & Tipper, 2007). Since gaze direction processing is a low-level ability, participants very often reach a ceiling effect in their Accuracy in gaze-related tasks, giving approximately 100% correct responses (*ibidem*). In these cases, an effect creating a difference of just 1-2% can represent a very effective manipulation.

The lack of statistically significant differences between included and excluded participants in RTs for both tasks is probably due to the large variation of RTs among different participants and different categories of stimuli and to the sensitivity of the measure in these experiments.

Next, it is important to consider the results in light of the appraisal theories (Sander et al., 2007). In Experiment 1, the increase in excluded participants' RTs in emotion recognition was mainly due to stimuli with direct gaze; in Experiment 2, the stimuli expressing all emotions but sadness presented the Exclusion * Task interaction effect. These results showed that modifying these social features (facial expression and gaze direction) modulated the previous effects of social exclusion. The result found in Experiment 1 seems to be counterintuitive given the "Tuning to

---

[2] Such a small variance can also explain why mixed effects models with Task as random effect could never converge: if within-task variance is so small, it is almost impossible to capture it with a random effect.

positivity" effect reported in the literature (DeWall et al., 2011), since direct gaze is a potentially re-inclusive signal, and stimuli with direct gaze are processed slower by excluded participants during emotion recognition. However, this result is much clearer considering the "social cognition impairment" effect caused by social exclusion: on the one hand, faces with direct gaze have a much stronger social meaning to the observer and, thus, are processed in a faster way in the appraisal of faces by included participants. On the other hand, excluded participants appear to be socially numb; therefore, they do not show this advantage for "socially enhanced" stimuli with direct gaze. The second result is even more interesting considering this hypothesis: stimuli conveying sadness do not show an Exclusion * Task interaction effect. While all the other emotions we considered have strong social meanings and are perceived either as a reward (happiness) or a possible threat (anger and fear), the processing of sadness does not bring an evolutionary advantage or have any survival value (i.e., avoiding dangers or obtaining rewards) and, thus, is less socially relevant (Lipp, Price, & Tellegen, 2009). Considering the social value of the other emotions, they present the "social cognition impairment", while sadness is not conveying socially relevant information and thus does not show any specific advantage or disadvantage for excluded participants.

As far as hypothesis (ii) is concerned, that the effects of social exclusion are moderated by participants' empathy, our results showed effects of moderation by the Empathy Quotient scores in Experiment 1. Specifically, participants higher in EQ tended to be faster in all tasks (main effect), and in emotion recognition tasks, excluded participants who scored "Low" or "Medium" in the EQ category were significantly slower than those who performed "Over the mean". The interpretation of this effect is very intuitive, since empathy by definition is related to social information processing (Baron-cohen & Wheelwright, 2004); therefore, people higher in empathy are expected to perform more quickly in tasks involving the processing of social information. It also indicates that EQ is a reliable measure of the construct of empathy. The second result (EQ category moderation) shows some sort of protective value of empathy: despite the "social cognition impairment", participants higher in empathy remain faster in social information processing and highly motivated in searching for possible re-inclusion, thus resulting in being less affected by the "social cognition impairment". These results, however, were not replicated in the second experiment, probably because of the smaller sample size, noisier data, and a slightly different experimental design. Therefore, although our data seem to suggest a protective value of empathy towards social exclusion, future research is needed to corroborate it.

Regarding our third hypothesis about an effect of gender differences (Pavlova, 2016) (see Williams & Sommer, 1997 for an example of the different effects of ostracism), our results showed that a difference between male and female participants in exclusion effects emerged clearly on both Accuracy and RTs in Experiment 2, while it almost reached statistical significance on Accuracy data in Experiment 1. In other words, excluded male participants overall tended to be less accurate and faster than included male participants, while excluded female participants showed a more accurate and slower performance than included female participants. Therefore, the participant's gender seems to play an important role in the way people respond to ostracism effects. On the one hand, excluded male participants' performance was in line with the effects reported in the literature in terms of emotional and cognitive numbness (Baumeister et al., 2007; Jamieson et al., 2010), here extended to include also the "social cognition impairment". In particular, they showed difficulties in a social cognition task caused by ostracism, as well as low interest in processing social information (as shown by lower RTs) by deploying less attentional resources. On the other hand, female participants seem to present higher motivation to be re-included. In fact, despite the difficulty they found in performing the tasks (indicated by higher RTs) caused by social exclusion to overcome the "social cognition impairment", excluded female participants put more effort in performing the tasks and had more motivation, as shown by higher accuracy compared to included female participants. This was also the case in Experiment 1, although this difference did not approach statistical significance, probably due to the methodological differences between the two experiments. Overall, these results extend our knowledge on gender differences in response to social exclusion.

A limitation of this study is the lack of a manipulation check concerning the effects of the Cyberball game before and after the game itself. Our best manipulation check on the Cyberball game was the NTS questionnaire. However, because of its nature, this questionnaire cannot be administered both before and after the manipulation. Future research should address this issue by using an implicit measure that is more sensitive than the PANAS (e.g., skin conductance), the administration of which could be repeated more than once within the same experiment. Despite this limitation, in Experiment 2 we found clear evidence of the efficacy of our Cyberball manipulation both after the Cyberball game and after the experimental tasks.

In conclusion, this study investigated for the first time the effects of social exclusion on two fundamental facial features (emotional expression and gaze direction) taken together. Contrary to what is known in the literature, we found that social information processing was not globally enhanced or impaired, i.e., not all social cues were affected in the same way by social exclusion. Gaze processing was specifically impaired by ostracism, probably because it has a crucial role in communicating important social aspects, i.e., not only social attention but also the comprehension of intentions and mental states. Moreover, this study also showed that male and female participants seem to react differently to social exclusion, and empathy seems to play a modulatory role in the detrimental effects of ostracism.

5. Appendix

Table 1:

Fixed effects included in the main analysis on Accuracy in Experiment 1.

Emotion
Task
Direction
Exclusion
Emotion * Task
Emotion * Direction
Emotion * Exclusion
Task * Direction
Task * Exclusion
Direction * Exclusion

Table 2:

Random effects included in the main analysis on Accuracy in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.4767	0.6904

Table 3:

Random effects included in the main analysis on Response Times in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.025190	0.15871
Emotion [Fear] | Subject	0.001823	0.04270
Emotion [Happiness] | Subject	0.002791	0.05283
Emotion [Sadness] | Subject	0.001392	0.03731
Direction | Subject	0.001456	0.03816

Table 4:

Random effects included in the analysis using Empathy Quotient scores as moderator on Response Times in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.023297	0.15263
Emotion [Fear] | Subject	0.001743	0.04175
Emotion [Happiness] | Subject	0.002753	0.05247
Emotion [Sadness] | Subject	0.001377	0.03711
Direction | Subject	0.001539	0.03923

Table 5:

Random effects included in the analysis using Empathy Quotient categories as moderator on Response Times in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.023447	0.15312
Emotion [Fear] | Subject	0.001956	0.04423
Emotion [Happiness] | Subject	0.002945	0.05427
Emotion [Sadness] | Subject	0.001398	0.03739
Direction | Subject	0.001499	0.03872

Table 6:

Fixed effects included in the analysis using Gender as moderator on Accuracy in Experiment 1.

Gender
Direction
Emotion
Task
Exclusion
Gender * Direction
Gender * Emotion
Gender * Task
Gender * Exclusion

Direction * Emotion
Direction * Task
Direction * Exclusion
Emotion * Task
Emotion * Exclusion
Task * Exclusion
Gender * Emotion * Task
Gender * Direction * Task

Table 7:

Random effects included in the analysis using Gender as moderator on Accuracy in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.4598	0.678

Table 8:

Random effects included in the analysis using Gender as moderator on Response Times in Experiment 1.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.040666	0.20166
Task | Subject	0.018872	0.13738
Direction | Subject	0.001633	0.04041

Table 9:

Fixed effects included in the main analysis on Accuracy in Experiment 2.

Emotion
Task
Direction
Exclusion
Task * Exclusion
Direction * Exclusion
Emotion * Exclusion

Emotion * Direction
Emotion * Task

Table 10:

Random effects included in the main analysis on Accuracy in Experiment 2.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.2725	0.522

Table 11:

Random effects included in the main analysis on Response Times in Experiment 2.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.039281	0.19819
Direction | Subject	0.001178	0.03432

Table 12:

Random effects included in the analysis using Empathy Quotient categories as moderator on Response Times in Experiment 2.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.0664971	0.25787
Direction | Subject	0.0007729	0.02780
Task | Subject	0.0302570	0.17395
Direction * Task | Subject	0.0037542	0.06127

Table 13:

Fixed effects included in the analysis using Gender as moderator on Accuracy in Experiment 2.

Gender
Direction
Emotion
Task

Exclusion
Gender * Direction
Gender * Emotion
Gender * Task
Gender * Exclusion
Direction * Emotion
Direction * Task
Direction * Exclusion
Emotion * Task
Emotion * Exclusion
Task * Exclusion
Gender * Direction * Emotion

Table 14:

Random effects included in the analysis using Gender as moderator on Accuracy in Experiment 2.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.1942	0.4407

Table 15

Random effects included in the analysis using Gender as moderator on Response Times in Experiment 2.

Random effect	**Explained variance**	**Std Dev**
Intercept | Subject	0.053962	0.23230
Task | Subject	0.025680	0.16025
Direction | Subject	0.001045	0.03233
Direction * Task | Subject	0.003370	0.05805

CHAPTER 3

THE BODY-INVERSION EFFECT

A meta-analytic review

1. Introduction

This chapter presents a meta-analysis of the literature about the *body-inversion effect*. In the introduction we discuss a systematic review of the studies related to face and body perception, in particular the configural processing of these stimuli, their neural correlates and the face and body inversion effects. Then, we focus specifically on the latter, by examining how this effect can be modulated by manipulating different features involved in configural processing, and by investigating the behaviour of clinical populations in which this effect is disrupted. This review was aimed at illustrating the ongoing debate in the literature about the processes involved in the body inversion effect.

Subsequently, the proper meta-analysis on the body inversion effect (and on how it can / cannot be modulated) is presented and discussed in the light of the reviewed literature.

1.1. Face and body perception

Faces and bodies provide extremely important non-verbal cues for social interaction, communication and comprehension. Psychological and neurocognitive research has focused mainly on face perception until now, considering the uniqueness of this stimulus and investigating how its perception differs from the perception of other objects (Kanwisher & Yovel, 2006; Rossion & Gauthier, 2002). In the last 15 years, however, many researchers have understood the importance of the body as a social stimulus and have investigated how it is perceived, considering many differences and commonalities with the perception of other social and non-social stimuli (Minnebusch & Daum, 2009).

Faces and bodies are different from a visual point of view, but they share some fundamental social features: both can convey information relevant for recognition of people’s identity and identification of their emotional state, gender, age and also intentions. Faces are symmetric and all share a common 3D configuration of critical elements (i.e., two eyes above the nose, above the mouth), and the same is for bodies (a torso, with a head on the top, two arms connected to the higher part and two legs to the lower part). The recognition and discrimination of different people require precise visual processing of shape, size and spatial relations of the features in both faces and bodies. To sum up, both categories of stimuli seem to be processed by specific cognitive mechanisms by means of the underlying specialized neural bases (Kanwisher & Yovel, 2006; Peelen & Downing, 2007b).

1.1.1. Configural processing in faces and bodies

It is now widely accepted that face perception depends on the detailed analysis of the configuration of facial features, also known as *configural processing* (Maurer, Le Grand, & Mondloch, 2002; McKone & Yovel, 2009). The definition of “configural processing” includes any processes involved in the perception of relations among the features of a stimulus, as opposite to analytic processing (Fig. 3.1b), characterized by feature-based processing mechanisms (Maurer et al., 2002).

Fig. 3.1: Examples of faces that differ (a) in second-order relations, and (b) in featural information (adapted from Maurer et al., 2002). The first (a) level of configural information is disrupted by face inversion, while featural processing (b) is less affected by inversion.

Maurer and colleagues (2002) defined three different types of configural face processing: (1) *first order spatial relations*, which can be defined as the relative coordinates in space of constituent parts of an object, such as the placement of the eyes above the nose. First-order relations help to define a stimulus as a face, since all faces share the same basic configuration. Evidence that first-order spatial relations are more important for faces than for other objects derives from the fact that scrambled faces are much more difficult to categorize and recognize than their scrambled object counterparts (Baenninger, 1994; Collishaw & Hole, 2000; Donnelly, Humphreys, & Sawyer, 1994). (2) *Holistic processing* refers to the fact that all features of a face are bound together into wholes (or *gestalts*). The face representation is not decomposed into individual parts, but it is integrated in a template representations (Farah, 1991; Farah, Tanaka, & Drain, 1995; Gauthier & Tarr, 2002). Holistic processing is not only based on internal facial features, but also on the external contours. The clearest demonstration of holistic facial processing is the *face composite effect* (Young, Hellawell, & Hay, 1987) (Fig. 3.2): two identical top halves of a face are perceived as being different if they are combined with different bottom parts. This effect shows that facial features cannot be processed independently. If the bottom and top halves are misaligned, the effect disappears. (3) *Second order spatial relations* refer to the spatial or metric distances among internal features (e.g., distance between the eyes, between the eyes and the nose, between the nose and the mouth, etc.) (Fig. 3.1a). The recognition of different faces requires the encoding of information about small variations in the spacing between different features (Diamond & Carey, 1986; Le Grand, Mondloch, Maurer, & Brent, 2001). One theory that may explain the use of second-order relations in face processing postulates that faces are encoded in terms of their deviation from a mentally represented average face that is abstracted from all the faces a person has seen (Valentine & Bruce, 1986). Second-order relational information refers to the deviation between the position of a particular point on a face (e.g., the outer edge of the eyes) and the position of that point on a prototype face, constructed by superimposing several faces together or averaging the positions of all face points over a set of faces (Carey, Schonen, & Ellis, 1992).

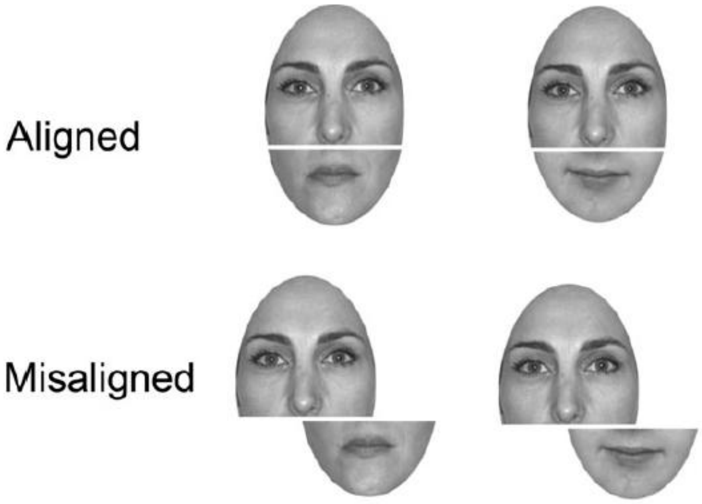


Fig. 3.2: Picture showing an example of the Face Composite Effect (adapted from Soria Bauser et al., 2015)

Maurer and colleagues (2002) left an open question by asking whether these different types of configural processing are independent of each other or hierarchically organized in a continuum. Further studies, especially investigating configural processing in bodies (Minnebusch & Daum, 2009 for a review; Reed, Stone, Grubb, & McGoldrick, 2006; Soria Bauser, Schriewer, & Suchan, 2015), highlighted the hierarchical nature of these mechanisms by disrupting different levels of the continuum and showing the impossibility to use higher level mechanisms (e.g., holistic processing) when lower level ones (e.g., first-order relations) were disrupted, for example, by scrambling facial features (Reed et al., 2006).

Another point on an hypothetical configural processing continuum refers to the *structural information* or *hierarchical structure* (Reed et al., 2006). This point was not originally considered by Maurer et al. (2002), but investigated in a systematic series of experiments by Reed and colleagues (2006). The authors demonstrated the existence of this configural process between the first-order relational information level and the holistic processing level (Fig. 3.3). The structural information is based on the proposal that recognition processes could work on the hierarchical structure of objects because particular features were embedded within an overall structure of the object (Marr, 1982). For example, unlike many objects, faces are recognized not only by the fact that the nose is below the eyes but also from the fact that the nose is in a particular position relative to the general structure of the face, thus, in the centre. The position of particular parts within the overall structural hierarchy of an object specifies another type of configural information, different from first-order information. First-order relationships provide information about the hierarchical structure of an object, whereas structural information defines the position of parts in the overall hierarchy. First-order relational information is thus necessary, but not sufficient, to define structural information.

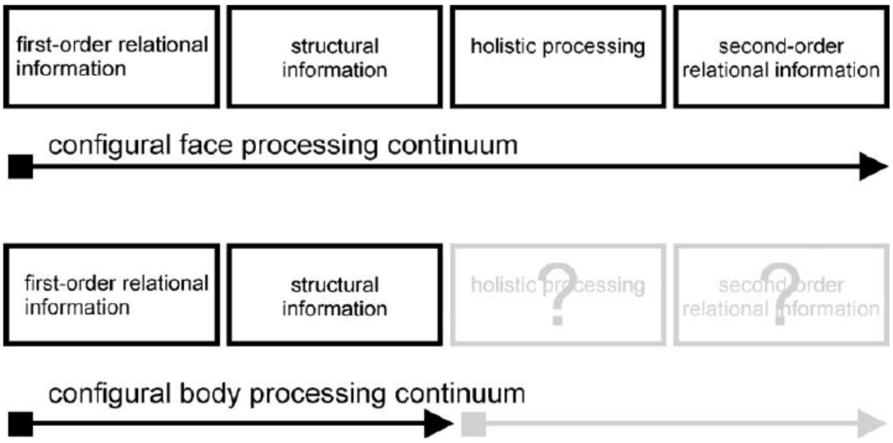


Fig. 3.3: Illustration of the configural face and body continuum (adapted from Minnebusch & Daum, 2009). It is relevant to highlight the position of the structural information processing, investigated in body configural processing by Reed and colleagues (2006).

The *face inversion effect* (FIE) is considered to be a critical evidence for configural face processing (Yin, 1969): the recognition of faces presented upside down is much more difficult than the recognition of upright faces, as demonstrated by longer time required to process inverted faces and higher error rates in face matching tasks. Although most objects are more difficult to recognize upside down than upright, inversion disproportionately disrupts the recognition of faces relative to the recognition of other objects (Carey et al., 1992; Yin, 1969). The FIE is thought to reflect configural processing and it clearly affects each of the different configural processing levels (Maurer et al., 2002). It is probably the most robust phenomenon in face processing literature, since it was found in different tasks and for both familiar and unfamiliar stimuli (Rossion & Gauthier, 2002).

Some years ago, it was clearly demonstrated that configural processing is fundamental also for the visual perception of human bodies (Reed, Stone, Bozova, & Tanaka, 2003; Stekelenburg & De Gelder, 2004). Reed and colleagues (2006) showed that faces and bodies partly share the same processing pathway, but configural recognition of bodies depends particularly on the structural information processing (Fig. 3.3). Configural processing of bodies has also been confirmed by studies that investigated the *body inversion effect* (BIE). This effect is analogous to the FIE: recognition of inverted body postures (compared to upright) yielded to slower reaction times and higher error rates (Reed et al., 2003, 2006). In fact, the BIE (in full bodies) per se does not allow any conclusions about the exact configural mechanism involved, and the amount of information needed for the body processing. Nevertheless, inversion effects were not observed for isolated body parts or scrambled bodies (disrupting respectively analytic processing and first-order information), showing that the whole body form, or at least one half of it (containing all information needed to access its structural hierarchy) is necessary for the configural processing (Reed et al., 2006). The study by Reed and colleagues (*ibidem*) showed the importance of structural information and first-order relations between body parts and the whole body context in order to perform configural body processing.

To summarize, the available findings show that human bodies and faces might share the same processing pathway during the early processing stages (first-order relations and structural information), while their perception might be dissociated at later processing stages (Fig. 3.3) (Minnebusch & Daum, 2009).

1.1.2. Neural bases of face and body perception

Studies aimed at investigating the neural bases and correlates of face and body perception are presented and discussed below. Studies employing the functional magnetic resonance imaging (fMRI) methodology were already presented (see Chapter 1), and revealed that specialized (and partly overlapping) cortical networks are involved in face and body perception. Psychophysiological studies performed by means of the electroencephalogram (EEG) or magnetoencephalogram (MEG) are reported below, since a large number of these studies focused on the FIE and BIE, with particular attention to the configural processes. This family of techniques

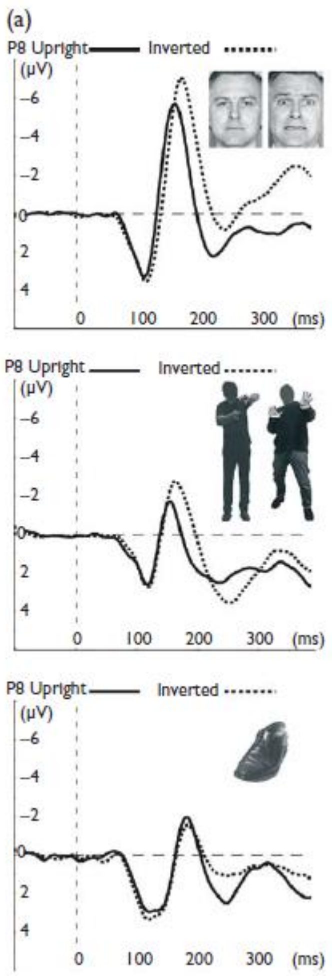


Fig.3.4: ERPs recorded at occipito-temporal location to upright (solid line) and inverted (dotted line) faces (top), bodies (middle), and objects (bottom). (adapted from Stekelenburg & de Gelder, 2004). The inversion effect can be clearly seen as larger and delayed N170 component in faces and bodies, but not objects.

has different temporal and spatial resolutions from fMRI technique, thus, it is important to consider both of them. The use of electrophysiological techniques allows an extremely high temporal resolution, but lower spatial resolution than fMRI, especially when studying the activity of subcortical structures. Event-related potentials (ERPs) represent the measured brain response that is the result of a specific event (sensory, cognitive or motor). ERPs are obtained by averaging the activity recorded by the M/EEG over several trials in a single condition (Luck & Kappenman, 2011).

A negative event-related potential (ERP) peaking around 170 ms after stimulus onset (named N170) is consistently elicited by human faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Rossion et al., 2000). This component presents the maximum amplitude over occipito-temporal areas, even though its exact neural source is not completely clear. In the FIE, N170 shows longer latency and often larger amplitude for inverted (compared to upright) faces (Eimer & Holmes, 2007; Itier & Taylor, 2004; Rossion et al., 2000; Rossion & Gauthier, 2002). This is not the case for objects (Fig 3.4). The N170 component is thought to be generated by the neural processes involved in structural encoding stages, where the representation of face configuration is created for recognition (Eimer, 2000; Jacques & Rossion, 2007).

Moreover, the P100 component, an early ERP component peaking around 90-120 ms after stimulus onset, is sensitive to processing of human faces. P100 was shown to be larger for faces than for objects and larger and delayed for inverted than upright faces (Itier & Taylor, 2004; Rossion et al., 2000). The P100 component appears to show an early global response to faces and most probably reflects the perception of a stimulus as a face (Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005).

A source localization analysis of these two components identified the source of P100 in the fusiform gyrus, while the source of N170 was localized in a occipito-temporo-parietal network comprising the fusiform face area (FFA), and the lateral occipito-temporal cortex (LOTC) (*ibidem*) (see also Chapter 1).

P100 and N170 components present many similarities and this fact raises a question about the exact timewindow in which differences between upright and inverted faces are processed, i.e., the timewindow of facial configural processing. Jacques & Rossion (2007) explored the relationship between behavioural performance (accuracy, RTs, efficiency based on both) and the electrophysiological FIE: they found that both P100 and N170 components were affected by face inversion, but behavioural FIE correlated only with the N170 amplitude. This result suggests that the behavioural FIE takes place during the perceptual structural encoding phase.

An effect of inversion on the N170 component was observed also for body perception: larger amplitude and longer latencies were observed in this component for inverted (compared to upright) bodies (Fig. 3.4) (Righart & de Gelder, 2007; Stekelenburg & De Gelder, 2004). This result corroborates the idea that body perception is supported by the underlying mechanism of configural processing, even though an inversion effect was not found on the P100 component as in faces.

Despite showing a similar inversion effect, some differences between face and body perception in the N170 component were found. First and foremost, N170 for bodies showed significantly smaller amplitude than for faces (Stekelenburg & De Gelder, 2004). The peak activity in this component while perceiving bodies was detected at a slightly longer latency, around 190 ms after stimulus onset, and for this reason it was named differently (N190) by some researchers (Thierry et al., 2006). Also the location of the N190 component differs from facial N170: it was detected over the right posterior extrastriate cortex (*ibidem*), even though the exact sites remain to be investigated in depth by using combined EEG-fMRI methodology.

These findings demonstrate that bodies are processed by specialized cortical structures that, on the one hand, share some communalities with face perception (configural processing) while, on the other hand, are at least in part dissociable from mechanisms involved in face and object perception. The precise pattern of similarities and differences is still to be determined and some processes specific of body perception will be investigated in further paragraphs.

1.2. Manipulation of body perception

Various sources showed that FIE is a very robust effect: it can be found also when performing different tasks, with familiar and unfamiliar faces, and also using scrambled stimuli (see Rossion & Gauthier, 2002 for a review; Soria Bauser & Suchan, 2013). On the contrary, the BIE was shown to be modulated or even cancelled using particular stimuli or under specific circumstances. The investigation of how the BIE can be modulated is presented below, considering the main topics actually debated in literature: (1) importance of the head for configural processing, (2) the body composite effect and body configural processing, (3) importance of using naked / clothed stimuli, (4) BIE in clinical populations. To note that the same variables are also taken into account during the meta-analysis (see Part 2).

1.2.1. Importance of the head

Starting in 2004, some fMRI studies began to investigate the influence of face perception when processing bodies: Cox, Meyers, & Sinha (2004) found that contextual cues (e.g., masked faces) elicit object-specific neural responses over FFA while processing bodies. Morris, Pelphrey,

& McCarthy (2006) showed that occipito-temporal activation elicited by bodies is modulated by the presence or absence of the face. These authors hypothesized that even masked faces, presented in the context of the body, might activate face-specific mechanisms and it was unclear whether faces, bodies, or both were fundamental for the results they found. The origin of this hypothesis stands in the fact that, in nature, body shapes include head and face and, thus, body processing may be based on both facial and bodily information.

In order to further test this hypothesis, Minnebusch, Suchan, & Daum (2009) investigated the behavioural and electrophysiological (N170) BIE using headless bodies as stimuli. They found the opposite inversion effect in headless bodies: participants showed significantly worse behavioural performance (efficiency scores) and larger and delayed N170 when processing upright headless bodies compared to inverted ones. The typical BIE was replicated for whole bodies (with masked face) in both behavioural and electrophysiological results. These findings proved their hypothesis: configural processing may be important for the recognition of human bodies with heads, representing a naturalistic silhouette, but not for bodies without heads. This implies that even masked faces might activate face-specific processing mechanisms to some degree, which in turn might be responsible for the reported inversion effect. Facial information (even if masked) may be thus responsible for configural processing of bodies.

A series of studies by the research group of Brandman & Yovel further investigated the role of facial information in the BIE. Yovel, Pelc, & Lubetzky (2010) found that the BIE is disrupted when removing the head from stimuli, but remains intact when removing the arms or a leg. This result demonstrated that the head has a special status in the processing of the human body and its presence is critical for intact body discrimination. The importance of (implicit) facial information in the BIE was also investigated in an fMRI study (Brandman & Yovel, 2010), in which face-selective areas (OFA and FFA) showed a pattern of activation reflecting behavioural BIE: their activation was shown to be sensitive to inversion of whole bodies, but not of headless bodies. Vice versa, body-selective areas were sensitive to inversion of both whole and headless bodies. These results, together with the findings of Cox et al. (2004), suggest a critical role for the head in the processing of human bodies: configural processing in BIE may thus be mediated by face-specific areas involved in head processing. From these findings, they hypothesized that the inversion effect found for faceless bodies may reflect a FIE resulting from contextual processing of body cues rather than an effect of body-selective processing. This hypothesis was tested in a following study (Brandman & Yovel, 2012), where a behavioural inversion effect was found also for faceless heads with minimal body context (head with only shoulders). The authors discuss this result as proving that faceless stimuli with adequate body context may be detected as faces, processed by face-specific mechanisms and thus generate a FIE.

The hypothesis formulated by these authors is in fact quite speculative, especially considering that many other studies found behavioural and electrophysiological BIEs using headless bodies (Arizpe, Mckean, Tsao, & Chan, 2017; Bonemei, Costantino, Battistel, & Rivolta, 2017a; Minnebusch, Keune, Suchan, & Daum, 2010; Mohamed, Neumann, & Schweinberger, 2011; R. A. Robbins & Coltheart, 2012; Susilo, Yovel, Barton, & Duchaine, 2013; Tao, Zeng, & Sun, 2014; Thierry et al., 2006). By any means, what can be demonstrated with high confidence by these findings is that FIE and BIE seem to rely on different mechanisms of configural processing (Yovel et al., 2010): while face processing depends on all different stages of configural processing (including holistic processing and second-order relations), body processing seems to rely more on first-order relations and structural information (disrupted by head removal). This statement is further supported by the literature about the body composite effect (see below).

1.2.2. Lessons from the body composite effect

The *face composite effect* (Young et al., 1987) is considered one of the demonstrations of holistic face processing since it shows that facial features cannot be processed independently. A series of studies by Soria Bauser and colleagues (Soria Bauser, Schriewer, & Suchan, 2015; Soria Bauser, Suchan, & Daum, 2011) investigated the different mechanisms of configural processing of face and body by combining inversion effect and composite effect. They found both behavioural (Soria Bauser, Suchan, & Daum, 2011) and electrophysiological (Soria Bauser, Schriewer, & Suchan, 2015) evidence of holistic and second-order relations processing for faces but not for bodies. As a matter of fact, they replicated FIE, BIE, and face composite effect, but they found no body composite effect. These findings show important differences in face and body processing: since inversion is thought to disrupt first-order relational information, holistic processing and second-order relational processing (Maurer et al., 2002), the differences they found might rely on the fact that composite effect has an impact on holistic processing but not on first-order relational information. Moreover, the fact that BIE was found in both aligned and misaligned bodies is further evidence for the absence of holistic processing in bodies. From the psychophysiological point of view (Soria Bauser, Schriewer, & Suchan, 2015), the P200 seems to be the component reflecting holistic and second-order relational information processing, while the N170 appears to be more linked to first-order relational information and structural information processing.

This hypothesis was further demonstrated by a study (Soria Bauser & Suchan, 2013) (not involving the composite effect) in which both behavioural and electrophysiological (N170) results showed that scrambling stimuli abolished the BIE but not the FIE. Since scrambling disturbs first-order relational information and structural information, these findings show that bodies are processed in a feature-based manner when this information is missing. On the contrary, FIE was not disrupted by scrambling, probably because the eye region (which remained intact in scrambled faces) activates face-specific brain processes (Itier, Alain, Sedore, & McIntosh, 2007; Nemrodov & Itier, 2011).

Considering these findings, face and body processing may share some early perceptual mechanisms, but they present important differences in configural processing.

1.2.3. The importance of clothes

A factor that was shown to modulate body perception and, in particular, the BIE is the amount of clothing depicted on body stimuli (Bonemei et al., 2017a; Hietanen & Nummenmaa, 2011). Hietanen & Nummenmaa (2011) showed that the N170 component was larger for naked bodies than for partially or completely clothed bodies, and even faces. These results suggest an enhanced visual processing of naked bodies, probably reflecting affective arousal and potentially beneficial in identifying potential mating partners and competitors. Bonemei et al. (2017) investigated the influence of clothing on the BIE and found behavioural inversion effects only for naked bodies (both with minimal and full body context, whole and headless) and not for clothed bodies. They discussed these findings as a demonstration of configural processing of naked bodies, while clothed bodies may trigger clothes-sensitive rather than body-sensitive perceptual mechanisms.

Clothed and naked bodies are both typically used in studies on body perception, but rarely the choice of one of the two categories is discussed. These findings suggest that, on the contrary, the choice of naked or clothed stimuli may be potentially confounding in interpreting results of the BIE or other phenomena related to body perception. For this reason, clothing was included as a potential moderator in our meta-analysis.

1.2.4. Clinical studies

One of the proofs typically used to demonstrate the uniqueness of body processing is the fact that a selective deficit in body perception comparable to prosopagnosia for faces has never been observed (Minnebusch & Daum, 2009; Peelen & Downing, 2007b). Body perception is most likely mediated by a distributed cortical network (see Chapter 1), therefore a damage to different components of the network may lead to specific and distinct body processing deficits.

Prosopagnosia is defined as a deficit in the ability to recognize a person by the face only (Bodamer, 1947; Rivolta, 2013). While *acquired prosopagnosia* is typically caused by a damage to bilateral occipito-temporal areas, *congenital* or *developmental prosopagnosia* (CP) is a condition characterized by a lifelong impairment in face recognition, and affecting around 2.5% of the general population (Kennerknecht et al., 2006). CP has been linked to a specific impairment in configural face processing (Palermo et al., 2011; Rivolta et al., 2014; Rivolta, Palermo, Schmalzl, & Williams, 2012). Since we already discussed that face and body perception partly share some configural mechanisms (Reed et al., 2006) and show overlapping neural representations (Peelen & Downing, 2007b), it is interesting to investigate how people affected by CP process faces and bodies. Righart & de Gelder (2007) first showed abnormalities in body processing in CP subjects, since both FIE and BIE were absent on the N170 component. Many other studies found behavioural results of impaired body processing in CP subjects (Biotti, Gray, & Cook, 2017; Moro et al., 2012; Rivolta, Lawson, & Palermo, 2016). These findings demonstrate that CP subjects might have a deficit in both configural face and body processing. This could be a further evidence for common configuration-based mechanisms shared between the two stimuli categories, suggesting a more general impairment of configural processing in CP subjects (Righart & de Gelder, 2007), which is critical for early stages of both stimuli encoding. However, it is important to avoid generalizing these results, especially given the high individual variability in CP subjects: Righart & de Gelder (*ibidem*) themselves found the electrophysiological BIE in one CP participant and Susilo, Yovel, Barton, & Duchaine (2013) found a preserved behavioural BIE in three out of four acquired prosopagnosic patients. These findings may suggest that not all CP subjects present a generally compromised configural processing: the causes underlying these differences still need to be investigated.

The presence of BIE was also investigated in the population affected by *Autism Spectrum Disorder* (ASD) (Reed et al., 2007). ASD is a family of neurodevelopmental disorders characterized by impairments in social interaction, verbal and non-verbal communication and stereotypic behaviours (APA, 2013). People affected by ASD often show difficulties in configural processing and enhanced detail-based processing, a type of behaviour formalized in the *weak central coherence* theory (Happé & Frith, 2006). Reed and colleagues' (2007) study found that ASD participants showed a preserved FIE, while the BIE was not present. They discussed their results as the fact that adults affected by ASD may have developed compensatory strategies for recognizing faces not used for body postures. These results also highlight, again, the fact that face and body processing differ in the configural mechanisms used.

The lack of BIE (with preserved FIE) was found also in patients affected by *Anorexia Nervosa* (AN) (Cosimo Urgesi et al., 2014). The authors explain this result as a specific impairment of configural body processing: disturbances of body perception in AN seems to be linked to specific alterations in the processing of body configurations with respect to the local processing of body part details.

Therefore we found that body processing may result impaired in different clinical conditions, either as a consequence of general configural processing deficit (as in CP population) or as a selective configural body processing impairment (as in ASD or AN patients).

1.3. Meta-analysis on the Body Inversion Effect

As we widely expressed, the BIE is a robust effect, replicated in many studies performed on typically developed population. Different studies on the BIE showed that body perception relies on configural mechanisms, partially shared with face processing (first-order relational information and structural information), and partially different (absence of holistic processing and second-order relational information). The BIE can be modulated by several manipulations of stimuli (and their consequent processing) or disrupted in different clinical (ASD, AN) or sub-clinical (CP) conditions.

In order to test the robustness of this effect and how it can be modulated, we decided to perform a meta-analysis on these studies. A meta-analysis is a statistical method that combines the results of different studies to assess the summary effect size (Borenstein, Hedges, Higgins, & Rothstein, 2009). The aim of a meta-analysis is to derive an estimate closest to the common effect size measured by all the studies, by performing a weighted average of the results and their variance. A method called *meta-regression* also allows to estimate how different predictors can modulate the effect size in the included studies. Therefore the meta-analysis, together with a systematic literature review, seems to be the most appropriate method to test the robustness and variability of the body inversion effect.

2. Methods

2.1. Literature search methodology

Search of relevant studies was conducted using electronic search of different databases: Google Scholar, Pubmed, Scopus, Mendeley, and Proquest Dissertations and Theses. The keywords used in searches were “body inversion” and “body inversion effect”. A supplementary approach used to identify relevant studies was searching references of different review articles (de Gelder et al., 2015; de Gelder, 2006; Minnebusch & Daum, 2009), together with requesting researchers known for their research on the BIE to provide any unpublished data.

2.2. Selection criteria

Studies were included in the current review and meta-analysis if they satisfied the following criteria:

- Studies examined perception of upright and inverted bodies and compared them in a statistical way. All studies reporting qualitative comparisons were excluded.
- Studies reported sufficient data to calculate an effect size.
- Participants could belong to clinical samples. Effect sizes were calculated separately for the non-clinical or control participants if a significant difference between samples was highlighted.
- Stimuli used in the study could be both real pictures or simulated 3-D body stimuli. Movies of biological motion were also included.
- Stimuli could be full-body or headless, clothed or naked, since these variables could represent a potential influence on BIE. Experiments presenting body parts, scrambled bodies,

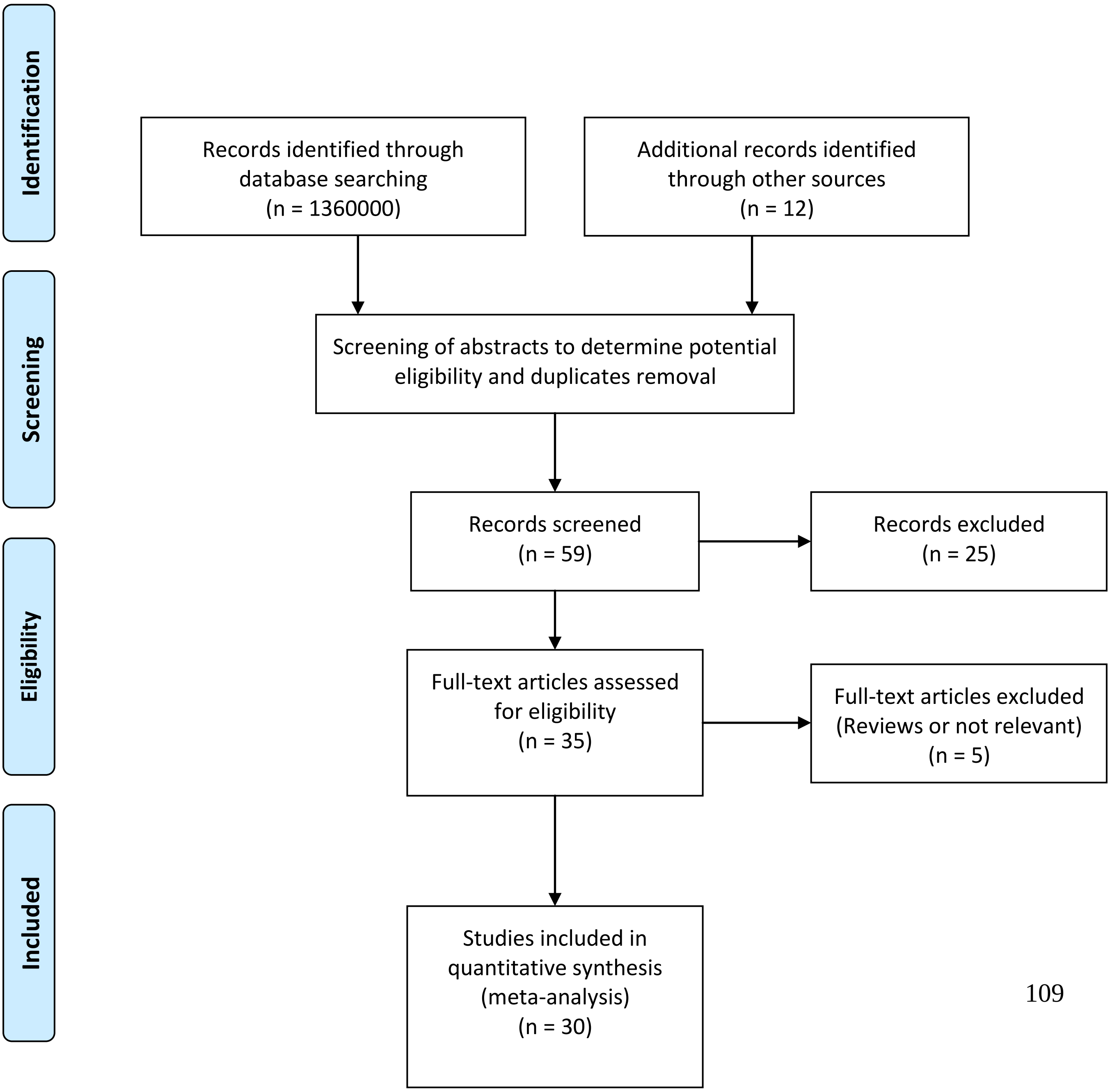
bodies with missing body parts, heads, misaligned body halves, anthropomorphised robots, without control body stimuli were excluded from the analysis.

All studies were cross-referenced to avoid duplicates in the meta-analysis. Review articles and chapters in books were excluded and only empirical studies were considered.

The selection process is represented by the following flow diagram.

59 studies were screened and 30 met all the previous criteria (total sample size = 977). The full table describing every study is reported in the appendix.

Selection Flow Diagram (adapted from PRISMA, 2009)



2.3. Meta-analytic methods

The whole meta-analysis was carried out using RStudio software (RStudio Inc., 2016). The package “compute.es” (Del Re, 2013) was used to estimate and transform effect size indices. The package “metafor” (Viechtbauer, 2010) was used to perform the meta-analysis and create the plots presented in the Results section.

The effect size index we used for all outcome measures was Cohen’s d, i.e. the difference between the means of two conditions (upright vs. inverted bodies) divided by their pooled standard deviation. The effect size was determined based on the reported statistics, including t, F, p values, and means and dispersion measures. When the effect was reported as “non-significant”, with no further information, the effect size was set to zero. 29 out of 30 studies presented a within-subjects or mixed between/within-subjects design. However, we decided to compute Cohen’s d assuming independence of samples: since effect size indices tend to be higher in within-subjects design than in between-subjects design (Lakens, 2013), we estimated Cohen’s d assuming no shared variance between samples in order to be conservative and provide an under estimation of the effect size.

Different measures of BIE were extracted from each study, because all studies reported more than one experiment, condition (e.g., whole bodies vs. headless bodies), population (clinical vs. non-clinical) or measurement. One effect size was computed for each of them, 113 measures in total extracted from 30 studies. Considered measures were behavioural (accuracy, d’, reaction times, inverse efficiency score, explicit judgements), electrophysiological (ERPs: P100, N170 and P200), from fMRI (activation of body-selective areas: EBA and FBA) and eye movement recordings (duration of the first fixation and total number of fixations).

Heterogeneity across sets of outcomes was assessed using the $Q_{\text{homogeneity}}$ statistic. A statistically significant result in the test on $Q_{\text{homogeneity}}$ represents high heterogeneity across the results of different studies. It is important to remember that the $Q_{homogeneity}$ tends to be always significant with a large number of studies considered (as every test assessing data distribution) (Cohen et al., 2013).

Since several datasets showed heterogeneous effect sizes, and because random effects models are more conservative than fixed effects parameters in these cases, effect sizes and confidence intervals (CIs) from a random effects model are presented. In random effects models, the true effects in the studies are assumed to have been sampled from a distribution of true effects, and both between- and within-study variability are taken into account.

The “file drawer problem” (Mullen, 1989) was dealt as follows. It defines the fact that only studies reporting statistically significant results are typically published in international peer-reviewed journals, while experiments showing null results tend to be “left behind” by researchers. In order to calculate the effect of potential data censoring or publication bias on the results of the meta-analysis, the “trim and fill” method (Duval & Tweedie, 2000a, 2000b) was used. Following this non-parametric method, a funnel plot of each measure’s effect size against the standard error (on the Y axis) was designed. If no publication bias was present, this plot was expected to have the shape of a funnel, because studies with smaller sample sizes (and thus, larger standard errors) have increasingly larger variation in estimates of their effect size because random variation becomes increasingly influential, while studies with larger sample sizes have smaller variation in effect sizes. With the trim and fill procedure, the studies with the highest effect size compared to their standard error (thus, out of the funnel shape), which are considered to be symmetrically unmatched by missing studies, are trimmed and their missing counterparts are “filled” as mirror images of the trimmed outcomes.

Another method typically used in meta-analyses is the Fail-safe method (Rosenthal, 1991). This method is aimed to estimate the number of studies with null result that should be added in literature to reduce the considered effect size to “non-significantly different from zero”. Typically, the fail-safe number (Nfs) is representative of the robustness of the effect size.

2.4. Meta-regression

As stated in the introduction, BIE was reported to be modulated by different variables (presence / absence of the head, clothing, etc.). For this reason, a meta-regression was carried out. A meta-regression is a method aimed to investigate the influence of one or more predictors used in the included studies. The influence of each predictor on combined effect sizes was tested with the $Q_{contrast}$ statistic in a mixed fixed-random effects model. A statistically significant $Q_{contrast}$ value indicates that the difference in effect size between subsets of studies is significant.

The predictors used in the meta-regression are:

1. Clothing: clothed (83 measures) or naked (30).
2. Head: full-body (84), headless (22) or both (7).
3. Pictures: real pictures (40), simulated 3-D stimuli (67) or biological motion (6).
4. Task: participants’ task was focused on: attractiveness judgement (3), composite illusion (12), continuous flash suppression (5), distortion (11), identity (13), orientation (4), letters discrimination (6), posture (56), stimulus category (3).
5. Measure: behavioural (80), ERPs (28), eyetracking (3), fMRI (2).

Variables 1-3 were particularly important regarding our hypotheses and their modulatory effects on BIE found in the literature; variables 4 and 5 were relevant to assess whether the high variability in the task performed and in the measure investigated influenced the body inversion effect size or not.

3. Results

3.1. Meta-analysis – overall effect

The combined effect size of the 30 studies (113 measurements) was d = 1.1292, total N = 977, 95% CI [0.99, 1.26], z = 16.37, p < .001. This result indicates a very large effect according to Cohen's (1988) and Sawilowsky's (2009) criteria. The results are represented by a forest plot in Fig. 3.5.

The $Q_{\text{homogeneity}}$ test showed a statistically significant result, highlighting the very heterogeneous set of outcomes: Q (112) = 496.13, p < .001. This result demonstrates the necessity of a random effects model, since it allows explaining larger variance compared to a fixed effect model.

3.2. Trim and fill method

The trim and fill method revealed that 25 measurements (Standard Error = 6.97) were trimmed and filled to create a symmetrical funnel plot (Fig. 3.6). These studies were probably subject to publication bias due to the null results. After implementing the trim and fill method, resulting adjusted combined effect size remained large and statistically significant: d = 0.8594, 95% CI [0.71, 1.01], z = 10.91, p < .001.

The fail-safe method showed a fail-safe number (Nfs) of 45923, i.e. 45923 studies with null result should be added in literature to reduce the considered effect size to "non-significantly different from zero" (Rosenthal, 1991). This result is larger than Rosenthal's (*ibidem*) criterion of 5k + 10 (k = the number of measures included in the meta-analysis), indicating that the overall effect size is very robust assuming a zero effect size.

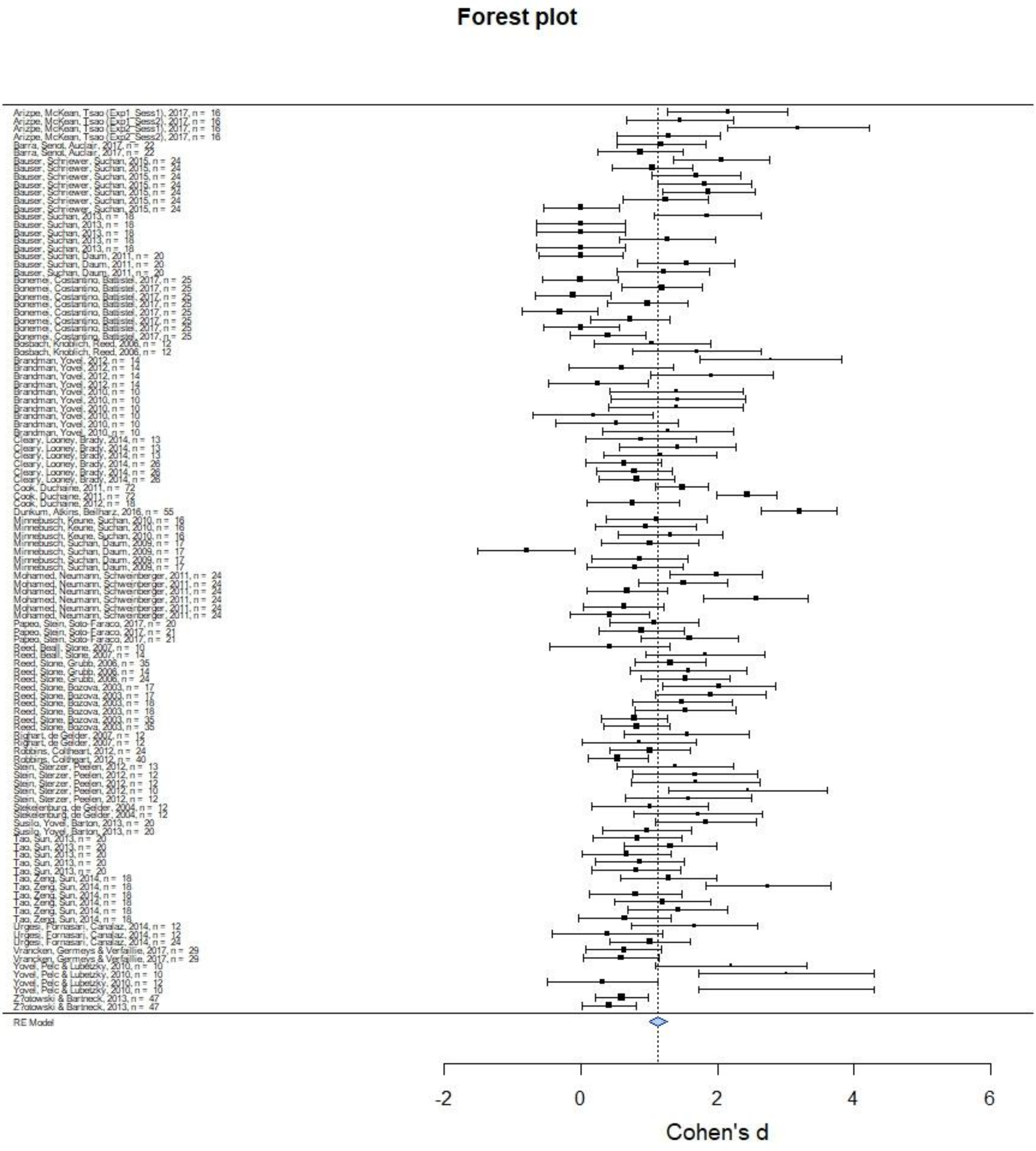


Fig. 3.5: The forest plot represents the effect size of each study, together with its 95% confidence interval (error bars) and sample size (represented by the squares' dimesion). The mean effect size (d = 1.1292) computed by the random effects model is represented by the diamond in the lower part of the plot, while the diamond's width represents the 95% confidence interval.

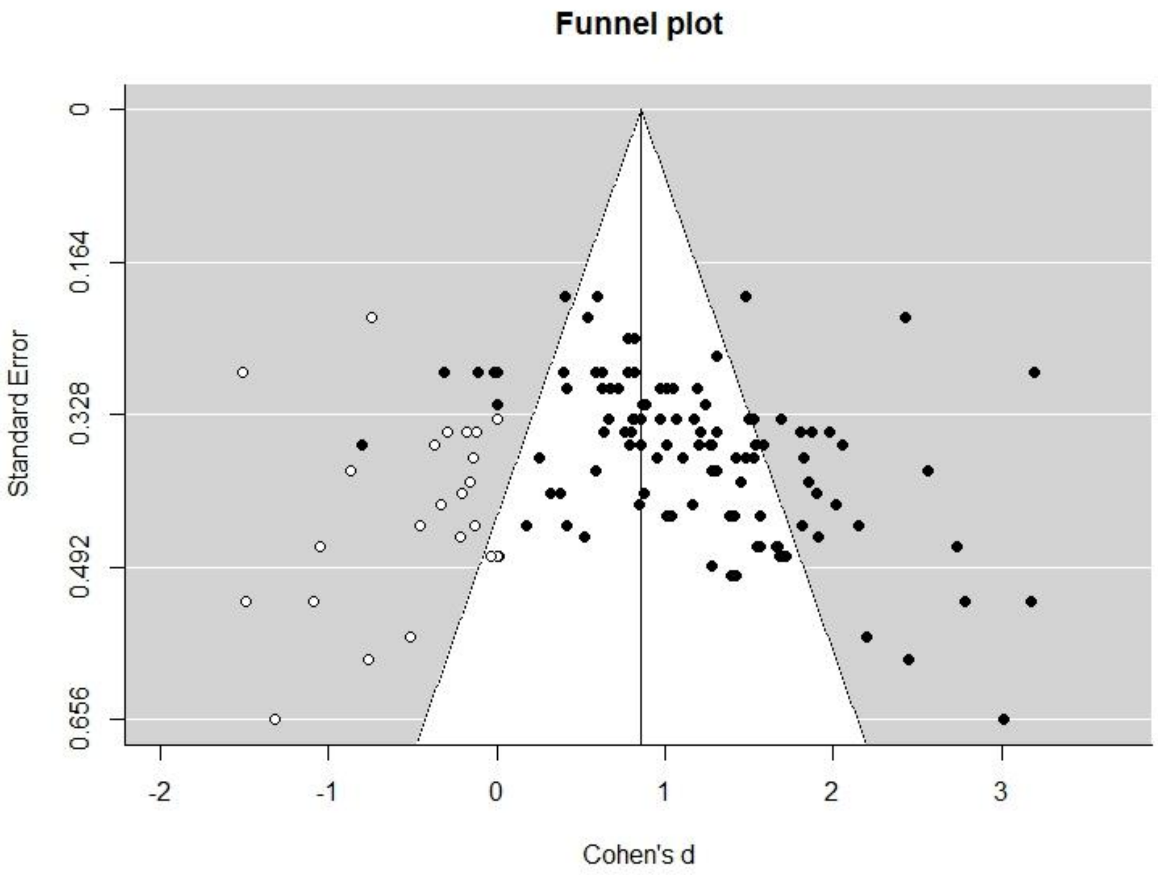


Fig. 3.6: The funnel plot represents included studies as black dots. In this plot the effect size is shown on the X axis and the standard error (inversely proportional to the sample size) on the Y axis. The white funnel shape represents the area where all studies should lie symmetrically if there were no publication bias, showing that studies with smaller sample sizes (and thus, larger standard errors) have increasingly larger variation in estimates of their effect size. The trim and fill method estimated 25 studies with null result, probably subject to publication bias, represented as white dots in the plot.

3.3. Meta-regression – moderators

The meta-regression was run in order to investigate the influence of any potential moderators, but it revealed no statistically significant differences among the levels of predictors we considered:

1. Clothing: clothed (d = 0.998, 95% CI [0.858, 1.138]), naked (d = 1.115, 95% CI [0.942, 1.288]), z = -0.655, p = .512.
2. Head: full-body (d = 1.068, 95% CI [0.923, 1.212]), headless (d = 0.935, 95% CI [0.791, 1.078]) or both (d = 0.863, 95% CI [0.646, 1.080]), z = 0.993, p = .321.

3. Pictures: real pictures (d = 0.984, 95% CI [0.839, 1.128]), simulated 3-D stimuli (d = 1.027, 95% CI [0.879, 1.175]) or biological motion (d = 1.359, 95% CI [1.169, 1.548]), z = -0.892, p = .372.
4. Task: participants' task was focused on: attractiveness judgement (d = 1.333, 95% CI [1.155, 1.511]), composite illusion (d = 1.143, 95% CI [0.994, 1.293]), continuous flash suppression (d = 1.115, 95% CI [0.953, 1.277]), distortion (d = 1.212, 95% CI [1.057, 1.366]), identity (d = 0.955, 95% CI [0.780, 1.131]), orientation (d = 0.948, 95% CI [0.838, 1.058]), letters discrimination (d = 0.869, 95% CI [0.749, 0.989]), posture (d = 0.986, 95% CI [0.841, 1.132]), stimulus category (d = 1.003, 95% CI [0.867, 1.140]), z = -0.378, p = .706.
5. Measure: behavioural (d = 1.049, 95% CI [0.894, 1.205]), ERPs (d = 0.980, 95% CI [0.850, 1.109]), eyetracking (d = 1.020, 95% CI [0.872, 1.168]), fMRI (d = 0.921, 95% CI [0.781, 1.061]), z = -0.382, p = .703.

4. Discussion

The body inversion effect (BIE) demonstrates the configural processing of body shapes (Reed et al., 2003, 2006), showing that recognition of body postures presented upside down is extremely more difficult than recognition of upright body postures. The BIE was replicated in several studies, but different manipulations were shown to disrupt this effect, e.g., removing the head from bodily stimuli or using clothed (compared to naked) stimuli. Thus, a meta-analysis and meta-regression were performed to test the robustness of this effect and how it can be modulated by different manipulations.

The main result of the meta-analysis shows that the BIE presents a very large overall effect size. This finding shows the robustness of this effect, i.e., inverted bodies were consistently more difficult to process than upright bodies, independently of different conditions and manipulations. Then we can deduct that configural body processing, as shown by differences caused by BIE, was demonstrated and consistent.

The $Q_{homogeneity}$ test showed large variability among different studies. This finding indicates that the BIE, even if consistent, can actually be modulated by stimulus manipulations, different tasks and it can display differences related to the different measures taken into account. This provides a further reason to perform a meta-regression and consider its results in the light of the literature, in order to find what variables may produce differences in the studies.

The trim and fill method showed a small publication bias in the studies that were included in the meta-analysis. This is quite common in the literature, since experiments with null results are generally less likely to be published (Duval & Tweedie, 2000a, 2000b). Even considering the estimated unpublished results, the effect size remained large and significantly different from zero. This, together with the very high fail-safe number, provides strong evidence for the robustness of the BIE, given the extremely low probability that its true effect size is "non-significantly different from zero" (Rosenthal, 1991).

The meta-regression revealed no statistically significant differences among the levels of the predictors. The absence of statistically significant effects shows that (1) the predictors discussed in literature (clothing, head presence and type of picture) may not predict changes in the effect size of BIE, while the large variance in the effect size is more likely to explain these differences, and (2) the BIE is manifested consistently and independently of the task performed by participants and the type of measure used.

Entire lines of research were aimed to highlight specific manipulations that could disrupt the BIE (see Paragraphs 1.2.1 and 1.2.3). One advantage of the meta-analytic methods is that the studies supporting these hypotheses are considered together with studies, which found no effect of the same manipulations. As a matter of fact, on the one hand some studies found specific effects of the head removal (Brandman & Yovel, 2010; Brandman & Yovel, 2012; Minnebusch, Suchan, & Daum, 2009; Yovel, Pelc, & Lubetzky, 2010) and of clothing (Bonemei et al., 2017a; Hietanen & Nummenmaa, 2011), discussing specific hypotheses regarding these differences. On the other hand, many studies found BIE using headless stimuli (Arizpe et al., 2017; Bonemei et al., 2017a; Minnebusch et al., 2010; Mohamed et al., 2011; Robbins & Coltheart, 2012; Susilo et al., 2013; Tao et al., 2014; Thierry et al., 2006). Moreover, most of the other studies included in the meta-analysis found BIE by using both naked and clothed stimuli indifferently. Considering both effect size and sample size in the meta-regression, these manipulations did not appear to affect the BIE in a statistically significant way. This finding does not necessarily mean that the hypotheses claimed by these authors are not valid, but they need further evidence and extensive replications in order to be robustly supported in the light of the present literature.

Even though the meta-regression did not yield statistically significant effects, marginal differences were found in the effects of Pictures and Task, due to non-overlapping confidence intervals among different levels of the predictors. Even though post-hoc comparisons cannot be performed in a meta-regression, it is known that two levels of a variable show a statistically significant difference if their 95% confidence intervals are not overlapping (Cohen et al., 2013). Considering these differences, Pictures effect showed that studies using biological motion revealed higher effect size than those using real pictures. This result may confirm that dynamic information represents a fundamental cue in configural body processing (Thompson, Clarke, Stewart, & Puce, 2005). Specialized visual areas in the posterior superior temporal sulcus (pSTS) produce selective neuronal response to movies of facial and bodily motion (Allison, Puce, & McCarthy, 2000; Puce & Perrett, 2003). This region is specialized in integrating form and dynamic cues, processing form-from-motion cues in the case of biological motion stimuli (Thompson et al., 2005). Also the *mirror-neuron system* was shown to be involved in perception of biological motion (Fox et al., 2016). The mirror-neuron system is a network of areas located over the rostral part of the inferior parietal lobule and the caudal part of the inferior frontal gyrus (Rizzolatti & Craighero, 2004), and is involved in both perception and execution of action. Also EBA and FBA, involved in structural encoding of body shape, are activated by viewing body actions (Astafiev, Stanley, Shulman, & Corbetta, 2004). These findings may suggest the involvement of a network including EBA, STS and the mirror-neuron system in biological motion configural processing (Thompson et al., 2005). The contribution of dynamic information may thus enhance the configural processing of these stimuli through this network. For the same reason, inversion, disturbing the overall stimuli configuration, may disrupt processing in the whole network and thus create a larger BIE, compared to BIE in static pictures.

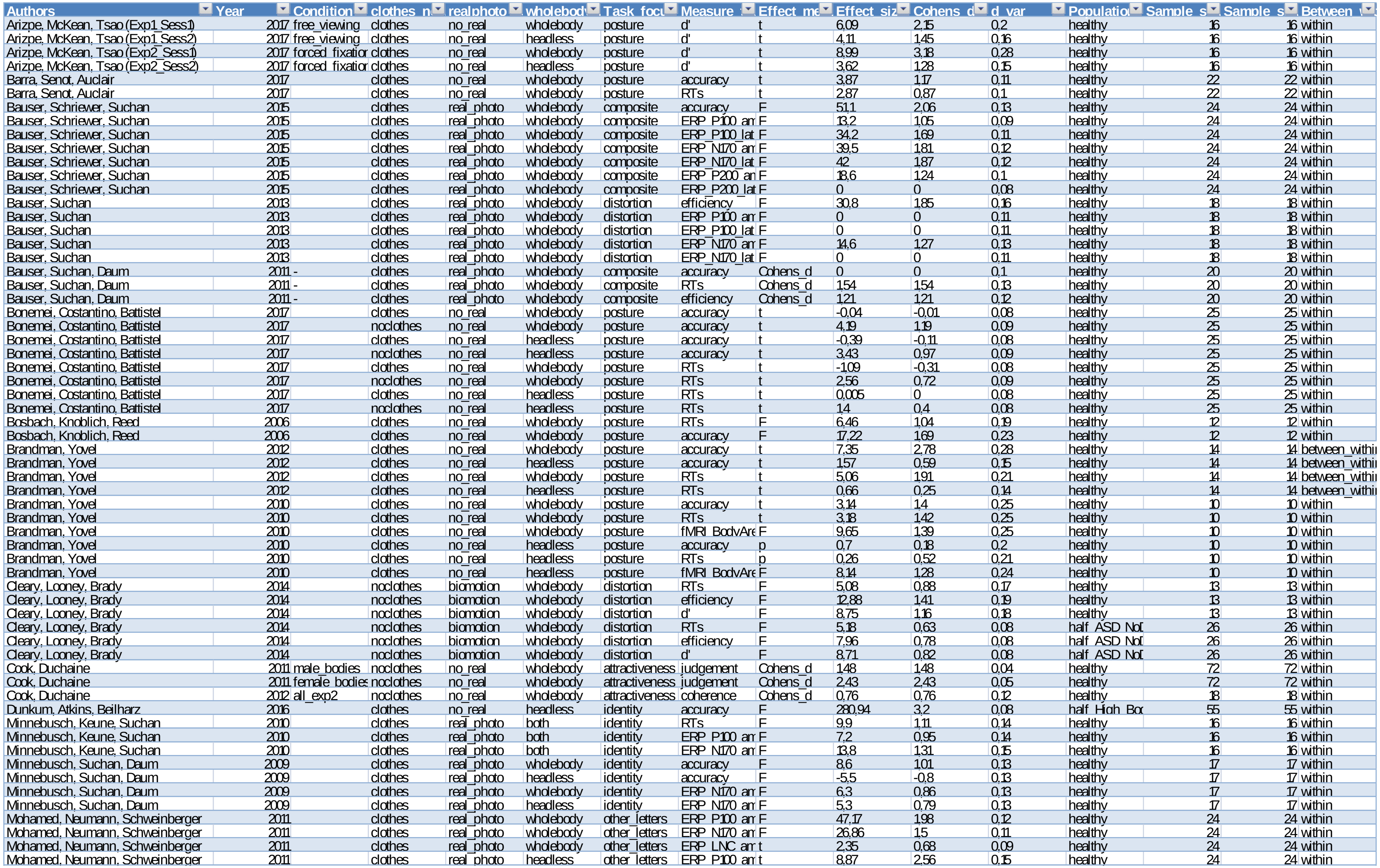
Also the Task predictor showed marginal differences: attractiveness judgement showed higher effect size than identity, orientation, letters, posture and category discrimination. Furthermore, letters discrimination showed a smaller effect size than distortion identification, composite effect and attractiveness judgement. The first difference refers to a study (Cook & Duchaine, 2011) in which the attractiveness judgement was used instead of the typical “sequential matching task”. This study was aimed to show that both faces and bodies recruit similar orientation-specific processes distinct from processes used for generic objects. An attractiveness judgement requires higher level processes than a purely perceptual task as the sequential matching task. Therefore, inversion disrupts the orientation-specific processes involved in the judgement, leading to a larger BIE than the BIE found in perceptual tasks. The second difference refers to a study (Mohamed et al., 2011) aimed to study the influence of the attentional load on the BIE: they found the electrophysiological BIE on the N170 component also when participants’ task was to discriminate a letter and bodies were presented as task-irrelevant distracters. The BIE they found in this task was significantly larger than zero, but in this meta-regression we found it to be smaller than the BIE found while explicitly processing bodies. This is not surprising, considering that attentional load was already proven to modulate face processing (Eimer & Holmes, 2007) and we know that faces and bodies partly share some configural processing mechanisms. Besides, all the tasks for which we found a difference (distortion identification, composite effect and attractiveness judgement) require high-level category-specific processes (Cook & Duchaine, 2011; Soria Bauser, Schriewer, & Suchan, 2015; Soria Bauser & Suchan, 2013; Soria Bauser, Suchan, & Daum, 2011) and, thus, high attentional load.

However, it is important to consider these differences with caution, since they represent results found in single studies. Further research will be needed to investigate these differences more in depth.

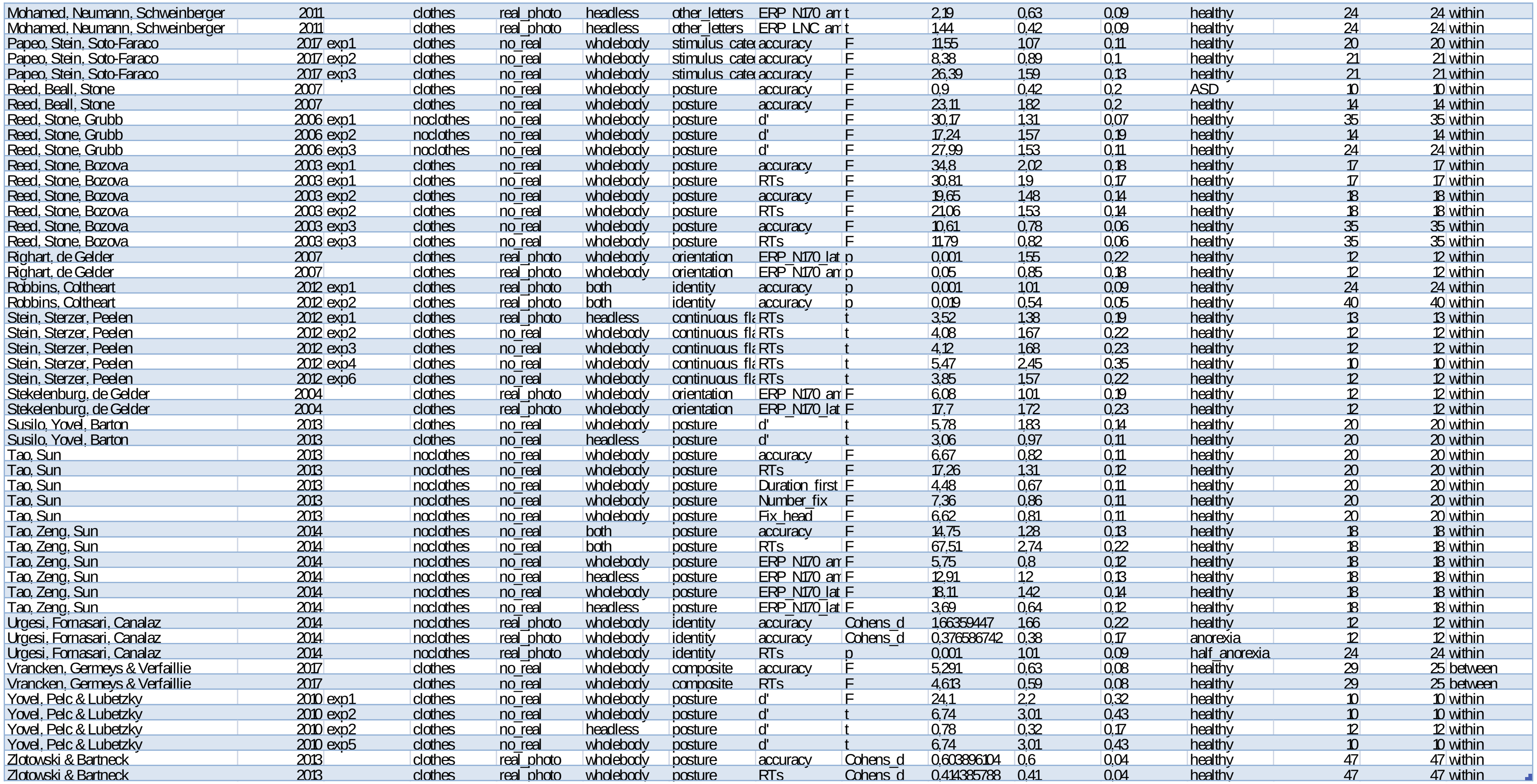
In conclusion, this meta-analysis showed that the BIE is a very robust effect, replicated in several studies, and it can be modulated by some manipulations of stimuli and tasks. However, further research is needed in order to understand the specific neurocognitive mechanisms involved in configural body processing and related BIE. This leads to the two following studies of my own research.

The first study was aimed to investigate the processes involved in BIE by analysing neurophysiological activity in the time-frequency domain. This methodology, exploring neural oscillations, already brought important insights in research on face processing (Tallon-Baudry & Bertrand, 1999) and, to our knowledge, was never used to explore neurocognitive mechanisms involved in BIE.

The second study is aimed to investigate the neural correlates of possible modulations of the BIE: we explored whether the psychophysiological BIE (in its ERP components) could be modulated by the emotion expressed by the stimuli through the emotional body language (de Gelder et al., 2015) and by the task performed by participants.



Authors	Year	Condition	clothes_n	realphoto	wholebody	Task_focu	Measure	Effect_me	Effect_siz	Cohens_d	d_var	Populatio	Sample_s	Sample_s	Between_v
Arizpe, McKean, Tsao (Exp1_Sess1)	2017	free_viewing	clothes	no_real	wholebody	posture	d'	t	6,09	2,15	0,2	healthy	16	16	within
Arizpe, McKean, Tsao (Exp1_Sess2)	2017	free_viewing	clothes	no_real	headless	posture	d'	t	4,11	1,45	0,16	healthy	16	16	within
Arizpe, McKean, Tsao (Exp2_Sess1)	2017	forced_fixatio	clothes	no_real	wholebody	posture	d'	t	8,99	3,18	0,28	healthy	16	16	within
Arizpe, McKean, Tsao (Exp2_Sess2)	2017	forced_fixatio	clothes	no_real	headless	posture	d'	t	3,62	1,28	0,15	healthy	16	16	within
Barra, Senot, Auclair	2017		clothes	no_real	wholebody	posture	accuracy	t	3,87	1,17	0,11	healthy	22	22	within
Barra, Senot, Auclair	2017		clothes	no_real	wholebody	posture	RTs	t	2,87	0,87	0,1	healthy	22	22	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	accuracy	F	51,1	2,06	0,13	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_P100_am	F	13,2	1,05	0,09	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_P100_lat	F	34,2	1,69	0,11	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_N170_am	F	39,5	1,81	0,12	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_N170_lat	F	42	1,87	0,12	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_P200_am	F	18,6	1,24	0,1	healthy	24	24	within
Bauser, Schriewer, Suchan	2015		clothes	real_photo	wholebody	composite	ERP_P200_lat	F	0	0	0,08	healthy	24	24	within
Bauser, Suchan	2013		clothes	real_photo	wholebody	distortion	efficiency	F	30,8	1,85	0,16	healthy	18	18	within
Bauser, Suchan	2013		clothes	real_photo	wholebody	distortion	ERP_P100_am	F	0	0	0,11	healthy	18	18	within
Bauser, Suchan	2013		clothes	real_photo	wholebody	distortion	ERP_P100_lat	F	0	0	0,11	healthy	18	18	within
Bauser, Suchan	2013		clothes	real_photo	wholebody	distortion	ERP_N170_am	F	14,6	1,27	0,13	healthy	18	18	within
Bauser, Suchan	2013		clothes	real_photo	wholebody	distortion	ERP_N170_lat	F	0	0	0,11	healthy	18	18	within
Bauser, Suchan, Daum	2011	-	clothes	real_photo	wholebody	composite	accuracy	Cohens_d	0	0	0,1	healthy	20	20	within
Bauser, Suchan, Daum	2011	-	clothes	real_photo	wholebody	composite	RTs	Cohens_d	1,54	1,54	0,13	healthy	20	20	within
Bauser, Suchan, Daum	2011	-	clothes	real_photo	wholebody	composite	efficiency	Cohens_d	1,21	1,21	0,12	healthy	20	20	within
Bonemei, Costantino, Battistel	2017		clothes	no_real	wholebody	posture	accuracy	t	-0,04	-0,01	0,08	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		noclothes	no_real	wholebody	posture	accuracy	t	4,19	1,19	0,09	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		clothes	no_real	headless	posture	accuracy	t	-0,39	-0,11	0,08	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		noclothes	no_real	headless	posture	accuracy	t	3,43	0,97	0,09	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		clothes	no_real	wholebody	posture	RTs	t	-1,09	-0,31	0,08	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		noclothes	no_real	wholebody	posture	RTs	t	2,56	0,72	0,09	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		clothes	no_real	headless	posture	RTs	t	0,005	0	0,08	healthy	25	25	within
Bonemei, Costantino, Battistel	2017		noclothes	no_real	headless	posture	RTs	t	1,4	0,4	0,08	healthy	25	25	within
Bosbach, Knoblich, Reed	2006		clothes	no_real	wholebody	posture	RTs	F	6,46	1,04	0,19	healthy	12	12	within
Bosbach, Knoblich, Reed	2006		clothes	no_real	wholebody	posture	accuracy	F	17,22	1,69	0,23	healthy	12	12	within
Brandman, Yovel	2012		clothes	no_real	wholebody	posture	accuracy	t	7,35	2,78	0,28	healthy	14	14	between_withi
Brandman, Yovel	2012		clothes	no_real	headless	posture	accuracy	t	1,57	0,59	0,15	healthy	14	14	between_withi
Brandman, Yovel	2012		clothes	no_real	wholebody	posture	RTs	t	5,06	1,91	0,21	healthy	14	14	between_withi
Brandman, Yovel	2012		clothes	no_real	headless	posture	RTs	t	0,66	0,25	0,14	healthy	14	14	between_withi
Brandman, Yovel	2010		clothes	no_real	wholebody	posture	accuracy	t	3,14	1,4	0,25	healthy	10	10	within
Brandman, Yovel	2010		clothes	no_real	wholebody	posture	RTs	t	3,18	1,42	0,25	healthy	10	10	within
Brandman, Yovel	2010		clothes	no_real	wholebody	posture	fMRI_BodyAre	F	9,65	1,39	0,25	healthy	10	10	within
Brandman, Yovel	2010		clothes	no_real	headless	posture	accuracy	p	0,7	0,18	0,2	healthy	10	10	within
Brandman, Yovel	2010		clothes	no_real	headless	posture	RTs	p	0,26	0,52	0,21	healthy	10	10	within
Brandman, Yovel	2010		clothes	no_real	headless	posture	fMRI_BodyAre	F	8,14	1,28	0,24	healthy	10	10	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	RTs	F	5,08	0,88	0,17	healthy	13	13	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	efficiency	F	12,88	1,41	0,19	healthy	13	13	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	d'	F	8,75	1,16	0,18	healthy	13	13	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	RTs	F	5,18	0,63	0,08	half_ASD_No	26	26	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	efficiency	F	7,96	0,78	0,08	half_ASD_No	26	26	within
Cleary, Looney, Brady	2014		noclothes	biomotion	wholebody	distortion	d'	F	8,71	0,82	0,08	half_ASD_No	26	26	within
Cook, Duchaine	2011	male_bodies	noclothes	no_real	wholebody	attractiveness	judgement	Cohens_d	1,48	1,48	0,04	healthy	72	72	within
Cook, Duchaine	2011	female_bodie	noclothes	no_real	wholebody	attractiveness	judgement	Cohens_d	2,43	2,43	0,05	healthy	72	72	within
Cook, Duchaine	2012	all_exp2	noclothes	no_real	wholebody	attractiveness	coherence	Cohens_d	0,76	0,76	0,12	healthy	18	18	within
Dunkum, Atkins, Beilharz	2016		clothes	no_real	headless	identity	accuracy	F	280,94	3,2	0,08	half_High_Bo	55	55	within
Minnebusch, Keune, Suchan	2010		clothes	real_photo	both	identity	RTs	F	9,9	1,11	0,14	healthy	16	16	within
Minnebusch, Keune, Suchan	2010		clothes	real_photo	both	identity	ERP_P100_am	F	7,2	0,95	0,14	healthy	16	16	within
Minnebusch, Keune, Suchan	2010		clothes	real_photo	both	identity	ERP_N170_am	F	13,8	1,31	0,15	healthy	16	16	within
Minnebusch, Suchan, Daum	2009		clothes	real_photo	wholebody	identity	accuracy	F	8,6	1,01	0,13	healthy	17	17	within
Minnebusch, Suchan, Daum	2009		clothes	real_photo	headless	identity	accuracy	F	-5,5	-0,8	0,13	healthy	17	17	within
Minnebusch, Suchan, Daum	2009		clothes	real_photo	wholebody	identity	ERP_N170_am	F	6,3	0,86	0,13	healthy	17	17	within
Minnebusch, Suchan, Daum	2009		clothes	real_photo	headless	identity	ERP_N170_am	F	5,3	0,79	0,13	healthy	17	17	within
Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	wholebody	other_letters	ERP_P100_am	F	47,17	1,98	0,12	healthy	24	24	within
Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	wholebody	other_letters	ERP_N170_am	F	26,86	1,5	0,11	healthy	24	24	within
Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	wholebody	other_letters	ERP_LNC_am	t	2,35	0,68	0,09	healthy	24	24	within
Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	headless	other_letters	ERP_P100_am	t	8,87	2,56	0,15	healthy	24	24	within



Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	headless	other_letters	ERP_N170_am	t	2,19	0,63	0,09	healthy	24	24	within
Mohamed, Neumann, Schweinberger	2011		clothes	real_photo	headless	other_letters	ERP_LNC_am	t	1,44	0,42	0,09	healthy	24	24	within
Papeo, Stein, Soto-Faraco	2017	exp1	clothes	no_real	wholebody	stimulus_cate	accuracy	F	11,55	1,07	0,11	healthy	20	20	within
Papeo, Stein, Soto-Faraco	2017	exp2	clothes	no_real	wholebody	stimulus_cate	accuracy	F	8,38	0,89	0,1	healthy	21	21	within
Papeo, Stein, Soto-Faraco	2017	exp3	clothes	no_real	wholebody	stimulus_cate	accuracy	F	26,39	1,59	0,13	healthy	21	21	within
Reed, Beall, Stone	2007		clothes	no_real	wholebody	posture	accuracy	F	0,9	0,42	0,2	ASD	10	10	within
Reed, Beall, Stone	2007		clothes	no_real	wholebody	posture	accuracy	F	23,11	1,82	0,2	healthy	14	14	within
Reed, Stone, Grubb	2006	exp1	noclothes	no_real	wholebody	posture	d'	F	30,17	1,31	0,07	healthy	35	35	within
Reed, Stone, Grubb	2006	exp2	noclothes	no_real	wholebody	posture	d'	F	17,24	1,57	0,19	healthy	14	14	within
Reed, Stone, Grubb	2006	exp3	noclothes	no_real	wholebody	posture	d'	F	27,99	1,53	0,11	healthy	24	24	within
Reed, Stone, Bozova	2003	exp1	clothes	no_real	wholebody	posture	accuracy	F	34,8	2,02	0,18	healthy	17	17	within
Reed, Stone, Bozova	2003	exp1	clothes	no_real	wholebody	posture	RTs	F	30,81	1,9	0,17	healthy	17	17	within
Reed, Stone, Bozova	2003	exp2	clothes	no_real	wholebody	posture	accuracy	F	19,65	1,48	0,14	healthy	18	18	within
Reed, Stone, Bozova	2003	exp2	clothes	no_real	wholebody	posture	RTs	F	21,06	1,53	0,14	healthy	18	18	within
Reed, Stone, Bozova	2003	exp3	clothes	no_real	wholebody	posture	accuracy	F	10,61	0,78	0,06	healthy	35	35	within
Reed, Stone, Bozova	2003	exp3	clothes	no_real	wholebody	posture	RTs	F	11,79	0,82	0,06	healthy	35	35	within
Righart, de Gelder	2007		clothes	real_photo	wholebody	orientation	ERP_N170_lat	p	0,001	1,55	0,22	healthy	12	12	within
Righart, de Gelder	2007		clothes	real_photo	wholebody	orientation	ERP_N170_am	p	0,05	0,85	0,18	healthy	12	12	within
Robbins, Coltheart	2012	exp1	clothes	real_photo	both	identity	accuracy	p	0,001	1,01	0,09	healthy	24	24	within
Robbins, Coltheart	2012	exp2	clothes	real_photo	both	identity	accuracy	p	0,019	0,54	0,05	healthy	40	40	within
Stein, Sterzer, Peelen	2012	exp1	clothes	real_photo	headless	continuous_fla	RTs	t	3,52	1,38	0,19	healthy	13	13	within
Stein, Sterzer, Peelen	2012	exp2	clothes	no_real	wholebody	continuous_fla	RTs	t	4,08	1,67	0,22	healthy	12	12	within
Stein, Sterzer, Peelen	2012	exp3	clothes	no_real	wholebody	continuous_fla	RTs	t	4,12	1,68	0,23	healthy	12	12	within
Stein, Sterzer, Peelen	2012	exp4	clothes	no_real	wholebody	continuous_fla	RTs	t	5,47	2,45	0,35	healthy	10	10	within
Stein, Sterzer, Peelen	2012	exp6	clothes	no_real	wholebody	continuous_fla	RTs	t	3,85	1,57	0,22	healthy	12	12	within
Stekelenburg, de Gelder	2004		clothes	real_photo	wholebody	orientation	ERP_N170_am	F	6,08	1,01	0,19	healthy	12	12	within
Stekelenburg, de Gelder	2004		clothes	real_photo	wholebody	orientation	ERP_N170_lat	F	17,7	1,72	0,23	healthy	12	12	within
Susilo, Yovel, Barton	2013		clothes	no_real	wholebody	posture	d'	t	5,78	1,83	0,14	healthy	20	20	within
Susilo, Yovel, Barton	2013		clothes	no_real	headless	posture	d'	t	3,06	0,97	0,11	healthy	20	20	within
Tao, Sun	2013		noclothes	no_real	wholebody	posture	accuracy	F	6,67	0,82	0,11	healthy	20	20	within
Tao, Sun	2013		noclothes	no_real	wholebody	posture	RTs	F	17,26	1,31	0,12	healthy	20	20	within
Tao, Sun	2013		noclothes	no_real	wholebody	posture	Duration_first	F	4,48	0,67	0,11	healthy	20	20	within
Tao, Sun	2013		noclothes	no_real	wholebody	posture	Number_fix	F	7,36	0,86	0,11	healthy	20	20	within
Tao, Sun	2013		noclothes	no_real	wholebody	posture	Fix_head	F	6,62	0,81	0,11	healthy	20	20	within
Tao, Zeng, Sun	2014		noclothes	no_real	both	posture	accuracy	F	14,75	1,28	0,13	healthy	18	18	within
Tao, Zeng, Sun	2014		noclothes	no_real	both	posture	RTs	F	67,51	2,74	0,22	healthy	18	18	within
Tao, Zeng, Sun	2014		noclothes	no_real	wholebody	posture	ERP_N170_am	F	5,75	0,8	0,12	healthy	18	18	within
Tao, Zeng, Sun	2014		noclothes	no_real	headless	posture	ERP_N170_am	F	12,91	1,2	0,13	healthy	18	18	within
Tao, Zeng, Sun	2014		noclothes	no_real	wholebody	posture	ERP_N170_lat	F	18,11	1,42	0,14	healthy	18	18	within
Tao, Zeng, Sun	2014		noclothes	no_real	headless	posture	ERP_N170_lat	F	3,69	0,64	0,12	healthy	18	18	within
Urgesi, Fornasari, Canalaz	2014		noclothes	real_photo	wholebody	identity	accuracy	Cohens_d	1,66359447	1,66	0,22	healthy	12	12	within
Urgesi, Fornasari, Canalaz	2014		noclothes	real_photo	wholebody	identity	accuracy	Cohens_d	0,376586742	0,38	0,17	anorexia	12	12	within
Urgesi, Fornasari, Canalaz	2014		noclothes	real_photo	wholebody	identity	RTs	p	0,001	1,01	0,09	half_anorexia	24	24	within
Vrancken, Germeys & Verfaillie	2017		clothes	no_real	wholebody	composite	accuracy	F	5,291	0,63	0,08	healthy	29	25	between
Vrancken, Germeys & Verfaillie	2017		clothes	no_real	wholebody	composite	RTs	F	4,613	0,59	0,08	healthy	29	25	between
Yovel, Pelc & Lubetzky	2010	exp1	clothes	no_real	wholebody	posture	d'	F	24,1	2,2	0,32	healthy	10	10	within
Yovel, Pelc & Lubetzky	2010	exp2	clothes	no_real	wholebody	posture	d'	t	6,74	3,01	0,43	healthy	10	10	within
Yovel, Pelc & Lubetzky	2010	exp2	clothes	no_real	headless	posture	d'	t	0,78	0,32	0,17	healthy	12	12	within
Yovel, Pelc & Lubetzky	2010	exp5	clothes	no_real	wholebody	posture	d'	t	6,74	3,01	0,43	healthy	10	10	within
Zlotowski & Bartneck	2013		clothes	real_photo	wholebody	posture	accuracy	Cohens_d	0,603896104	0,6	0,04	healthy	47	47	within
Zlotowski & Bartneck	2013		clothes	real_photo	wholebody	posture	RTs	Cohens_d	0,414385788	0,41	0,04	healthy	47	47	within

Table describing all the studies included in the meta-analysis and all the specific measures that were used.

CHAPTER 4

NEURAL OSCILLATIONS INVOLVED IN FACE- AND BODY-INVERSION EFFECTS

Theta- and Gamma- band activity discriminates face, body and object perception

1. Introduction[3]

As we discussed, an electrophysiological marker specifically related to configural processing was found by means of the event-related potentials (ERPs) technique. Much evidence demonstrates the existence of a face- and body-sensitive ERP negative component that peaks at around 170 ms post stimulus onset (N170), which reflects early perceptual processing of the human visual system (Bentin, Deouell, & Soroker, 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion & Gauthier, 2002). Given that the N170 component is larger and delayed for inverted faces and bodies, it is believed that this component reflects early perceptual structural encoding (Rossion et al., 2000; Stekelenburg & de Gelder, 2004; Watanabe, Kakigi, & Puce, 2003).

ERPs reflect brain activity that is phase-locked (i.e. evoked) to the stimulus onset and they are calculated by averaging the EEG signal from all trials. They, however, hide information deriving from induced (non-phase locked) activity, which provides important information, especially in the cognitive domain (Donner & Siegel, 2011; Uhlhaas & Singer, 2010). Induced activity can be extracted on a single trial level and can be retrieved by time-frequency analyses, also known as time-frequency representations (TFRs), on different frequency bands (Donner & Siegel, 2011; Oostenveld, Fries, Maris, & Schoffelen, 2011).

In the primate visual system, high-frequency, low amplitude gamma-band (> 25 Hz) activity has been suggested to mediate perceptual binding, and the grouping of visual information (Singer & Gray, 1995; Tallon-Baudry & Bertrand, 1999). According to the “representational hypothesis” (*ibidem*), induced gamma synchronization is a signature of bottom-up feature binding (also related to holistic processing of faces) and top-down matching between the perceived stimulus and an internal object representation of it. This definition seems to imply that gamma-band oscillations

---

[3] The study presented in this Chapter was carried out at the University of East London, in collaboration with Prof. Davide Rivolta.

represent a marker of holistic processing and second-order spatial information processing (Maurer et al., 2002). Evidence suggests enhanced gamma oscillations induced by faces over occipito-temporal areas, when compared to control stimuli such as houses or scrambled stimuli (Gao et al., 2012; Zion-Golumbic & Bentin, 2007; Zion-Golumbic, Golan, Anaki, & Bentin, 2008). Since these oscillations show a FIE (i.e., upright faces induce greater gamma synchronization when compared to inverted faces), it is likely that this activity reflects the inability of the visual system to bind facial features of inverted faces in a representation (Anaki et al., 2007; Dobel, Junghöfer, & Gruber, 2011; Lachaux et al., 2005; Matsuzaki, Schwarzlose, Nishida, Ofen, & Asano, 2015; Moratti, Méndez-Bértolo, Del-Pozo, & Strange, 2014; Uono et al., 2016).

Theta-band activity (typically represented in the 4-7 or 5-7 Hz range), correlates with various cognitive and attentional mechanisms, such as motor planning and imagery, mental rotation, spatial attention, and working memory (Ptak, Schnider, & Fellrath, 2017). It has been shown that cortico-hippocampal interactions mediate theta activity in cognition (Başar, 1999), since it is the spontaneous rhythm of different limbic structures. Albeit not specifically linked to the FIE, theta-band connections between limbic structures and visual cortex were reported in various emotional paradigms (Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2001; Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2002; Başar, Güntekin, & Öniz, 2006; Güntekin & Başar, 2009, 2014) and in several experiments involving facial recognition and facial emotional expressions (Başar, Güntekin, & Öniz, 2006; Güntekin & Başar, 2009, 2014). In those studies, occipital and occipito-temporal areas showed greater theta synchronization when processing emotionally arousing visual stimuli or faces showing emotional expressions, at latencies around 200-500 ms post-stimulus. Furthermore, enhanced theta-gamma coupling induced by upright faces (compared to inverted faces) has been shown in the right inferior occipital gyrus (IOG), after 200 ms post-stimulus onset (Sato et al., 2014). These results were interpreted as evidence that right-IOG gamma-activity conducts rapid and multistage (i.e., both featural and holistic) face processing, in coherence with theta oscillations transmitted from other brain regions. In particular, as demonstrated in a further study (Sato et al., 2017), theta-gamma coupling shows bidirectional modulatory effects between the IOG and limbic structures (i.e., the amygdala). This suggests a subcortico-cortical fast communication dedicated to the efficient processing of faces. These findings suggest that occipital theta-band oscillations may represent a marker of the fast early perceptual processing of highly salient stimuli. This processing is based on the subcortical route including superior colliculus, pulvinar and the amygdala, in the model suggested by Adolphs et al. (Adolphs, 2002a, 2002b) (see Chapter 1).

Although critical in person recognition, faces do not represent the only stimuli on which we rely on; person recognition also relies heavily on body processing. Similar to faces, bodies constitute fundamental mediums for emotional expression and communication (see Chapter 1, de Gelder, de Borst, & Watson, 2015 for a review). At the cognitive and psychophysiological level, however, body and face processing share some perceptual mechanisms. Body inversion, like faces, causes a drop in performance (i.e., Body-Inversion Effect, BIE) (Bonemei, Costantino, Battistel, & Rivolta, 2017b; Reed et al., 2003), which suggests a reliance on configural mechanisms and, as for faces, the N170 is larger and delayed for inverted bodies (Stekelenburg & De Gelder, 2004). Even though both face and body perception rely on configural processing, these stimulus categories may involve different stages of configural processing, to different extent (see Chapter 3 Section 1.1.1, Reed, Stone, Grubb, & McGoldrick, 2006).

Although the ERP correlates of the BIE have been investigated, no study comparing TFR activity in Face and Body perception has been conducted and it is not known whether some differences also exist at the TFR level as they exist at behavioural level. Despite sharing some perceptual and cognitive mechanisms, these stimuli are known to convey different information: faces convey information related both to identity and to emotional expressions (Haxby et al., 2000), while bodies are known to express mainly emotional information, through the emotional body language (de Gelder et al., 2015), and less information about person identity. Thus, in the current study we compared neural oscillations elicited by the presentation of upright and inverted faces to those elicited by bodies and houses. Houses were chosen as control stimuli since, as bodies and faces, they can vary in specific features and in their configuration (involving holistic processing vs. second-order relational processing, Maurer et al., 2002), but they are not social stimuli. Specifically, we decided to investigate gamma and theta band activity given that the former is a specific marker of feature binding and representation matching processes (Tallon-Baudry & Bertrand, 1999) and can inform us about the involvement of holistic processing of the stimuli, while the latter is involved in the processing of facial identity, expression and emotionally arousing stimuli (Başar, Güntekin, & Öniz, 2006; Güntekin & Başar, 2009, 2014), thus it can tell us how these different pieces of information are involved in FIE and BIE. On the one hand, we expected to find greater gamma-band activity when participants were processing upright than inverted faces. On the other hand, based on the previous literature showing the importance of theta and gamma band activity in feature binding and facial recognition processes (Güntekin & Başar, 2014; Tallon-Baudry & Bertrand, 1999), we also expected to find some differences among our stimulus categories in theta and gamma activity. More specifically, if the processes disrupted by Face and Body Inversion are the same, then a similar pattern of oscillatory activity should be elicited by the inversion of both these two categories of stimuli, while a different one should be found for inverted houses. By contrast, if this is not the case, we expected to find different oscillatory patterns for each of the three categories.

2. Methods

2.1. Participants

Twenty-four healthy participants (11 M; mean age: 28.2 ± 5.8 years) were recruited for the experiment mainly among university students and their acquaintances. One participant was excluded from the analyses due to technical problems related to data quality. All participants gave written informed consent before enrolment in this study and were screened for contraindications to EEG: exclusion criteria included the presence of a history of any neurological or psychiatric disease, use of active drugs, abuse of any drugs (including nicotine and alcohol) as well as any skin condition that could have been worsened by the use of the EEG cap. The study was approved by the local Ethics Committee of the University of East London (UEL) and was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants had normal or corrected-to-normal vision and were right-handed.

2.2. Stimuli

A total of 96 pictures were presented to each participant (one per trial). 32 pictures of faces were extracted from the Radboud Faces Database (RaFD), (Langner et al., 2010), 32 pictures of bodies were extracted from the Bodily Expressive Action Stimulus Test (BEAST), (Beatrice de Gelder & Van den Stock, 2011), and 32 pictures of houses were extracted from the dataset used in a previous EEG experiment (Negrini, Brkic, Pizzamiglio, Premoli, & Rivolta, 2017). All pictures representing faces and bodies conveyed neutral expression, depicted 32 different actors for faces and 32 for bodies (balanced for gender). Half of the pictures were presented upright and the other half inverted.

All pictures were converted into black and white and cropped to a blank background using Adobe Photoshop CS5 software (Adobe Systems Inc., 2011) and had a dimension of 7 x 10.5 cm, which subtend a visual angle of 4° x 6° on a 22-inch LCD monitor positioned 100 cm away from the participants. In order to match all stimuli's low-level visual features, mean luminance was manipulated using MATLAB® R2016a (The Mathworks Inc., 2016) and the SHINE toolbox (Willenbockel et al., 2010).

2.3. Procedure

After signing informed consent, the EEG cap was put on (see next section for details) and participants were conducted and sat in a dimly illuminated electrically-shielded room. There the cap was connected to the EEG amplifier and participants began the experiment. The experiment was run using E-Prime® 2.0 software (Psychological Software Tools Inc., 2007). Participants were presented with 96 stimuli divided in 3 blocks of 32 stimuli that were randomly presented, using a permutated blocks order for each participant. Before each block, 5 trials were presented as training, a feedback on participants' response was given. Each trial consisted of a fixation cross shown for one second, the stimulus was displayed for 500 ms, followed by a response screen (max duration: 5 s), during which the participant could respond. Participants' task was to detect if the stimulus was presented upright or inverted, by pressing one out of two buttons on an EGI® Chronos response box. After the response (or after 5 s of response screen) a grey screen was presented for one second, before beginning the next trial.

2.4. EEG data recording and analysis

EEG data were recorded using a high-density 128-channel Hydrocel Geodesic Sensor Net (Electrical Geodesic Inc., EGI, Eugene, OR, USA) referenced to the vertex (Tucker, 1993). The EEG signal was amplified with EGI NetAmps 400, digitized at 1000 Hz sampling rate, and recorded. No filters were applied during signal recording. Electrodes impedances were kept below 50 kΩ during the whole experimental procedure.

EEG data were analyzed using MATLAB® R2016a version (The Mathworks Inc., 2016) house-made scripts, EEGLAB (Delorme & Makeig, 2004) and FieldTrip toolboxes (Oostenveld et al., 2011). A band-pass filter (1–100Hz) and a notch filter (50 Hz) were applied in order to limit the signal of interest and remove the power line noise. Data were subsequently segmented into epochs (i.e., trials) of 2000 ms length, starting from the presentation of the fixation cross and ending 500 ms after the presentation of the response screen. Each trial was baseline-corrected by removing the values averaged over a period of 1000 ms (from 1000 to 0 ms before stimulus), during which participants were looking at the fixation cross. After visual inspection, trials affected by prominent artifacts (i.e., major muscle movement and electric artifacts) were removed, and bad channels were deleted. On average, 90 trials per participant were included in the analysis. The signal was referenced to the common average of all electrodes (Dien, 1998), and Independent Component Analysis (ICA) was applied to remove remaining artifacts related to muscular and ocular activity. After removing the remaining artifacts using ICA, noisy channels were spatially interpolated.

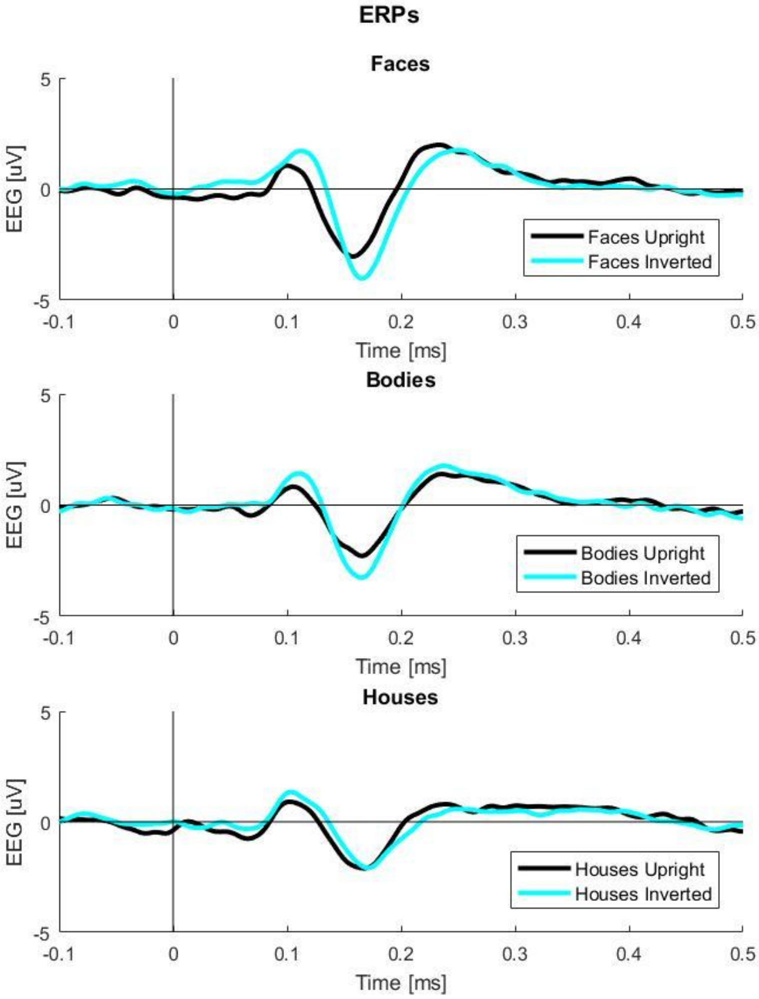


Fig. 4.1: Plots of ERP activity calculated over 11 right occipito-temporal electrodes, averaged over 23 participants, separated for three category of stimuli (Faces, Bodies, Houses). In each plot, the black line represents upright stimuli, while the cyan line represents inverted stimuli. This picture clearly shows larger and delayed N170 components (negative deflections around 170 ms post-stimulus onset) for inverted faces and bodies, but not houses.

In order to obtain ERPs, all trials of each condition were averaged for each participant (Fig. 4.1). N170 component amplitude was computed by averaging the activity in the range 140-200 ms. The exact timewindow was defined by visual inspection of the butterfly plots of each condition.

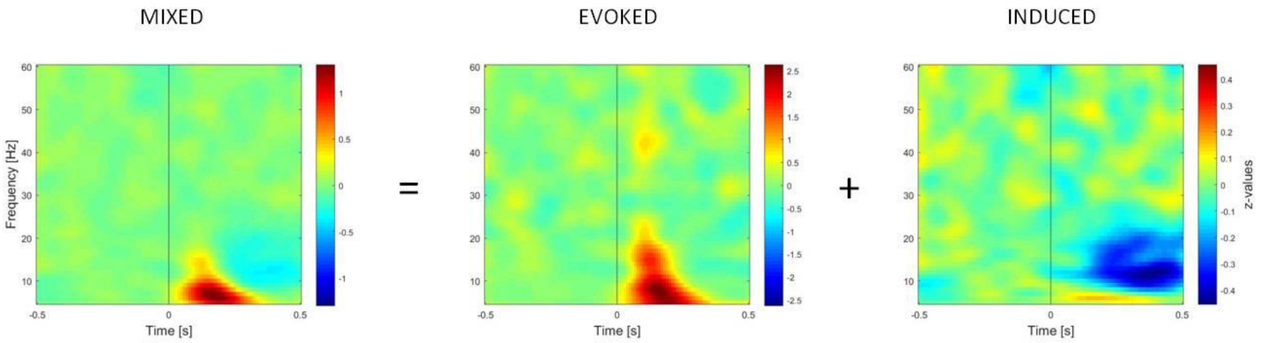


Fig. 4.2: The time-frequency representations (TFRs) of mixed, evoked (phase-locked) and induced (non phase-locked) activity, calculated over 11 right occipito-temporal electrodes (Region Of Interest determined by literature on the Face Inversion Effect), averaged over 23 participants. The activity elicited by upright faces is shown. The picture shows how induced activity is determined by computing the TFR of evoked activity (on ERPs averaged across trials) and subtracting it from mixed activity, at single-trial level.

Time-frequency representations (TFRs) of oscillatory power changes were computed, separately for each of the 6 stimulus categories (faces upright and inverted, bodies upright and inverted, houses upright and inverted). Time-frequency power spectra were estimated using Morlet wavelet analysis based on 3.5 cycles at the lowest frequency (5 Hz) increasing to 18 cycles at the highest considered frequency (60 Hz) (time steps: 10 ms, frequency steps: 1 Hz) (Oostenveld et al., 2011). We divided neuronal response components into evoked (i.e., phase-locked) vs. induced (i.e., non-phase-locked) by stimuli (Fig. 4.2) (Cohen et al., 2013; David, Kilner, & Friston, 2006; Donner & Siegel, 2011; Herrmann, Rach, Vosskuhl, & Strüber, 2014). The TFR of the induced response was then isolated by subtracting the individual time-domain average from each trial before calculating the TFRs of the single trials (Cohen et al., 2013; Premoli et al., 2017). This approach was adopted since we performed single-trial normalization by z-transforming the TFR of each trial for each frequency. The z-transformation was performed on the respective mean and standard deviation derived from the full trial length. Following the z-transformation, an absolute baseline correction for each trial was performed by subtracting the average of the -400 to -100 ms period for each frequency to ensure z-values represent a change from the baseline (Premoli et al., 2017). The baseline correction timewindow (-400 to -100 ms) was chosen in order to avoid evoked time-frequency activity that could be found some ms before the stimulus onset in low frequencies. Subsequently, TFRs were averaged across trials per experimental condition. After performing this procedure, the result consisted of an event related spectral perturbation (ERSP) measure that is robustly normalized based on the single trial level (Grandchamp & Delorme, 2011). In the end, TFRs were cropped to the time of interest (-500 to 500 ms), removing time-frequency bins at the trial edges for which no values could be computed. Values were averaged across frequency bins to calculate the power within the two frequency bands: theta (5-7 Hz) and gamma (28-45 Hz), which are considered to be the most representative frequency ranges in the study of social visual stimuli (Güntekin & Başar, 2014).

The gamma range limits were chosen since phase-locked and time-locked gamma oscillations following visual stimulations are detectable in the 28-45 Hz range in different timewindows (Basar, 2012). In particular, the focus of our work was on induced activity and to this end we used the TFR, since it is the only technique allowing to study it.

2.5. Statistical analyses

In order to compare the sensor-level EEG data among different stimulus conditions, non-parametric cluster-based permutation analyses (Monte-Carlo method based on paired *t*-statistics) (Maris & Oostenveld, 2007) were performed. This method was shown to be extremely accurate in solving the multiple comparisons problem in M/EEG data, thus avoiding false positive and false negative results, also in comparison with other broadly used approaches (i.e., bootstrap-based and Bayesian approaches) (Maris, 2012). Considering data separated for frequency range and timewindow, *t*-values exceeding an *a priori* threshold of $p < .05$ were clustered based on neighbouring electrodes. Cluster-level statistics were calculated by taking the sum of the *t*-values within every cluster. The comparisons were done with respect to the maximum values of summed *t*-values. By means of a permutation test (i.e., randomizing data across conditions and re-running the statistical test 1500 times), we obtained a reference distribution of the maximum of summed cluster *t*-values to evaluate the statistic of the actual data. Clusters in the dataset were considered to be significant at an alpha level of .05 if < 5% of the permutations (N = 1500) used to construct the reference distribution yielded a maximum cluster-level statistic larger than the cluster-level value observed in the original data.

In order to test whether our data replicated previous findings, three paired-samples *t*-tests were performed separately on ERPs, computed by averaging trials for each participant in each condition. These comparisons investigated the inversion effect in different categories (faces upright vs. inverted, bodies upright vs. inverted, houses upright vs. inverted) on the N170 component. Successively, the ERPs differences between upright and inverted stimuli were computed for the three categories (faces, bodies and houses) by subtracting averaged μV values in the inverted condition from those in the upright condition, for each timepoint. These differences were, then, compared by performing three paired-samples *t*-tests in order to test any interaction effects (face inversion vs. body inversion, face inversion vs. house inversion, body inversion vs. house inversion).

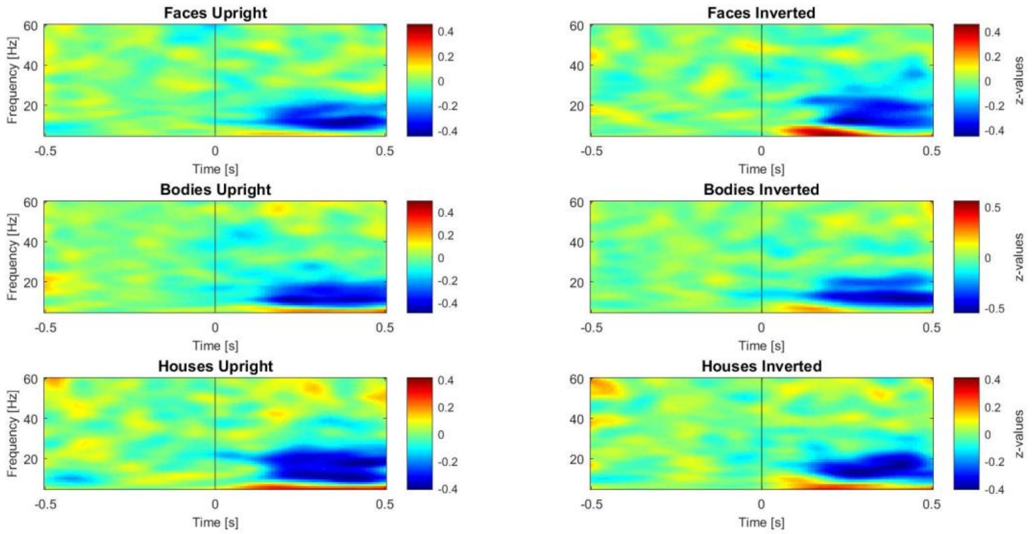


Fig. 4.3: Plots of induced time-frequency activity calculated over 11 right occipito-temporal electrodes, averaged over 23 participants, separated for each category of stimuli. This picture allows to observe differences in patterns of activity for every category, in particular over theta (5-7 Hz) and gamma (28-45 Hz).

Then, three paired-samples *t*-tests were performed separately on induced data, in order to investigate the inversion effect in different category comparisons (faces upright vs. inverted, bodies upright vs. inverted, houses upright vs. inverted). For these tests, the activity in different frequency ranges was separated, as described above. One timewindow of interest (TOI) was defined by both referring to existing literature on the topic and visual inspection of occipital singleplots of activity (Fig. 4.3): the time of interest was set at 250-500 ms for induced activity. This TOI was chosen because induced activity (especially in gamma range) typically starts around 280 ms after the presentation of the stimulus, and is clearly disentangled from evoked activity at this latency (Tallon-Baudry & Bertrand, 1999), while 500 ms was chosen as the limit of the TOI because it is the time when the response screen was presented, so we expect a different, motor-related activity, after this timewindow. In the timewindow z-transformed values were averaged across time bins for each frequency.

3. Results

3.1. ERP analysis

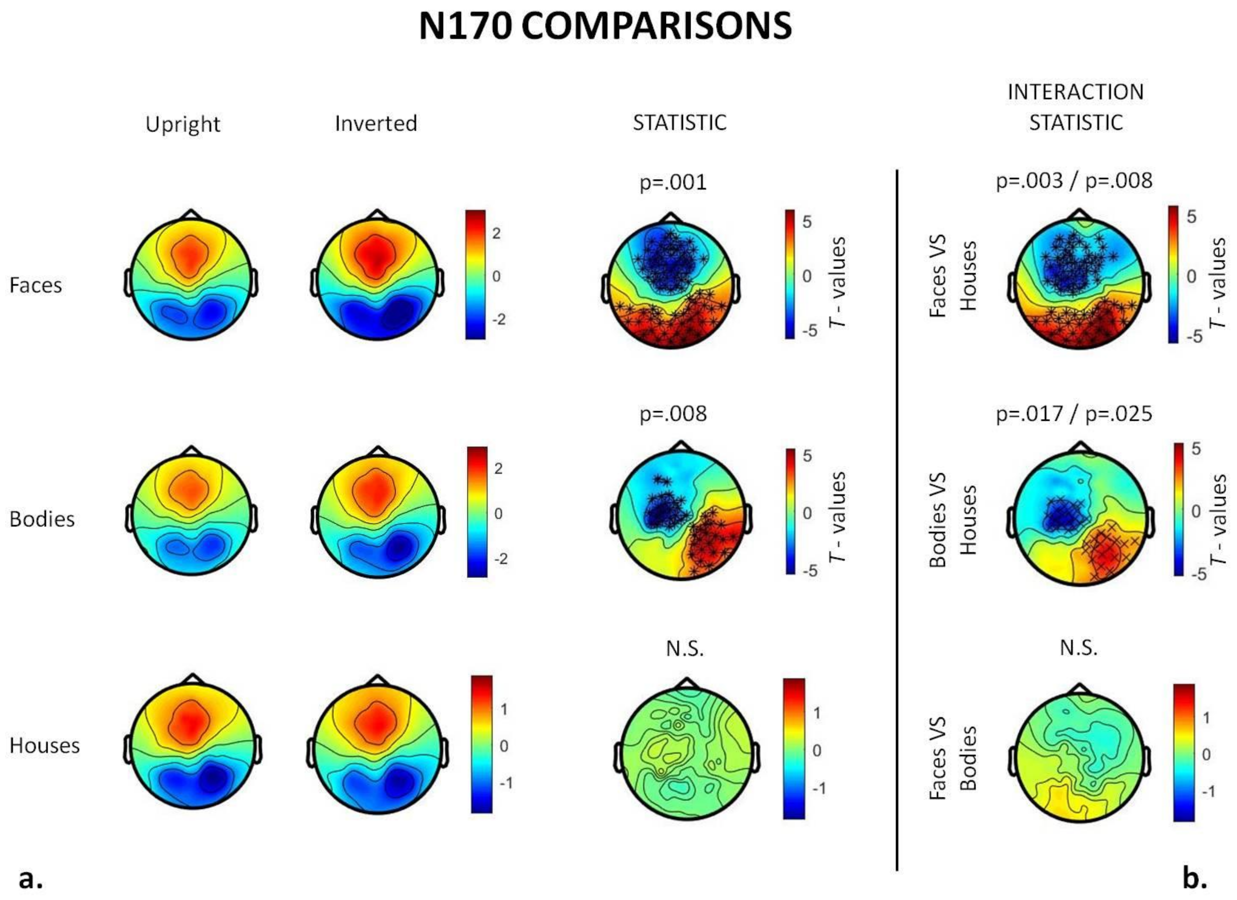


Fig. 4.4: Summary of results related to ERPs. All topographies were obtained by calculating the average voltage over the timewindow of interest for N170 components (i.e., 140-200 ms after stimulus onset).

(A) The topographies show the activity evoked by upright and inverted faces (first row), bodies (second row) and houses (third row). The third column of topographies shows clusters where statistically significant differences between upright and inverted stimuli were found, by means of non-parametric cluster-based permutation tests. Inverted faces and bodies showed larger N170 (occipitotemporal areas) and VPP (Vertex Positive Potential, frontal areas) than upright ones.

(B) The topographies show the results of the comparisons between Inversion Effects (interaction effects): the first and the second pictures show that Face Inversion and Body Inversion lead to a significantly different change of activity over the previously reported areas, when compared to house inversion. The third picture shows that Face and Body Inversion did not differ in a statistically significant way.

Inverted faces showed significantly larger N170 component than upright faces over a large bilateral occipitotemporal cluster of 34 electrodes (*p* = .001) and a frontal cluster of 48 electrodes (*p* = .001). Similarly, inverted bodies showed significantly larger N170 component than upright bodies, over a right occipitotemporal cluster (22 electrodes) (*p* = .008) and a left frontal cluster (23 electrodes) (*p* = .008). No statistically significant differences were found between upright and inverted houses (Fig. 4.4a).

Results also revealed a significant interaction between face inversion and house inversion, over a bilateral occipitotemporal cluster (29 electrodes) (*p* = .008) and a frontal cluster (44 electrodes) (*p* = .003), suggesting that face inversion generates an increase in N170 amplitude which is significantly higher than the increase generated by house inversion. Moreover, a significant interaction between body inversion and house inversion was found over a right occipitotemporal cluster (19 electrodes) (*p* = .025) and a left frontal cluster (20) (*p* = .017), suggesting that the increase in N170 amplitude generated by body inversion is significantly higher than the increase generated by house inversion. Face inversion and body inversion showed no statistically significant differences (Fig. 4.4b).

3.2. Induced activity

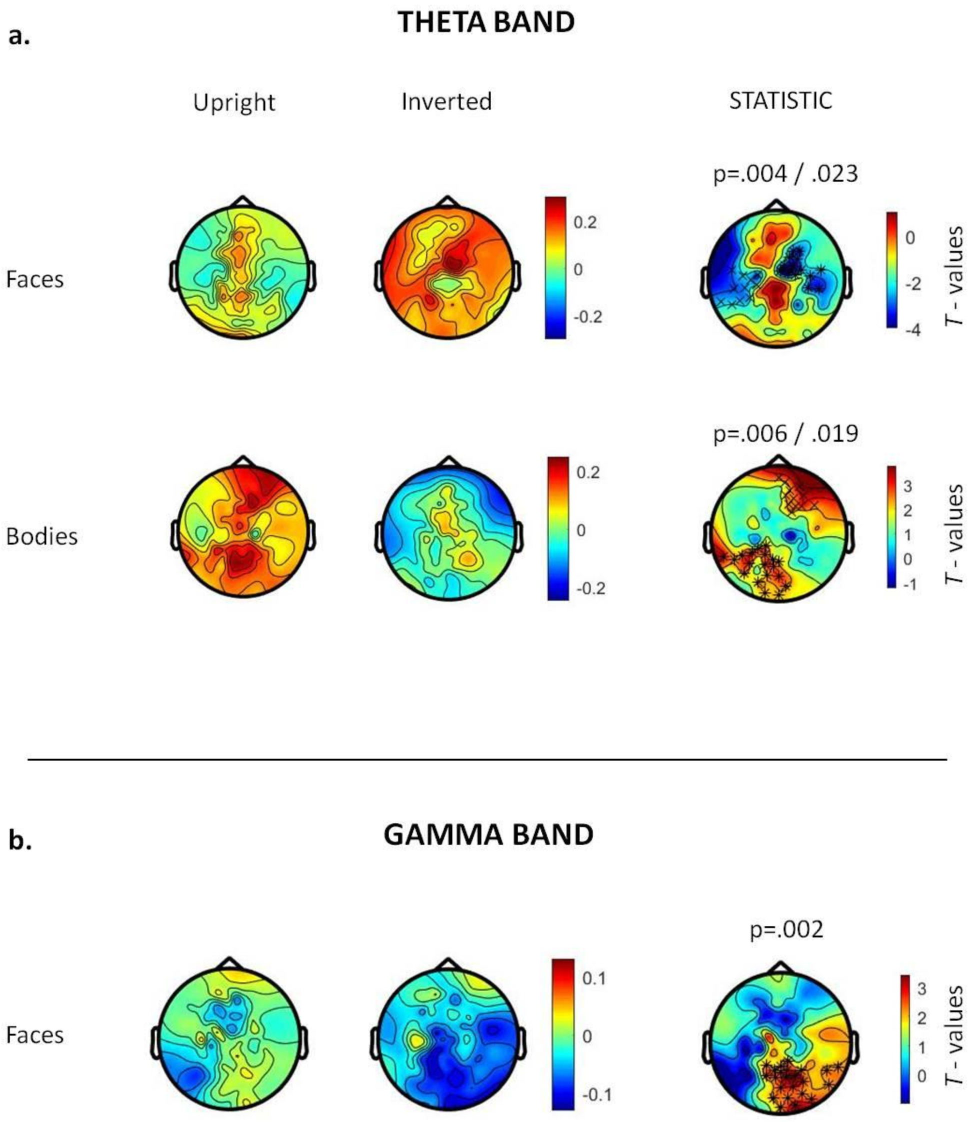


Fig. 4.5: Summary of results related to induced activity. All topographies were obtained by calculating the average power over the timewindow of interest for induced activity (i.e., 250-500 ms after stimulus onset).

(A) The topographies show the activity induced by upright and inverted faces (first row) and bodies (second row) in theta band (5-7 Hz). The third column of topographies shows clusters where statistically significant differences between upright and inverted stimuli were found, by means of non-parametric cluster-based permutation tests. Increased theta synchronization is highlighted for inverted faces (vs. upright faces) over a right fronto-parietal and a left parietal cluster, whereas upright bodies (vs. inverted bodies) showed to induce a significantly stronger theta synchronization over a left-lateralized occipito-temporal cluster and a right prefrontal cluster.

(B) The topographies representing gamma-band (28-45 Hz) activity induced by upright and inverted faces are shown. The statistical comparison highlighted a stronger gamma synchronization for upright faces (vs. inverted faces) over a right occipito-temporal cluster.

In the 250-500 ms timewindow a psychophysiological FIE showed that inverted faces, as compared to upright faces, showed stronger theta synchronization in a right fronto-parietal cluster (14 electrodes) (*p* = .004) and in a left parietal cluster (10 electrodes) (*p* = .023) (Fig. 4.5a). Participants also showed a stronger theta synchronization induced by upright bodies (as compared to inverted bodies) in a left-lateralized occipito-temporal cluster (19 electrodes) (*p* = .006) and in a right prefrontal cluster (12 electrodes) (*p* = .019).

The analysis of gamma-band activity showed stronger synchronization for upright faces as compared to inverted faces (*p* = .002) over a right-lateralized occipito-temporal cluster of electrodes (21 electrodes) (Fig. 4.5b).

No other inversion effects were statistically significant.

4. Discussion

At the behavioural level, face and body inversion effects have a similar magnitude (Reed et al., 2003) and are supposedly mediated by a disruption of the configural processing (Bonemei et al., 2017). The psychophysiological marker of configural processing, the N170 (Rossion & Gauthier, 2002), also showed similarities between the two categories of visual stimuli (Stekelenburg & De Gelder, 2004; Watanabe et al., 2003). Our results, replicating previous evidence, showed the presence of the FIE and BIE on the N170 component, thus suggesting a common disruption of configural processing in face and body processing. The N170 effect was found over a spread bilateral occipito-temporal region for faces, whereas it was more lateralized on the right hemisphere for bodies. Also this finding replicates previous literature (Gliga & Dehaene-Lambertz, 2005).

Our investigation of induced neural oscillations, however, revealed clear differences in the psychophysiological correlates of the FIE and BIE. Specifically, face inversion induced a synchronization in theta band over bilateral fronto-parietal areas and a desynchronization in gamma band over occipito-temporal areas (developing to the right side), whereas body inversion induced a desynchronization in theta band over left occipito-temporal and right prefrontal areas. Therefore, it is important to try to differentiate between the theta synchronization found for inverted faces and theta synchronization found for upright bodies: it is fundamental to remember that cerebral activity in the same frequency band may have completely different functions in different cortical (and sub-cortical) areas and in different timewindows (Başar, 1999).

It is possible that the theta band synchronization associated with the FIE reflected an increase in attentional resources towards inverted faces, needed to rapidly recognize their orientation. Theta band activity, as a matter of fact, has been related to attentional, cognitive and memory performance in different tasks (Başar, 1999; Klimesch, 1999), and it has been associated specifically to feature-based attentional functions (Harris, Dux, Jones, & Mattingley, 2017). Feature-based attention is involved in inverted face processing, since the typical holistic processing used for faces is disrupted with the inversion (Maurer et al., 2002). Besides, the cortical areas in which the difference in theta band was found could reflect activity in areas involved in the dorsal frontoparietal attentional network (Corbetta, Kincade, & Shulman, 2002; Lückmann, Jacobs, & Sack, 2014; Ptak, 2012; Ptak et al., 2017).

Even though it is known that upright faces automatically capture attention through a stimulus-driven bottom-up mechanism (Sato & Kawahara, 2015), this is not the case for inverted faces (Ariga & Arihara, 2017; Langton, Law, Burton, & Schweinberger, 2008; Sato & Kawahara, 2015; Tomonaga & Imura, 2009). Therefore, inverted faces are processed more in a feature-based fashion rather than holistically. Hence, it is likely that an explicit attentional (top-down) effort is required in order to process the facial features that cannot be bound in a configuration, since holistic processing is disrupted by inversion. This attentional resources deployment might be what triggers the increased theta activation in the frontoparietal network.

This interpretation is coherent with the stronger gamma synchronization induced by upright faces in the right occipital area, which is in line with previous findings (Anaki et al., 2007; Rodriguez et al., 1999), since holistic processing is disrupted for inverted faces and their features cannot be bound and matched to a stereotypical configuration. Specifically, as in the present study, while upright faces can be directly processed in an holistic way (gamma-band activity), thus easily recognized, inverted faces need more feature-based attentional resources (theta synchronization) to be recognized as faces, since part-based processing requires higher resources. These results could also be related to theta-gamma coupling (Sato et al., 2014, 2017): simultaneous theta desynchronization and gamma synchronization could reflect the rapid communication between cortical and subcortical brain regions. This is in line with the interpretation related to the deployment of attentional resources, since the amygdala, along with other subcortical structures can direct attention on the basis of the evaluation/appraisal of the stimulus (Nummenmaa & Calder, 2009). The replication of previous findings in gamma band demonstrates the reliability of the experimental paradigm and of the task we used, thus granting stronger reliability to our novel results found in theta band.

In contrast, body inversion induced greater theta synchronization over left occipito-temporal and right prefrontal areas for upright bodies only, whereas no differences were found in the gamma band. These results may suggest that, while the differences that emerged during face processing might be more related to the holistic processing of the stimulus, so as inverted faces require a stronger cognitive effort to be recognized, body processing appears to be more related to lower-level configural processing (i.e., first-order spatial information and structural hierarchy; Reed, Stone, Grubb, & McGoldrick, 2006) and feature-based processing already in upright bodies. Both upright and inverted bodies need the deployment of attentional resources in order to be processed, since feature-based processing seems to be more involved in the structural encoding of this category of stimuli. This might be the reason why the BIE does not induce any differences in theta band over the frontoparietal attentional network. This interpretation is supported by findings showing that holistic processing – investigated with a different method (the composite illusion) – may not be involved in the perception of human body shapes (Soria Bauser, Suchan, & Daum, 2011; Soria Bauser, Schriewer, & Suchan, 2015; Soria Bauser & Suchan, 2013). As a matter of fact, it has never been demonstrated that holistic processing and second-order spatial information are part of configural body processing (Minnebusch & Daum, 2009), whereas first-order spatial information and structural information were proven to be strongly involved in it (Reed et al., 2006).

This interpretation is also supported by the fact that, for body processing, we found an activity that is very similar to the activity classically associated with the activation of limbic structures. As stated earlier, theta-band activity is the spontaneous rhythm of different limbic structures (Başar, 1999), and occipital areas show theta synchronization during processing of emotionally salient stimuli and facial expressions because these oscillations are most probably coupled with hippocampal theta generators (cortico-hippocampal interactions) (Miller, 1991). The involvement of limbic structures is plausible also if we consider that occipito-temporal synchronized theta oscillations were reported during the processing of emotionally arousing visual stimuli, at latencies similar to our timewindow of interest for induced activity (200-500 ms post-stimulus) (Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2001; Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2002; Başar, Güntekin, & Öniz, 2006; Güntekin & Başar, 2009, 2014).

Although the bodies showed in this study were not conveying any specific emotion, processing of emotional information in bodies seems to take place at the level of structural encoding: indeed, in our study the greater theta synchronization emerged over two areas that were also involved in de Gelder et al.'s (2015) network associated with the visuomotor perception of emotional body language (lateral occipital cortex and premotor cortex). This processing is disrupted when bodies are inverted, as indicated by a desynchronization of theta activity. The absence of differences in gamma activity further supports this interpretation, showing that body processing is not mediated by a holistic process of feature binding, but relies much more on different levels of configural processing. Thus, body processing seems to share the same limbic-cortical neural bases of emotional stimuli processing. This processing path may be related to the same subcortical path (involving the amygdala) found for early perceptual processing of emotionally salient stimuli (Adolphs, 2002a, 2002b) and involved in reflex-like processing of emotional body language hypothesized by de Gelder et al.'s (2006, 2015) model. The involvement of this subcortical path in body processing was already demonstrated in patients with cortical blindness or neglect (Tamietto et al., 2015; Van den Stock, Tamietto, Hervais-Adelman, Pegna, & de Gelder, 2015). In these patients, stronger connections between subcortical regions and extrastriate visual areas led to the recognition of bodies above chance level, despite the incapability to see consciously these stimuli.

Further investigation with specific neuroimaging techniques is needed to corroborate this interpretation.

Besides, the occipito-temporal synchronization shows a clear lateralization to the left hemisphere. Until now, literature reported right lateralization for ERPs involved in body processing (Gliga & Dehaene-Lambertz, 2005; de Gelder et al., 2015 for a review), similarly to what we found for the N170. On the other hand, no previous studies have investigated oscillations in body processing. Considering that induced activity completely excludes evoked (time-locked) oscillations (i.e., activity related to ERPs), the left occipito-temporal induced synchronization represents a novel finding: while the early stages of body processing are mostly lateralized in the right hemisphere, a later (over 250 ms post-stimulus) stage of processing seems to be lateralized in the left one and is exhibited by induced oscillations. This result could imply an involvement of bilateral occipito-temporal cortices in different stages of body processing, showing an important difference with mostly right-lateralized faces processing. This new result needs to be corroborated in future research.

Upright and inverted houses did not show statistically significant differences in any of the considered frequency bands, confirming that this class of stimuli is less (or not at all) subject to inversion effect.

The main limitation of the study is its explorative nature. Important and novel results were found, that could shed some new light on commonalities and differences between face and body processing. Though, these results need further confirmatory research in replications, both by using analogous techniques to study oscillatory activity and by means of other neuroimaging techniques, aimed in particular to explore the relationship between subcortical (limbic) and cortical processes.

In conclusion, we found new evidence showing that the psychophysiological mechanisms mediating Face and Body Inversion Effects present important differences, in line with some behavioural and psychophysiological findings (Soria Bauser, Suchan, & Daum, 2011; Soria Bauser, Schriewer, & Suchan, 2015; Soria Bauser & Suchan, 2013). As well as replicating some previous findings, our face processing results showed to be subjected to feature-binding processes (represented by occipital gamma activity). We showed that inversion can disrupt these processes and seems to require more attentional resources (theta fronto-parietal activity). On the contrary, the BIE appears to be less related to holistic processing and more to lower levels of configural processing. It also appears to be linked with the neural activity indicative of limbic processes (as shown by left occipito-temporal theta activity).

CHAPTER 5

INVERSION AND EMOTIONAL EXPRESSIONS BOTH AFFECT VISUAL PROCESSING OF FACES AND BODIES, BUT INDEPENDENTLY

An ERP study

1. Introduction[4]

In this study we investigated how emotional expressions can interact with structural encoding of social stimuli. This was done by studying the ERP correlates of face and body inversion effects, using stimuli that conveyed neutral vs. emotional expressions.

With regards to theoretical models of face processing discussed in Chapter 1, Bruce & Young’s (1986) model postulated that facial expression analysis occurred after structural encoding of the facial representation, by means of a bottom-up process. Haxby, Hoffman, & Gobbini (2000) theorised a model in which the early perception of facial features (in inferior occipital areas) occurs before the processing of emotional expressions (together with other changeable aspects of faces in STS), by means of both feed-forward (bottom-up) and feed-back (top-down) connections. The first model would, thus, suggest that structural encoding is completely independent of emotional expression, while the second seems to imply that, albeit occurring after the encoding of facial features, emotional expression processing can be influenced later by top-down information.

Neurocognitive models describing recognition of emotional expressions (Adolphs, 2002a, 2002b) suggest that a fast perceptual processing of highly salient (and potentially dangerous) stimuli occurs very early (around 100-120 ms after stimulus onset) and takes advantage of connections between the superior colliculus and the amygdala, and thalamo-cortical connections. The detailed perception and encoding of the stimulus represents a later stage (around 170 ms after onset) and involves connections between the inferior occipital cortex and STS, the fusiform gyrus, amygdala and orbitofrontal cortex. In the third late stage (over 300 ms after onset), the conceptual knowledge of the emotion expressed by the facial stimulus is achieved via re-entrant feed-back connections from the amygdala and the orbitofrontal cortex to all levels of the visual processing

---

[4] The study presented in this Chapter was carried out at the University of East London, in collaboration with Prof. Davide Rivolta.

stream and somatosensory cortex, thus modulating visual cortices as a function of the emotional content of the stimuli (Amaral, Price, Pitkanen, & Carmichael, 1992). Similarly, de Gelder's (2006) model posits the presence of a rapid non-conscious automated system for reflex-like emotion recognition (including mainly subcortical structures) and a cortical system for detailed visuo-motor perception of emotional body language, in combination with past experience and memory. The connection between these two systems is represented by the amygdala.

By only considering theoretical models, we cannot conclude whether processing of emotional expression and structural encoding are completely independent (Bruce & Young, 1986), interact at a late stage (Haxby et al., 2000), or have reciprocal influences since early stages of perception (Adolphs, 2002a, 2002b; de Gelder, 2006).

Several experimental studies investigated the influence of emotional expression on structural encoding by testing whether neutral or emotional expression modulated N170, the ERP component related to structural encoding and holistic processing of faces (Rossion & Gauthier, 2002a). The first results appeared to be in favour of *dual theories* (i.e. claiming that structural encoding and facial expression processing are parallel and independent processes). Eimer & Holmes (2002) found that fearful faces, compared to neutral ones, increased frontal positivity with a remarkably early onset: starting from 120 ms post-stimulus, it affected N1 (smaller amplitude) and *vertex positive potential* (VPP, analogous to N170 in latency, peaking over frontocentral areas) (larger amplitude) components, followed by increased late frontocentral positivity (starting at 250 ms post-stimulus). These results were linked to an initial rapid detection of facial expression in prefrontal areas involved in the detection of emotionally significant stimuli, followed by subsequent higher level stages of emotional face processing, such as the conscious evaluation of emotional content. No influence of emotional expression on the N170 component was found, proving no influence of emotional expression on structural encoding. In a follow-up study, Eimer, Holmes, & McGlone (2003) found the same effect for all the six basic emotional expressions (Ekman & Friesen, 1976), showing that these results do not reflect emotion-specific processes, which may occur in separate neural areas at later latencies (Eimer & Holmes, 2007). Sato and colleagues (2001) showed that emotional expression (happy and fearful) in faces elicited larger N270 component over posterior temporal areas, ascribed to the control by amygdala re-entrant projections. Also Krolak-Salmon et al. (2001) and Leppänen, Kauppinen, Peltola, & Hietanen (2007) found the influence of emotional expressions on occipito-temporal components later than N170: between 250 and 550 ms post stimulus for all expressions (Krolak-Salmon et al., 2001) and 190–290 ms post-stimulus (P2 component) only for fearful expression and not for happy (Leppänen et al., 2007). All these findings seem to exclude an influence of emotional expression on structural encoding, whereas they identified later psychophysiological correlates of conscious evaluation of emotional content (represented by the latest stage in Adolphs' model).

Vice versa, the findings from several other studies supported *integrated theories*, arguing for integrated rather than segregated mechanisms in the processing of identity and emotional expressions. Batty & Taylor (2003) first found global effects of emotion on P1 occipito-temporal component (around 100 ms post-stimulus), while latency and amplitude differences among emotional expressions were seen on N170 component. Positive emotions evoked N170 significantly earlier than negative emotions and the amplitude of N170 evoked by fearful faces was larger than neutral or surprised faces. Ashley, Vuilleumier, & Swick (2004) found effects of emotional expression on N170, not selective for any specific emotions, and specific effects in later occipital and frontocentral components. Further studies reported larger amplitude for various emotional expression on both P1 and N170 (Rigato et al., 2009; Valdés-Conroy, Aguado, Fernández-Cahill, Romero-Ferreiro, & Diéguez-Risco, 2014) or N170 only (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007 (only fear, not happiness); Wronka & Walentowska, 2011). These findings are consistent with an early automatic encoding of facial expressions during the structural encoding stage or at even earlier stages (Batty & Taylor, 2003; Rigato et al., 2009).

In order to understand the consistency among these findings, a meta-analysis that included 57 studies was recently performed to investigate the N170 sensitivity to facial expressions (Hinojosa, Mercado, & Carretié, 2015). Results showed a mean effect size of -0.332, significantly different from zero and, thus, clearly supporting an effect of larger N170 for emotional than neutral faces. This result finally supports integrated theories, showing an influence of emotional expression on structural encoding of faces. Furthermore, this N170 sensitivity is heterogeneous, with angry, fearful and happy faces eliciting the largest N170 amplitudes. Considering this overall finding, integrated models of perception of emotional expressions (Adolphs, 2002a, 2002b) seem to be reliable for facial expressions.

Little is known, however, on body emotion expressions. Stekelenburg & de Gelder (2004) studied ERP correlates of fearful expressions in faces and bodies. As predicted by models discussed above, results show larger occipitotemporal N170 and P2 components for fearful faces, together with larger frontocentral N2. For bodies, however, N170 was not influenced by emotional expression, while larger frontal VPP and a sustained fronto-central negativity (around 300-500 ms post stimulus) were found for fearful bodies (compared to neutral ones). In a following study, van Heijnsbergen, Meeren, Grèzes, & de Gelder (2007) found that fearful bodies showed earlier latency of occipito-temporal P1 and frontocentral VPP, while the N170 component was unaffected by the emotional expression. Meeren, Hadjikhani, Ahlfors, Hämäläinen, & de Gelder (2016) found (in an MEG study) increased amplitude in a positive parietal component for fearful (compared to neutral) bodies as early as 80 ms after stimulus onset. These findings seem to suggest that decoding of bodily expression occurs in the early stages of visual processing and does not influence the structural encoding of these stimuli (as pointed out by the absence of N170 modifications). This hypothesis could be in line with the differences in configural processing between faces and bodies, discussed in Chapter 3. However, few studies are available to assess the effect of emotional expression on structural encoding of bodies.

Since inversion was also shown to affect structural encoding of both faces and bodies (at all levels for faces, only at first-order spatial information and structural hierarchy levels for bodies) (see Chapter 3), in the current study the effects of different emotional expressions were investigated in combination with FIE and BIE. Studies investigating the interaction between inversion effect and emotional expressions in bodies (Stekelenburg & de Gelder, 2004; Meeren et al., 2016) and faces (Ashley et al., 2004; Eimer & Holmes, 2007; Righart & De Gelder, 2006) did not lead to clear and unambiguous results. According to the literature, inversion disrupts structural encoding of these stimuli, while emotional expressions enhance it (at least in faces). Studying the interaction between these two manipulations could bring important insights and answer some questions, such as: can emotional expressions influence the structural encoding of inverted stimuli (in which configural processing is disrupted)? In which way enhancement due to expression and disruption due to inversion may interact? What are the cognitive mechanisms involved in these processes and their neural bases? The aim of the present study was to answer these questions.

Another critical variable to consider is the task performed by participants. Several studies investigated the influence of the task on emotional expressions processing (Krolak-Salmon, Fischer, Vighetto, & Mauguiere, 2001; Valdés-Conroy, Aguado, Fernández-Cahill, Romero-Ferreiro, & Diéguez-Risco, 2014; Wronka & Walentowska, 2011; Hinojosa et al, 2015 for a review) (see also Chapter 1 Section 4). These authors manipulated explicit vs. implicit processing of emotional information by asking participants to identify emotion vs. gender in the faces they were shown. They found important differences, since the influence of emotional expression on different components (N170 or later components) disappeared or was reduced when participants were asked to identify the gender. These results show the importance of an explicit vs. implicit processing of the emotional expression in an experimental paradigm studying it (see also Ricciardelli, Lugli, Pellicano, Iani, & Nicoletti, 2016). Therefore, in the current study, we decided to ask participants to identify emotional expressions over two blocks and gender over the remaining two.

Some hypotheses were examined in this study, considering the literature. We expected (i) behavioural (lower accuracy) and electrophysiological (larger N170 component) inversion effects for both faces and bodies, but not for objects; (ii) enhancement of N170 (and probably other components as P1 and P2) due to emotional expressions in faces; (iii) a possible dissociation of the effects of emotional expressions in different components between faces and bodies, since they are processed through partially dissociable configural mechanisms; (iv) an interaction of the effects of emotional expression and inversion, since both were proven to influence the structural encoding of social stimuli; (v) larger effects of emotional expressions during the task related to emotion than during the task related to gender.

The current study was composed of two experiments: Experiment 1 was aimed to investigate the influence of emotional expressions and inversion on different ERP components elicited by faces and bodies. Experiment 2 addressed only hypothesis (i), by investigating psychophysiological FIE and BIE in comparison to the presentation of houses. Data collected in Experiment 2 were also analysed in the time-frequency domain in the study presented in the previous Chapter.

2. Methods

2.1. Participants

Twenty-four healthy participants (11 M; mean age: 28.2 ± 5.8 years) were recruited for the experiment among university students and their acquaintances. One participant was excluded from the analyses due to technical problems related to data quality. All participants gave written informed consent before enrolment in this study and were screened for contraindications to EEG: exclusion criteria included the presence of a history of any neurological or psychiatric disease, use of active drugs, abuse of any drugs (including nicotine and alcohol), as well as any skin condition that could have been worsened by the use of the EEG cap. The study was approved by the local Ethics Committee of the University of East London (UEL) and was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants had normal or corrected-to-normal vision and were right-handed.

2.2. Stimuli

In Experiment 1, 128 pictures were presented twice (once per experimental block, see Procedure) to each participant (one per trial). 64 pictures of faces were extracted from the Radboud Faces Database (RaFD), (Langner et al., 2010) and 64 pictures of bodies were extracted from the Bodily Expressive Action Stimulus Test (BEAST) (Beatrice de Gelder & Van den Stock, 2011). Half pictures of faces and bodies conveyed neutral expression, half conveyed four different emotional expressions: happiness, sadness, anger and fear (8 stimuli each). The pictures depicted 32 different actors for faces and 32 for bodies (balanced for gender). Half of the pictures were presented upright and the other half inverted.

Stimuli used in Experiment 2 were already described in the previous Chapter.

All pictures were converted into black and white and cropped to a blank background using Adobe Photoshop CS5 software (Adobe Systems Inc., 2011) and had a dimension of 7 x 10.5 cm, which subtend a visual angle of 4° x 6° on a 22-inch LCD monitor positioned 100 cm away from participants. In order to match all stimuli's low-level visual features, mean luminance was manipulated using MATLAB® R2016a (The Mathworks Inc., 2016) and the SHINE toolbox (Willenbockel et al., 2010).

2.3. Procedure

After signing informed consent, participants wore the EEG cap (see next section for details) and were conducted and sat in a dimly illuminated electrically-shielded room. There the cap was connected to the EEG amplifier and participants began the experiments. Both Experiments 1 and 2 were run using E-Prime® 2.0 software (Psychological Software Tools Inc., 2007).

In Experiment 1, participants were presented with 256 stimuli divided in 4 blocks of 64 stimuli that were randomly presented, using a permutated blocks order for each participant: faces and bodies were alternatively presented on even (2 and 4) or odd (1 and 3) blocks. Before each block, 5 trials were presented as training and a feedback on participants' response was given. Each trial consisted of a fixation cross shown for one second, the stimulus was displayed for 500 ms, followed by a response screen (max duration: 5 s), during which the participant could respond. Participants' task was to detect if the stimulus was male or female in the first (or last) two blocks, or if it was emotional or neutral in the last (or first) two blocks, by pressing one out of two buttons on an EGI® Chronos response box. After the response (or after 5 s of response screen) a grey screen was presented for one second, before beginning the next trial. Only in the emotions task, after responding "emotional", the participant was asked to choose one out of four emotions (happiness, sadness, anger, fear) that best represented the stimulus she/he had seen, by pressing one out of four buttons on the response box. The screen asking the exact emotion had no time limit and was terminated by participant's response.

The procedure of Experiment 2 was already presented in the previous Chapter.

2.4. EEG data recording and analysis

EEG data were recorded using a high-density 128-channel Hydrocel Geodesic Sensor Net (Electrical Geodesic Inc., EGI, Eugene, OR, USA) referenced to the vertex (Tucker, 1993). The EEG signal was amplified with EGI NetAmps 400, digitized at 1000 Hz sampling rate, and recorded. No filters were applied during signal recording. Electrodes impedances were kept below 50 kΩ during the whole experimental procedure.

EEG data were analyzed using MATLAB® R2016a version (The Mathworks Inc., 2016) house-made scripts, EEGLAB (Delorme & Makeig, 2004) and FieldTrip toolboxes (Oostenveld et al., 2011). A band-pass filter (0.5–100Hz) and a notch filter (50 Hz) were applied in order to limit the signal of interest and remove the power line noise. Data were subsequently segmented into epochs (i.e., trials) of 2000 ms length, starting from the presentation of the fixation cross and ending 500 ms after the presentation of the response screen. Each trial was baseline-corrected by removing the values averaged over a period of 1000 ms (from 1000 to 0 ms before stimulus), during which participants were looking at the fixation cross. After visual inspection, trials affected by prominent artifacts (i.e. major muscle movement and electric artifacts) were removed, and bad channels were deleted. Also trials in which participants gave wrong responses were removed. On average, 90 trials per participant in Experiment 1 and 240 in Experiment 2 were included in the analysis. The signal was referenced to the common average of all electrodes (Dien, 1998), and Independent Component Analysis (ICA) was applied to remove remaining artifacts related to muscular and ocular activity.

After removing the remaining artifacts using ICA, noisy channels were spatially interpolated. Before calculating ERPs, data were downsampled to 250 Hz and band-pass filtered in the range 1-45 Hz. All trials were then divided in categories, considering stimulus category, inversion, task and emotion in Experiment 1, and only stimulus category and inversion in Experiment 2. For each participant, all trials in each category were averaged in order to obtain ERPs.

In order to define a timewindow of interest (TOI) for each ERP component, we referred to both existing literature and visual inspection of butterfly plots representing activity of all upright and inverted conditions (Fig. 5.1). Three different TOIs were thus defined: 80-135 ms after stimulus onset for P1, 140-200 ms for N170, and 200-350 ms for P2.

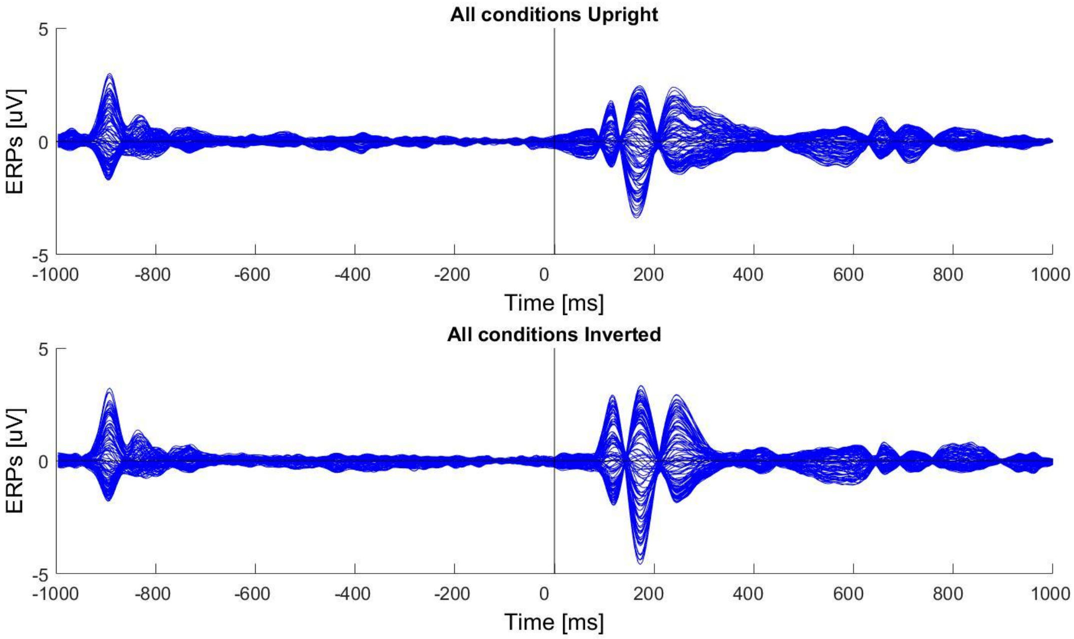


Fig. 5.1: Corresponding event related potentials (ERPs) traces (butterfly plots) for all electrodes as averaged across all trials presented upright (first panel) and inverted (second panel) ("0" indicates stimulus onset). Three major components can be observed at three TOIs: 80-135 ms after stimulus onset (P1), 140-200 ms (N170), and 200-350 ms (P2).

Considering our a-priori hypotheses, we defined two occipitotemporal regions of interest (ROIs) by referring to both literature and visual inspection of all-conditions average multiplot and one topographic plot for each TOI (Fig. 5.2). The two ROIs (left and right clusters) included five occipitotemporal symmetrical channels each. Electrophysiological peaks amplitude in μV was extracted from these channels for the three TOIs in each participant, and then averaged across the five channels of each ROI.

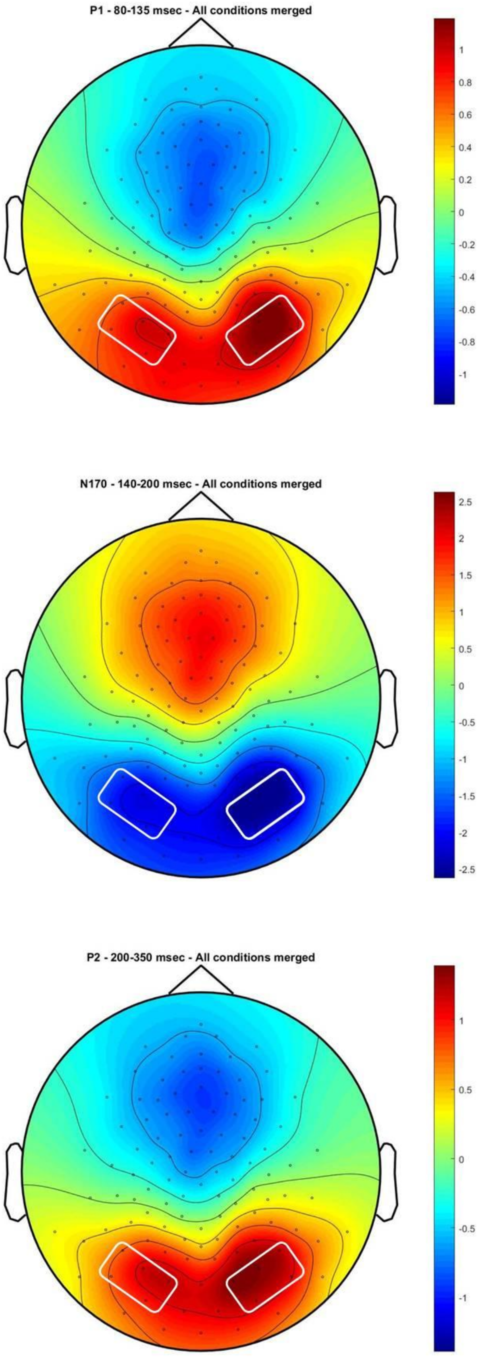


Fig. 5.2: Topographic plots representing scalp distributions of neural activity averaged through all experimental conditions. Each plot represents the TOI corresponding to one ERP component: P1 (80-135 ms), N170 (140-200 ms) and P2 (200-350 ms). The two occipito-temporal ROIs (of 5 electrodes each) are marked by white rectangles.

2.5. Statistical analyses

Statistical analyses were performed using R-Studio software (version 0.99.902, RStudio Inc., 2016). Plots were created using the open-source package “ggplot2” (Wickham, 2009). Mixed Effect Linear Model analyses were run using the open-source packages “lme4” (Bates, Maechler, Bolker, & Walker, 2014) and “lmerTest” (Kuznetsova et al., 2015). Post-hoc comparisons were performed using the open-source package “lsmeans” (Lenth, 2016). R^2 computations were performed using the open-source package “MuMIn” (Barton, 2016).

Participants’ accuracy data from Experiment 1 were analysed by using a generalised linear mixed-effects model (GLMM) computed on a binomial distribution, allowing thus to analyse accuracy at a single-trial level. This model included as independent variables Stimulus (2 levels, Faces vs. Bodies), Inversion (2 levels, Upright vs. Inverted), Task (2 levels, if participants were asked to identify Emotion vs. Gender) and Emotion (5 levels, Neutral vs. Happy vs. Sad vs. Angry vs. Fearful), in a full factorial design. In this GLMM, the significance of each effect was estimated performing LRTs with corresponding null models.

Participants’ accuracy data from Experiment 2 were not analysed since they reached a ceiling effect (~ 94%) due to the basic task (identifying orientation).

The peak amplitude values were then analysed by using linear mixed-effects models (LMM). Three LMMs were performed on Experiment 1, one for each component (P1, N170, P2), and one was performed for N170 in Experiment 2, since it was carried out in order to have confirmatory results on N170.

Models used to analyse data from Experiment 1 included as independent variables Stimulus (2 levels, Faces vs. Bodies), Inversion (2 levels, Upright vs. Inverted), Task (2 levels, Emotion vs. Gender), Emotion (5 levels, Neutral vs. Happy vs. Sad vs. Angry vs. Fearful) and Side (Left vs.

Right cluster), in a full factorial design. The model used to analyse data from Experiment 2 included as independent variables Stimulus (3 levels, Faces vs. Bodies vs. Houses), Inversion (2 levels, Upright vs. Inverted) and Side (Left vs. Right cluster), in a full factorial design. The significance of each effect was estimated using the Satterthwaite approximation for degrees of freedom in LMMs.

Since the most appropriate use of these models is under debate (Barr, Levy, Scheepers, & Tily, 2013; Bates, Kliegl, Vasishth, & Baayen, 2015), it is important to specify the decisional pipeline we followed to decide which random effects were to be included in the models. First, only random effects that allowed the model to converge were included. We included only random effects that presented a correlation $|r| < .80$ with other random effects in order to avoid overfitting. Whenever we needed to choose a random effect, we performed a Likelihood Ratio Test (LRT) with a null model and included the random effect only if the LRT resulted as statistically significant. This last criterion showed that the proportion of explained variance was significantly higher than in the null model. All post-hoc comparisons were performed using Tukey's honest significant difference.

3. Results

3.1. Experiment 1 – Accuracy

Random effects only include random intercept (explained variance = 0.138, st dev = 0.3715). The R^2 calculations of the model were as follows: Marginal R^2 (considering only the variance explained by fixed effects) = 0. 268 and Conditional R^2 (considering also the variance explained by random effects) = 0. 298 (Nakagawa & Schielzeth, 2013). The statistically significant fixed effects were as follows: Stimulus: χ^2 (1) = 6.902, p = .009; Inversion: χ^2 (1) = 50.137, p < .001; Task: χ^2 (1) = 316.26, p < .001; Emotion: χ^2 (4) = 10.79, p = .029; Stimulus * Emotion: χ^2 (4) = 71.93, p < .001; Inversion * Task: χ^2 (1) = 32.992, p < .001; Inversion * Emotion: χ^2 (4) = 29.94, p < .001; Task * Emotion: χ^2 (4) = 62.042, p < .001; Stimulus * Task * Emotion: χ^2 (4) = 32.916, p < .001.

Main effects: *Stimulus* effect showed that participants were significantly more accurate when processing faces (mean = 0.861) than bodies (mean = 0.837). *Inversion* effect showed that upright (mean = 0.880) were better recognized than inverted (mean = 0.818) stimuli. *Task* effect showed that participants were more accurate in gender recognition (mean = 0.928) than in emotion recognition (mean = 0.770). The only statistically significant difference found in *Emotion* effect showed that happy stimuli (mean = 0.872) are recognized more accurately than angry stimuli (mean = 0.829, z = -2.566, p = .030).

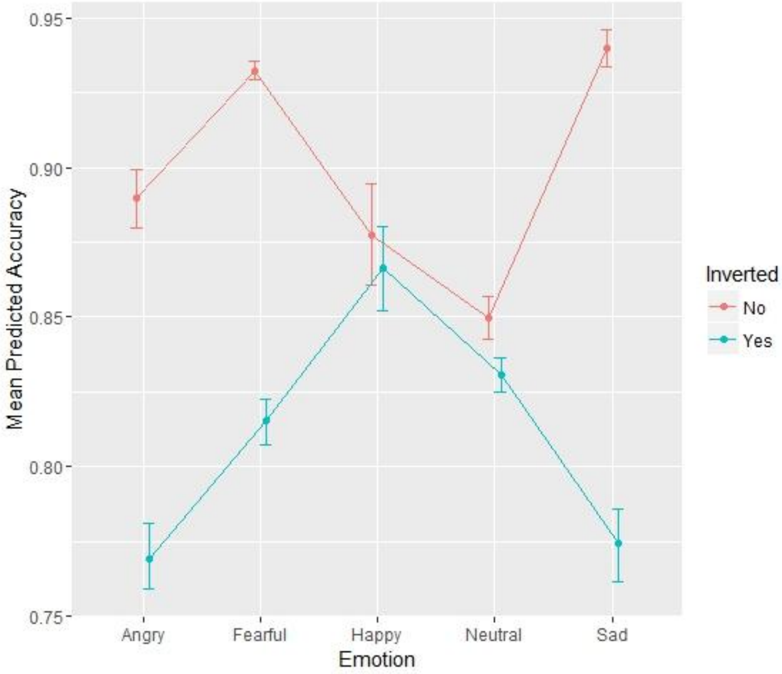


Fig. 5.3: Plot representing the effects of emotion in upright (red line) and inverted (blue line) stimuli on participants' Accuracy in Experiment 1. In this and following plots dots represent the mean value and error bars represent 95% confidence intervals.

Interaction effects: *Inversion * Task* effect showed that inversion effect is stronger for gender (upright mean = 0.971, inverted mean = 0.885, z = 8.752, p < .001) than emotion processing (upright mean = 0.790, inverted mean = 0.750, z = 4.282, p < .001), even though both were statistically significant. *Inversion * Emotion* effect (Fig. 5.3) showed that stimuli conveying all emotions but happiness presented an inversion effect in accuracy (angry upright mean = 0.890, angry inverted mean = 0.769, *z* = 5.421, p < .001; fearful upright mean = 0.932, fearful inverted mean = 0.815, *z* = 4.455, p < .001; neutral upright mean = 0.850, neutral inverted mean = 0.831, *z* = 4.137, p = .001; sad upright mean = 0.940, sad inverted mean = 0.774, *z* = 6.747, p < .001; happy upright mean = 0.878, happy inverted mean = 0.866, *z* = 1.898, p = .671). Comparisons based on emotions revealed that, in inverted stimuli, happiness was recognised better than anger (*z* = 4.150, p = .001) and sadness (*z* = 3.881, p = .004); angry stimuli were also recognized less accurately than neutral stimuli (*z* = -3.333, p = .029). In upright stimuli, the only significant difference showed that sadness was recognised more accurately than neutral stimuli (*z* = 3.330, p = .030).

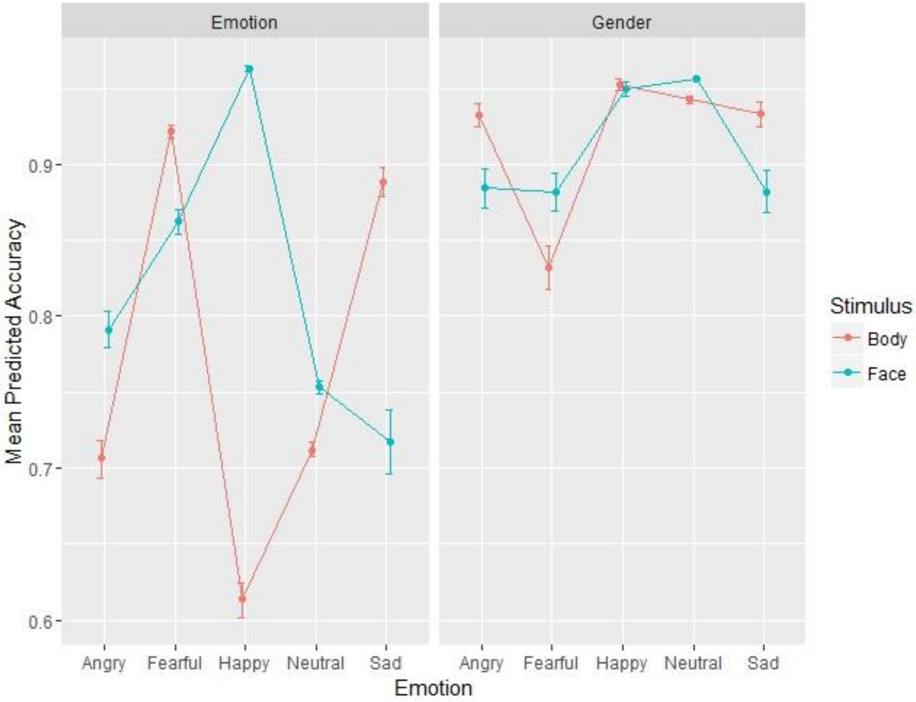


Fig. 5.4: Plot representing the effects of emotional expression in faces (blue line) and bodies (red line) on participants' Accuracy in Experiment 1, divided by the task performed by participants (emotion or gender recognition).

Post-hoc comparisons of interaction effects *Stimulus * Emotion* and *Task * Emotion* will not be presented, because their 3-way interaction *Stimulus * Task * Emotion* is presented below (Fig. 5.4). In the comparisons based on stimuli, only in the emotion recognition task (Fig. 5.4, first panel), happiness was recognized with higher accuracy when conveyed by faces (mean = 0.963) than by bodies (mean = 0.614, *z* = 6.860, p < .001), while sadness presented higher accuracy when conveyed by bodies (mean = 0.889) than by faces (mean = 0.717, *z* = 4.003, p = .010). The comparisons based on performed tasks revealed higher accuracy in gender recognition than in emotion recognition when processing angry bodies (gender mean = 0.933, emotion mean = 0.707, *z* = 5.867, p < .001), happy bodies (gender mean = 0.953, emotion mean = 0.614, *z* = 7.044, p < .001), neutral bodies (gender mean = 0.943, emotion mean = 0.712, *z* = 10.870, p < .001) and sad faces (gender mean = 0.882, emotion mean = 0.717, *z* = 5.069, p < .001). The comparisons based on emotions revealed that most differences were present in the emotion recognition task: in bodies, anger (mean = 0.707) was recognized less accurately than fear (mean = 0.922, *z* = -4.926, p < .001) and sadness (mean = 0.889, *z* = -4.549, p < .001), fear was also recognized better than happiness (mean = 0.614, *z* = 6.394, p < .001) and neutral stimuli (mean = 0.712, *z* = 5.416, p < .001), and also sad bodies were recognized better than happy (*z* = 6.168, p < .001) and neutral ones (*z* = 5.119, p < .001); concerning faces, happy faces (mean = 0.963) were recognised with higher accuracy than angry (mean = 0.791, *z* = 4.406, p = .002), neutral (mean = 0.754, *z* = 5.500, p < .001), and sad faces (mean = 0.717, *z* = 5.279, p < .001). In the gender recognition task, the only significant difference based on emotions was found between fearful bodies (mean = 0.832) and neutral bodies (mean = 0.957, *z* = -3.946, p = .012). Comparisons based on emotional expressions are synthesized in the following table:

EXPERIMENT 1 – ACCURACY

EMOTION identification task		**GENDER identification task**	
FACES	**BODIES**	**FACES**	**BODIES**
Happy > angry, neutral, sad	Fearful > angry, happy, neutral	None	Neutral > fearful
	Sad > angry, happy, neutral		

3.2. Experiment 1 – P1 component

Included random effects are listed in Table 1 (in Appendix). The R^2 calculations of the model were as follows: Marginal $R^2 = 0.100$ and Conditional $R^2 = 0.709$.

Statistically significant fixed effects were as follows: Stimulus: F (1, 22) = 15.786, p < .001; Inversion: F (1, 22.01) = 54.822, p < .001; Emotion: F (4, 1644.30) = 23.438, p < .001; Stimulus * Inversion: F (1, 1644.28) = 19.074, p < .001; Stimulus * Side: F (1, 1644.03) = 4.145, p = .042; Inversion * Side: F (1, 1644.03) = 7.561, p = .006.

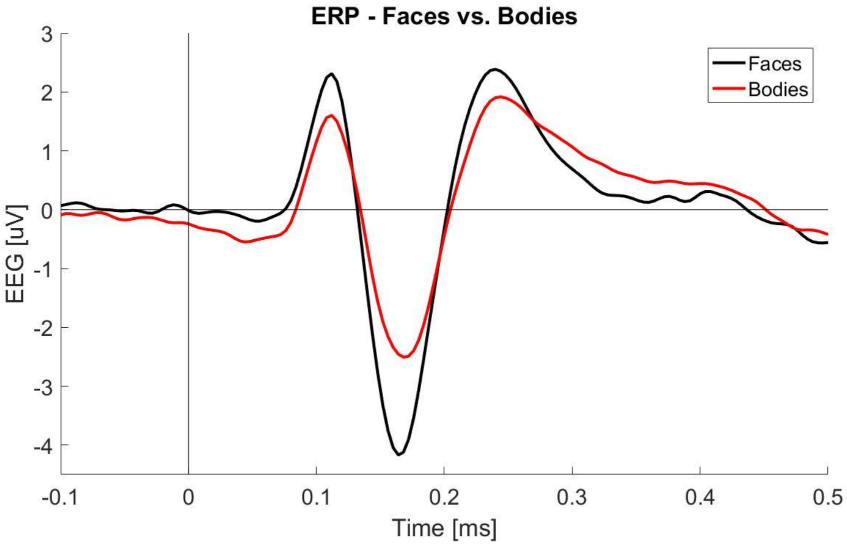


Fig. 5.5: Grand-averaged ERP activity elicited by faces (black line) and bodies (red line) in Experiment 1, averaged through the 10 occipito-temporal electrodes considered in the two ROIs. The activity is averaged through inversion, emotion and task variables.

Main effects: *Stimulus* effect (Fig. 5.5) showed that, on average, faces (mean = 3.426) presented a larger P1 component than bodies (mean = 2.892). *Inversion* effect (Fig. 5.6) revealed that inverted stimuli (mean = 3.644) exhibited a larger P1 component than upright ones (mean = 2.675). Post-hoc comparisons in *Emotion* effect (Fig. 5.7) showed that neutral stimuli (mean = 2.579) exhibited a smaller P1 component than all other emotional stimuli (angry mean = 3.300, *t* = -

7.553, p < .001; fearful mean = 3.290, *t* = -7.412, p < .001; happy mean = 3.372, *t* = -8.311, p < .001, sad mean = 3.251, *t* = -7.048, p < .001).

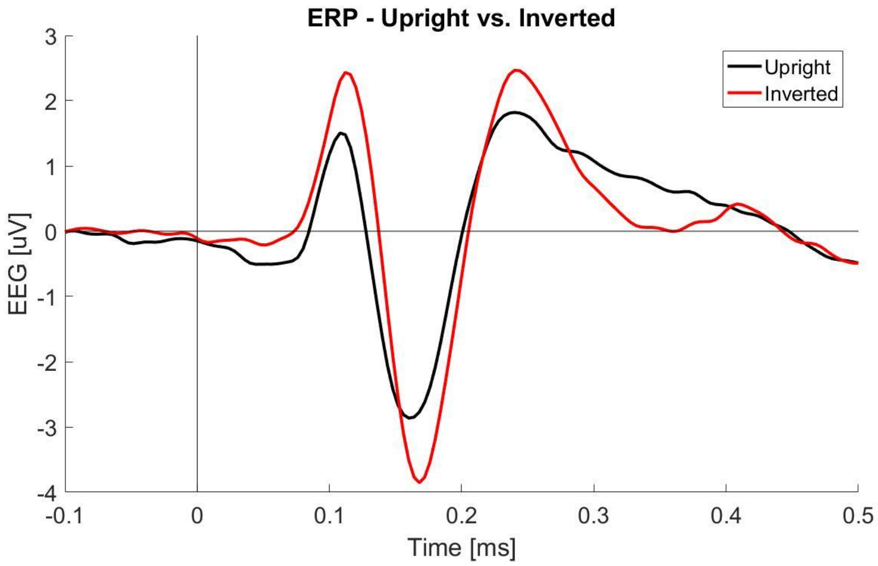


Fig. 5.6: Grand-averaged ERP activity elicited by upright (black line) and inverted (red line) stimuli in Experiment 1, averaged through the 10 occipito-temporal electrodes considered in the two ROIs. The activity is averaged through stimulus, emotion and task variables.

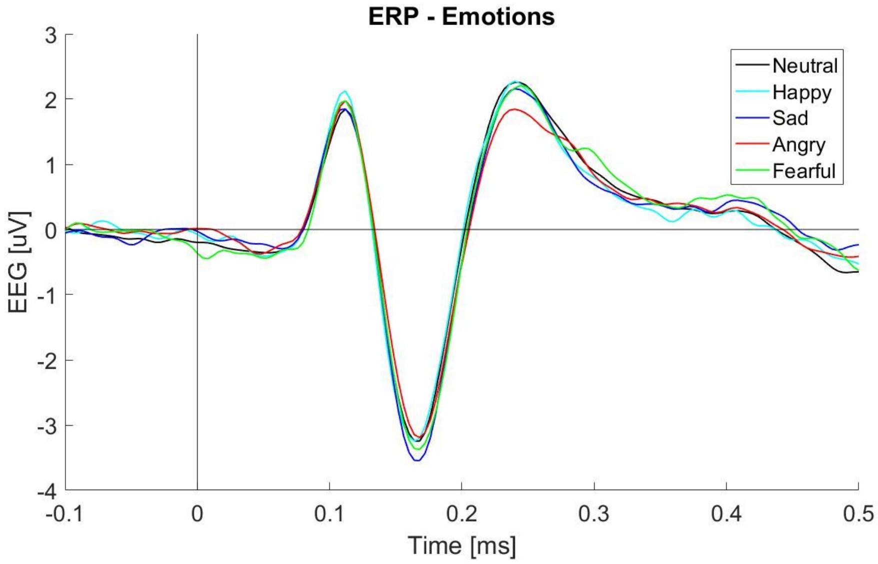


Fig. 5.7: Grand-averaged ERP activity elicited by neutral (black line), happy (cyan line), sad (blue line), angry (red line) and fearful (green line) stimuli in Experiment 1, averaged through the 10 occipito-temporal electrodes considered in the two ROIs. The activity is averaged through stimulus, inversion and task variables.

Interaction effects: *Stimulus * Inversion* effect showed that inversion effect was stronger for faces (upright mean = 2.810, inverted mean = 4.051, *t* = 8.549, p < .001) than for bodies (upright mean = 2.541, inverted mean = 3.243, *t* = 4.885, p < .001), even though both were statistically significant. *Stimulus * Side* effect revealed that P1 component was significantly larger for faces than for bodies on both sides, but this difference is larger over the right cluster (faces mean = 3.792, bodies mean = 3.135, *t* = 4.459, p < .001) than over the left cluster (faces mean = 3.061, bodies mean = 2.648, *t* = 2.787, p = .042). *Inversion * Side* effect showed that the inversion effect was larger over the right cluster (upright mean = 2.897, inverted mean = 4.032, *t* = 7.874, p < .001) than over the left cluster (upright mean = 2.454, inverted mean = 3.257, *t* = 5.562, p < .001), even though both were statistically significant.

3.3. Experiment 1 – N170 component

Included random effects are listed in Table 2 (in Appendix). The R^2 calculations of the model were as follows: Marginal R^2 = 0.126 and Conditional R^2 = 0.835.

The statistically significant fixed effects were as follows: Stimulus: F (1, 22.01) = 32.731, p < .001; Inversion: F (1, 22.89) = 83.442, p < .001; Emotion: F (1, 1644.65) = 20.034, p < .001; Side: F (1, 22) = 5.915, p = .024; Stimulus * Inversion: F (1, 1644.62) = 12.260, p < .001; Stimulus * Emotion: F (4, 1644.65) = 5.054, p < .001; Inversion * Side: F (1, 1644.23) = 11.791, p < .001; Stimulus * Task * Emotion: F (4, 1644.65) = 2.629, p = .033.

Main effects: *Stimulus* effect (Fig. 5.5) revealed that N170 component was larger for faces (mean = -5.580) than for bodies (mean = -3.849). *Inversion* effect (Fig. 5.6) showed that N170 component was larger for inverted stimuli (mean = -5.170) than for upright ones (mean = -4.256). Post-hoc comparisons performed on *Emotion* effect (Fig. 5.7) revealed that neutral stimuli (mean = -4.195) elicited a smaller N170 component compared to all emotional stimuli (angry mean = -4.658, *t* = 4.605, p < .001; fearful mean = -4.946, *t* = 7.368, p < .001; happy mean = -4.766, *t* = -5.687, p < .001; sad mean = -4.999, *t* = 7.975, p < .001); furthermore, angry stimuli exhibited a significantly smaller N170 when compared to fearful (*t* = 2.770, p = .045) and sad stimuli (*t* = 3.385, p = .007). *Side* effect revealed larger N170 components on the right cluster (mean = -5.233) than on the left one (mean = -4.191).

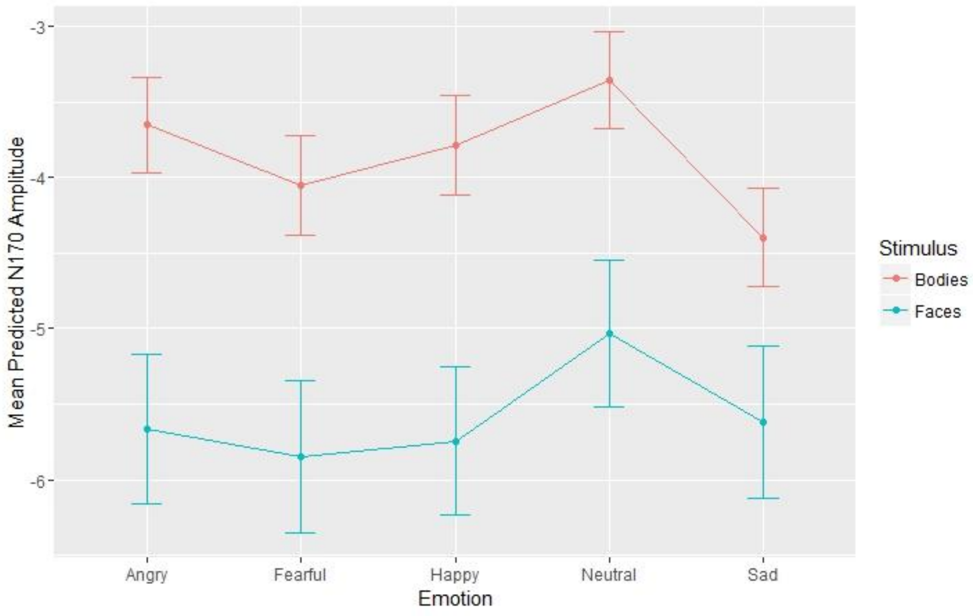


Fig. 5.8: Plot representing the effects of emotion in bodies (red line) and faces (blue line) on N170 in Experiment 1.

Interaction effects: *Stimulus * Inversion* effect revealed that inversion effect is larger for faces (upright mean = -5.006, inverted mean = -6.162, *t* = 9.571, p < .001) than for bodies (upright mean = -3.506, inverted mean = -4.192, *t* = 5.814, p < .001), even though both are statistically significant. Post-hoc comparisons performed on *Stimulus * Emotion* effect (Fig. 5.8) revealed specific patterns: sad bodies (mean = -4.396) showed larger N170 component than angry (mean = -3.652, *t* = -5.239, p < .001), happy (mean = -3.787, *t* = -4.290, p < .001) and neutral (mean = -3.357, *t* = -7.316, p < .001) bodies; in addition, fearful bodies (mean = -4.054) showed larger N170 than neutral ones (*t* = -4.903, p < .001); whereas neutral faces (mean = -5.033) revealed smaller N170 components compared to all emotional stimuli (angry mean = -5.663, *t* = 4.436, p < .001; fearful mean = -5.848, *t* = 5.516, p < .001; happy mean = -5.746, *t* = 5.017, p < .001; sad mean = -5.615, *t* = 3.973, p = .003). Moreover, for all emotions, faces showed larger N170 than bodies (all *t*s > 3.6, all ps < .03). *Inversion* * *Side* effect showed that inversion effect is stronger on the right cluster (upright mean = -4.667, inverted mean = -5.803, *t* = 9.545, p < .001) than on the left cluster (upright mean = -3.845, inverted mean = -4.538, *t* = 5.844, p < .001), even if both are statistically significant.

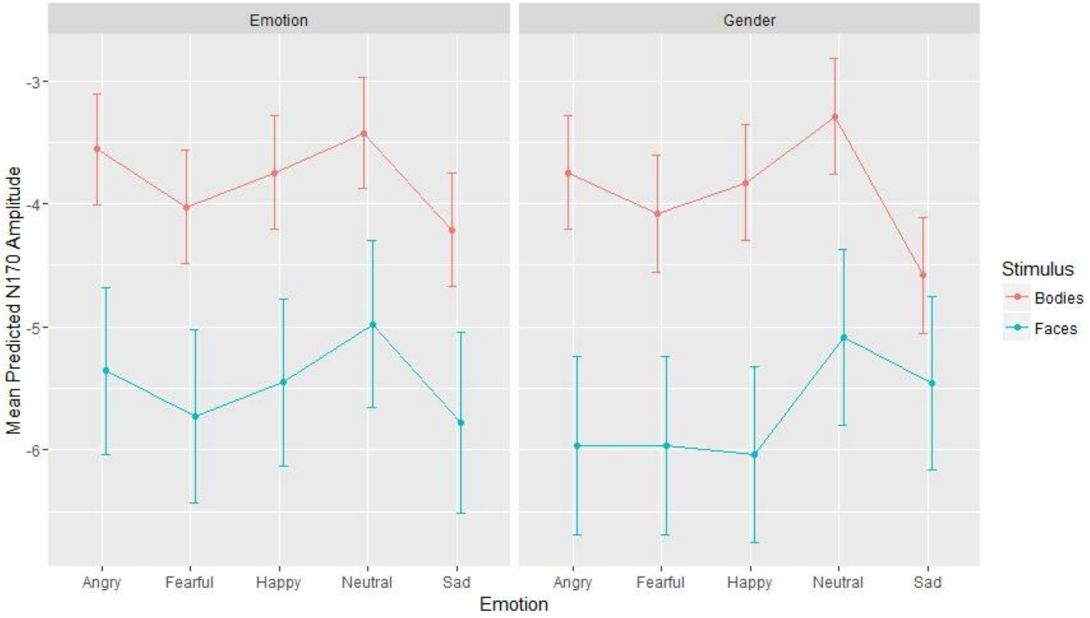


Fig. 5.9: Plot representing the effects of emotion in bodies (red line) and faces (blue line) on N170 in Experiment 1, divided by the task performed by participants (emotion or gender recognition).

Post-hoc tests performed on *Stimulus* * *Task* * *Emotion* effect (Fig. 5.9) revealed specific patterns. The comparisons based on emotions showed important differences while participants were performing the gender recognition task: bodies revealed the same pattern found in the Stimulus * Emotion effect, since sad bodies (mean = -4.580) showed larger N170 component than angry (mean = -3.747, *t* = -4.145, p = .006), happy (mean = -3.828, *t* = -3.741, p = .026) and neutral bodies (mean = -3.290, *t* = -6.419, p < .001), and also fearful bodies (mean = -4.081) showed larger N170 than neutral bodies (*t* = -3.937, p = .013); faces also showed a pattern very similar to the one found in the Stimulus * Emotion effect: neutral faces (mean = -5.088) revealed smaller N170 component than angry (mean = -5.967, *t* = 4.371, p = .002), fearful (mean = -5.966, *t* = 4.370, p = .002) and happy faces (mean = -6.040, *t* = 4.738, p < .001). On the contrary, in the emotion recognition task, both sad faces and bodies (faces mean = -5.780, bodies mean = -4.213) showed significantly larger N170 component than their neutral counterpart (faces mean = -4.977, *t* = -3.763, p = .024; bodies mean = -3.423, *t* = -3.928, p = .013). The comparisons based on the performed task revealed no statistically significant differences (all ps > .4). The comparisons based on stimuli showed that for all tasks and emotions faces exhibited larger N170 component than bodies (all *t*s > 4.2, all ps < .013), except for sad stimuli in the gender recognition task (faces mean = -5.459, bodies mean = -4.580, *t* = 2.465, p = .614). Comparisons based on emotional expressions are synthesized in the following table:

EXPERIMENT 1 – N170

EMOTION identification task		**GENDER identification task**	
FACES	**BODIES**	**FACES**	**BODIES**
Sad > neutral	Sad > neutral	Neutral < angry, fearful, happy	Fearful > neutral
			Sad > angry, happy, neutral

3.4. Experiment 1 – P2 component

Included random effects are listed in Table 3 (in Appendix). The R^2 calculations of the model were as follows: Marginal R^2 = 0.056 and Conditional R^2 = 0.733.

The statistically significant fixed effects were as follows: Stimulus: F (1, 22.03) = 7.550, p = .012; Inversion: F (1, 22.01) = 6.786, p = .016; Emotion: F (4, 1622.49) = 33.301, p < .001; Side:

F (1, 22) = 4.774, p = .040; Inversion * Side: F (1, 1622.02) = 7.200, p = .007; Stimulus * Task * Emotion: F (4, 1622.49) = 2.500, p = .041.

Main effects: *Stimulus* effect (Fig. 5.5) revealed that faces (mean = 4.024) elicit a larger P2 than bodies (mean = 3.760). *Inversion* effect (Fig. 5.6) showed that inverted stimuli (mean = 4.065) exhibited a larger P2 component than upright ones (mean = 3.719). Post-hoc comparisons performed on *Emotion* effect (Fig. 5.7) revealed that neutral stimuli (mean = 3.323) showed smaller P2 component than all emotional stimuli (angry mean = 3.976, *t* = -7.985, p < .001; fearful mean = 4.206, *t* = -10.667, p < .001, happy mean = 3.929, *t* = -7.411, p < .001; sad mean = 4.027, *t* = -8.711, p < .001), and also happy stimuli showed a significantly smaller P2 than fearful ones (*t* = -3.267, p = .010). *Side* effect showed that P2 component resulted to be larger over the right cluster (mean = 4.162) then over the left cluster (mean = 3.621).

Interaction effects: *Inversion * Side* interaction effect revealed that inversion effect on P2 showed to be statistically significant only over the right cluster (upright mean = 3.919, inverted mean = 4.407, *t* = -3.401, p = 0.010) and not over the left one (upright mean = 3.519, inverted mean = 3.723, *t* = -1.454, p = .477).

*Stimulus * Task * Emotion* interaction effect (Fig. 5.10) showed specific patterns that were analysed using post-hoc comparisons. Comparisons based on emotions revealed that for bodies, while performing both tasks, P2 component was significantly smaller for neutral bodies than for any other emotional body (Emotion recognition task: neutral mean = 2.969, angry mean = 3.824, *t* = -5.227, p < .001; fearful mean = 3.972, *t* = -6.133, p < .001; happy mean = 3.750, *t* = -4.779, p < .001; sad mean = 3.693, *t* = -4.429, p = .001. Gender recognition task: neutral mean = 3.250, angry mean = 3.891, *t* = -3.919, p = .014; fearful mean = 4.277, *t* = -6.281, p < .001; happy mean = 3.953, *t* = -4.301, p = .003; sad mean = 4.017, *t* = -4.694, p < .001). For faces, most evident differences were found during the gender recognition task: neutral faces (mean = 3.485) showed smaller P2 component than angry (mean = 4.307, *t* = -5.024, p < .001), fearful (mean = 4.389, *t* = -

5.528, p < .001) and sad faces (mean = 4.080, *t* = -3.635, p = .038); on the contrary, during the emotion recognition task, only the difference between neutral (mean = 3.587) and sad faces (mean = 4.330, *t* = -4.660, p < .001) showed smaller P2 component. Comparisons based on stimuli revealed a significant difference between sad faces (mean = 4.330) and bodies (mean = 3.694, *t* = 3.607, p = .046) during the emotion recognition task. Comparisons based on performed tasks revealed no statistically significant differences. Comparisons based on emotional expressions are synthesized in the following table:

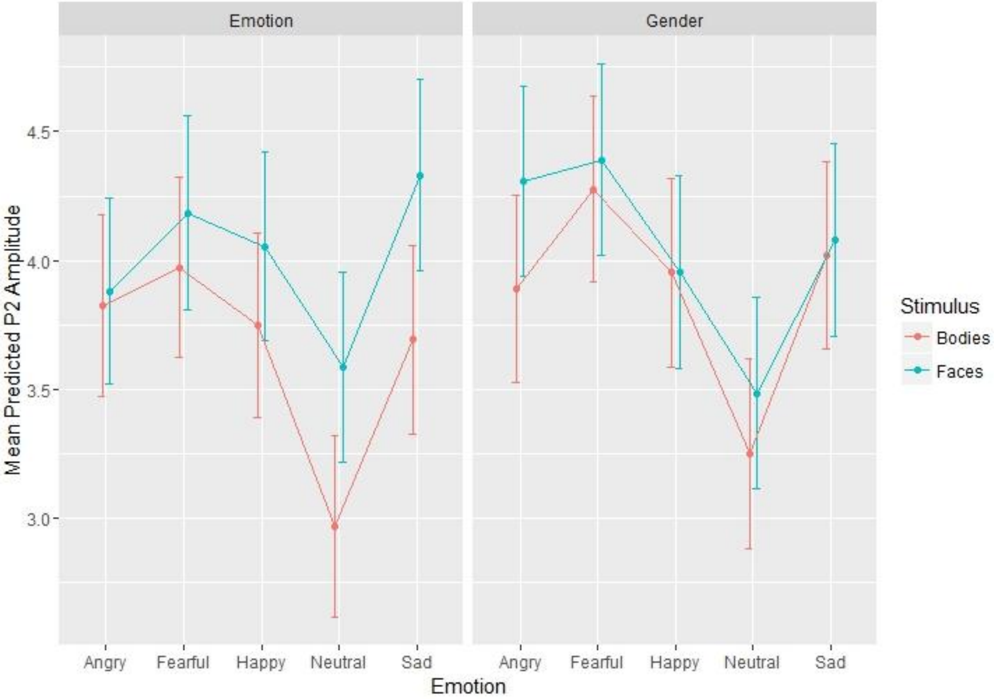


Fig. 5.10: Plot representing the effects of emotion in bodies (red line) and faces (blue line) on P2 in Experiment 1, divided by the task performed by participants (emotion or gender recognition).

EXPERIMENT 1 – P2

EMOTION identification task		GENDER identification task	
FACES	**BODIES**	**FACES**	**BODIES**
Neutral < sad	Neutral < angry, fearful, happy, sad	Neutral < angry, fearful, sad	Neutral < angry, fearful, happy, sad

3.5. Experiment 2 – N170 component

Included random effects are listed in Table 4 (in Appendix). The R^2 calculations of the model were as follows: Marginal R^2 = 0.134 and Conditional R^2 = 0.906.

The statistically significant fixed effects were as follows: Stimulus: F (2, 22) = 23.6032, p < .001; Inversion: F (1, 176) = 30.1787, p < .001, Side: F (1, 22) = 9.7711, p = .005; Stimulus * Inversion: F (2, 176) = 10.6729, p < .001.

Main effects: *Stimulus* effect showed that faces (mean = -4.522) exhibited larger N170 component than bodies (mean = -3.217, *t* = -5.778, p < .001) and houses (mean = -2.627, *t* = -6.520, p < .001); also bodies showed larger N170 than houses (*t* = -2.556, p = .046). *Inversion* effect revealed that upright stimuli (mean = -3.170) showed smaller N170 than inverted ones (mean = -3.740). *Side* effect showed that N170 was generally larger over the right cluster (mean = -3.965) than over the left one (mean = -2.946).

Interaction effect: post-hoc comparisons performed on *Stimulus * Inversion* effect (Fig. 5.11) revealed the presence of a statistically significant inversion effect for faces (upright mean = -4.000, inverted mean = -5.045, *t* = 5.802, p < .001) and bodies (upright mean = -2.839, inverted mean = -3.594, *t* = 4.199, p < .001), but not for houses (upright mean = -2.671, inverted mean = -2.584, *t* = -0.485, p = 0.997).

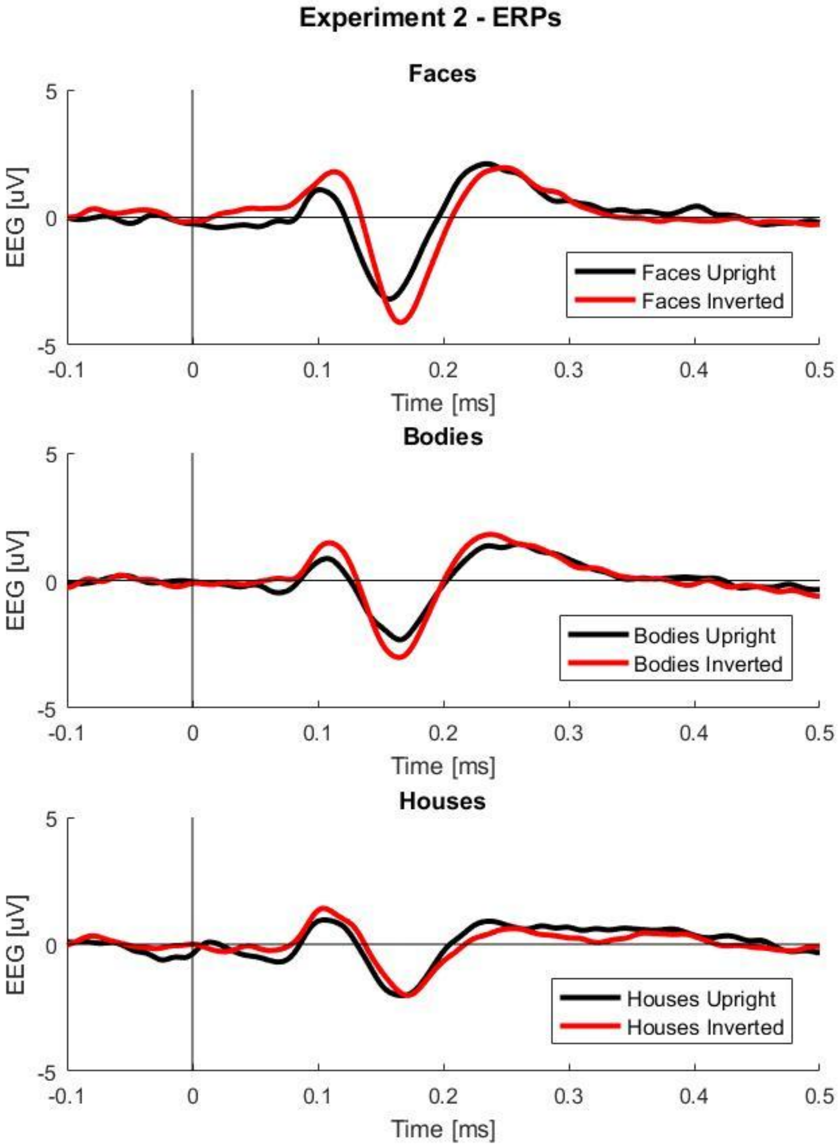


Fig. 5.11: Grand-averaged ERP activity elicited by upright (black line) and inverted (red line) faces (first panel), bodies (second panel) and houses (third panel) in Experiment 2, averaged through the 10 occipito-temporal electrodes considered in the two ROIs.

4. Discussion

Emotional expressions were shown to enhance the structural encoding of facial stimuli (Batty & Taylor, 2003; Hinojosa et al., 2015), while few results are available for bodies perception (Stekelenburg & De Gelder, 2004; van Heijnsbergen et al., 2007) and they seem to show that structural encoding of bodies is unaffected by emotional expressions. Inversion was proven to disrupt structural encoding of both faces (Rossion & Gauthier, 2002a; Yin, 1969) – relying on all levels of configural processing (Maurer et al., 2002) – and bodies (Reed et al., 2003) – relying mostly on first-order relational information and structural hierarchy processing (Reed et al., 2006).

The aim of this study was to investigate how different emotional expressions and inversion effect may interact on the structural encoding of faces and bodies. To do this, behavioural accuracy and psychophysiological activity in different stages (occipito-temporal ERP components: P1, N170, P2) were analysed while inverted and upright pictures of faces and bodies expressing 4 possible emotions (happiness, sadness, anger, fear – compared to emotional neutrality) were presented to participants. Their task was to identify either the stimulus gender or the emotion expressed.

The below hypotheses were tested in this study. For clarity, they are presented separately, together with the summary of the most relevant results for that hypothesis and their discussion.

4.1. Hypothesis 1

According to the first hypothesis, we expected behavioural (lower accuracy) and electrophysiological (larger N170 component) inversion effects for both faces and bodies, but not for objects, considering previous literature showing these effects (Reed et al., 2003; Rossion & Gauthier, 2002; Stekelenburg & De Gelder, 2004; Yin, 1969).

Considering behavioural performance, only the accuracy in Experiment 1 was analysed, since accuracy in Experiment 2 reached a ceiling effect. This analysis revealed a main effect of inversion: independently of the stimulus, upright faces and bodies were processed more easily than inverted ones, thus replicating the inversion effect.

The key result for this hypothesis was the analysis of N170 amplitude in Experiment 2: the Stimulus * Inversion effect revealed that inverted faces and bodies showed larger N170 components than upright ones, while inverted and upright houses showed no statistically significant differences (Fig. 5.11). This result replicates previous literature, proving the disruption of configural processing by inversion in faces and bodies, and no configural processing involved in objects perception (Stekelenburg & De Gelder, 2004).

In ERP analysis of Experiment 1 data, the inversion effect was present on all the investigated components: P1, N170 and P2 were all larger for inverted stimuli than for upright ones (see Fig. 5.6). Besides, the Stimulus * Inversion interaction effects showed that in P1 and N170 the inversion effect was stronger for faces, even though statistically significant for both.

Some studies already found the presence of inversion effect also on P1 (Itier & Taylor, 2004; Minnebusch, Keune, Suchan, & Daum, 2010; Rossion et al., 1999, 2000) and P2 components (Soria Bauser et al., 2015). The P1 component is a low-level early perceptual component and is related to the cognitive mechanisms often described as “recognizing the stimulus as a face” (or a body) (Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier & Taylor, 2004; Righart & de Gelder, 2007; Rossion et al., 1999, 2000; Soria Bauser, Schriewer, & Suchan, 2015; Thierry et al., 2006), while the P2 component is typically related to higher levels of perceptual processing, as integration of information coming from different neural networks (Adolphs, 2002a, 2002b) or refined holistic processing (Soria Bauser et al., 2015). These results show, thus, that inversion can affect stimulus encoding at all stages, from the early coarse encoding, to structural encoding, to refined and integrated holistic processing.

The novel result is that inversion effect seems to affect more faces than bodies on the early components related to stimulus encoding. FIE and BIE were typically described as having comparable effect sizes (Bonemei et al., 2017a; Reed et al., 2003; Stekelenburg & De Gelder, 2004), while specific components analyses highlighted this result. This is probably related to the differences in configural processing involved in face and body perception. If configural body processing relies only on first-order information and structural hierarchy (Reed et al., 2006) inversion may represent a "less impairing" disruption of body processing, compared to face processing, which requires all levels of configural processing (Maurer et al., 2002). Thus, bodies may be encoded using a part-based strategy more easily than faces, showing that the shape of single body parts is more relevant in body processing than single facial features in face processing.

Two other groups of results replicating previous literature are discussed here below.

Lateralization of ERP components

A main effect of Side showed larger N170 and P2 components on the right hemisphere than on the left one. The significant interaction effect Inversion * Side was statistically significant on all components, showing that the inversion effect was larger on the right side for P1 and N170, while it was statistically significant *only* on the right side for P2. Moreover, the P1 component revealed larger amplitude for faces than bodies, and this difference was larger on the right side than on the left one.

These results replicate previous results found for right lateralization of face (Rossion, 2014) and body processing (Gliga & Dehaene-Lambertz, 2005; Minnebusch & Daum, 2009), especially on N170 component. Lateralization of P2 component shows that also higher levels of visual holistic processing are mostly occurring in the right hemisphere. This finding is further corroborated by the lateralization of the inversion effect: if configural processing of faces and bodies is preferentially located on the right side, also inversion (disrupting configural processing) should display larger effects in the right hemisphere.

The P1 component showed very early increased selectivity for faces on the right side. This selectivity was generalised for both stimuli in later stages of processing (N170 and P2). Facial stimuli seem to be coded as a face and fed in the specialized processing pathway (in the right hemisphere) sooner than bodies. Therefore, the visual system seems to be more rapidly tuning on face than body processing. This interpretation is discussed also in the next paragraph.

Stimulus effects

In all analyses, faces showed overall higher accuracy and larger P1, N170, and P2 components than bodies (Fig. 5.5). These results replicate previous findings (Stekelenburg & De Gelder, 2004) which found larger N170 for faces than bodies, and generalize them to all the ERP components. This corroborates the previous explanation: the visual system, at all processing stages, seems to be more rapidly (and easily) tuning on face than body processing.

Taking into account these results, one could argue that bodies showed smaller ERP components because only faces are processed in a configural way and bodies are processed analytically, as objects. On the contrary, the results from Experiment 2 showed that N170 for bodies is significantly larger than for objects, showing that the structural encoding of these stimuli relies on configural processing and both faces and bodies are encoded as configural *gestalts*.

4.2. Hypothesis 2

The second hypothesis postulated an enhancement of N170 (and probably other components as P1 and P2) due to emotional expressions in faces, as widely demonstrated in the literature (Hinojosa et al., 2015 for a review).

On P1 no specific effect of emotion on face processing was found, but the main effect of Emotion showed that neutral stimuli (faces and bodies) presented smaller P1 than all emotional stimuli (Fig. 5.7). On N170, the Stimulus * Emotion interaction effect (Fig. 5.8) indicated the same trend for faces. Specifically, neutral faces presented smaller N170 than all emotional faces. On the P2 component no Stimulus * Emotion effect was statistically significant, but the Stimulus * Task * Emotion showed that, during the task requiring gender discrimination[5], neutral faces showed smaller P2 than all negative emotional faces (sad, angry, fearful). On the other hand, during the emotion discrimination task only sad faces showed larger P2 than neutral ones.

This pattern of results provides important insights about the face processing route. P1 seems to show a fast coarse differentiation between emotionally arousing vs. non-arousing stimuli. No differences among diverse emotions or between faces and bodies were found. This result appears to be consistent with the early action of the colliculo-pulvinar–amygdala pathway involved in fast emotional appraisal of the stimulus (Adolphs, 2002a, 2002b). In the second stage of face processing (N170), all emotional expressions influenced the structural encoding of faces. This result replicates previous findings for happy, angry and fearful faces (Hinojosa et al., 2015), and extends this effect also to sadness, showing no significant differences among specific expressions. In P2, we found the precise discrimination of emotional positive vs. negative valence thanks to the appraisal of the emotion, i.e., only faces with negative valence (sad, angry, fearful) showed larger P2 than neutral

---

[5] Effects related to the task performed by participants are discussed in Paragraph 4.5.

ones. This appraisal is more sophisticated than the fast appraisal indicated by P1, since it can categorize the negative vs. positive emotional valence. It may reflect a match with the cognitive system (memory and previous experience related to facial expressions) in a higher-level, more conceptualized processing, based on feed-back connections from orbitofrontal cortex and amygdala to visual processing areas (Adolphs, 2002a, 2002b).

4.3. Hypothesis 3

The third hypothesis considered the possibility of a dissociation of the effects of emotional expressions in different components between faces and bodies, since they are processed through partially dissociable configural mechanisms (Reed et al., 2006).

As regards the analysis on behavioural accuracy, the difference found in the Stimulus * Task * Emotion interaction effect (in the emotion discrimination task)[6] are summarized and discussed. During the emotion recognition task, faces showed higher accuracy for happy expression compared to angry, neutral and sad expressions, whereas fearful and sad bodies displayed higher accuracy than neutral, angry and happy ones. Furthermore, comparisons based on the stimulus showed that happiness was recognized better through faces than through bodies, and sadness was recognized better through bodies than through faces.

Regarding ERP components, faces and bodies showed on P1 the same pattern of results described in Paragraph 4.2, as no significant Stimulus * Emotion effect was found. On N170 bodies showed specific differences among emotions (Fig. 5.8): sad bodies showed larger N170 than angry, happy and neutral ones, while fearful bodies presented larger N170 than neutral ones. On P2 all emotional bodies showed larger amplitude than neutral ones, in both tasks.

---

[6] See note 5.

After a first rapid coarse processing through the subcortical pathway (reflected in P1), an appraisal of the behavioural approach-avoidance tendency appears to be performed at the structural encoding level for bodies. As a matter of fact, avoidance-oriented emotional expressions (fear and sadness) showed larger N170 components than neutral and approach-oriented expressions (happiness and anger). What influences this stage seems, thus, not to be the emotion, but the tendency to approach or avoid the observer. Approach-avoidance tendency is expressed more easily through the body than through the face because approach and avoidance behaviours naturally require a movement of the body. Our visual system seems thus to be tuned to perceive the implied tendency to move as part of the body structure. This interpretation is supported by studies observing the activation of visual areas designated for motion processing while observing still images of implied motion (Allison et al., 2000; Kourtzi & Kanwisher, 2000) and increased bilateral N170 when watching movies of biological motion (Puce & Perrett, 2003). Movement (even implied) seems to be a key feature in body encoding. For body processing, the subcortical pathway may play a key role not only at the earliest processing stage (P1), but also at the structural encoding stage: the amygdala was proven to be a key structure in discriminating approach- and avoidance-oriented behaviour (expression and gaze, in this case) (Adams, Gordon, Baird, Ambady, & Kleck, 2003) and the same pattern was found on N170 for bodies in our study. Further neuroimaging research focusing on the neural bases of approach and avoidance in faces and bodies is required to confirm this hypothesis.

The proper emotional expression encoding in bodies seems to occur at P2 latency (Fig.6.10). The emotional content of bodies is clearly categorized only at this stage, through a precise appraisal obtained by using a top-down conceptual processing and categorization of the emotion. Therefore, the emotional expression discrimination is slower and less immediate than in faces, i.e., it requires a higher-level processing and conceptualization. On the other hand, emotional expressions of faces are already processed at the structural encoding stage, showing that (for the human visual system) faces are probably the most appropriate stimulus category to convey emotions. This may also be the reason why facial expressions are a universal and “spontaneous” mean to convey emotions (Ekman & Friesen, 1971), while body postures typically require a specific training to be fully understood.

Behavioural results for bodies exactly reflected the results found in N170: avoidance-oriented expressions are categorized better than approach-oriented and neutral expressions. Therefore, participants’ accuracy for bodily expression recognition mostly reflects the structural encoding of these stimuli, corroborating the interpretation linked to the importance of implied motion in body processing. On the other hand, behavioural results for faces reflected a well-known perceptual effect, the *happy face advantage* (Shimamura, Ross, & Bennett, 2006): faces showing a happy expression are processed more easily, faster, and are recognized better. This reinforcing effect is most likely what drives the facial expression result in our study. P1 and N170 components did not show this clear advantage for happy expression, which displayed the same increased amplitude as all other facial expressions. Probably the neural bases of this effect can be found at later stages of processing, since the P2 component showed increased amplitude only for facial expressions with negative valence.

Consequently, we can conclude that face and body structural encoding are affected by emotional expressions in a different way, as suggested by the different stages in which they are processed.

4.4. Hypothesis 4

The fourth hypothesis postulated an interaction of the effects of emotional expression and inversion, since both were proven to influence the structural encoding of social stimuli (Hinojosa et al., 2015; Reed et al., 2003).

Considering accuracy results, the interaction effect Emotion * Inversion (Fig. 5.3) showed that inverted stimuli were more difficult to be processed for all emotions except for happiness, which revealed no behavioural inversion effect. No statistically significant interaction of Emotion * Inversion, or higher level interactions including this effect, were found in psychophysiological data.

The behavioural result can be easily explained considering again the *happy face advantage* (Shimamura et al., 2006): happy expression boosts the encoding of the stimulus, so that both emotional expression and gender can be easily recognized in inverted stimuli, in which the configural processing was disrupted. This result, together with the effects of emotional expressions on N170, corroborates the interpretation of an influence of emotional expression on the structural encoding of social stimuli.

Even though the influence of both inversion and emotional expressions (with different trajectories for faces and bodies) were found on the neural encoding of these stimuli, they did not interact on psychophysiological activation. In other words, emotional expressions can boost the structural encoding, independently of its configural or part-based processing. The most likely explanation of this finding is that this “emotional boost” may occur through fast processing in the rapid subcortical stream (Adolphs, 2002a, 2002b), *independently* of further slower processing through visual cortices, which may differ in configural or analytical (as suggested by inversion effects). The independence of these mechanisms may be due to the different aims of the two streams: on the one hand, the subcortical pathway (on which emotional expressions act) performs a rougher stimulus processing aimed to extract the valence through a fast appraisal of emotional information. On the other hand, the cortical pathway (on which inversion acts) processes stimuli in a smoother way, performing a precise configural encoding aimed to identify the social stimulus and its peculiarities (identity, familiarity, etc.). The different targets of these pathways proves that their functional independence may represent indeed an advantage. Thinking from a phylogenetic point of view, the rapid recognition of the emotional expression of another individual may help a person to understand signals of danger, reward, approach or avoidance (in the case of bodies). The recognition of these signals independently of the configural processing may be an advantage in situations where the individual may process only a part of the social stimulus (e.g., the expression of the eye region or the mouth region, an arm ready to throw a punch) or in conditions of low visibility, in which the other individual cannot be clearly seen and identified. This skill could potentially play an important role in survival, and could explain why this process bypasses the configural processing aimed to identity recognition or higher-level processes.

Whereas these two pathways were typically described as slightly faster (subcortical) and slower (cortical) in their processing, we found that inversion and emotional expressions affected visual processing of social stimuli at all stages (P1, N170, P2). Even though most studies have focused only on the N170 component, it is not news that face and body inversion affects also P1 (Itier & Taylor, 2004; Minnebusch, Keune, Suchan, & Daum, 2010; Rossion et al., 1999, 2000) and P2 components (Soria Bauser et al., 2015), as already discussed in Paragraph 4.1. The same goes for the influence of emotional expressions (Batty & Taylor, 2003; Krolak-Salmon et al., 2001; Rigato et al., 2009; Stekelenburg & De Gelder, 2004; Valdés-Conroy et al., 2014). Therefore, we can conclude that both pathways can affect processing of social stimuli at all stages, from early recognition of the stimulus as a face/body (P1), to structural encoding and configural processing (N170), to conceptual categorization of the stimulus (P2).

4.5. Hypothesis 5

According to hypothesis number 5 we would expect larger effects of emotional expressions during the emotion discrimination task than during the gender discrimination task.

Behavioural and psychophysiological data will be presented and discussed separately, in order to make the discussion easier to read.

Behavioural results showed that the emotion discrimination task had overall lower accuracy than gender discrimination. The Task * Inversion interaction effect demonstrated that the inversion effect is larger during the gender discrimination task. The Task * Emotion interaction effect showed that emotion discrimination task displayed lower accuracy than gender discrimination task for all emotions except for fear, in which no differences were found. In the Stimulus * Task * Emotion (Fig. 5.4), comparisons based on the task showed that the previous result was mainly driven by bodies (for angry, happy and neutral bodies) and by only sad faces. The comparisons based on the emotion revealed that most of the differences among emotions were found during the emotion discrimination task.

The overall task difference showed that the emotion discrimination task was more difficult than the gender discrimination task: while gender needed only a two-choice response (male vs. female), emotion recognition required a two-choice response (neutral vs. emotional) followed by a four-choice response (discriminating among specific emotions) in the “emotional” case. Therefore, the chance level was much lower in the second case. Moreover, some studies investigating the difference between gender and emotion processing found consistently that participants showed lower accuracy and slower RTs for expression than gender recognition (Krolak-Salmon et al., 2001; Wronka & Walentowska, 2011), showing that it is typically experienced as a more difficult task.

The larger behavioural inversion effect found during the gender discrimination task is a further demonstration that, as discussed above, emotional expression processing may not require full configural processing, while gender recognition may require it since this task needs to process unchangeable aspects of the face in a full configuration (Haxby et al., 2000).

Comparisons based on the task showed no difference for fear: the fearful expression is highly recognizable in all tasks and stimuli (see Fig. 5.4) because it is a very arousing emotion, easy to recognize since it conveys alarm for a possible danger (Ekman & Friesen, 1971). Differences based on task were mainly conveyed by bodies (angry, happy and neutral): as discussed in Paragraph 4.3, avoidance-oriented expressions (i.e., sadness and fear) are easily conveyed and recognized through bodies, while the discrimination of other emotions is more difficult; at the same time, gender is easier to discriminate through bodies since it is based on clear features. For this reason, the gender discrimination task showed high accuracy for all emotions and exhibited significant differences with the recognition of approach-oriented (and neutral) emotions. With regard to sadness, various sources prove that it is one of the most difficult emotions to recognize though facial expression (together with disgust and surprise), also given that it exerts the lowest influence on the N170 component (Hinojosa et al., 2015). This effect may lead the difference found for sadness between gender and emotion discrimination tasks.

Most of the differences among emotions were found during the emotion discrimination task, when they were explicitly processed. This effect highlights the fact that probably, during gender discrimination, the emotional information was filtered by the visual system in order to process only invariant information related to gender through a top-down mechanism. On the other hand, the emotional information was explicitly processed during the other task, leading to the differences found in accuracy.

As far as electrophysiological results are concerned, no effects of task were found on the P1 component, while the Stimulus * Task * Emotion interaction effect was found to be statistically significant on both N170 and P2. The comparisons based on emotions revealed that most significant differences in N170 (and in P2 for faces) were found during the gender discrimination task (and on both tasks in P2 for bodies). Moreover, the comparisons based on the stimulus revealed that faces elicited larger N170 than bodies in all conditions, except for sad stimuli during the gender discrimination task.

The importance of the gender discrimination task to elicit differences among emotions seems to be counterintuitive, but may be interpreted in association with the behavioural results. The visual system processes the emotional information through the subcortical pathway in an automatic and fast way. When participants were requested to process the stimulus gender, a *conflict* was probably created between the incoming emotional information and the information required by the task. Therefore, a top-down mechanism filtering the automatically processed emotional information is required. N170 and P2 components may display larger differences in amplitude among emotions for this reason: their amplitude may reflect the cognitive effort needed to filter the task-irrelevant emotional information. Consequently, if a larger ERP component is associated with a specific emotion, it could mean that the emotional information interfering with the gender discrimination was more salient. This explanation is coherent with the behavioural results, in which almost no differences among emotions were found during the gender discrimination task[7].

The lack of a significant difference between sad faces and bodies during gender discrimination on N170 component may be explained as follows. As discussed in Paragraph 4.3, N170 was increased for avoidance-oriented emotions in bodies, showing that the structural encoding of these stimuli was enhanced. During gender discrimination, the cognitive system needs to filter this emotional information (as described above). The emotional information of sad bodies was probably so salient that N170 amplitude for these stimuli reached the amplitude for sad faces (much higher for other emotions). However, this effect was not found in fearful bodies (also avoidance-oriented), probably due to the arousal difference between these emotions. This aspect should be investigated in further research.

4.6. Conclusions

This study was aimed to investigate the influence of inversion and different emotional expressions on the visual processing of faces and bodies, using both behavioural (accuracy) and electrophysiological (ERPs) measures. The key findings were (i) behavioural and

---

[7] The possible reason why comparisons based on emotions were found in both tasks on P2 for bodies was discussed in Paragraph 4.3.

psychophysiological inversion effects for both faces and bodies on all occipito-temporal ERP components (P1, N170, P2), shown by lower accuracy and larger ERP amplitude for inverted stimuli. This result proved that inversion disrupts configural processing of both stimulus categories; (ii) emotional expressions influenced visual processing of both faces and bodies, but with different trajectories. Faces showed specific effects of emotional expressions during the structural encoding stage (N170), while body perception discriminated approach and avoidance during this stage and specific emotions only through following top-down conceptualization (P2); (iii) no interaction of these two effects. This result demonstrated a functional independence of the two neurocognitive pathways involved in social stimuli processing (subcortical and cortical) (Adolphs, 2002a, 2002b). These pathways were proven to act during all stages of visual processing.

This study first investigated in depth how these two pathways are differently involved in all the diverse stages of face and body visual processing, and assessed their functional independence.

The aim of future research will be the investigation of these mechanisms through different techniques (e.g., neuroimaging techniques, source localization) or focusing on different aspects (e.g., influence of attention in different tasks, focus on the approach-avoidance related features).

5. Appendix

Table 1:

Experiment 1 – Random effect included in LMM on P1.

Random effect	Explained variance	Std Dev
Intercept | Subject	3.5307	1.8790
Stimulus | Subject	0.3307	0.5750
Side | Subject	2.5641	1.6013
Inversion | Subject	0.3077	0.5548
Task | Subject	0.1720	0.4147

Table 2:

Experiment 1 – Random effect included in LMM on N170.

Random effect	Explained variance	Std Dev
Intercept | Subject	3.5821	1.8926
Stimulus | Subject	2.3460	1.5317
Side | Subject	2.2896	1.5131
Inversion | Subject	0.1345	0.3667
Task | Subject	0.1756	0.4190
Stimulus : Side | Subject	1.2623	1.1235

Table 3:

Experiment 1 – Random effect included in LMM on P2.

Random effect	Explained variance	Std Dev
Intercept | Subject	2.7547	1.6597
Stimulus | Subject	0.3321	0.5763
Side | Subject	1.3375	1.1565
Inversion | Subject	0.4619	0.6796
Task | Subject	0.1716	0.4142
Stimulus : Inversion | Subject	0.8468	0.9202

Table 4:

Experiment 2 – Random effect included in LMM on N170.

Random effect	Explained variance	Std Dev
Intercept | Subject	4.0480	2.0120
Stimulus:Faces | Subject	0.8019	0.8955
Stimulus:Houses | Subject	0.8489	0.9214
Side | Subject	2.1971	1.4823

Final remarks

Perceptual mechanisms involved in visual processing of faces and bodies have been broadly studied (see Chapters 1 and 3). They involve dissociable neural networks, which are thought to involve configural processing of face and body information, as demonstrated by face- and body-inversion effects. Moreover, effects of emotional expressions and behavioural tendency to approach/avoidance are believed to play an important role in the encoding of both these stimuli.

The studies presented in this thesis showed new important findings in this field. First of all, we demonstrated that processing of facial features can be modulated. Indeed, social exclusion was proven to cause a (small but consistent) impairment in gaze direction discrimination, a key facial feature for social interaction. This finding demonstrates an important interplay between reflective and reflexive systems in the social cognitive neuroscience theoretical framework (Lieberman, 2007), indicating an actual interplay between controlled and automatic processes. Moreover, qualitative differences in processing of faces and bodies were found. A dissociation was found in neural oscillations involved in face- and body-inversion effects, suggesting that different configural processes are involved in the visual encoding of body and face. This result corroborates and expands the literature concerning commonalities and differences between face and body perception (Minnebusch & Daum, 2009; Reed, Stone, Grubb, & McGoldrick, 2006; Soria Bauser, Schriewer, & Suchan, 2015). Emotional expressions and inversion were both shown to affect the encoding of these stimuli, but through independent and non-interacting perceptual processes. Furthermore, we found that emotional expressions, when conveyed by faces or by bodies, were processed by partially dissociable perceptual mechanisms, as demonstrated by different ERP response patterns.

From a theoretical point of view, these findings shed new light on different processes involved in the perception of social stimuli. Future research will be aimed to explore more in depth these processes. For instance, the modulation of body perception by social exclusion is yet to be investigated. Bodily emotional expressions can easily convey to the observer information concerning approach/avoidance behavioural tendencies (as was discussed in Chapter 5), which are strictly related to social inclusion or exclusion. Therefore, assuming the interaction between interrelated automatic and controlled processes, we could expect a modulation of bodily expressions encoding caused by social exclusion, as we saw for gaze direction processing.

Additionally, in the research presented in this thesis, only static pictures of body shapes and bodily emotional expressions were used. The contribution of dynamic information to visual encoding of bodies is crucial (Allison et al., 2000; Kourtzi & Kanwisher, 2000; Puce & Perrett, 2003). Consequently, investigating how dynamic information may contribute to configural processing of body shapes and bodily emotional expressions (by using biological motion displays) would be a fundamental development.

Another possible development of this research is exploring the neural and anatomical bases of the effects found by means of neuroimaging techniques (e.g., fMRI), in order to investigate a potential specific role of a subcortical route (e.g., involving colliculus-pulvinar-amygdala, Adolphs, 2002a, 2002b). Also the use of other face and body effects different from inversion (e.g., the composite effect), aimed to manipulate specific stages of configural processing (holistic processing, in this case) may be useful to underline the differences between face and body processing. As we discussed (Maurer, Le Grand, & Mondloch, 2002; Minnebusch & Daum, 2009; Chapter 3), configural visual processing can be distinguished in different stages, i.e., first-order spatial relations, structural hierarchy, holistic processing and second-order spatial relations. The role of holistic processing (processing a stimulus as a *gestalt* and not as a sum of features) is crucial in face perception, while it is more discussed in body perception (Minnebusch & Daum, 2009). Our findings, together with other recent findings (Soria Bauser, Schriewer, & Suchan, 2015; Soria Bauser & Suchan, 2013), seem to suggest that configural processing of body relies on stages different from holistic processing. However, as stated above, further research involving manipulations specifically affecting holistic processing is needed.

The investigation of face and body visual encoding in clinical (e.g., autism spectrum disorder) or sub-clinical populations (e.g., congenital prosopagnosia), which are specifically impaired in perception of social stimuli, could contribute to a better understanding of specific deficits in face and/or body perception, or a possible general impairment of configural processing, as suggested by some recent findings (Rivolta, Lawson, & Palermo, 2017). At the same time, the investigation of developmental trajectories of these processes in infants could increase our comprehension of the perception of social stimuli.

In conclusion, the research presented in this thesis brought various significant insights in the field of social cognition and social cognitive neuroscience, but there is still a long way to go. Developments of this research are countless and it is exciting to think how much is yet to know about cognition, the way we perceive, interact with, and (sometimes) understand what surrounds us.

References

Adams, R. B., Ambady, N., Macrae, C. N., & Kleck, R. E. (2006). Emotional expressions forecast approach-avoidance behavior. *Motivation and Emotion*, *30*(2), 179–188. https://doi.org/10.1007/s11031-006-9020-2

Adams, R. B. J., & Kleck, R. E. (2005). Effects of Direct and Averted Gaze on the Perception of Facially Communicated Emotion. *Emotion*, *5*(1), 3–11. https://doi.org/10.1037/1528-3542.5.1.3

Adams, R. B., & Kleck, R. E. (2003). Perceived gaze direction and the processing of facial display of emotion. *Psychological Science*, *14*(6), 644–647. https://doi.org/10.1046/j.0956-7976.2003.psci_1479.x

Adams Jr., R. B., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science*, *300*(5625), 1536. https://doi.org/10.1126/science.1082244

Adobe Systems Incorporated (2011). Adobe Photoshop Cs5. *Methods*.

Adolphs, R. (1999). The Human Amygdala and Emotion. *The Neuroscientist*, *5*(2), 125–137. https://doi.org/10.1177/107385849900500216

Adolphs, R. (2002a). Neural systems for recognizing emotion. *Current Opinion in Neurobiology*, *12*(2), 169–177. https://doi.org/10.1016/S0959-4388(02)00301-X

Adolphs, R. (2002b). Recognizing Emotion From Facial Expressions : *Behavioral and Cognitive Neuroscience Reviews*, *1*(1), 21–62. https://doi.org/10.1177/1534582302001001003

Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature Reviews. Neuroscience*, *4*(3), 165–78. https://doi.org/10.1038/nrn1056

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, a R. (2000). A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *The Journal of Neuroscience*, *20*(7), 2683–2690. https://doi.org/123123123

Adolphs, R., Tranel, D., & Damasio, A. R. (2003). Dissociable neural systems for recognizing emotions. *Brain and Cognition*, *52*(1), 61–69. https://doi.org/10.1016/S0278-2626(03)00009-5

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*(6507), 669–672. https://doi.org/10.1038/372669a0

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. R. (1995). Fear and the human amygdala. *Journal of Neuroscience*, *15*, 5879–5891.

Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., … Damasio, A. R. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia*, *37*(10), 1111–1117. https://doi.org/10.1016/S0028-3932(99)00039-1

Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2001). Affective picture processing: Event-related synchronization within individually defined human theta band is modulated by valence dimension. *Neuroscience Letters*, *303*(2), 115–118. https://doi.org/10.1016/S0304-3940(01)01703-7

Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2002). Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *International Journal of Psychophysiology*, *44*(1), 67–82. https://doi.org/10.1016/S0167-8760(01)00194-5

Akechi, H., Senju, A., Kikuchi, Y., Tojo, Y., Osanai, H., & Hasegawa, T. (2010). The effect of gaze direction on the processing of facial expressions in children with autism spectrum disorder: An ERP study. *Neuropsychologia*, *48*(10), 2841–2851. https://doi.org/10.1016/j.neuropsychologia.2010.05.026

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*(7), 267–278. https://doi.org/10.1016/S1364-6613(00)01501-1

Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In *The Amygdala: Neurobiological Aspects of Emotion, Memory, and Mental Dysfunction* (pp. 1–66).

American Psychiatric Association (2013). *DSM 5*. *American Journal of Psychiatry*. https://doi.org/10.1176/appi.books.9780890425596.744053

Anaki, D., Zion-Golumbic, E., & Bentin, S. (2007). Electrophysiological neural mechanisms for detection, configural analysis and recognition of faces. *NeuroImage*, *37*(4), 1407–1416.

https://doi.org/10.1016/j.neuroimage.2007.05.054

Anderson, A. K., & Phelps, E. A. (2000). Expression Without Recognition: Contributions of the Human Amygdala to Emotional Communication. *Psychological Science*, *11*(2), 106–111. https://doi.org/10.1111/1467-9280.00224

Ariga, A., & Arihara, K. (2017). Attentional capture by spatiotemporally task-irrelevant faces: supportive evidence for Sato and Kawahara (2015). *Psychological Research*. https://doi.org/10.1007/s00426-017-0869-3

Arizpe, J. M., Mckean, D. L., Tsao, J. W., & Chan, A. W. (2017). Where You Look Matters for Body Perception : Preferred Gaze Location Contributes to the Body Inversion Effect. *PLoS ONE*, 1–24. https://doi.org/10.7910/DVN/ZSI2D1

Artuso, C., & Palladino, P. (2015). Social updating : The role of gaze direction in updating and memorizing emotional faces. *Social Cognition*, *33*(6), 543–561. https://doi.org/10.1521/soco.2015.33.6.543

Artuso, C., Palladino, P., & Ricciardelli, P. (2012). How do we update faces? Effects of gaze direction and facial expressions on working memory updating. *Frontiers in Psychology*, *3*(SEP), 1–10. https://doi.org/10.3389/fpsyg.2012.00362

Ashley, V., Vuilleumier, P., & Swick, D. (2004). Time course and specificity of event-related potentials to emotional expressions. *Neuroreport*, *15*(1), 211–6. https://doi.org/10.1097/01.wnr.0000091411.19795.f5

Astafiev, S. V, Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, *7*(5), 542–548. https://doi.org/10.1038/nn1241

Baenninger, M. (1994). The development of face recognition: featural or configurational processing? *Journal of Experimental Child Psychology*, *57*, 377–396. https://doi.org/10.1006/jecp.1994.1018

Baron-Cohen, S. (2004). The essential difference.

Baron-cohen, S., & Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger’s syndrome or high functioning autism, and normal sex differences. *J. Autism Dev. Disord.*, *34*(2), 163–175.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013a). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013b). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Barton, K. (2016). MuMIn: Multi-Model Inference.

Basar, E. (2012). Multiple oscillations and phase locking in human gamma responses: an essay in search of eigenvalues. *NeuroQuantology*.

Başar, E. (1999). *Brain function and oscillations: Volume II, Integrative brain function. Neurophysiology and cognitive processes*. *Springer series in synergetics*.

Başar, E., Güntekin, B., & Öniz, A. (2006). Chapter 4 Principles of oscillatory brain dynamics and a treatise of recognition of faces and facial expressions. *Progress in Brain Research*, *159*(6), 43–62. https://doi.org/10.1016/S0079-6123(06)59004-1

Bates, D., Kliegl, R., Vasishth, S., & Baayen, H. (2015). Parsimonious Mixed Models. Retrieved from http://arxiv.org/abs/1506.04967

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R Package Version*.

Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, *17*(3), 613–620. https://doi.org/10.1016/S0926-6410(03)00174-5

Baumeister, R. F., Brewer, L. E., Tice, D. M., & Twenge, J. M. (2007). Thwarting the need to belong: Understanding the interpersonal and inner effects of social exclusion. *Social and Personality Psychology Compass*, *1*(1), 506–520. https://doi.org/doi:10.1111/j.1751-9004.2007.00020.x

Baumeister, R. F., DeWall, C. N., Ciarocco, N. J., & Twenge, J. M. (2005). Social Exclusion Impairs Self-Regulation. *Journal of Personality and Social Psychology*, *88*(4), 589–604. https://doi.org/10.1037/0022-3514.88.4.589

Baumeister, R. F., & Leary, M. R. (1995). the Need To Belong - Desire for Interpersonal Attachments As a Fundamental Human-Motivation. *Psychological Bulletin*, *117*(3), 497–529.

https://doi.org/0033-2909

Baumeister, R. F., Twenge, J. M., & Nuss, C. K. (2002). Effects of social exclusion on cognitive processes: anticipated aloneness reduces intelligent thought. *Journal of Personality and Social Psychology*, *83*(4), 817–27. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12374437

Becchio, C., Sartori, L., & Castiello, U. (2010). Toward You: The Social Side of Actions. *Current Directions in Psychological Science*, *19*(3), 183–188. https://doi.org/10.1177/0963721410370131

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of Face Perception in Humans. *Journal of Cognitive Neuroscience*, *8*(6), 551–565. https://doi.org/10.1162/jocn.1996.8.6.551

Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: evidence from developmental prosopagnosia. *Neuroreport*, *10*(4), 823–7. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10208555

Bernstein, M. J., Young, S. G., Brown, C. M., Sacco, D. F., & Claypool, H. M. (2008). Adaptive responses to social exclusion: Social rejection improves detection of real and fake smiles. *Psychological Science*, *19*(10), 981–983. https://doi.org/10.1111/j.1467-9280.2008.02187.x

Biotti, F., Gray, K. L. H., & Cook, R. (2017). Impaired body perception in developmental prosopagnosia. *Cortex*, *93*, 41–49. https://doi.org/10.1016/j.cortex.2017.05.006

Blair, R. J. R., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain*, *122*(5), 883–893. https://doi.org/10.1093/brain/122.5.883

Bodamer, J. (1947). Die Prosop-Agnosie - Die Agnosie des Physiognomieerkennens. *Archiv Für Psychiatrie Und Nervenkrankheiten Vereinigt Mit Zeitschrift Für Die Gesamte Neurologie Und Psychiatrie*, *179*(1–2), 6–53. https://doi.org/10.1007/BF00352849

Bonemei, R., Costantino, A. I., Battistel, I., & Rivolta, D. (2017a). The perception of (naked only) bodies and faceless heads relies on holistic processing: Evidence from the inversion effect. *British Journal of Psychology*, 1–12. https://doi.org/10.1111/bjop.12271

Bonemei, R., Costantino, A. I., Battistel, I., & Rivolta, D. (2017b). The perception of (naked only) bodies and faceless heads relies on holistic processing: Evidence from the inversion effect.

British Journal of Psychology. https://doi.org/10.1111/bjop.12271

Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2009). *Introduction to Meta Analysis*. UK: Wiley. https://doi.org/10.1007/BF03342659

Brandman, T., & Yovel, G. (2010). The Body Inversion Effect Is Mediated by Face-Selective, Not Body-Selective, Mechanisms. *Journal of Neuroscience*, *30*(31), 10534–10540. https://doi.org/10.1523/JNEUROSCI.0911-10.2010

Brandman, T., & Yovel, G. (2012). A face inversion effect without a face. *Cognition*, *125*(3), 365–372. https://doi.org/10.1016/j.cognition.2012.08.001

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.2044-8295.1986.tb02199.x/full

Bruyer, R., Laterre, C., Seron, X., Feyereisen, P., Strypstein, E., Pierrard, E., & Rectem, D. (1983). A case of prosopagnosia with some preserved covert remembrance of familiar faces. *Brain and Cognition*, *2*(3), 257–284. https://doi.org/10.1016/0278-2626(83)90014-3

Burton, A. M., Bruce, V., & Johnston, R. A. (1990). Understanding face recognition with an interactive activation model. *British Journal of Psychology*. https://doi.org/10.1111/j.2044-8295.1990.tb02367.x

Calder, A. J. (1996). Facial Emotion Recognition after Bilateral Amygdala Damage: Differentially Severe Impairment of Fear. *Cognitive Neuropsychology*, *13*(5), 699–745. https://doi.org/10.1080/026432996381890

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience*, *3*(11), 1077–1078. https://doi.org/10.1038/80586

Calder, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience*. https://doi.org/10.1038/35072584

Carey, S., Schonen, S. D., & Ellis, H. D. (1992). Becoming a Face Expert. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *335*(1273), 95–103. https://doi.org/10.1098/rstb.1992.0012

Carlston, D. E. (Ed.). (2013). *The Oxford handbook of social cognition*. Oxford University Press.

Carraro, L., Dalmaso, M., Castelli, L., Galfano, G., Bobbio, A., & Mantovani, G. (2016). The appeal of the devil’s eye: social evaluation affects social attention. *Cognitive Processing*, (November). https://doi.org/10.1007/s10339-016-0785-2

Carter-Sowell, A. R., Chen, Z., & Williams, K. D. (2008). Ostracism increases social susceptibility. *Social Influence*, *3*(3), 143–153. https://doi.org/10.1080/15534510802204868

Champely, S. (2016). pwr: Basic Functions for Power Analysis.

Chow, R. M., Tiedens, L. Z., & Govan, C. L. (2008). Excluded emotions: The role of anger in antisocial responses to ostracism. *Journal of Experimental Social Psychology*, *44*(3), 896–903. https://doi.org/10.1016/j.jesp.2007.09.004

Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences*.

Cohen, J., Cohen, P., West, S., & Aiken, L. (2013). *Applied multiple regression/correlation analysis for the behavioral sciences* (3rd ed.). Routledge.

Cohen, M. X., Donner, T. H., Akam, T., Kullmann, D., Botvinick, M., Braver, T., … Cohen, J. (2013). Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *Journal of Neurophysiology*, *110*(12), 2752–63. https://doi.org/10.1152/jn.00479.2013

Collishaw, S. M., & Hole, G. J. (2000). Featural and configurational processes in the recognition of faces of different familiarity. *Perception*, *29*(8), 893–909. https://doi.org/10.1068/p2949

Cook, R., & Duchaine, B. (2011). A look at how we look at others: Orientation inversion and photographic negation disrupt the perception of human bodies. *Visual Cognition*, *19*(4), 445–468. https://doi.org/10.1080/13506285.2010.541892

Corbetta, M., Kincade, J. M., & Shulman, G. L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. *Journal of Cognitive Neuroscience*, *14*(3), 508–523. https://doi.org/10.1162/089892902317362029

Costall, A. (1995). Socializing Affordances. *Theory & Psychology*, *5*(4), 467–481. https://doi.org/10.1177/0959354395054001

Cox, D., Meyers, E., & Sinha, P. (2004). Contextually Evoked Object-Specific Responses in Human Visual Cortex. *Science*, *304*(April), 115–117. https://doi.org/10.1126/science.1093110

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., … Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: a functional magnetic resonance imaging study. *Human Brain Mapping*, *9*(2), 93–105. https://doi.org/10.1002/(SICI)1097-0193(200002)

Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L., Parvizi, J., & Hichwa, R. D. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, *3*(10), 1049–56. https://doi.org/10.1038/79871

David, O., Kilner, J. M., & Friston, K. J. (2006). Mechanisms of evoked and induced responses in MEG/EEG. *NeuroImage*, *31*(4), 1580–1591. https://doi.org/10.1016/j.neuroimage.2006.02.034

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nat Rev Neurosci*, *7*(3), 242–249. https://doi.org/10.1038/nrn1872

de Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1535), 3475–3484. https://doi.org/10.1098/rstb.2009.0190

de Gelder, B., de Borst, A. W., & Watson, R. (2015). The perception of emotion in body expressions. *Wiley Interdisciplinary Reviews: Cognitive Science*, *6*(2), 149–158. https://doi.org/10.1002/wcs.1335

de Gelder, B., & Van den Stock, J. (2011). The bodily expressive action stimulus test (BEAST). Construction and validation of a stimulus basis for measuring perception of whole body expression of emotions. *Frontiers in Psychology*, *2*(AUG). https://doi.org/10.3389/fpsyg.2011.00181

de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport*, *10*(18), 3759–3763. https://doi.org/10.1097/00001756-199912160-00007

De Jaegher, H. (2009). Social understanding through direct perception? Yes, by interacting. *Consciousness and Cognition*, *18*(2), 535–542. https://doi.org/10.1016/j.concog.2008.10.007

Del Re, A. C. (2013). Package “compute. es”: Compute effect sizes. *R Package Version*.

Delorme, A., & Makeig, S. (2004). Eeglab. *Journal of Neuroscience Methods*, *134*, 9–21.

Devine, P. G., Hamilton, D. L., & Ostrom, T. M. (Eds.). (1994). *Social cognition: Impact on social* *psychology* (Academic Press). San Diego, CA. Retrieved from http://psycnet.apa.org/record/1994-97895-000

DeWall, C. N., & Baumeister, R. F. (2006). Alone but Feeling No Pain: Effects of Social Exclusion on Physical Pain Tolerance and Pain Threshold, Affective Forecasting, and Interpersonal Empathy. *Journal of Personality and Social Psychology*, *91*(1), 1–15. https://doi.org/10.1037/0022-3514.91.1.1

DeWall, C. N., Maner, J. K., & Rouby, D. A. (2009). Social exclusion and early-stage interpersonal perception: Selective attention to signs of acceptance. *Journal of Personality and Social Psychology*, *96*(4), 729–741. https://doi.org/10.1037/a0014634

DeWall, C. N., Twenge, J. M., Koole, S. L., Baumeister, R. F., Marquez, A., & Reid, M. W. (2011). Automatic emotion regulation after social exclusion: Tuning to positivity. *Emotion*, *11*(3), 623–636. https://doi.org/10.1037/a0023534

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*(2), 107–117. https://doi.org/10.1037/0096-3445.115.2.107

Di Paolo, E., & De Jaegher, H. (2012). The interactive brain hypothesis. *Frontiers in Human Neuroscience*, *6*(June), 1–16. https://doi.org/10.3389/fnhum.2012.00163

Dien, J. (1998). Issues in the application of the average reference: Review, critiques, and recommendations. *Behavior Research Methods, Instruments, & Computers*, *30*(1), 34–43. https://doi.org/10.3758/BF03209414

Dobel, C., Junghöfer, M., & Gruber, T. (2011). The role of gamma-band activity in the representation of faces: Reduced activity in the fusiform face area in congenital prosopagnosia. *PLoS ONE*, *6*(5). https://doi.org/10.1371/journal.pone.0019550

Donnelly, N., Humphreys, G. W., & Sawyer, J. (1994). Stimulus factors affecting the categorisation of faces and scrambled faces. *Acta Psychologica*, *85*(3), 219–234. https://doi.org/10.1016/0001-6918(94)90036-1

Donner, T. H., & Siegel, M. (2011). A framework for local cortical oscillation patterns. *Trends in Cognitive Sciences*, *15*(5), 191–199. https://doi.org/10.1016/j.tics.2011.03.007

Downing, P. E., Chan, W.-Y., Peelen, M. V, Dodds, C. M., & Kanwisher, N. (2006). Domain

Specificity in Visual Cortex. *Cerebral Cortex*, *16*(10), 1453–1461. https://doi.org/10.1093/cercor/bhj086

Downing, P. E., Jiang, Y., m. Shuman, & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470–2473.

Downing, P. E., & Peelen, M. V. (2016). Body selectivity in occipitotemporal cortex: Causal evidence. *Neuropsychologia*, *83*, 138–148. https://doi.org/10.1016/j.neuropsychologia.2015.05.033

Downing, P. E., Wiggett, A. J., & Peelen, M. V. (2007). Functional Magnetic Resonance Imaging Investigation of Overlapping Lateral Occipitotemporal Activations Using Multi-Voxel Pattern Analysis. *Journal of Neuroscience*, *27*(1), 226–233. https://doi.org/10.1523/JNEUROSCI.3619-06.2007

Draine, S. (2014). Inquisit 4. Seattle: Millisecond Software.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze Perception Triggers Reflexive Visuospatial Orienting. *Visual Cognition*, *6*(5), 509–540. https://doi.org/10.1080/135062899394920

Duval, S., & Tweedie, R. (2000a). A Nonparametric “Trim and Fill” Method of Accounting for Publication Bias in Meta-Analysis. *Journal of the American Statistical Association*, *95*(449), 89–98. https://doi.org/10.1080/01621459.2000.10473905

Duval, S., & Tweedie, R. (2000b). Trim and Fill: A Simple Funnel-Plot-Based Method of Testing and Adjusting for Publication Bias in Meta-Analysis. *Biometrics*, *56*(2), 455–463. https://doi.org/10.1111/j.0006-341X.2000.00455.x

Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces - Evidence from event-related brain potentials. *Cognitive Brain Research*, *10*(1–2), 145–158. https://doi.org/10.1016/S0926-6410(00)00038-0

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, *13*(4), 427–431. https://doi.org/10.1097/00001756-200203250-00013

Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, *45*(1), 15–31. https://doi.org/10.1016/j.neuropsychologia.2006.04.022

Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cogn Affect Behav Neurosci*, *3*(2), 97–110. https://doi.org/10.3758/CABN.3.2.97

Eisenberger, N. I. (2015). Social Pain and the Brain: Controversies, Questions, and Where to Go from Here. *Annual Review of Psychology*, *66*(1), 601–629. https://doi.org/10.1146/annurev-psych-010213-115146

Eisenberger, N. I., & Cole, S. W. (2012). Social neuroscience and health: neurophysiological mechanisms linking social ties with physical health. *Nature Neuroscience*, *15*(5), 669–74. https://doi.org/10.1038/nn.3086

Eisenberger, N. I., Jarcho, J. M., Lieberman, M. D., & Naliboff, B. D. (2006). An experimental study of shared sensitivity to physical pain and social rejection. *Pain*, *126*(1–3), 132–138. https://doi.org/10.1016/j.pain.2006.06.024

Eisenberger, N. I., & Lieberman, M. D. (2004). Why rejection hurts: A common neural alarm system for physical and social pain. *Trends in Cognitive Sciences*, *8*(7), 294–300. https://doi.org/10.1016/j.tics.2004.05.010

Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does Rejection Hurt? An fMRI Study of Social Exclusion. *Science*, *290*(2003), 290–292. https://doi.org/10.1126/science.1089134

Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology*, *17*(2), 124–129. https://doi.org/10.1037/h0030377

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect* (CA: Consul). Palo Alto.

Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. *Cerebral Cortex*, *17*(10), 2400–2406. https://doi.org/10.1093/cercor/bhl148

Farah, M. J. (1991). Patterns of co-occurrence among the associative agnosias: Implications for visual object representation. *Cognitive Neuropsychology*, *8*(1), 1–19. https://doi.org/10.1080/02643299108253364

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology. Human Perception and Performance*, *21*(3), 628–634. https://doi.org/10.1037/0096-1523.21.3.628

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., … Van Ijzendoorn, M. H. (2016). Assessing Human Mirror Activity With EEG Mu Rhythm: A Meta-Analysis. *Psychological Bulletin, 142*(3), 291–313. https://doi.org/10.1037/bul0000031

Frijda, N. (1986). The emotions: Studies in emotion and social interaction. *Paris: Maison de Sciences de l'Homme*.

Frischen, A., Bayliss, A. P., & Tipper, S. P. (2007). Gaze cueing of attention: Visual attention, social cognition, and individual differences. *Psychological Bulletin*, *133*(4), 694–724. https://doi.org/10.1037/0033-2909.133.4.694

Frith, C. D., & Frith, U. (2008). Implicit and Explicit Processes in Social Cognition. *Neuron, 60*(3), 503–510. https://doi.org/10.1016/j.neuron.2008.10.032

Frith, U., & Frith, C. (2010). The social brain: allowing humans to boldly go where no other species has been. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1537), 165–176. https://doi.org/10.1098/rstb.2009.0160

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., … Politi, P. (2009). Functional atlas of emotional faces processing: A voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry and Neuroscience*, *34*(6), 418–432. https://doi.org/10.1016/S1180-4882(09)50077-7

Gallese, V. (2003). The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology*. https://doi.org/10.1159/000072786

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*(9), 396–403. https://doi.org/10.1016/j.tics.2004.07.002

Gao, Z., Goldstein, A., Harpaz, Y., Hansel, M., Zion-Golumbic, E., & Bentin, S. (2012). A magnetoencephalographic study of face processing: M170, gamma-band oscillations and source localization. *Human Brain Mapping, 34*(8), 1783–1795. https://doi.org/10.1002/hbm.22028

Gardner, W. L., Pickett, C. L., & Brewer, M. B. (2000). Social Exclusion and Selective Memory: How the Need to belong Influences Memory for Social Events. *Personality and Social Psychology Bulletin*, *26*(4), 486–496. https://doi.org/10.1177/0146167200266007

Gauthier, I., & Bukach, C. (2007). Should we reject the expertise hypothesis? *Cognition*, *103*(2), 322–330. https://doi.org/10.1016/j.cognition.2006.05.003

Gauthier, I., & Tarr, M. J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(2), 431–446. https://doi.org/10.1037//0096-1523.28.2.431

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The Fusiform “Face Area” is Part of a Network that Processes Faces at the Individual Level. *Journal of Cognitive Neuroscience*, *12*(3), 495–504. https://doi.org/10.1162/089892900562165

Gauthier, Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform “face area” increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*(6), 568–73. https://doi.org/10.1038/9224

Gliga, T., & Dehaene-Lambertz, G. (2005). Structural encoding of body and face in human infants and adults. *Journal of Cognitive Neuroscience*, *17*, 1328–1340. https://doi.org/10.1162/0898929055002481

Gonsalkorale, K., & Williams, K. D. (2007). The KKK won’t let me play: ostracism even by a despised outgroup hurts. *European Journal of Social Psychology*, *37*(6), 1176–1186. https://doi.org/10.1002/ejsp.392

Gorno-Tempini, M. L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., … Nichelli, P. (2001). Explicit and Incidental Facial Expression Processing: An fMRI Study. *NeuroImage*, *14*(2), 465–473. https://doi.org/10.1006/nimg.2001.0811

Grandchamp, R., & Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology*, *2*(SEP), 1–14. https://doi.org/10.3389/fpsyg.2011.00236

Grèzes, J., Pichon, S., & de Gelder, B. (2007). Perceiving fear in dynamic body expressions. *NeuroImage*, *35*(2), 959–967. https://doi.org/10.1016/j.neuroimage.2006.11.030

Güntekin, B., & Başar, E. (2009). Facial affect manifested by multiple oscillations. *International Journal of Psychophysiology*, *71*(1), 31–36. https://doi.org/10.1016/j.ijpsycho.2008.07.019

Güntekin, B., & Başar, E. (2014). A review of brain oscillations in perception of faces and emotional pictures. *Neuropsychologia*, *58*(1), 33–51.

https://doi.org/10.1016/j.neuropsychologia.2014.03.014

Hadjikhani, N., & De Gelder, B. (2003). Seeing Fearful Body Expressions Activates the Fusiform Cortex and Amygdala. *Current Biology*, *13*(24), 2201–2205. https://doi.org/10.1016/j.cub.2003.11.049

Happé, F., & Frith, U. (2006). The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, *36*(1), 5–25. https://doi.org/10.1007/s10803-005-0039-0

Hariri, A. R., Bookheimer, S. Y., & Mazziotta, J. C. (2000). Modulating emotional responses: effects of a neocortical network on the limbic system. *Neuroreport*, *11*(1), 43–48. https://doi.org/10.1097/00001756-200001170-00009

Harris, A. M., Dux, P. E., Jones, C. N., & Mattingley, J. B. (2017). Distinct roles of theta and alpha oscillations in the involuntary capture of goal-directed attention. *NeuroImage*, *152*(October 2016), 171–183. https://doi.org/10.1016/j.neuroimage.2017.03.008

Hartgerink, C. H. J., van Beest, I., Wicherts, J. M., & Williams, K. D. (2015). The ordinal effects of ostracism: a meta-analysis of 120 Cyberball studies. *PloS One*, *10*(5), e0127002. https://doi.org/10.1371/journal.pone.0127002

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233. https://doi.org/10.1016/S1364-6613(00)01482-0

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, *51*(1), 59–67. https://doi.org/10.1016/S0006-3223(01)01330-0

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*(1), 189–199. https://doi.org/10.1016/S0896-6273(00)80690-X

Heider, F., & Simmel, M. (1944). An experimental study of apparent behaviour. *The American Journal of Psychology*, *57*(2), 243–259. https://doi.org/10.2307/1416950

Herrmann, C., Rach, S., Vosskuhl, J., & Strüber, D. (2014). Time–frequency analysis of event-related potentials: a brief tutorial. *Brain Topography*. Retrieved from http://link.springer.com/article/10.1007/s10548-013-0327-5

Herrmann, M. J., Ehlis, A.-C., Muehlberger, A., & Fallgatter, A. J. (2005). Source Localization of Early Stages of Face Processing. *Brain Topography*, *18*(2), 77–85. https://doi.org/10.1007/s10548-005-0277-7

Hietanen, J. K., & Nummenmaa, L. (2011). The naked truth: The face and body sensitive N170 response is enhanced for nude bodies. *PLoS ONE*, *6*(11), 25–27. https://doi.org/10.1371/journal.pone.0024408

Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience and Biobehavioral Reviews*, *55*, 498–509. https://doi.org/10.1016/j.neubiorev.2015.06.002

Hodzic, A., Kaas, A., Muckli, L., Stirn, A., & Singer, W. (2009). Distinct cortical networks for the detection and identification of human body. *NeuroImage*, *45*(4), 1264–1271. https://doi.org/10.1016/j.neuroimage.2009.01.027

Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. *Human Brain Mapping*, *30*(3), 951–962. https://doi.org/10.1002/hbm.20558

Hornak, J., Rolls, E. T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia*, *34*(4), 247–261. https://doi.org/10.1016/0028-3932(95)00106-9

Iacoboni, M. (2009). Imitation, Empathy, and Mirror Neurons. *Annual Review of Psychology*, *60*(1), 653–670. https://doi.org/10.1146/annurev.psych.60.110707.163604

Itier, R. J., Alain, C., Sedore, K., & McIntosh, A. R. (2007). Early Face Processing Specificity: It’s in the Eyes! *Journal of Cognitive Neuroscience*, *19*(11), 1815–1826. https://doi.org/10.1162/jocn.2007.19.11.1815

Itier, R. J., & Taylor, M. J. (2004). Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *NeuroImage*, *21*(4), 1518–1532. https://doi.org/10.1016/j.neuroimage.2003.12.016

Jacques, C., & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, *36*(3), 863–876. https://doi.org/10.1016/j.neuroimage.2007.04.016

Jamieson, J. P., Harkins, S. G., & Williams, K. D. (2010). Need Threat Can Motivate Performance After Ostracism. *Personality and Social Psychology Bulletin*, *36*(5), 690–702. https://doi.org/10.1177/0146167209358882

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *17*(11), 4302–11. https://doi.org/10.1098/Rstb.2006.1934

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2109–2128. https://doi.org/10.1098/rstb.2006.1934

Kawasaki, H., Adolphs, R., Kaufman, O., Damasio, H., Damasio, A. R., Granner, M., … Howard, M. A. (2001). Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nature Neuroscience*, *4*(1), 15–16. https://doi.org/10.1038/82850

Kennerknecht, I., Grueter, T., Welling, B., Wentzek, S., Horst, J., Edwards, S., & Grueter, M. (2006). First report of prevalence of non-syndromic hereditary prosopagnosia (HPA). *American Journal of Medical Genetics, Part A*, *140*(15), 1617–1622. https://doi.org/10.1002/ajmg.a.31343

Kesler-West, M. L., Andersen, A. H., Smith, C. D., Avison, M. J., Davis, C. E., Kryscio, R. J., & Blonder, L. X. (2001). Neural substrates of facial emotion processing using fMRI. *Cognitive Brain Research*, *11*(2), 213–226. https://doi.org/10.1016/S0926-6410(00)00073-2

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*(2–3), 169–195. https://doi.org/10.1016/S0165-0173(98)00056-3

Klucharev, V., & Sams, M. (2004). Interaction of gaze direction and facial expressions processing: ERP study. *Neuroreport*, *15*(4), 621–625. https://doi.org/10.1097/00001756-200403220-00010

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 48–55. https://doi.org/10.1162/08989290051137594

Krolak-Salmon, P., Fischer, C., Vighetto, A., & Mauguiere, F. (2001). Processing of facial emotion expression: Spatio-temporal data as assessed by scalp event-related potentials. *European*

Journal of Neuroscience, *13*, 987–994. https://doi.org/10.1046/j.0953-816X.2001.01454.x

Kurucz, J., & Feldmar, G. (1979). Prosopo-Affective Agnosia Associated with Chronic Organic Brain Syndrome. *Journal of the American Geriatrics Society*, *27*(5), 225–230. https://doi.org/10.1111/j.1532-5415.1979.tb03347.x

Kuznetsova, A., Brockhoff, P., & Christensen, R. (2015). Package "lmerTest." *R Package Version*. Retrieved from http://cran.uib.no/web/packages/lmerTest/lmerTest.pdf

Lachaux, J. P., George, N., Tallon-Baudry, C., Martinerie, J., Hugueville, L., Minotti, L., … Renault, B. (2005). The many faces of the gamma band response to complex visual stimuli. *NeuroImage*, *25*(2), 491–501. https://doi.org/10.1016/j.neuroimage.2004.11.052

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. *Frontiers in Psychology*, *4*(NOV), 1–12. https://doi.org/10.3389/fpsyg.2013.00863

Lane, R. D., Fink, G. R., Chau, P. M., & Dolan, R. J. (1997). Neural activation during selective attention to subjective emotional responses. *Neuroreport*, *8*(18), 3969–3972. https://doi.org/10.1097/00001756-199712220-00024

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D. H. J., Hawk, S. T., & van Knippenberg, A. (2010). Presentation and validation of the Radboud Faces Database. *Cognition & Emotion*, *24*(8), 1377–1388. https://doi.org/10.1080/02699930903485076

Langton, S. R. H., Law, A. S., Burton, A. M., & Schweinberger, S. R. (2008). Attention capture by faces. *Cognition*, *107*(1), 330–342. https://doi.org/10.1016/j.cognition.2007.07.012

Lazarus, R. S. (1991). Progress on a cognitive-motivational-relational theory of emotion. *American Psychologist*, *46*(8), 819–834. https://doi.org/10.1037/0003-066X.46.8.819

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature*, *410*(April), 890. https://doi.org/10.1016/j.echo.2007.08.009

Lenth, R. (2016). Least-squares means: the R Package lsmeans. *J Stat Softw*. Retrieved from https://www.jstatsoft.org/article/view/v069i01/v69i01.pdf

Leppänen, J. M., Kauppinen, P., Peltola, M. J., & Hietanen, J. K. (2007). Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions. *Brain Research*, *1166*(1), 103–109. https://doi.org/10.1016/j.brainres.2007.06.060

Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP Study of Emotional Face Processing in the Adult and Infant Brain. *Child Development*, *78*(1), 232–245. https://doi.org/10.1111/j.1467-8624.2007.00994.x

Lieberman, M. D. (2007). Social Cognitive Neuroscience: A Review of Core Processes. *Annual Review of Psychology*, *58*(1), 259–289. https://doi.org/10.1146/annurev.psych.58.110405.085654

Lieberman, M. D., Gaunt, R., Gilbert, D. T., & Trope, Y. (2002). Reflexion and reflection: A social cognitive neuroscience approach to attributional inference, *34*, 199–249. https://doi.org/10.1016/S0065-2601(02)80006-5

Lipp, O. V., Price, S. M., & Tellegen, C. L. (2009). Emotional faces in neutral crowds: Detecting displays of anger, happiness, and sadness on schematic and photographic images of faces. *Motivation and Emotion*, *33*(3), 249–260. https://doi.org/10.1007/s11031-009-9136-2

Luck, S. J., & Kappenman, E. S. (Eds.). (2011). *The Oxford handbook of event-related potential components* (Oxford Uni).

Lückmann, H. C., Jacobs, H. I. L., & Sack, A. T. (2014). The cross-functional role of frontoparietal regions in cognition: Internal attention as the overarching mechanism. *Progress in Neurobiology*, *116*, 66–86. https://doi.org/10.1016/j.pneurobio.2014.02.002

Lyyra, P., Wirth, J. H., & Hietanen, J. K. (2017). Are you looking my way? Ostracism widens the cone of gaze. *The Quarterly Journal of Experimental Psychology*, *70*(8), 1713–1721. https://doi.org/10.1080/17470218.2016.1204327

Macdonald, G., & Leary, M. R. (2005). Why does social exclusion hurt? The relationship between social and physical pain. *Psychol Bull*, *131*(2), 202–223. https://doi.org/10.1037/0033-2909.131.2.202

Maner, J. K., DeWall, C. N., Baumeister, R. F., & Schaller, M. (2007). Does social exclusion motivate interpersonal reconnection? Resolving the “porcupine problem”. *Journal of Personality and Social Psychology*, *92*(1), 42–55. https://doi.org/10.1037/0022-3514.92.1.42

Maris, E. (2012). Statistical testing in electrophysiological studies. *Psychophysiology*, *49*(4), 549–565. https://doi.org/10.1111/j.1469-8986.2011.01320.x

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data.

Journal of Neuroscience Methods, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Marr, D. (1982). Vision.

Marsh, K. L., Richardson, M. J., & Schmidt, R. C. (2009). Social Connection Through Joint Action and Interpersonal Coordination. *Topics in Cognitive Science*, *1*(2), 320–339. https://doi.org/10.1111/j.1756-8765.2009.01022.x

Matsuzaki, N., Schwarzlose, R. F., Nishida, M., Ofen, N., & Asano, E. (2015). Upright face-preferential high-gamma responses in lower-order visual areas: Evidence from intracranial recordings in children. *NeuroImage*, *109*, 249–259. https://doi.org/10.1016/j.neuroimage.2015.01.015

Maurage, P., Joassin, F., Philippot, P., Heeren, A., Vermeulen, N., Mahau, P., … de Timary, P. (2012). Disrupted Regulation of Social Exclusion in Alcohol-Dependence: An fMRI Study. *Neuropsychopharmacology*, *37*(9), 2067–2075. https://doi.org/10.1038/npp.2012.54

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*(6), 255–260. https://doi.org/10.1016/S1364-6613(02)01903-4

McKone, E., & Robbins, R. (2007). The evidence rejects the expertise hypothesis: Reply to Gauthier & Bukach. *Cognition*, *103*(2), 331–336. https://doi.org/10.1016/j.cognition.2006.05.014

McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychonomic Bulletin & Review*, *16*(5), 778–797. https://doi.org/10.3758/PBR.16.5.778

Meeren, H. K. M., Hadjikhani, N., Ahlfors, S. P., Hämäläinen, M. S., & de Gelder, B. (2016). Early Preferential Responses to Fear Stimuli in Human Right Dorsal Visual Stream - A Meg Study. *Scientific Reports*, *6*(April), 24831. https://doi.org/10.1038/srep24831

Miller, R. (1991). *Cortico-Hippocampal Interplay and the Representation of Contexts in the Brain*. *Studies of Brain Function* (Vol. 17). https://doi.org/10.1007/978-3-662-21732-0

Minnebusch, D. A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. *Neuroscience and Biobehavioral Reviews*, *33*(7), 1133–1144.

https://doi.org/10.1016/j.neubiorev.2009.05.008

Minnebusch, D. A., Keune, P. M., Suchan, B., & Daum, I. (2010). Gradual inversion affects the processing of human body shapes. *NeuroImage*, *49*(3), 2746–2755. https://doi.org/10.1016/j.neuroimage.2009.10.046

Minnebusch, D. A., Suchan, B., & Daum, I. (2009). Losing your head: behavioral and electrophysiological effects of body inversion. *Journal of Cognitive Neuroscience*, *21*(5), 865–74. https://doi.org/10.1162/jocn.2009.21074

Mohamed, T. N., Neumann, M. F., & Schweinberger, S. R. (2011). Combined effects of attention and inversion on event-related potentials to human bodies and faces. *Cognitive Neuroscience*, *2*(3–4), 138–146. https://doi.org/10.1080/17588928.2011.597848

Moratti, S., M??ndez-B??rtolo, C., Del-Pozo, F., & Strange, B. A. (2014). Dynamic gamma frequency feedback coupling between higher and lower order visual cortices underlies perceptual completion in humans. *NeuroImage*, *86*, 470–479. https://doi.org/10.1016/j.neuroimage.2013.10.037

Moro, V., Pernigo, S., Avesani, R., Bulgarelli, C., Urgesi, C., Candidi, M., & Aglioti, S. M. (2012). Visual body recognition in a prosopagnosic patient. *Neuropsychologia*, *50*(1), 104–117. https://doi.org/10.1016/j.neuropsychologia.2011.11.004

Moro, V., Urgesi, C., Pernigo, S., Lanteri, P., Pazzaglia, M., & Aglioti, S. M. (2008). The Neural Basis of Body Form and Body Action Agnosia. *Neuron*, *60*(2), 235–246. https://doi.org/10.1016/j.neuron.2008.09.022

Morris, J. P., Pelphrey, K. A., & McCarthy, G. (2006). Occipitotemporal activation evoked by the perception of human bodies is modulated by the presence or absence of the face. *Neuropsychologia*, *44*(10), 1919–1927. https://doi.org/10.1016/j.neuropsychologia.2006.01.035

Morris, J. S., de Gelder, B., Weiskrantz, L., & Dolan, R. J. (2001). Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*, *124*(6), 1241–1252. https://doi.org/10.1093/brain/124.6.1241

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, *383*(6603), 812–815. https://doi.org/10.1038/383812a0

Morris, J. S., Ohman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, *393*(6684), 467–470. https://doi.org/10.1038/30976

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating “unseen” fear. *Proceedings of the National Academy of Sciences*, *96*(4), 1680–1685. https://doi.org/10.1073/pnas.96.4.1680

Mullen, B. (1989). *Advanced basic meta-analysis: Version 1.10* (Psychology). Hillsdale, NJ: Erlbaum.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/DOI 10.1111/j.2041-210x.2012.00261.x

Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., … Kojima, S. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neurophysiology*, *82*(3), 1610–1614.

Narumoto, J., Yamada, H., Iidaka, T., Sadato, N., Fukui, K., Itoh, H., & Yonekura, Y. (2000). Brain regions involved in verbal or non-verbal aspects of facial emotion recognition. *Neuroreport*, *11*(11), 2571–2576. https://doi.org/10.1097/00001756-200008030-00044

Negrini, M., Brkic, D., Pizzamiglio, S., Premoli, I., & Rivolta, D. (2017). Neurophysiological correlates of featural and spacing processing for face and non-face stimuli. *Frontiers in Psychology*, *8*(MAR). https://doi.org/10.3389/fpsyg.2017.00333

Nemrodov, D., & Itier, R. J. (2011). The role of eyes in early face processing: A rapid adaptation study of the inversion effect. *British Journal of Psychology*, *102*(4), 783–798. https://doi.org/10.1111/j.2044-8295.2011.02033.x

Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2004.01.004

Nummenmaa, L., & Calder, A. J. (2009). Neural mechanisms of social attention. *Trends in Cognitive Sciences*, *13*(3), 135–143. https://doi.org/10.1016/j.tics.2008.12.006

O’Toole, A. J., Roark, D. A., & Abdi, H. (2002). Recognizing moving faces: A psychological and neural synthesis. *Trends in Cognitive Sciences*, *6*(6), 261–266. https://doi.org/10.1016/S1364-6613(02)01908-3

Ochsner, K. N., & Lieberman, M. D. (2001). The Emergence of Social Cognitive Neuroscience. *American Psychologist*. https://doi.org/10.1037//0003-066X.56.9.717

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*. https://doi.org/10.1155/2011/156869

Otten, M., & Jonas, K. J. (2013). Out of the group, out of control? The brain responds to social exclusion with changes in cognitive control. *Social Cognitive and Affective Neuroscience*, *8*(7), 789–794. https://doi.org/10.1093/scan/nss071

Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia*, *49*(5), 1226–1235. https://doi.org/10.1016/j.neuropsychologia.2011.02.021

Paulus, A., & Wentura, D. (2015). It Depends: Approach and Avoidance Reactions to Emotional Expressions are Influenced by the Contrast Emotions Presented in the Task. *Journal of Experimental Psychology. Human Perception and Performance*, *41*(5), 1–16. https://doi.org/10.1037/xhp0000130

Pavlova, M. A. (2016). Sex and gender affect the social brain: Beyond simplicity. *Journal of Neuroscience Research*, *0*. https://doi.org/10.1002/jnr.23871

Peelen, M. V., & Downing, P. E. (2007a). Using multi-voxel pattern analysis of fMRI data to interpret overlapping functional activations. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2006.10.009

Peelen, M. V., & Downing, P. E. (2017). Category selectivity in human visual cortex: Beyond visual object recognition. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2017.03.033

Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, *49*(6), 815–822. https://doi.org/10.1016/j.neuron.2006.02.004

Peelen, M. V, & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, *93*(1), 603–8. https://doi.org/10.1152/jn.00513.2004

Peelen, M. V, & Downing, P. E. (2007b). The neural basis of visual body perception. *Nature*

Reviews. Neuroscience, *8*(8), 636–48. https://doi.org/10.1038/nrn2195

Phillips, M. L., Bullmore, E. T., Howard, R., Woodruff, P. W. R., Wright, I. C., Williams, S. C. R., … David, A. S. (1998). Investigation of facial recognition memory and happy and sad facial expression perception: An fMRI study. *Psychiatry Research - Neuroimaging*, *83*(3), 127–138. https://doi.org/10.1016/S0925-4927(98)00036-5

Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., … Gray, J. A. (1998). Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1408), 1809–1817. https://doi.org/10.1098/rspb.1998.0506

Phillips, M. L., Young, a. W., Senior, C., Brammer, M., Andrew, C., Calder, a. J., … David, a. S. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature*, *389*(October), 495–498. https://doi.org/10.1038/39051

Pickett, C. L. (2004). Getting a Cue: The Need to Belong and Enhanced Sensitivity to Social Cues. *Personality and Social Psychology Bulletin*, *30*(9), 1095–1107. https://doi.org/10.1177/0146167203262085

Pizzagalli, D., Regard, M., & Lehmann, D. (1999). Rapid emotional face processing in the human right and left brain hemispheres: an ERP study. *Neuroreport*, *10*(13), 2691–2698. https://doi.org/10.1097/00001756-199909090-00001

Premoli, I., Bergmann, T. O., Fecchio, M., Rosanova, M., Biondi, A., Belardinelli, P., & Ziemann, U. (2017). The impact of GABAergic drugs on TMS-induced brain oscillations in human motor cortex. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2017.09.023

Ptak, R. (2012). The Frontoparietal Attention Network of the Human Brain : Action , Saliency , and a Priority Map of the Environment. https://doi.org/10.1177/1073858411409051

Ptak, R., Schnider, A., & Fellrath, J. (2017). The Dorsal Frontoparietal Network: A Core System for Emulated Action. *Trends in Cognitive Sciences*, *21*(8), 589–599. https://doi.org/10.1016/j.tics.2017.05.002

Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London, Series B*, *358*(1431), 435–45. https://doi.org/10.1098/rstb.2002.1221

R Core Team. (2016). R: A language and environment for statistical computing. Version 3.3.2.

Reddy, V. (2003). On being the object of attention: Implications for self-other consciousness. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(03)00191-8

Reddy, V. (2008). *How infants know minds* (Harvard Un).

Reed, C. L., Beall, P. M., Stone, V. E., Kopelioff, L., Pulham, D. J., & Hepburn, S. L. (2007). Brief report: Perception of body posture - What individuals with autism spectrum disorder might be missing. *Journal of Autism and Developmental Disorders*, *37*(8), 1576–1584. https://doi.org/10.1007/s10803-006-0220-0

Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, *14*(4), 302–8. https://doi.org/10.1111/1467-9280.14431

Reed, C. L., Stone, V. E., Grubb, J. D., & McGoldrick, J. E. (2006). Turning configural processing upside down: part and whole body postures. *Journal of Experimental Psychology. Human Perception and Performance*, *32*(1), 73–87. https://doi.org/10.1037/0096-1523.32.1.73

Ricciardelli, P., Bricolo, E., Aglioti, S., & Chelazzi, L. (2002). My eyes want to look where your eyes are looking: exploring the tendency to imitate another individual’s gaze. *Neuroreport*.

Ricciardelli, P., Lugli, L., Pellicano, A., Iani, C., & Nicoletti, R. (2016). Interactive effects between gaze direction and facial expression on attentional resources deployment: the task instruction and context matter. *Scientific Reports*, *6*(21706), 1–12. https://doi.org/10.1038/srep21706

Richardson, M. J., Marsh, K. L., & Baron, R. M. (2007). Judging and actualizing intrapersonal and interpersonal affordances. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(4), 845–859. https://doi.org/10.1037/0096-1523.33.4.845

Rietveld, E. (2008). Situated normativity: The normative aspect of embodied cognition in unreflective action. *Mind*, *117*(468), 973–997. https://doi.org/10.1093/mind/fzn050

Rigato, S., Farroni, T., & Johnson, M. H. (2009). The shared signal hypothesis and neural responses to expressions and gaze in infants and adults. *Social Cognitive and Affective Neuroscience*, *5*(1), 88–97. https://doi.org/10.1093/scan/nsp037

Rigato, S., Menon, E., Farroni, T., & Johnson, M. H. (2013). The shared signal hypothesis: Effects of emotion-gaze congruency in infant and adult visual preferences. *British Journal of Developmental Psychology*, *31*(1), 15–29. https://doi.org/10.1111/j.2044-835X.2011.02069.x

Righart, R., & de Gelder, B. (2007). Impaired face and body perception in developmental prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.0707753104

Righart, R., & De Gelder, B. (2006). Context influences early perceptual analysis of faces - An electrophysiological study. *Cerebral Cortex*, *16*(9), 1249–1257. https://doi.org/10.1093/cercor/bhj066

Riva, P., & Andrighetto, L. (2012). “Everybody feels a broken bone, but only we can feel a broken heart”: Group membership influences the perception of targets’ suffering. *European Journal of Social Psychology*, *42*(7), 801–806. https://doi.org/10.1002/ejsp.1918

Riva, P., Romero Lauro, L. J., DeWall, C. N., Chester, D. S., & Bushman, B. J. (2014). Reducing aggressive responses to social exclusion using transcranial direct current stimulation. *Social Cognitive and Affective Neuroscience*, 352–356. https://doi.org/10.1093/scan/nsu053

Riva, P., Williams, K. D., & Gallucci, M. (2014). The relationship between fear of social and physical threat and its effect on social distress and physical pain perception. *Pain*, *155*(3), 485–493. https://doi.org/10.1016/j.pain.2013.11.006

Riva, P., Wirth, J. H., & Williams, K. D. (2011). The consequences of pain: The social and physical pain overlap on psychological responses. *European Journal of Social Psychology*, *41*(6), 681–687. https://doi.org/10.1002/ejsp.837

Rivolta, D. (2013). *Prosopagnosia - When All Faces Look the Same*. *Media*. https://doi.org/10.1007/978-3-642-40784-0

Rivolta, D., Lawson, R. P., & Palermo, R. (2016). More than just a problem with faces: Altered body perception in a group of congenital prosopagnosics Davide. *Water*, *44*(0), 320–327.

Rivolta, D., Lawson, R. P., & Palermo, R. (2017). More than just a problem with faces: altered body perception in a group of congenital prosopagnosics. *Quarterly Journal of Experimental Psychology*, *70*(2), 276–286. https://doi.org/10.1080/17470218.2016.1174277

Rivolta, D., Palermo, R., Schmalzl, L., & Williams, M. A. (2012). Investigating the Features of the M170 in Congenital Prosopagnosia. *Frontiers in Human Neuroscience*, *6*. https://doi.org/10.3389/fnhum.2012.00045

Rivolta, D., Woolgar, A., Palermo, R., Butko, M., Schmalzl, L., & Williams, M. A. (2014). Multi-voxel pattern analysis (MVPA) reveals abnormal fMRI activity in both the “core” and “extended” face network in congenital prosopagnosia. *Frontiers in Human Neuroscience*, *8*(November), 925. https://doi.org/10.3389/fnhum.2014.00925

Rizzolatti, G., & Craighero, L. (2004). The Mirror-Neuron System. *Annual Review of Neuroscience*, *27*(1), 169–192. https://doi.org/10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*(4), 264–274. https://doi.org/10.1038/nrn2805

Roark, D. A., Barrett, S. E., Spence, M. J., Abdi, H., & O’Toole, A. J. (2003). Psychological and Neural Perspectives on the Role of Motion in Face Recognition. *Behavioral and Cognitive Neuroscience Reviews*, *2*(1), 15–46. https://doi.org/10.1177/1534582303002001002

Robbins, R. A., & Coltheart, M. (2012). The effects of inversion and familiarity on face versus body cues to person recognition. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(5), 1098–1104. https://doi.org/10.1037/a0028584

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34–79. https://doi.org/10.1016/j.cognition.2006.02.008

Rodriguez, E., George, N., Lachaux, J. P., Martinerie, J., Renault, B., & Varela, F. J. (1999). Perception’s shadow: long-distance synchronization of human brain activity. *Nature*, *397*(6718), 430–433. https://doi.org/10.1038/17120

Rosenthal, R. (1991). *Meta-Analytic Procedures for Social Research*. 2455 Teller Road, Thousand Oaks California 91320 United States of America : SAGE Publications, Inc. https://doi.org/10.4135/9781412984997

Rossion, B. (2014). Understanding face perception by means of human electrophysiology. *Trends in Cognitive Sciences*, *18*(6), 310–318. https://doi.org/10.1016/j.tics.2014.02.013

Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J. M. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology*, *50*(3), 173–189. https://doi.org/10.1016/S0301-0511(99)00013-7

Rossion, B., Dricot, L., Devolder, A., Bodart, J.-M., Crommelinck, M., Gelder, B. de, & Zoontjes,

R. (2000). Hemispheric Asymmetries for Whole-Based and Part-Based Face Processing in the Human Fusiform Gyrus. *Journal of Cognitive Neuroscience*, *12*(5), 793–802. https://doi.org/10.1162/089892900562606

Rossion, B., & Gauthier, I. (2002). How does the brain process upright and inverted faces? *Behavioral and Cognitive Neuroscience Reviews*, *1*(1), 63–75. https://doi.org/10.1177/1534582302001001004

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport*, *11*(1), 69–74. https://doi.org/10.1097/00001756-200001170-00014

RStudio Inc. (2016). RStudio, integrated development environment for R. Version: 1.0.44. Boston, Massachusetts.

Ruggieri, S., Bendixen, M., Gabriel, U., & Alsaker, F. (2013a). Cyberball. *Swiss Journal of Psychology*, *72*(2), 103–109. https://doi.org/10.1024/1421-0185/a000103

Ruggieri, S., Bendixen, M., Gabriel, U., & Alsaker, F. (2013b). Do Victimization Experiences Accentuate Reactions to Ostracism? An Experiment Using Cyberball. *International Journal of Developmental Science*, *7*(1), 25–32. https://doi.org/10.3233/DEV-1312114

Runeson, S., & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology: General*, *112*(4), 585–615. https://doi.org/10.1037/0096-3445.112.4.585

Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology*, *19*(3), 470–480. https://doi.org/10.1080/09541440600757426

Sato, S., & Kawahara, J. I. (2015). Attentional capture by completely task-irrelevant faces. *Psychological Research*, *79*(4), 523–533. https://doi.org/10.1007/s00426-014-0599-8

Sato, W., Kochiyama, T., Uono, S., Matsuda, K., Usui, K., Inoue, Y., & Toichi, M. (2014). Rapid, high-frequency, and theta-coupled gamma oscillations in the inferior occipital gyrus during face processing. *Cortex*, *60*, 52–68. https://doi.org/10.1016/j.cortex.2014.02.024

Sato, W., Kochiyama, T., Uono, S., Matsuda, K., Usui, K., Usui, N., … Toichi, M. (2017). Bidirectional electric communication between the inferior occipital gyrus and the amygdala during face processing. *Human Brain Mapping*, *0*(August 2016). https://doi.org/10.1002/hbm.23678

Sato, W., Kochiyama, T., Yoshikawa, S., & Matsumura, M. (2001). Emotional expression boosts early visual processing of the face: ERP recording and its decomposition by independent component analysis. *Neuroreport*, *12*(4), 709–714. https://doi.org/10.1097/00001756-200103260-00019

Satpute, A. B., & Lieberman, M. D. (2006). Integrating automatic and controlled processes into neurocognitive models of social cognition. *Brain Research*, *1079*(1), 86–97. https://doi.org/10.1016/j.brainres.2006.01.005

Sawilowsky, S. S. (2009). New Effect Size Rules of Thumb. *Journal of Modern Applied Statistical Methods*, *8*(2), 597–599. https://doi.org/10.22237/jmasm/1257035100

Scherer, Klaus R.; Schorr, Angela; Johnstone, T. (2001). *Appraisal processes in emotions: Theory, methods, research*. *Oxford University Press* (Oxford Uni). https://doi.org/10.1017/CBO9781107415324.004

Scherer, K. R. (1992). What Does Facial Expression Express? In *International Review of Studies on Emotion* (pp. 139–165). John Wiley & Sons.

Scherer, K., Scherer, K., & Ekman, P. (1984). On the nature and function of emotion: A component process approach. *Approaches to Emotion*.

Schilbach, L. (2010). A second-person approach to other minds. *Nature Reviews Neuroscience*, *11*(6), 449–449. https://doi.org/10.1038/nrn2805-c1

Schilbach, L., Bzdok, D., Timmermans, B., Fox, P. T., Laird, A. R., Vogeley, K., & Eickhoff, S. B. (2012). Introspective Minds: Using ALE meta-analyses to study commonalities in the neural correlates of emotional processing, social & unconstrained cognition. *PLoS ONE*, *7*(2). https://doi.org/10.1371/journal.pone.0030920

Schilbach, L., Eickhoff, S. B., Cieslik, E. C., Kuzmanovic, B., & Vogeley, K. (2012). Shall we do this together? Social gaze influences action control in a comparison group, but not in individuals with high-functioning autism. *Autism*, *16*(2), 151–162. https://doi.org/10.1177/1362361311409258

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., & Vogeley, K. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences*, *36*(4), 441–462. https://doi.org/10.1017/S0140525X12002452

Schindler, K., Van Gool, L., & de Gelder, B. (2008). Recognizing emotions expressed by body pose: A biologically inspired neural model. *Neural Networks*, *21*(9), 1238–1246. https://doi.org/10.1016/j.neunet.2008.05.003

Schmolck, H., & Squire, L. R. (2001). Impaired perception of facial emotions following bilateral damage to the anterior temporal lobe. *Neuropsychology*, *15*(1), 30–38. https://doi.org/10.1037//0894-4105.15.1.30

Schneider, F., Habel, U., Kessler, C., Salloum, J. B., & Posse, S. (2000). Gender differences in regional cerebral activity during sadness. *Human Brain Mapping*, *9*(4), 226–238. https://doi.org/10.1002/(SICI)1097-0193(200004)9:4<226::AID-HBM4>3.0.CO;2-K [pii]

Schneider, W., Eschman, A., & Zuccolotto, A. (2007). E-Prime® 2.0. Pittsburg: Psychological Software Inc.

Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological Review*, *84*(1), 1–66. https://doi.org/10.1037/0033-295X.84.1.1

Schultz, A. (1972). *The phenomenology of the social world* (Heinemann).

Schwarzlose, R. F. (2005). Separate Face and Body Selectivity on the Fusiform Gyrus. *Journal of Neuroscience*, *25*(47), 11055–11059. https://doi.org/10.1523/JNEUROSCI.2621-05.2005

Selya, A. S., Rose, J. S., Dierker, L. C., Hedeker, D., & Mermelstein, R. J. (2012). A practical guide to calculating Cohen’s f 2, a measure of local effect size, from PROC MIXED. *Frontiers in Psychology*, *3*(APR), 1–6. https://doi.org/10.3389/fpsyg.2012.00111

Sherman, S. J., Judd, C. M., & Park, B. (1989). Social cognition. In *(1989). Porter, Lyman W (Ed), Rosenzweig, Mark R (Ed), Annual review of psychology, Vol. 40. (pp.281 326). Palo Alto, CA, US: Annual Reviews, Inc. ix, 707 pp.*

Shimamura, A. P., Ross, J. G., & Bennett, H. D. (2006). Memory for facial expressions: The power of a smile. *Psychonomic Bulletin & Review*, *13*(2), 217–222. https://doi.org/10.3758/BF03193833

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, *18*(1), 555–86. https://doi.org/10.1146/annurev.ne.18.030195.003011

Slavich, G. M., Way, B. M., Eisenberger, N. I., & Taylor, S. E. (2010). Neural sensitivity to social rejection is associated with inflammatory responses to social stress. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(33), 14817–14822. https://doi.org/10.1073/pnas.1009164107

Smith, E. R., & DeCoster, J. (1999). Associative and rule-based processing: A connectionist interpretation of dual-process models. In *Dual-process theories in social psychology*. (pp. 323–336).

Soria Bauser, D. A., Schriewer, E., & Suchan, B. (2015). Dissociation between the behavioural and electrophysiological effects of the face and body composite illusions. *British Journal of Psychology*, *106*, 414–432. https://doi.org/10.1111/bjop.12101

Soria Bauser, D. A., & Suchan, B. (2013). Behavioral and electrophysiological correlates of intact and scrambled body perception. *Clinical Neurophysiology*, *124*(4), 686–696. https://doi.org/10.1016/j.clinph.2012.09.030

Soria Bauser, D. A., Suchan, B., & Daum, I. (2011). Differences between perception of human faces and body shapes: Evidence from the composite illusion. *Vision Research*, *51*(1), 195–202. https://doi.org/10.1016/j.visres.2010.11.007

Staebler, K., Renneberg, B., Stopsack, M., Fiedler, P., Weiler, M., Roepke, S., … Silk, K. R. (2011). Facial emotional expression in reaction to social exclusion in borderline personality disorder. *Psychological Medicine*, *41*(9), 1929–1938. https://doi.org/10.1017/S0033291711000080

Stekelenburg, J. J., & de Gelder, B. (2004). The neural correlates of perceiving human bodies: An ERP study on the body-inversion effect. *Neuroreport*, *15*(3), 487–491. https://doi.org/10.1097/01.wnr.0000119730.93564.e8

Streit, M., Ioannides, a a, Liu, L., Wölwer, W., Dammers, J., Gross, J., … Müller-Gärtner, H. W. (1999). Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Brain Research. Cognitive Brain Research*, *7*(4), 481–491. https://doi.org/10.1016/S0926-6410(98)00048-2

Sugase, Y., Yamane, S., Ueno, S., & Kawano, K. (1999). Global and fine information coded by single neurons in the temporal visual cortex. *Nature*, *400*(6747), 869–873. https://doi.org/10.1038/23703

Susilo, T., Yovel, G., Barton, J. J. S., & Duchaine, B. (2013). Face perception is category-specific: Evidence from normal body perception in acquired prosopagnosia. *Cognition*, *129*(1), 88–94. https://doi.org/10.1016/j.cognition.2013.06.004

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*(4), 151–162. https://doi.org/10.1016/S1364-6613(99)01299-1

Tamietto, M., Castelli, L., Vighetti, S., Perozzo, P., Geminiani, G., Weiskrantz, L., & de Gelder, B. (2009). Unseen facial and bodily expressions trigger fast emotional reactions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(42), 17661–17666. https://doi.org/10.1073/pnas.0908994106

Tamietto, M., Cauda, F., Celeghin, A., Diano, M., Costa, T., Cossa, F. M., … de Gelder, B. (2015). Once you feel it, you see it: Insula and sensory-motor contribution to visual awareness for fearful bodies in parietal neglect. *Cortex*, *62*, 56–72. https://doi.org/10.1016/j.cortex.2014.10.009

Tao, W., Zeng, W., & Sun, H. (2014). Behavioral and electrophysiological measures of the body inversion effect: the contribution of the limb configurations. *Neuroreport*, 1–10. https://doi.org/10.1097/WNR.0000000000000234

Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI Analysis of Body and Body Part Representations in the Extrastriate and Fusiform Body Areas. *Journal of Neurophysiology*, *98*(3), 1626–1633. https://doi.org/10.1152/jn.00012.2007

The Mathworks Inc. (2016). MATLAB (R2016a). *The MathWorks Inc.* https://doi.org/10.1007/s10766-008-0082-5

ThePrismaGroup:, Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. (2009). Preferred Reporting Items for Systematic reviews and Meta Analyses: The Prisma Statement. *PLoS Med*, *6*(7716), 1–15. https://doi.org/10.1371/journal.pmed1000097

Thierry, G., Pegna, A. J., Dodds, C., Roberts, M., Basan, S., & Downing, P. (2006). An event-related potential component sensitive to images of the human body. *NeuroImage*, *32*(2), 871–879. https://doi.org/10.1016/j.neuroimage.2006.03.060

Thompson, J. C., Clarke, M., Stewart, T., & Puce, A. (2005). Configural Processing of Biological Motion in Human Superior Temporal Sulcus. *Journal of Neuroscience*, *25*(39), 9059–9066. https://doi.org/10.1523/JNEUROSCI.2129-05.2005

Tomonaga, M., & Imura, T. (2009). Faces capture the visuospatial attention of chimpanzees (Pan troglodytes): evidence from a cueing experiment. *Frontiers in Zoology*, *6*(1), 14. https://doi.org/10.1186/1742-9994-6-14

Tucker, D. M. (1993). Spatial sampling of head electrical fields: the geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, *87*(3), 154–163. https://doi.org/10.1016/0013-4694(93)90121-B

Twenge, J. M., Baumeister, R. F., DeWall, C. N., Ciarocco, N. J., & Bartels, J. M. (2007). Social exclusion decreases prosocial behavior. *Journal of Personality and Social Psychology*, *92*(1), 56–66. https://doi.org/10.1037/0022-3514.92.1.56

Twenge, J. M., Baumeister, R. F., & Tice, D. M. (2001). If You Can't Join Them , Beat Them : Effects of Social Exclusion on Aggressive Behavior. *Journal of Personality and Social Psychology*, *81*(6), 1058–1069. https://doi.org/10.1037//0022-3514.81.6.1058

Twenge, J. M., Catanese, K. R., & Baumeister, R. F. (2003). Social Exclusion and the Deconstructed State: Time Perception, Meaninglessness, Lethargy, Lack of Emotion, and Self-Awareness. *Journal of Personality and Social Psychology*, *85*(3), 409–423. https://doi.org/10.1037/0022-3514.85.3.409

Uhlhaas, P. J., & Singer, W. (2010). Abnormal neural oscillations and synchrony in schizophrenia. *Nature Reviews. Neuroscience*, *11*(2), 100–13. https://doi.org/10.1038/nrn2774

Uono, S., Sato, W., Kochiyama, T., Kubota, Y., Sawada, R., Yoshimura, S., & Toichi, M. (2016). Time Course of Gamma-Band Oscillation Associated with Face Processing in the Inferior Occipital Gyrus and Fusiform Gyrus : A Combined fMRI and MEG Study, *0*. https://doi.org/10.1002/hbm.23505

Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic stimulation of extrastriate body area impairs visual processing of nonfacial body parts. *Current Biology*, *14*(23), 2130–2134. https://doi.org/10.1016/j.cub.2004.11.031

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial Magnetic Stimulation Reveals Two Cortical Pathways for Visual Body Processing. *Journal of*

Neuroscience, *27*(30), 8023–8030. https://doi.org/10.1523/JNEUROSCI.0789-07.2007

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, *10*(1), 30–31. https://doi.org/10.1038/nn1815

Urgesi, C., Fornasari, L., Canalaz, F., Perini, L., Cremaschi, S., Faleschini, L., … Brambilla, P. (2014). Impaired configural body processing in anorexia nervosa: Evidence from the body inversion effect. *British Journal of Psychology*, *105*(4), 486–508. https://doi.org/10.1111/bjop.12057

Valdés-Conroy, B., Aguado, L., Fernández-Cahill, M., Romero-Ferreiro, V., & Diéguez-Risco, T. (2014). Following the time course of face gender and expression processing: A task-dependent ERP study. *International Journal of Psychophysiology*, *92*(2), 59–66. https://doi.org/10.1016/j.ijpsycho.2014.02.005

Valentine, T., & Bruce, V. (1986). The effects of distinctiveness in recognising and classifying faces. *Perception*, *15*(5), 525–535. https://doi.org/10.1068/p150525

van Beest, I., & Williams, K. D. (2006). When inclusion costs and ostracism pays, ostracism still hurts. *Journal of Personality and Social Psychology*, *91*(5), 918–28. https://doi.org/10.1037/0022-3514.91.5.918

Van den Stock, J., Tamietto, M., Hervais-Adelman, A., Pegna, A. J., & de Gelder, B. (2015). Body Recognition in a Patient with Bilateral Primary Visual Cortex Lesions. *Biological Psychiatry*, *77*(7), e31–e33. https://doi.org/10.1016/j.biopsych.2013.06.023

van Heijnsbergen, C. C. R. J., Meeren, H. K. M., Grèzes, J., & de Gelder, B. (2007). Rapid detection of fear in body expressions, an ERP study. *Brain Research*, *1186*(1), 233–241. https://doi.org/10.1016/j.brainres.2007.09.093

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, *36*(August).

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, *30*(3), 829–841. https://doi.org/10.1016/S0896-6273(01)00328-2

Watanabe, S., Kakigi, R., & Puce, A. (2003). The spatiotemporal dynamics of the face inversion effect: A magneto- and electro-encephalographic study. *Neuroscience*, *116*(3), 879–895. https://doi.org/10.1016/S0306-4522(02)00752-2

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology*, *54*(6), 1063–1070. https://doi.org/10.1037/0022-3514.54.6.1063

Way, B. M., Taylor, S. E., & Eisenberger, N. I. (2009). Variation in the μ-opioid receptor gene (OPRM1) is associated with dispositional and neural sensitivity to social rejection. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(35), 15079–15084. https://doi.org/10.1073/pnas.0812612106

Wegner, D. M., & Vallacher, R. R. (1977). *Implicit psychology: An introduction to social cognition* (Oxford Uni).

Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion*, *1*(1), 70–83. https://doi.org/10.1037//1528-3542.1.1.70

Wickham, H. (2009). ggplot2: elegant graphics for data analysis.

Wild, B., Erb, M., & Bartels, M. (2001). Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: Quality, quantity, time course and gender differences. *Psychiatry Research*, *102*(2), 109–124. https://doi.org/10.1016/S0165-1781(01)00225-6

Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: the SHINE toolbox. *Behavior Research Methods*, *42*(3), 671–684. https://doi.org/10.3758/BRM.42.3.671

Williams, K. D. (2007). Ostracism. *Annual Review of Psychology*, *58*(1), 425–452. https://doi.org/10.1146/annurev.psych.58.110405.085641

Williams, K. D. (2009). *Chapter 6 Ostracism. A Temporal Need-Threat Model. Advances in Experimental Social Psychology* (1st ed., Vol. 41). Elsevier Inc. https://doi.org/10.1016/S0065-2601(08)00406-1

Williams, K. D., Cheung, C. K. T., & Choi, W. (2000). Cyberostracism: effects of being ignored over the internet. *Journal of Personality and Social Psychology*, *79*(5), 748–762. https://doi.org/10.1037/0022-3514.79.5.748

Williams, K. D., & Jarvis, B. (2006). Cyberball: a program for use in research on interpersonal ostracism and acceptance. *Behavior Research Methods*, *38*(1), 174–180. https://doi.org/10.3758/BF03192765

Williams, K. D., & Sommer, K. L. (1997). Social ostracism by coworkers: Does rejection lead to loafing or compensation? *Personality and Social Psychology Bulletin*, *23*(7), 693–706. https://doi.org/0803973233

Wirth, J. H., Sacco, D. F., Hugenberg, K., & Williams, K. D. (2010). Eye Gaze as Relational Evaluation: Averted Eye Gaze Leads to Feelings of Ostracism and Relational Devaluation. *Personality and Social Psychology Bulletin*, *36*(7), 869–882. https://doi.org/10.1177/0146167210370032

Wronka, E., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology*, *48*(8), 1047–1056. https://doi.org/10.1111/j.1469-8986.2011.01180.x

Wyer, R. S. J. [Ed], & Srull, T. K. [Ed]. (1984). Handbook of social cognition. 1st edition. *Handbook of Social Cognition*.

Wyer, R. S. J. [Ed], & Srull, T. K. [Ed]. (1994). Handbook of social cognition. 2nd edition. *Handbook of Social Cognition*.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141–145. https://doi.org/10.1037/h0027474

Young, A., Hellawell, D., & Hay, D. (1987). Configural information in face perception. *Perception*, *16*(July), 747–759. https://doi.org/10.1068/p160747

Yovel, G., Pelc, T., & Lubetzky, I. (2010). It's all in your head: why is the body inversion effect abolished for headless bodies? *Journal of Experimental Psychology. Human Perception and Performance*, *36*(3), 759–767. https://doi.org/10.1167/9.8.460

Zadro, L., Hawes, D. J., Iannuzzelli, R. E., Godwin, A., MacNevin, G., Griffiths, B., & Gonsalkorale, K. (2013). Ostracism and Children: A Guide to Effectively Using the Cyberball Paradigm With a Child Sample. *International Journal of Developmental Science*, *7*(1), 7–11. https://doi.org/10.3233/DEV-1312112

Zadro, L., Williams, K. D., & Richardson, R. (2004). How low can you go? Ostracism by a computer is sufficient to lower self-reported levels of belonging, control, self-esteem, and meaningful existence. *Journal of Experimental Social Psychology*, *40*(4), 560–567. https://doi.org/10.1016/j.jesp.2003.11.006

Zion-Golumbic, E., & Bentin, S. (2007). Dissociated neural mechanisms for face detection and configural encoding: Evidence from N170 and induced gamma-band oscillation effects. *Cerebral Cortex*, *17*(8), 1741–1749. https://doi.org/10.1093/cercor/bhl100

Zion-Golumbic, E., Golan, T., Anaki, D., & Bentin, S. (2008). Human face preference in gamma-frequency EEG activity. *NeuroImage*, *39*(4), 1980–7. https://doi.org/10.1016/j.neuroimage.2007.10.025