UNIVERSITÀ DEGLI STUDI DI PADOVA

DIPARTIMENTO DI PSICOLOGIA GENERALE

Corso di Dottorato in Psychological Sciences

Ciclo XXXI

USING EMOTIONAL MOVIES TO CHARACTERIZE CORTICAL DYNAMICS IN EMOTIONS AND INDIVIDUAL DIFFERENCES IN EMPATHY

Coordinatore: Ch.mo Prof. Giovanni Galfano

Supervisore: Ch.mo Prof. Alessandro Angrilli

Co-Supervisore: Ch.ma Prof.ssa Chiara Spironelli

Dottorando: Antonio Maffei

Table of Contents

OVERVIEW 7

1 EMOTIONS, EMPATHY AND THE BRAIN 10
1.1 Emotions as a multifaceted phenomenon 10
1.1.1 Discrete emotions and affective dimensions 11
1.1.2 Brain substrates for emotions 16
1.2 Empathy and its building blocks 22
1.2.1 Cognitive Empathy 23
1.2.2 Affective Empathy 24
1.2.3 Individual differences in empathy and emotions 26

2 INDUCING EMOTIONS IN THE LAB 30
2.1 Pictures 30
2.2 Sounds and Music 34
2.3 Movies 37

3 AIM OF THE PROJECT 40

4 STUDY 1: E-MOVIE-EXPERIMENTAL MOVIES FOR INDUCTION OF EMOTIONS: AN INNOVATIVE DATABASE OF FILM CLIPS WITH NORMATIVE DATA AND SEX DIFFERENCES 42
4.1 Abstract 42
4.2 Introduction 43
4.3 Methods 49
4.4 Results 54
4.5 Discussion 62

5 STUDY 2: AFFECTIVE CONTENT SHAPES CORTICAL REACTIVITY TO NATURALISTIC STIMULI: EVIDENCES FROM OSCILLATORY EEG DYNAMICS AND SOURCE IMAGING 68
5.1 Abstract 68
5.2 Introduction 69
5.3 Methods 73
5.4 Results 77

5.5 Discussion 83

6 STUDY 3: CORTICAL REACTIVITY TO EMOTIONAL MOVIES IS SHAPED BY VIEWER'S EMPATHY: EVIDENCES FROM GAMMA EEG ACTIVITY 89

6.1 Abstract 89

6.2 Introduction 90

6.3 Methods 94

6.4 Results 101

6.5 Discussion 105

7 STUDY 4: PRIMARY PSYCHOPATHIC TRAITS ARE ASSOCIATED WITH REDUCED CORTICAL REACTIVITY TO UNPLEASANT EMOTIONAL MOVIES 111

7.1 Abstract 111

7.2 Introduction 112

7.3 Methods 115

7.4 Results 122

7.5 Discussion 127

8 GENERAL DISCUSSION 132

8.1 Summary of the findings 132

8.2 Limitations 137

8.3 Conclusions and Future Directions 138

REFERENCES 141

APPENDIX I 160

APPENDIX II 163

Overview

The ability to experimentally manipulate participants' affective state represents the cornerstone of every research in affective neuroscience. In order to be effective, mood induction should be strong, ecological and characterized by low demand for the participants. Among many available techniques, film clips fully satisfy these criteria, but are still used only in a minority of researches employing mood induction procedures, despite their superior efficacy compared to other approaches. A critical factor contributing to their limited use might be the lack of a standardized databases of film clips, explicitly designed to meet the above criteria while still being suited for the inherent constraints posed by the setting of a typical psychophysiological experiment.

The present thesis will introduce, in Study 1, the E-MOVIE (Experimental MOVies for Induction of Emotions) database, which includes 39 film excerpts that resulted from the efforts to overcome the limitations of existing collections of emotional film clips for experimental use. The first important feature of E-MOVIE is represented by the six film categories considered: Erotic, Scenery, Sadness, Compassion, Fear and Neutral. They aim at providing a wide covering of the pleasantness/unpleasantness spectrum, while still providing a refined characterization of affective states usually thought to overlap. A second, critical, feature of E-MOVIE is the standardized duration of the clips. An average length of two minutes (with a variability between clips of ± 10 seconds) was selected, which makes these clips long enough to provide an intense emotional experience, while still allowing a sufficient number of repetitions during experiments.

In Study 2, EEG was used to characterize the cortical dynamics associated with affective states elicited by emotional movies. In response to a subset of eighteen of the most effective clips, results showed that activity at different frequency bands tracked different dimensions of the emotional experience. Alpha activity was mostly modulated by the arousal dimension, with a larger alpha inhibition, a measure of cortical activation, observed in response to the most arousing clips. Beta activity was instead sensitive to the valence dimension, especially to the unpleasantness of the clips. Analysis of the neural generators of the activity observed at the scalp, revealed that alpha modulation reflected mostly the activity of parietal brain regions involved in attention, high-order integration as well as self-referential cognition. Temporal regions involved in processing of affective and social features of the stimulus were instead involved in the response observed in the beta rhythm.

The second part of this work will show two studies that, taking advantage of the unique characteristics of film clips, tried to deal with the important issue of understanding how emotional reactivity is influenced by individual differences in empathy. Indeed, movies are an ideal tool to study empathy, since enjoying a movie is founded on the ability to understand characters' intentions (cognitive empathy) and share characters' feelings (affective empathy). Moreover, individual differences in empathy modulate how a person responds to affective cues (especially the ones social in nature) in everyday life, but they are almost uniquely studied using an empathy-for-pain paradigm, which may fail to capture the complex dynamics occurring in everyday life.

In Study 3, individual differences in dispositional empathy have been assessed in a sample of students, and two groups with high and low trait empathy have been identified. These groups were presented with four categories of emotional movies (Erotic, Compassion, Fear and Neutral) while their EEG activity was monitored. Results showed that in term of subjective experience of emotions, high empathy was linked with a greater perceived arousal pointing toward a general increased emotional sensitivity in high empathic individuals. This conclusion was bolstered by the analysis of cortical activity which showed that high empathy individuals were characterized by larger cortical activity in the gamma band in response to all the emotional movies, while low empathy individuals showed an aversive specific brain response. Moreover, analysis at source level revealed that in response to Compassion clips, selected explicitly to elicit an empathic response in the viewer, high empathic participants' brain activity in the inferior parietal lobule, a region crucial in the empathy network, was predictive of experienced arousal. This suggested that levels of dispositional empathy might moderate cortical and subjective response in response to others' sufferance.

Finally, Study 4 aimed at addressing the role of empathy in emotional responding by focusing on individuals with a consistent lack of this psychological dimension, i.e. individuals with high primary psychopathy. The analysis of subjective and cortical response to emotional movies in two groups of participants selected for being high and low in primary psychopathy, revealed that the former are characterized by a reduced reactivity to negative emotional clips (Fear and Compassion). Source analysis also revealed that individuals with high psychopathic traits show a large deactivation, when processing threatening stimuli, in a large network of brain regions involved in visual attention, emotion and social cognition, suggesting that the reduced affective experience results from the lack of integration between regions involved in attention and multimodal integration (lyngual gyrus, cuneus, precuneus) and social cognition (inferior parietal lobule, middle frontal gyrus).

Taken together, this work provides a new standardized collection of experimental stimuli that are tailored for use in psychophysiology and neuroimaging. The results from study 2 give new insights on how affective content impacts brain processing of a complex, dynamic stimulus, like a movie, and results from studies 3 and 4 aim at establishing a new perspective on how empathy interacts with processing of affective stimuli and emotional reactivity, exploiting the naturalistic setting achievable with emotional movies.

Keywords: *Emotions, Empathy, EEG, Film clips, Psychopathy, Individual differences, Personality*

Chapter 1

Emotions, Empathy and the Brain

1.1. Emotions as a multifaceted phenomenon

Despite centuries of philosophical investigations and decades of systematic scientific enquiry, a complete agreed-upon definition of emotion is still far from being achieved. This lack of consensus has been generally interpreted as the result of conflictual positions among different disciplines, theories and authors, but it is better accounted by acknowledging the inherent complexity of the phenomenon itself. Indeed, each time an emotion takes place, there are at least three interdependent facets that contribute to the process: subjective experience, behavioral manifestation and physiological activation. The subjective facet represents the rich component of experienced feelings arising with an emotion, which are usually expressed using language (Lindquist, Satpute, & Gendron, 2015). The behavioral facet refers instead to the changes in behavior occurring with an emotion. A paradigmatic example of the behavioral component of emotions, is represented by the freezing behavior occurring after the encounter with a threatening stimulus, observable in both animals and humans (Mulligan & Scherer, 2012).

Finally, the physiological changes occurring with an emotion represent the complex interaction between the brain and the body, needed to deploy the resources to cope with the situation that gives rise to the emotion. A pumping heart and sweating hands in front of a threat are two distinctive physiological correlates of this emotional activation, that result from the bi-directional interaction between cortical and subcortical regions (which role is to perceive and recognize a stimulus as a threat) and the autonomic nervous system (which is role is to provide the body with the resources needed to cope).

It is important to stress that the differential contribution of these three components is not fixed but dynamic and prone to changes. This is evident in the dissociations that occur among different facets (i.e. increase in physiological activation in absence of overt behavioral manifestations) and within them (i.e. directional fractionation of autonomic responses showing divergent pattern of changes), which contribute to the wide variability that characterizes the spectrum of emotions and the variability that characterizes how emotions vary across individuals.

1.1.1 Discrete emotions and affective dimensions

Although the term emotion is used to describe affective phenomena in general, in everyday life and everyday language, we can recognize a wide variety of *emotions*. A long-time standing question in emotion research asks if these represent different *basic* emotions independent from each other, or instead they are the result of the combination of different levels of some fundamental dimensions.

The categorical perspective states that affective phenomena can be characterized in term of a set of discrete *primary* emotions, each capturing a family of affective states that share the same experiential characteristics (Ekman & Cordaro, 2011). The most common characterization identifies Fear, Happiness, Disgust, Anger, Sadness and Surprise as fundamental emotions, even if it is a matter of debate how many basic emotions can be identified, with some authors suggesting that the number of primary emotions is larger (Ekman & Cordaro, 2011). Despite these contrasts, all the authors advocating this perspective agree to consider the basic emotions universal, as the result of the evolutionary process which provided the organism with a set of behaviors tailored to support distinct survival functions. A strong argument in favor of this perspective is represented by the evidence of discrete configurations of facial expression, that are unambiguously associated with each of six basic emotions (Ekman, 1992; Ekman & Cordaro, 2011). Moreover, the trans-cultural presence of these facial expressions is generally provided as an evidence of the universality of these affective states.

According to the categorical approach, basic emotions should also be characterized by distinctive physiological reaction patterns, predicting that a unique combination of changes in different physiological measures should be able to differentiate one emotion from another. For what concerns activity of the autonomic nervous system (ANS), the idea of specialized responses in support of different affective states dates back to the seminal conceptualization of emotion made by William James, but the evidences in support for this prediction are far from definitive, especially in human research. In a recent review, Kreibig (2010) showed that, although it is possible to identify partially segregated response patterns for different discrete emotions within ANS reactivity, the degree of specificity in autonomic response is affected by numerous factors, like the emotions considered, the number of physiological measures considered, the emotion elicitation technique used. Another review made by Mauss and Robinson (2009) further suggested that the theoretical prediction of discrete autonomic patterns matching discrete emotional states has only limited support from empirical researches. Considering that ANS activity is affected by a several psychological and physical factors which are not necessarily related to emotions (Kreibig, 2010), it may be limited to conceptualize autonomic reactivity as a patterned response serving solely affective reactivity. Limited support for the correspondence between discrete affective state and discrete physiological states is found also for what concerns the activity of the central nervous system. Paradigmatic is the case of amygdala, which activity has been traditionally considered as the hallmark of fear, according to the crucial role played by this brain structure in the associative learning based on aversive conditioning (LeDoux, 2003). Recent advances are progressively suggesting to reconsider amygdala activity as the neural correlate of an overarching mechanism of detection of emotional significance in sensory stimulation, not restricted to fearful and threatening stimuli but sensitive to biological significance in general (Pessoa, 2010; Pessoa & Adolphs, 2010). Another example is represented by the activity in the insular cortices, which is consistently observed when the emotion of disgust is experienced (Phillips et al., 1997). New studies have highlighted that activation of the insula is not a unique correlate of disgust as initially thought (Schienle et al., 2002), but rather a mechanism necessary for the cortical integration of interoceptive information coming from the rest of the organism (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). As a consequence, insular activity occurs in response to disgusting stimuli (due to the large autonomic response associated with them) as well as painful stimuli but also sexually arousing stimuli.

Taken together, these evidences highlight that a categorical view of emotions is limited and not conclusive. An alternative view of affective phenomena is represented by the *dimensional* perspective of emotions.

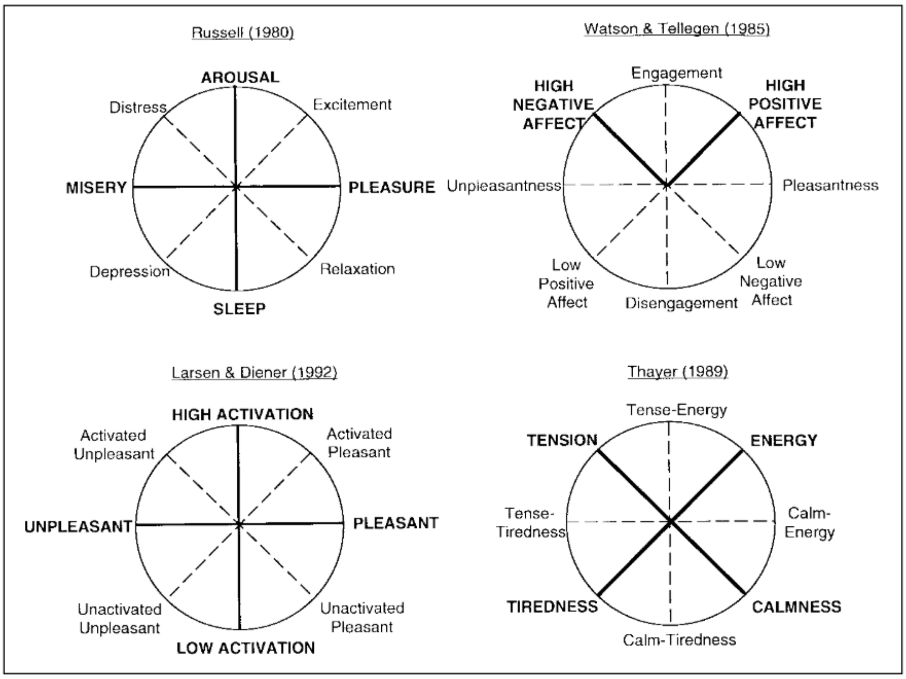

Figure 1.1 Dimensional models of emotions. Schematic representations of four bi-dimensional models of affect. (Adapted from Feldman-Barrett and Russell, 1999)

This approach is grounded on the idea that, despite the many features that make different emotions seemingly discrete entities, they can be efficiently described by a limited number of fundamental factors, differentially combined (Feldman-Barrett & Russell, 1999). The most distinctive one is represented by the positive-negative dimension, usually referred to as valence. This dimension easily captures the intuitive distinction that characterizes emotional states and emotional behaviors, although this distinction is coarse-grained and too simplistic. A complementary dimension is represented by the arousal, which characterizes an emotion along the calm-activated axis. The combination of valence and arousal factors, provides a two-dimensional space that effectively maps the complex variety of emotional states (Feldman-Barrett & Russell, 1999). Convincing arguments in support of this perspective comes from studies investigating affective self-reports as well as studies investigating psychophysiological reactivity to emotional stimuli. Nevertheless, it has been argued that the exclusive combination of valence and arousal fails to account for the differences in certain emotional states. This is the case for fear and anger, which can be both described as negative in valence and are both characterized by an activated state for what concerns the arousal dimension, though they lead to markedly different behavioral manifestations. To resolve this ambiguity a third factor should be considered, that is a motivational dimension arranged along the axis delimited by the behavioral tendency to approach and the behavioral tendency to withdraw from the source of the affective state (Davidson, 1992; Lang & Bradley, 2010). Even though the direction of the motivational drive might resemble the valence dimension (positive affect leads to approach, negative affect leads to withdraw), the psycho-physiological features of the affective states associated with anger clarify how motivational tendency and valence represents non-redundant affective dimensions (Harmon-Jones, Gable, & Peterson, 2010). Indeed, the motivational tendency that characterizes anger has an opposite direction of the motivational tendency occurring when feeling scared, although in the valence-arousal space anger occupies a position close to the one occupied by fear. Usually, in order to cope with a threat eliciting a fearful emotional state, the predominant behavioral tendency is to withdraw from the threat, while anger is characterized by the action tendency to seek conflict, approaching the source of the emotion experienced. Interestingly, this motivational dimension has been traditionally associated with a distinctive neural correlate represented by the asymmetrical activation of the frontal region of the two brain hemisphere (Coan & Allen, 2004; Davidson, 2004; Reznik & Allen, 2018). Affective states associated with an approaching motivation, both positive and negative, are linked with a greater left frontal activity while a withdrawing motivation is associated with a relatively larger activity in the right hemisphere. As a consequence, psychological experience of anger is associated with left frontal activation, while fear is associated with a right frontal activity (Harmon-Jones & Allen, 1998).

In conclusion, although the categorical and dimensional perspectives of emotions have been traditionally viewed as contrasting positions, incompatible with each other, it has been progressively acknowledged that both these theoretical approaches should be taken into account to understand the nature of emotion as a complex psychophysiological phenomenon (Harmon-Jones, Harmon-Jones, & Summerell, 2017). Only with the adoption of an integrated perspective it is possible to acknowledge that discrete emotions are likely to exist to maximize the survival chances of the organism, exploiting highly selected behaviors, but at the same time fundamental affective dimensions are critical to characterize psychological processes shared across, apparently distinct, emotional states. Therefore, it is very likely that fear, as an emotional state supporting the quest for self-protection, reflects a *basic* affective state, but also that the heightened attention toward a salient emotional stimulus is not a unique feature of fear, reflecting instead the effect of arousal, thus characterizing with varying intensity a multitude of affective states.

1.1.2 Brain substrates for emotions

The complexity of emotion is not restricted to its characterization as a psychological phenomenon, but extends to its characterization as a neurophysiological process, since a wide range of brain regions, continuously interacting, is involved in emotions and motivated behaviors.

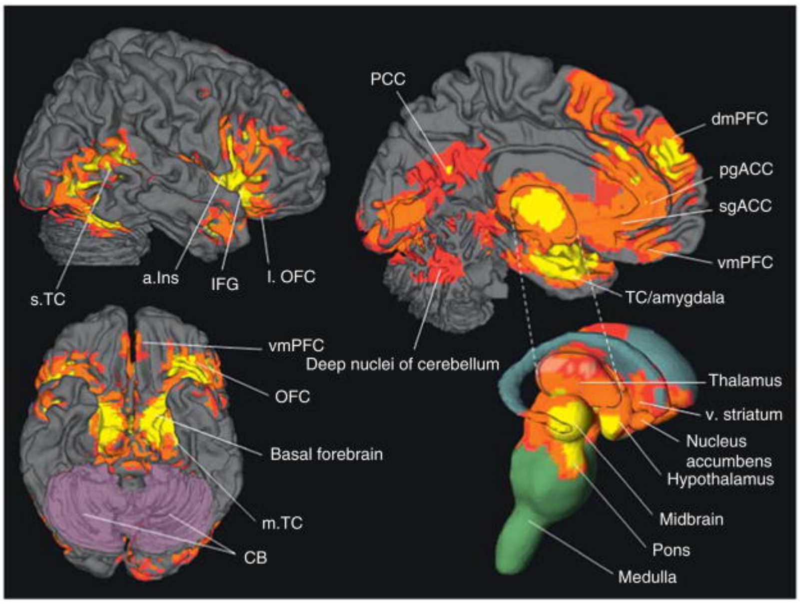

Figure 1.2 Brain regions involved in affect. This image is the result of a meta-analysis of 165 neuroimaging studies of emotion and shows the dimension and the complexity of the network of regions implicated in affect (Adapted from Feldman Barrett & Bliss-Moreau, 2009)

Traditionally, the neurophysiological investigation of emotions has focused on subcortical nuclei, aiming at uncover the role of these structures phylogenetically conserved across different species. Among them, amygdala, a small almond-shaped structure located deep in the temporal lobe, plays a crucial role in emotional/motivational processes due to its large number of anatomical connections with other regions of the brain, which make it a necessary central station along the processing pathway of incoming sensory stimuli (LeDoux, 2003; Phelps & LeDoux, 2005). Indeed, direct connections with the thalamus project to the amygdala a coarse-grained representation of the sensory stimulus, sufficient to provide a fast detection of those features that are motivationally relevant and trigger a cascade of autonomic modifications that support behavioral responses. This *subcortical* pathway has been described in detail in the rat brain in the context of fear conditioning and considers the lateral part of the amygdala as the target of afferent projections from the thalamus, while the central nucleus represents the efferent portion of the amygdaloid complex from which stem projections (direct or mediated by the bed nucleus of the stria terminalis) toward the periacqueductal grey, the lateral portion of hypothalamus and the paraventricular nucleus of hypothalamus. These efferent projections then mediate the behavioral manifestations of fear, like the freezing mediated by the PAG, and its associated changes in autonomic homeostasis (i.e. cardiovascular and skin conductance modifications) and hormonal secretion, mediated by the lateral hypothalamus and the paraventricular nucleus of the hypothalamus, respectively.

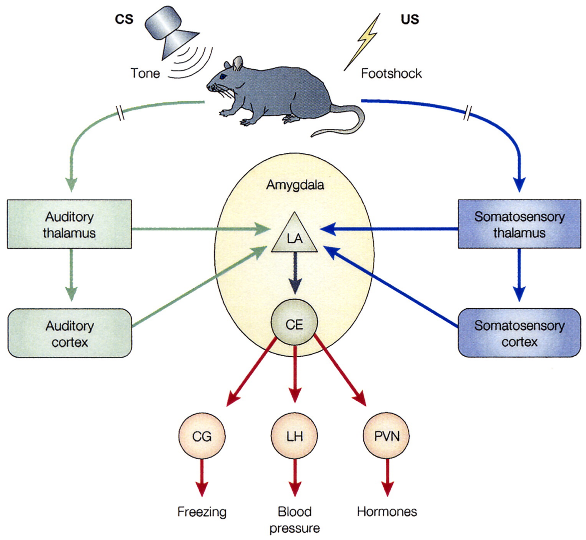

Figure 1.3 The role of amygdala in threat conditioning. Schematic representation of the neural circuit, centered around amygdaloid nuclei, that mediates behavioral response to threat. (Adapted from Phelps and LeDoux, 2005)

The main advantages of this pathway is that it is fast, which explains its crucial role in mediating response to threat, but is limited because it operates on a raw sensory input. A second pathway exists, along which amygdala receives afferent fibers from sensory cortices, allowing elaboration on a fine-grained representation of the input. This *cortical* pathway characterized by the bi-directional connection between the amygdala and the cortex, is thought to be responsible for the complex interactions existing between emotional and cognitive processes, especially the influence of emotion on attention (Pessoa & Adolphs, 2010). Indeed, emotional stimuli are elaborated preferentially and with greater intensity compared with stimuli characterized by low affective relevance, which is reflected in a greater brain activity in primary and secondary sensory cortices as well as brain regions deputed to higher-order integration following the presentation of emotionally charged stimuli (Peter J. Lang & Bradley, 2010; Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004). It is important to highlight that this phenomenon characterizes in similar fashion pleasant and unpleasant emotional stimuli (Weymar & Schwabe, 2016), supporting the idea that the functional role of amygdala lies in computation of stimulus significance, rather than in the simple detection of threat.

Nevertheless, the computation of its significance represents only a portion of this complex process of reacting toward a stimulus. The computation of stimulus' rewarding properties represents another, critical, step. Traditionally, neurophysiologists have identified in the dopaminergic neurons located in the ventral striatum and the ventral tegmental area the subcortical stations necessary for the pleasant experience of reward (Schultz, Dayan, & Montague, 1997; Schultz, 2015). Indeed, these brain regions have been demonstrated to be involved in food intake and sexual desire (Volkow, Wang, & Baler, 2010), activities that share the feature of being highly rewarding, and their abnormal activity has been linked to addictive behaviors, in general, and specifically to food and drug abuse (Volkow, Wise, & Baler, 2017). These evidences contributed to the diffuse view, among experts as well as laymen, that these regions are the "pleasure centers" of the brain and that experience of pleasure critically depends on dopamine. Actually, these regions are involved in the continuous computation, from sensory input, of predictions about the potential rewarding value of the stimuli with which the organism interacts (Floresco, 2015; Schultz, 2015).

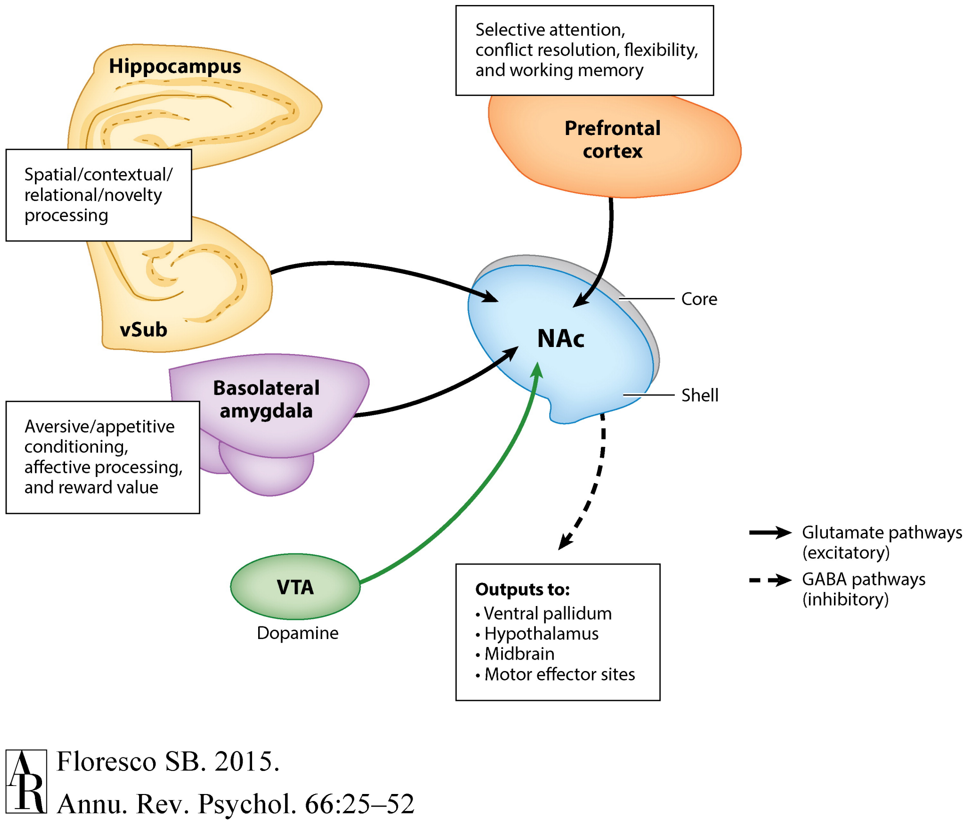

Figure 1.4 Afferent and Efferent projections to dopaminergic structures. This figure shows a schematic representation of the pathways that connect the *nucleus accumbens* and the *ventral tegmental area* with other brain regions, highlighting the multifaceted role played by these dopaminergic regions in emotion, cognition and behavior. (Adapted from Floresco, 2015)

Studies conducted on the brains of different species (i.e. primates, rats, mice) showed that the firing of these dopaminergic neurons depends on the contextual probability of association between a stimulus and a reward (i.e. food) and that the plastic modulation of this process mediates learning (Schultz, 2015). As a consequence, activity within these brain areas can be considered critical for every emotional state that is characterized by an approach motivation to gain a reward, from relatively simple behaviors like foraging and sexual mating to more complex states like attachment, affiliation and, eventually, love (Bartels & Zeki, 2004; Lakatos et al., 2000).

So far it seems that emotions and motivation largely depend on activity in subcortical structures (i.e. amygdala, striatum) with the cortex acting simply as a sensory receiver and motor effector, instead the functions played by the neocortex in emotions are essential. A vast literature capitalizing on the study of brain damaged patients, since the first description of the Phineas Gage case, demonstrated the leading the frontal lobe role in affect and motivation. The classical neuropsychological perspective viewed differentiated functions for the frontal areas of the two hemispheres, according to the evidences that indicated that a damage to the right frontal lobe leads to flattened affect, and a damage to the left leads to behavioral disinhibition and severe impairment in emotional regulation and control. Modern cognitive neuropsychology, taking advantage of recent brain imaging techniques, highlighted that different subregions within frontal areas are involved in different aspects of emotional behavior. The ventromedial portion of the prefrontal cortex, also defined orbitofrontal cortex, due to its vast afferent and efferent connectivity with, among others, insula, somatosensory cortices, amygdala and striatum, has a fundamental role in the integration of interoceptive information and affective bodily modifications, and uses this information to support decision making and, more generally initiate and regulate behavior (Bechara, Damasio, & Damasio, 2000; Pollatos, Gramann, & Schandry, 2007). The dorsolateral portion of frontal cortex (dlPFC) has been instead linked to the motivational dimension of approach/avoidance, with the right dlPFC linked to avoidance motivation and the left dlPFC linked to approach (Reznik & Allen, 2018). Interestingly, evidences in support to this characterization of the dlPFC showed that its asymmetrical association with motivational direction acts as trait moderator of individual's affective behavior (Davidson, 2002). Thus, individuals that are characterized at rest by larger left activity have a larger tendency to indulge in appetitive/approaching behaviors and more sensitive to rewards. On contrast, individuals characterized by larger right frontal activity show a greater propensity to withdrawal and behavioral inhibition. These findings also translate to affective disorders, especially depression, showing that patients affected by depression have at rest larger right frontal activity (assessed by means of EEG), left dlPFC non-invasive stimulation leads to improvement of affective symptomatology (Schutter, 2009) and neurofeedback of frontal activity improves negative affect (Mennella, Patron, & Palomba, 2017).

Meta-analyses of brain activity in emotions revealed that frontal lobes are not the only region of the cortex involved, though their functions have a major impact, showing that affective processing requires the integrated participation of many cortical districts. Besides primary sensory cortices, which role in emotions depends on their deep interconnections with subcortical regions (as detailed in the previous section), occipital as well as parietal and temporal areas are involved in affect. This evidence marks the idea of emotion as a distributed process (Wager et al., 2015), contrasting earlier modular perspectives, and emphasize the importance of investigating this phenomenon using a brain network perspective. In the last years cognitive neuroscience has witnessed a surge of studies investigating brain networks, defined as pattern of regions which show direct anatomical connections or functional associations (i.e. they are co-activated at rest or during a task). The emerging branch of *network neuroscience* (Bassett & Sporns, 2017) supports the idea that brain networks subtend general-domain functions (rather than domain-specific processes), and are involved in the generation of complex cognition and behaviors through their integrated recruitment. Emotions should then be viewed as arising from the activity of the majority of known functional networks (i.e. the salience network, the default mode network, the dorsal attentional network, the executive control network). It is by means of their fine-tuned integrated activity that the brain can (ap)percept the environment (both external and internal) and rapidly extract salient features, compute their motivational value, select and implement the most appropriate behavior, and then continuously monitoring and adjusting it. As a consequence, this demands to interpret brain activity related to emotions by referring to the context within which they unravel, considering the specificities of what is triggering the emotional response rather than considering emotions as a separated process, functionally independent from other mental activities.

From this standpoint an important factor that should be considered to understand emotions, and the brain activity that generates them, is that in humans emotions are deeply interconnected with the social nature of our species. Thus, to gain a better comprehension is critical to consider how the ability to understand and share feelings of others influences our own emotional responding.

1.2 Empathy and its building blocks

The warm feeling of joy when seeing a person cheering and the poignant sensations that come from looking at people grieving at a funeral are typical cases in which individual's emotions arise from a social interactions. These are common and (quasi-)automatic experiences grounded in the psychological process called empathy. As it often occurs in psychology and cognitive neuroscience, empathy does not have a simple, clear-cut definition (Batson, 2009a). It is instead construed as multicomponent construct, with its facets carved to capture distinct features of the construct. According to the traditional approach, empathy is built on top of two distinct abilities. One related to the explicit understanding of others' thoughts, intentions, motivations, defined *cognitive empathy*, and another related to the psychological and physiological sharing of others' emotions, defined *affective empathy*.

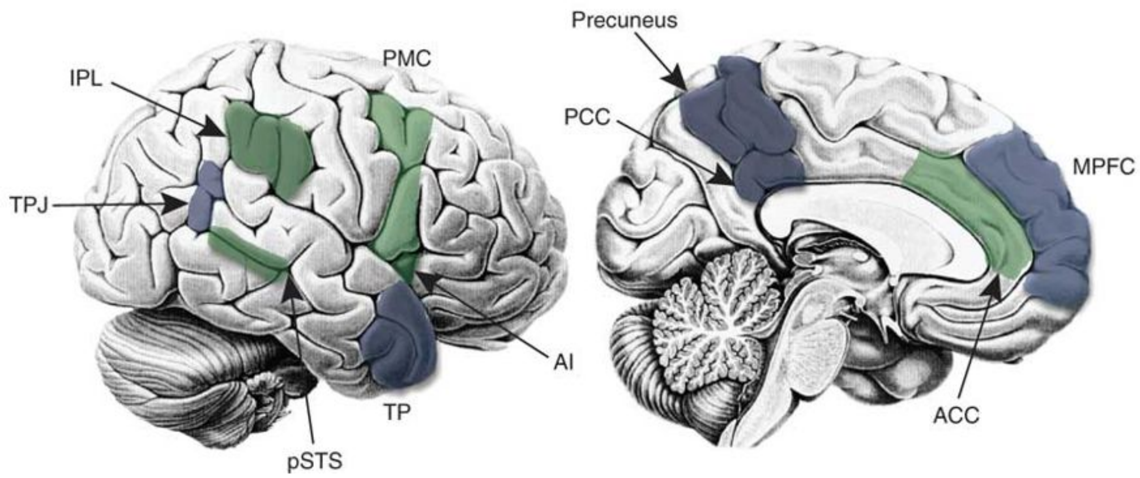

Figure 1.5 Brain regions supporting empathy. This image shows the contribution of different brain regions in the cognitive (blue) or affective (green) facets of empathy. IPL, inferior parietal lobule; TPJ, temporoparietal junction; pSTS, posterior superior temporal sulcus; TP, temporal pole; AI, anterior insula; PMC, premotor cortex; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; MPFC, medial prefrontal cortex. (Adapted from Zaki and Ochsner, 2012)

1.2.1 Cognitive empathy

The cognitive component of empathy has been the focus of a large corpus of investigations stemming from early works on children with atypical development, especially children affected by autistic spectrum disorders (Baron-Cohen & Wheelwright, 2004). Indeed, a distinctive feature of autistic children is that they lack a normal development of the *mind-reading* ability that mediates the understanding of others' actions and intentions. This impairment determines the major dysfunctions that ASD patients bear for what concerns their social functioning, and improvement of their ability to correctly catch and interpret social cues about others' mental state is the final aim of many treatment approaches to ASD (Begeer et al., 2011).

Neuroimaging studies employing tasks probing the cognitive side of empathy, such as asking participants to explicitly infer the feelings and the goals of another person, revealed that this process relies on the activity of several distinct brain regions, located in temporal, parietal and frontal areas (Zaki & Ochsner, 2012). Specifically, the core network of cognitive empathy involves mainly the temporoparietal junction, the temporal pole, the precuneus and the medial prefrontal cortex.

Within this network, the frontal cortex is thought to integrate self-referential processing, mediated by the precuneus (and, more generally, by the default mode network) with autobiographical memory, mediated by temporal regions, in order to provide the individual with the ability to understand and adopt the cognitive perspective of another person, without confounding it with his/her own.

1.2.2. Affective empathy

The ability to infer what another person is thinking, or the reason making him/her behave in a specific manner, represents only one side of story. The full picture of empathy is completed only when considering the ability to resonate with the others' emotions. Indeed, the emotional component is the most representative facet of empathy, so much that in folk psychology affect sharing and empathy are considered as interchangeable concepts. In the context of cognitive neuroscience instead, the affective facet of empathy refers specifically to the process of sharing, both psychologically and physiologically, the emotions displayed by another person (Batson, 2009a; Zaki & Ochsner, 2012). A critical feature of this process is that there is no confusion between the feelings of the empathizer and the ones of the target person (Batson, 2009a; Davis, 1983).

The dominant theoretical model for the neurobiology of affect sharing proposes that the third-person experience of emotions of others is founded on the recycling mechanism of the neural circuits deputed for experiencing emotions in first-person (De Waal & Preston, 2017; Preston & de Waal, 2002). This model has received large support in the last fifteen years from studies that used empathy for pain as experimental paradigm. These studies showed that the brain regions that are usually activated during the experiencing of physical pain are also active when viewing other people receiving a physical painful stimulation Specifically, activity in the insular cortex, especially in its anterior portion, has been consistently reported to play a central role in mapping this self-other emotional resonance (Singer, 2006; Singer et al., 2004). Indeed, a series of studies consistently reported activation of brain regions involved in processing of the emotional aspects of pain, centered around the insula, while those involved in the sensory perception of pain were activated only by first-hand experience of pain, not by vicarious experience (Singer et al., 2004). Furthermore, the evidence that individual variability in insular activity elicited during this empathy-eliciting task covaries with individual difference in trait empathy bolstered this view, making insular activity a hallmark of the empathic sharing of the feelings of others in pain.

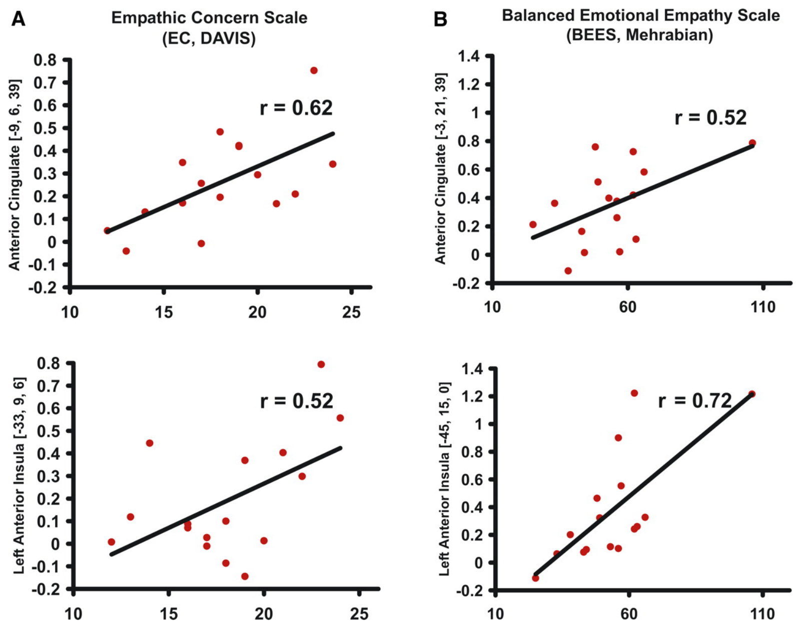

Figure 1.6 Correlation between insular activity and trait empathy. This image shows the covariation between activity in anterior insula elicited by view of others in pain and individual levels of trait empathy. (Adapted from Singer et al., 2004)

Together with insula, studies reported also activity in parietal regions, especially in the inferior parietal lobe (Zaki & Ochsner, 2012). The association of empathy with neural activity in the inferior lobule of the parietal cortex dates back to the first description in the macaque's brain of mirror neurons (Rizzolatti, Fogassi, & Gallese, 2001). Mirror neurons represent a specific class of neurons marked by a unique property, that is they fire both during the execution of a specific action as well as during the simple observation of the same action. Also neurons in human parietal cortex are characterized by this property (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008), and has been demonstrated that they are involved in others' action understanding. This involvement lead theorists to advance that the mirror property of this class of neurons might constitute a general mechanism that supports our understanding of the social world in which we behave. Using the same neural circuits involved in the actual execution of a behavior, the brain produces an inner "simulation" of the same behavior that determines the process of understanding it and, above all, sharing its associated feelings (De Waal & Preston, 2017).

1.2.3 Individual differences in empathy and emotions

Although empathy is a fundamental ability, its expression is not constant throughout our species (Hein & Singer, 2008). One of the most striking evidence of individual differences in empathy is represented by the role of gender. Men and women tend to show different pattern of response in the two subcomponents of empathy. As excellently reviewed by Christov-Moore and colleagues (2014), women are characterized by greater affective empathy, tend to show greater emotional responsivity in tasks that require empathic sharing and are characterized by greater tendency to act prosocially compared to men. Men on the other side seem to have a slight advantage in tasks that require mentalizing. It is interesting that these gender differences are reflected in morphological and functional diversity in the male and female brain, suggesting that they are founded in ontogenetic and phylogenetic biological differences, rather than being the unique effect of culturally mediated influences (Banissy, Kanai, Walsh, & Rees, 2012).

More generally speaking it is also possible to acknowledge that individual differences in empathy are related to different behavioral outcomes. For instance, people characterized by greater empathy are usually observed to indulge more frequently in prosocial behaviors. On the other hand, antisocial tendencies are usually observed in individuals characterized by being less empathic. Moreover, it is important to recognize that these different behavioral outcomes are mediated by differences in emotional experience and reactivity, as a function of empathy. This highlights the importance of understanding how individual differences in empathy are related to differences in the affective experience and reactivity to emotional stimuli.

For instance, using an emotion recognition paradigm, consisting in recognizing emotional states in pictures of faces, Besel and Yuille (2010) observed that individuals with higher levels of affective empathy are characterized by a greater ability to recognize emotions in others, especially fear. Moreover, high emotional empathy has been associated with greater facial reactivity to emotional displays in others' faces (Dimberg, Andréasson, & Thunberg, 2011). Increased emotional reactivity has been also observed in terms of greater physiological response in individuals with high empathy, interestingly without differences related to the hedonic valence (Mehrabian, Young, & Sato, 1988). On the other hand, low levels of emotional empathy are usually related with blunted emotional reactivity. Indeed, recognition of facial affect showing distress cues is deficient in individuals with low empathy and antisocial tendencies (Marsh & Blair, 2008). Moreover, psychophysiological reactivity to emotional stimuli in general, and threatening stimuli specifically, is markedly abnormal in individuals affected by psychopathy, a complex psychopathological condition characterized by low levels of affective empathy (Patrick, 1994; Sutton, Vitale, & Newman, 2002; Verona, Patrick, & Curtin, 2004). Similar patterns have been also observed for what concerns the cortical processing of stimuli depicting others in pain: individuals with low levels of empathy and high emotional detachment, were characterized by a reduced brain response in the neural circuits involved in empathy for pain (Seara-Cardoso, Viding, Lickley, & Sebastian, 2015).

Taken together, these reviewed evidences point toward a strong impact of empathy in the mediation of individual's emotional reactivity, but are characterized by several limitations that demand further investigation.

One of the most common objections toward those who study empathy is represented by how this construct is operationalized in the laboratory context and, more importantly, how it is experimentally manipulated. Indeed the artificiality of the experimental approach employed represents a major pitfall, which seriously prevents a complete understanding of this phenomenon, and the achievement of results that can be translated more efficiently outside of basic research (Zaki & Ochsner, 2012). A general criticism concerns that the two facets of empathy are usually studied as separate, non-interacting processes, without acknowledging that in everyday life they are deeply interweaved and interacting. Moreover, for what concerns the process of experience sharing/affective empathy, the golden standard of experimental paradigm is represented by the empathy-for-pain paradigm, which might be limited. The main problem with this kind of paradigm is that pain is a highly salient affective stimulus characterized by its idiosyncrasies that make it very specific, thus limiting the generalizability of results to other, more ecological contexts. This is particularly relevant for what concerns the understanding of the neural correlate of affective empathy, especially the role of the insula. Indeed, considering the peculiar role that bodily sensations play in pain (either self-experienced or vicariously experienced) and the central role that the insula has in interoception and in the computations supporting central-periphery integration, it is hard to disambiguate the real contribution of empathy as a general process from the specificity of pain in the insular activation observed in response to others' pain (Zaki & Ochsner, 2012).

The problem of artificiality also impacts negatively the investigation of how empathy interacts with emotional reactivity. Indeed, the limited ecological validity of the emotional states induced in the laboratory represents a long standing issue in the field that demands efforts to identify and adopt more suited approaches for emotional induction.

Chapter 2

Inducing Emotions in the Lab

The ability to experimentally recreate the emotional states that occur naturally in everyday life is the most critical aspect in the study of affective phenomena. At the very beginning of emotion science, researchers put a great deal of effort in identifying the most effective strategies to prompt a strong emotional experience (and reaction) in their participants, using emotional probes that today might appear odd, at least. Classic is the example of Landis (1924) who, in order to study facial expression of emotions, asked his participants to put their hand in a basket containing living frogs. The major issue with this quest for the emotional strength of the experimental induction was the lack of consistency in the methods used across different labs and experiments, which were characterized by large differences that eventually limited the cross-comparisons of results obtained through different methodologies. Progressively, the need of consistency across affective scientists rose, leading to the development and validation of databases of emotional stimuli, created explicitly with the purpose of providing the community with tools to use in the experiments. Currently it is possible to recognize three different media that gained that largest diffusion, pictures, sounds and music, and movies. In the following paragraphs the strength and limits of each of this technique will be reviewed.

2.1 Pictures

Images are the foremost used class of stimuli for emotion elicitation, a leading position that largely depends on the availability of numerous picture databases that gained large popularity among scholars. The International Affective Picture System (IAPS), developed and maintained by Lang and Bradley (1999), was the first effort to standardize emotional pictures for experimental use. Currently this database includes more than 900 color pictures rated along three different dimensions, valence, arousal and dominance, this latter defined as the perceived degree of control one is able to exert over that emotional state. The IAPS was the first standardized database of emotional stimuli, and its major strength lies in its widespread usage. Indeed, the large diffusion of the IAPS made it the golden standard for experimental induction of emotions, especially in the field of psychophysiology and neuroscience, contributing to its continuing cross-validation. Moreover, IAPS slides provided solid grounds for interesting studies aiming at understanding the interaction between affective and attentive processes, and the contribution of basic perceptual information in the generation of emotional responses. On the other hand, its vast diffusion might represent also a limit of the field. Indeed, considering that emotions in the lab are increasingly operationalized as the affective reactivity prompted by the view of IAPS slides, it might lead to neglect the inherent limits of this database. In general, the most common criticism to the IAPS is represented by the lack of uniformity in the quality of the pictures included and by the limited control of the number and types of the categories included. Another limit is that some pictures, mostly threatening and erotic pictures, are heavily influenced by the cultural norms of the time in which they were originally selected (1970's and 1980's), resulting obsolete and insufficient for affective induction when used today.

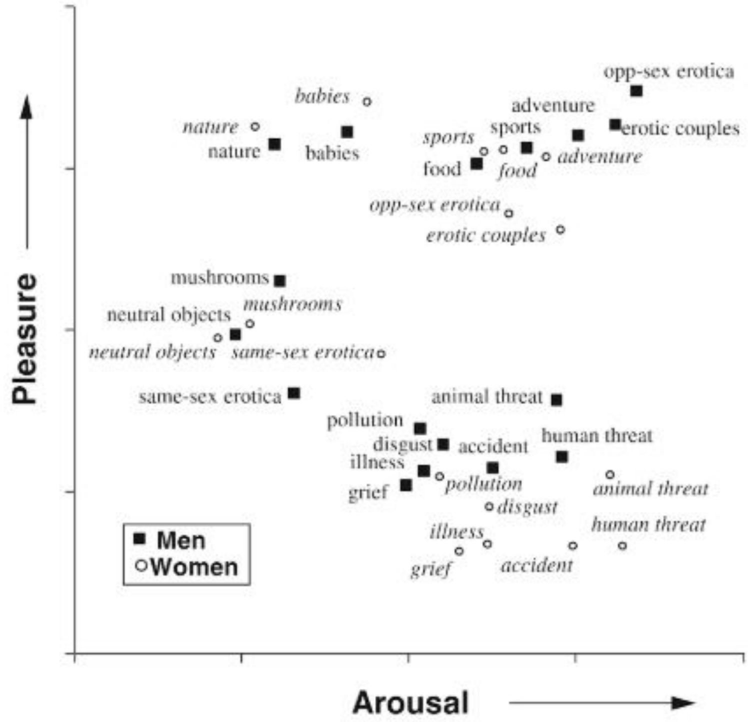

Figure 2.1 Affective space of the IAPS. Distribution of the images comprised in IAPS along the two-dimensional valence-arousal affective space, divided per gender and picture content. (Adapted from Lang and Bradley, 2007)

In recent years, alternatives to the IAPS have been developed with the aim to overcome the aforementioned limitations. One of the most comprehensive collection of affective images is the Nencki Affective Picture System (NAPS), which includes 1,356 high-resolution color images arranged in five categories, namely people, faces, animals, objects, and landscapes (Marchewka, Zurawski, Jednoróg, & Grabowska, 2014). The images were validated along valence and arousal dimensions, as in the IAPS, plus a third approach-avoidance dimension. The major strength of the NAPS is represented by the high number of pictures included, which favors its usage in experiments that require an elevated number of repetitions (i.e. ERPs, fMRI), and their being recent and in high resolution. Nevertheless, the major limitation of the NAPS is represented by the lack of highly pleasant and highly arousing images. Thus, in order to overcome this, the authors introduced a specific subset of images, the NAPS-ERO, comprising only erotic images (Wierzba et al., 2015). This set is characterized by the inclusion of new erotic material, updated to current cultural norms, and adapted to both genders and different sexual orientations, providing an optimal alternative to IAPS erotic images.

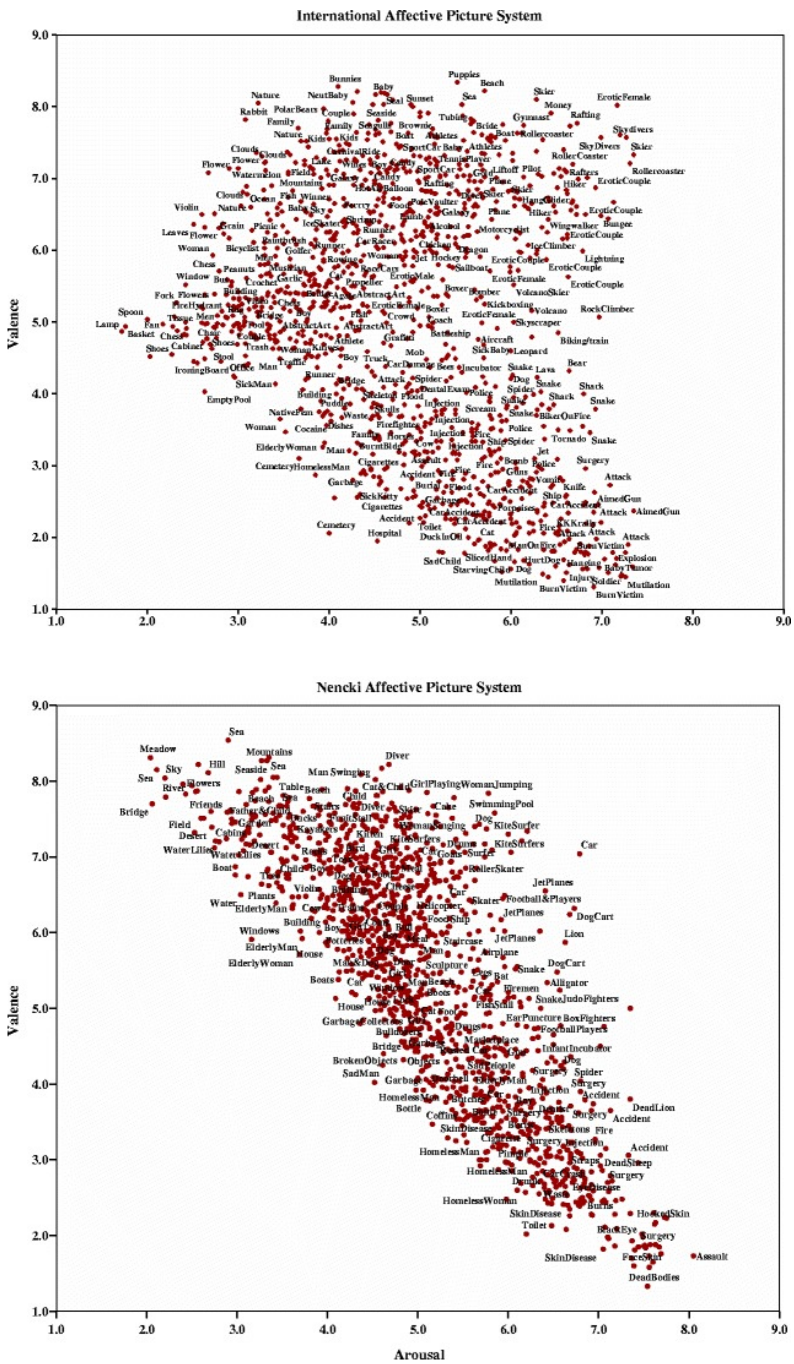

Figure 2.2 Comparisons of the affective space distribution of the IAPS (top panel) and NAPS (bottom panel). (Adapted from Marchewka et al., 2014)

Finally, an even newer database of emotional pictures, named OASIS (Open Affective Standardized Image Set), has been published very recently (Kurdi, Lozano, & Banaji, 2017).

This new database comprises 900 pictures selected from four different categories (animals, objects, people, and scenes) evaluated along valence and arousal dimensions. Although in term of image quality the pictures included in OASIS are not superior to the ones included in the IAPS, they have the unique feature of being free of any copyright.

In the context of affective images, it is also necessary to mention a specific class of picture databases, that is databases including only images of emotional faces. Originally, the first collection of emotional facial expression was the Ekman's POFA (Picture Of Facial Affect) (1976), which has been widely used in experiments focusing on emotion recognition, as well as on the social influence of facial displays of emotions. Despite its diffusion this collection is limited by several factors, first and foremost the inclusion of greyscale images only and the limited number of individuals portrayed. Both these limitations have been overcome by a newer set named KDEF (Karolinska Directed Emotional Faces) which was built with the explicit purpose of providing researchers with an updated and more versatile set of pictures, depicting 7 emotional expressions in both genders under the same conditions (Lundqvist, Flykt, & Öhman, 1998). Unfortunately, an important element not addressed in neither of this picture sets is the ethnic diversity of the people portrayed, which is instead the major focus of the NimStim database. The NimStim is one of the most comprehensive collection of standardized pictures of emotional expressions, including facial expressions across a vast range of ethnic groups (African-American, European-American, Asian-American and Latino-American).

2.2 Sounds and Music

Auditory perception represents a rapid, precise and effective mechanism that helps the brain to map the external world by its sounds. Hence, it is not surprising that sounds very often carry to the listener's ear (and brain) emotional information and trigger an affective reaction. These unique properties have been exploited for long in the context of emotional induction, but compared to visual images, the use of auditory material has been less structured. It is possible to distinguish two approaches in the use of auditory stimuli for emotions elicitation. One strategy is founded on the use of natural sounds that are associated with specific events, thus with a clear emotional meaning. Another approach consists instead in the use of human-made musical pieces, often derived from the classical music repertoire.

The International Affective Digitized Sound (IADS) system (Bradley & Lang, 2007) is the largest collection of emotional sounds available for experimental use. It includes 111 sounds of varying nature, like animals' calls (i.e. a dog growling) or baby crying, and was developed according to the same theoretical principles that guided the development of the IAPS, that is a dimensional view of emotional phenomena founded on the three dimensions of valence, arousal and dominance, although an analysis of the affect elicited in terms of emotional categories has also been published (Stevenson & James, 2008). This database was originally developed to capture the unique contribution of sounds in the generation of an affective response in everyday life, in which vision and hearing interact (Bradley & Lang, 2000). Analysis of self-report and subjective emotional evaluation showed that, in general, the affective profile prompted by sounds does not differ drastically from the one elicited by the view of emotional slides, even if the overall emotional modulation seems to be weaker (Bradley & Lang, 2000). Nevertheless, it is interesting that, for some specific combination of sounds and pictures, the results showed a dissociation across the two sensory domains. This is the case of bees, which are rated as affectively neutral when presented as a visual stimulus while are judged to be unpleasant and arousing when their buzzing is presented (Bradley & Lang, 2000).

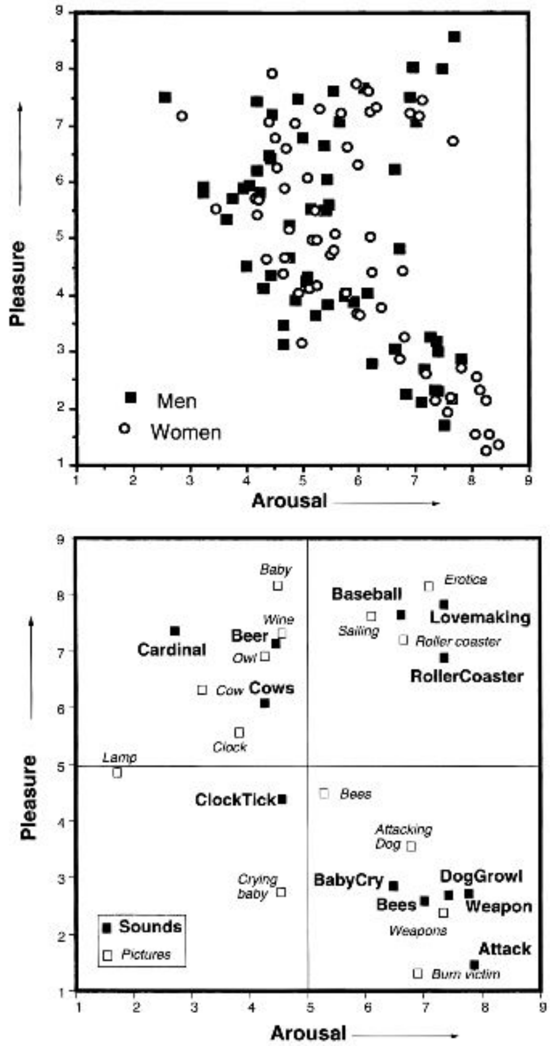

Figure 2.3 Characterization of the IADS database. Top panel shows the distribution of the ratings, separated per gender, for valence and arousal. Bottom panel shows the distribution of both IADS and IAPS stimuli in the affective space, highlighting that for some semantic context the ratings are very similar across domains, while for others there is a dissociated response toward visual and auditory stimuli. (Adapted from Bradley and Lang, 2000)

Emotion elicitation trough music listening is another very successful approach for mood induction by means of auditory stimuli. Characterization of music-induced emotions has a long tradition (Zentner, Grandjean, & Scherer, 2008), and songs have been especially used for the elicitation of complex affective states (Feldmann-Barrett et al., 2010; Scherer, 2004), like nostalgia, which are not easily evoked using natural sounds or static images. Indeed, the dynamicity of songs is the prominent feature that drives the emotion, with negative valenced affect arising from low pitch, slow tempo, and minor mode, while major mode and high pitch is linked with positive mood (Västfjäll, 2001). Unfortunately, for what concerns the use of music, there are not equivalent databases of songs for emotional induction, that can allow the selection of specific stimuli for each experiment. The absence of this kind of standardization seriously limits the use of this technique, despite the interest that music-elicited emotions arise in affective scientists (Scherer, 2004).

2.3 Emotional Movies

The use of movies for emotion elicitation has been constantly rising in recent years but it is an experimental approach that spans several decades of research (Rottenberg, Ray, & Gross, 2007). The unique contribution of movies in the mechanism of emotion elicitation is represented by the use of dynamic display of images, usually combined with sounds and music. This combination allow the researcher to take advantage of the power of both visual and auditory stimuli within a continuous narrative that makes the viewer feeling immerged, thus increasing the naturalism of the affective experience prompted (Rottenberg et al., 2007).

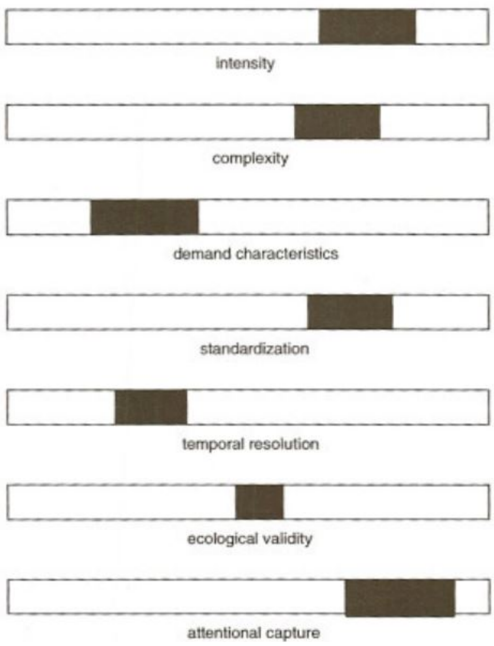

Figure 2.4 Efficacy of film clips as an emotion elicitation procedure. The image summarize the strengths (and the weaknesses) of film clips for mood induction, characterizing their potential along different dimensions. (Adapted from Rottenberg, Ray and Gross, 2007)

At the beginning of the use of movies in emotion science, researchers often relied on one or few movies, usually selected based on informal rules and tailored for the specific experiment. This limited a wider diffusion of this technique, despite its efficacy. Progressively, the need for standardized stimuli laid the foundations for the first efforts to systematize a selection of emotional movies (Philippot, 1993), and today the success of film clips as a technique for mood induction largely depends on the availability of multiple standardized databases.

In term of diffusion, the Gross and Levenson's (1995) film collection (revised and updated in Rottenberg et al., 2007) is the most used. It was developed according to a categorical perspective of affective phenomena, and includes 16 film clips, selected for their ability to elicit effectively and discretely seven different emotional states (Amusement, Contentment, Sadness, Anger, Disgust, Surprise and Fear). The advantage of this database lies in the extensive validation received in more than two decades of use but has two important limits: the first is represented by the low number of clips included, and the second by the fact that the clips are selected from old movies, thus they might be potentially unsuited for younger participants. This latter problem has been partially overcome by newer collections of film clips, like the one developed by Gabert-Quillen and colleagues (2015), which nevertheless suffers from the limit of the inclusion of only a limited number of excerpts (eighteen). A larger database is the one presented by Schaefer and colleagues (2010). In this work, the authors provided a large collection of 70 clips rated along both affective dimensions (i.e. positive and negative affect) and multiple emotional categories. Interestingly, each clip was also rated in term of the ability to elicit the so called "mixed-emotions", namely complex affective states that can be considered as blends of some basic emotions. The idea of mixed-affect has been further extended in a recent work by Samson and colleagues (2015). In this work, the authors collected ratings of positive, negative and mixed feelings for 133 short clips

(22-30 seconds in length), providing the first comprehensive database of videos for elicitation of mixed emotional states, specifically the emotional mixture of positive (amusement) and negative affect.

Finally, an interesting work is the Emotional Movie Database (Carvalho, Leite, Galdo-Álvarez, & Gonçalves, 2012), which includes 52 film clips rated along valence and arousal dimensions. The EMDB is the only available film set explicitly standardized adopting a dimensional view of affect and, more importantly, validated not only in terms of self-report of emotional experience but also using a psychophysiological assessment of the affective reactivity of the viewer. To make their clips suited for psychophysiological experiments, the authors placed emphasis on controlling the duration of the clips, which last 40 seconds each, which is a unique feature of this database compared to the others. On the other hand, the EMDB has a major issue represented by the inclusion of clips without soundtrack. Although, it allows the researcher to independently manipulate the auditory system, for instance presenting startle probes superimposed with the clips, this feature might reduce the overall effectiveness of the clips in eliciting a strong emotional experience, considering the decisive contribution of the score to boost the affective potential of a movie (Cohen, 2001). Generally speaking, each of the available databases has its own strength and limitations, which mostly concern the categories of film included and the characteristics of the clips (i.e. duration, audio track). This highlights the need for further efforts in exploring new paths and broadening the number of film sets for emotional induction, in order to take a full advantage of the power of movies for mood induction.

Chapter 3

Aim of the project

Despite the interest and the growing research efforts, emotion science is still in its infancy for what concerns the understanding of the neural mechanisms that give rise to the complex emotions occurring in everyday life. One of the most critical issue of the current approach of affective neuroscience is represented by the use of oversimplified experimental models of human emotions, sacrificing naturalism and ecology for an easy-to-control experimental setting. This limit also seriously impacts the investigations of empathy and its interaction with affective processes. The aim of the following experiments is to contribute to overcoming this limit, adopting an experimental approach of emotion elicitation trough films able to recreate in the laboratory a naturalistic experience of emotions. This represents the essential condition for an accurate understanding of emotions from a neuroscientific perspective.

Thus, the starting point of the present work is represented by the development of a new comprehensive database of emotional film clips, the first in Italian language, explicitly designed for use in psychophysiology and neuroimaging. This database should be able to fill the gaps present in the sets currently available, thus providing a new tool for exploring the physiological substrate of affective experience, especially its neural basis. Indeed, this work will present the investigation of the differential brain activity associated with different affective states. Although there is a growing literature showing how the brain process complex and dynamic stimuli like film clips, there are very few studies that aimed at characterizing how this brain activity is affected by the emotional content of the movie itself. Finally, considering the deep tie between emotional experience and individual differences in empathy, and the unique characteristics of movie clips that make them an ideal tool to probe empathic reactions to others emotion, this work will investigate, in two separate studies, how people selected for having extreme high empathy and high emotional detachment traits differ in their subjective and neural reaction to affective movies, from people with low expression of these traits.

Chapter 4

STUDY 1: E-MOVIE-Experimental MOVies for Induction of Emotions: an innovative database of film clips with normative data and sex differences.

4.1 Abstract

The need for a validated set of emotional clips to elicit emotions in more ecological experiments is increasing. Here we present the validation of a new database of emotional films, named E-MOVIE, which includes, 39 excerpts arranged in six categories, Erotic, Fear, Sadness, Neutral, and the new Scenery and Compassion. The clips of the database are characterized by homogenous durations of approximately two minutes, which make them suitable for psychophysiological research. In order to study the affective profile prompted by each category 174 participants (112 women) rated the movies on multiple dimensions. Erotic clips were effective in the elicitation of a positive emotional state, characterized by high levels of arousal and excitement. On the other hand, Fear clips (selected without blood to avoid disgust reaction) prompted an affect characterized by high arousal, low valence and high levels of reported fear and anxiety. Women reported greater unpleasantness, distress, anxiety and jittery than men to the three negative categories. Compassion clips, characterized by the depiction of crying characters, was able to induce an affective state dominated by sadness and feeling touched, consistent with an empathic reaction to emotional sufferance. Sadness clips, instead, elicited an affective state characterized by sadness together with distress and angst. We also demonstrated that clips depicting natural environments (i.e. Scenery) prompted in the viewer a surprised, inspired affective state, characterized by high valence and arousal (especially in males), a result which suggests that their past categorization as neutral stimuli was inaccurate and problematic.

4.2 Introduction

The induction of an emotional state in the lab represents a long-standing issue in the investigations of human emotions (Rottenberg et al., 2007). A critical aspect, faced by experimenters in this field, concerns the need to find a balance between the psychometric control of the main perceptual variables (brightness, color, sound level, sound tone, duration, etc.), and the ability to induce an effective, ecological and spontaneous emotion in the lab. There are many different methods available for emotion induction, each with advantages and limitations, and these are: emotional imagery, presentation of visual stimuli (slides and videos), presentation of sound or music, recollection of autobiographical memories and, more recently, virtual reality (Bradley & Lang, 2007; Felnhofer et al., 2015; Lang et al., 1999; P J Lang, Kozak, Miller, Levin, & McLean, 1980; Zentner et al., 2008)

Affective pictures are one of the most widely used tool, comprising many important characteristics that made its usage widespread. Pictures are indeed a class of stimuli very easy to implement in an experiment, providing the experimenter with the flexibility to switch between different presentation paradigms. They can be used in a great variety of experimental designs, from simple passive viewing to more complex designs, in which slide presentation is mixed with other tasks. Moreover, they put low demand to participants, making easy their use with different populations (i.e. children, clinical samples). Another useful feature of pictures is that they provide to experimenters the ability of controlling the perceptual characteristics of the stimuli, and even to experimentally manipulate them(De Cesarei, Loftus, Mastria, & Codispoti, 2017), thus allowing a great overall control. Finally, it is important to acknowledge that the great diffusion of pictures as a mean of emotion elicitation is due to the great availability of validated databases of pictorial stimuli, such as the universally acknowledged

International Affective Pictures System (Lang et al., 2008), POFA (Ekman & Friesen, 1976), KDEF (Lundqvist et al., 1998), NAPS (Marchewka et al., 2014).

Nevertheless, images have some important limitations that can be surpassed by other methods. One of the most critical shortcomings of pictures is that they are static, therefore the affective experience prompted by picture viewing is neither strong, nor ecological enough compared to that induced with a dynamic modality, such as video presentation (Westermann, Stahl, & Hesse, 1996).

Indeed, film clips allow a multimodal stimulation of the viewer, with a simultaneous and coherent engagement of both the visual and the auditory sensory systems. In the context of mood induction, they are suitable for elicitation of basic emotions, like Fear or Disgust, as well as for the induction of more complex feelings (Rottenberg et al., 2007; Schaefer et al., 2010). Furthermore, the recent diffusion of modern video editing software applications has made very easy to select and edit video clips for experimental use.

Two seminal works in this field have been done by Philippot (1993) and Gross and Levenson (1995), who first systematically investigated the effectiveness of movie excerpts for emotional induction and built a validated dataset of stimuli. Their works have been followed in recent years by new efforts for providing extended, wider, and updated datasets of short movies (Gabert-Quillen et al., 2014; Gilman et al., 2017; Jenkins & Andrewes, 2012; Rottenberg et al., 2007; Samson et al., 2015; Schaefer et al., 2010; von Leupoldt et al., 2007). Each of this dataset has distinct strengths, aiming at filling the gap in the availability of standardized stimuli, which has limited the application of this method. The present work sought to contribute to this process, by focusing on those aspects in emotional film validation that, so far, received less attention.

A review of the existing libraries of film clips shows that there is a wide variability in the duration of the stimuli included, with clips lasting less than a minute (Carvalho et al., 2012;

Samson et al., 2015) to clips with durations of over seven minutes (Schaefer et al., 2010). What is more surprising is that this variability is large within most of databases (Gross & Levenson, 1995 ; Hewig et al.,2005;Schaefer et al., 2010). This inconsistency is due to the fact that different films are able to elicit the same target affect in different ways (i.e. different plots, different scenes, different soundtracks), leaving researchers with stimuli which vary in their duration. Moreover, some emotions could arise from very brief stimulation, like Disgust or Fear, while secondary, complex emotions, characterized by lower biological relevance, need more time to develop (e.g. disappointment). Although this is a minor issue for those studies based on self-report evaluation only, large variations between the experimental stimuli may lead to a problematic interpretation of the results, and this is particularly true in the field of psychophysiology and neuroscience (in which having stimuli with equal or, at least, comparable durations represents an essential requirement).

For what concerns the optimal duration of an emotional stimulus there are no clues in the literature, and past authors did not explicitly address this issue when building their sets. Since there is no clear criterion for deciding how long should last a stimulation for eliciting an emotion, most authors of past databases used, as proper duration, the integrity of the scene, a choice which led to the quoted large variability of film duration within many databases. Here we decided to include only clips with completed scenes of approximately two minutes duration, according to a theoretical perspective that views the emotional experience as a phasic phenomenon superimposed to a tonic affective state (Rottenberg et al., 2007). Such duration should be long enough to provide the viewer with an understanding of the plot, leading to a coherent and stable change of his/her affective state. Shorter clips (i.e. one minute or less) may not be long enough to induce a complex emotion, engage the attention of the viewer and making possible the process of “willing suspension of disbelief” (Frijda, 1989; Rottenberg et al., 2007), which is critical for the ecology of the emotional experience achieved through film watching. On the other hand, using longer clips (i.e. three minutes or more) may increase the difficulty to disengage from the stimulus, thus prompting carryover effects on the following excerpts within the experimental paradigm. In addition, using longer excerpts could potentially impact the number of stimuli employed in an experimental paradigm with multiple clips, hence reducing the generalizability of the results.

Another critical issue addressed in the present work regards the film categories that should be included and their target affective states. Most of the available databases generally include stimuli selected from thriller and horror movies in order to elicit Fear and Disgust, covering the spectrum of the negative affect. On the other hand, less agreement has been found in the selection of film categories for the elicitation of positive emotions. The general approach adopted so far was the inclusion of clips extracted from film comedies and/or stand-up comedy, in order to target positive affective states most commonly reported as Joy, Happiness and Amusement. This selection strategy of existing database has been developed within the theoretical framework of the "basic emotion theory" (Ekman, 1992). Nevertheless, there are some exceptions like the work of Samson and colleagues (2015) which relied on a simpler classification among positive, negative and mixed emotional states, and the work of Carvalho and colleagues (2012) which was based on a dimensional view of emotions.

In the present research, we sought to build a dataset including film categories able to cover the spectrum of both positive and negative affective states and to introduce some new categories that have rarely or never been considered. In general, very homogenous categories have been developed to avoid cross-contamination among different emotions underlying confounded/borderline categories (see e.g. below past research on Fear often confounded with Disgust).

Concerning the range of negative emotions, we decided to include the categories of Fear, Sadness and Compassion. In the past, clips selected to elicit Fear consisted of scenes characterized by tense and threatening situations that are often accompanied by the depiction of violence, blood and/or mutilation. Although these clips are very powerful in eliciting an affective reaction in the viewer, there is evidence that stimuli characterized by the depiction of blood and wounds elicit a large overlapping between the feelings of Fear and Disgust (Schaefer et al., 2010), thus reducing the homogeneity of the selected category. Moreover, it was repeatedly proven that stimuli depicting blood and mutilation represent a category which prompt very distinctive physiological reactions (Palomba, Sarlo, Angrilli, Mini, & Stegagno, 2000; Sarlo, Buodo, Poli, & Palomba, 2005), therefore including clips featuring these kind of elements could lead to confounded emotions and, eventually, bias the results. Thus, we decided to focus exclusively on clips able to elicit feelings of fear and anxiety related to the anticipation of a threat, without the depiction of violence and blood, and aiming at inducing a “pure” fear experience.

Sadness is another category that has consistently been included in previous validations, usually comprising clips depicting scenes of grief and loss, whose typical feature is the representation of one or more crying characters. Here we aimed to operate a finer distinction within the broad category of sadness-eliciting clips, by retaining in the Sadness category clips featuring themes of loneliness and helplessness, while the selection of excerpts featuring scenes of characters crying for a loss or a separation to a novel category, was defined Compassion. Crying is a behavior evolved to communicate distress to others, seeking for help and prompting a motivated approach (Gross, Fredrickson, & Levenson, 1994; Hendriks, Croon, & Vingerhoets, 2008; Hendriks & Vingerhoets, 2006), therefore clips depicting crying scenes are expected to evoke feelings of sadness through a mechanism of emotional resonance (Decety & Meyer, 2008), which also determines feeling of compassion, empathic concern and prosocial tendency. Instead, clips featuring scenes of loneliness, without showing any crying character, will prompt a sad emotional state, characterized also by angst and distress, but relatively less empathy for others.

For what concerns the elicitation of positive emotions, we decided to include the Erotic and Scenery categories. Stimuli depicting erotic scenes have been largely used in past research, with both pictures and films, as a powerful source of pleasant and high arousal emotional state, that could be considered as a complement to the affect elicited by threatening stimuli(Bianchin & Angrilli, 2012; Margaret M. Bradley, Codispoti, Sabatinelli, & Lang, 2001; Codispoti, Surcinelli, & Baldaro, 2008; Stevens & Hamann, 2012; Wierzba et al., 2015). Interestingly, while erotic clips have been widely used in past isolated studies on emotions as single non validated strong positive stimulations, previous standardized and validated datasets of film clips for emotional induction largely neglected this category of contents, with the exception of the work of Carvahlo and colleagues (2012).

Unlike erotic scenes, clips depicting natural landscapes (we termed them "Scenery") have been already included in other databases (Carvalho et al., 2012; Rottenberg et al., 2007), but they have been used as clips inducing a Neutral condition. Here we argue against this definition and use, after analyzing the growing body of research(Hartig, Evans, Jamner, Davis, & Gärling, 2003; Johnsen, Rydstedt, & Rydstedt, 2013; Kaplan, 1995; Ulrich, 1981; Ulrich et al., 1991; van den Berg, Koole, & van der Wulp, 2003) that showed that exposure to natural environments and landscapes, both direct and indirect (like exposure trough pictures and videos), has a positive effect on mood, emotional well-being and facilitates recovery form stressful events. Therefore, in the light of past evidence, using these stimuli as affectively neutral category seems inappropriate. They should rather be considered as elicitors of positive affect. Starting with the mentioned analysis of past literature and dataset we have developed and validated a first set of 39 clips divided into six homogenous emotional categories.

4.3 Method

Participants

One hundred and seventy-four students from University of Padova (112 females and 62 males) were enrolled in this study, in different phases and classes, in exchange of credit courses or monetary reward (13 €). Mean age of the sample was 21.3 years (s.d. = 2.6 years). The investigation was approved by the local Ethics Committee, has been conducted according to the principles expressed in the Declaration of Helsinki and all the participants gave their written consent to participate in the study.

Stimuli

Thirty-nine excerpts from commercial motion pictures have been selected and edited for being included in our validation sample according to several criteria: 1) lasting approximately two minutes, 2) providing a consistent and easily to understand development of the plot (without sudden changes or transitions), 3) showing the most arousing part of the clip in the second minute, 4) to form highly homogenous categories of clips. The clips were a-priori divided into six categories of interest, thus the sample was arranged as showed in Table 1.

All the selected clips were presented with their original audio in Italian language, with the exception of Scenery clips which were presented with a musical soundtrack. It is worth to acknowledge that, although some of the clips here included have been a-priori selected without looking at past literature, a few of them resulted to be already present in other databases (Carvalho et al., 2012; Gross & Levenson, 1995; Schaefer et al., 2010). However most of the clips of E-MOVIE are new in the literature, especially the excerpts included in the Erotic and Scenery categories.

A single, continuous, clip was obtained after editing the excerpts with Adobe Premiere CS5, with a final resolution of 1280x720 pixels. Within the final clip, the order of the excerpts was pseudo-randomized, namely there were no two consecutive excerpts belonging to the same category.

FILM	CATEGORY	VALENCE	AROUSAL
Lust [1]	*EROTIC*	M = 6 (1.4) F = 5.3 (1.7)	M = 5.2 (2) F = 5.6 (2.3)
Lust [2]	*EROTIC*	M = 5.7 (1.7) F = 4.8 (2)	M = 5.7 (1.8) F = 5.6 (2.1)
Monster's Ball	*EROTIC*	M = 6.8 (1.3) F = 5.7 (1.7)	M = 6.1 (2) F = 5.7 (2.2)
The Notebook	*EROTIC*	M = 6.3 (1.2) F = 6.7 (1.6)	M = 5.2 (1.7) F = 6.2 (1.7)
Underworld	*EROTIC*	M = 6.4 (1) F = 6.2 (1.4)	M = 4.6 (2) F = 5.1 (2.2)
Supernatural	*EROTIC*	M = 6 (1.2) F = 6.2 (1.3)	M = 4.1 (1.9) F = 5.1 (2)
40 Days and 40 Nights	*EROTIC*	M = 6 (1.7) F = 6.4 (1.6)	M = 4.5 (1.9) F = 5.2 (2)
Bbc's Planet Earth: Seasonal Forests	*SCENERY*	M = 6.5 (1.6) F = 6.3 (1.4)	M = 4.5 (2.3) F = 3.4 (2.4)
Bbc's Planet Earth: Deserts	*SCENERY*	M = 6.2 (1.6) F = 5.8 (1.4)	M = 4.9 (2.4) F = 4.2 (2.5)
Bbc's Planet Earth: Fresh Water	*SCENERY*	M = 6.7 (1.5) F = 6.7 (1.5)	M = 4.9 (2.5) F = 4.3 (2.4)
Bbc's Planet Earth: Mountains	*SCENERY*	M = 6.6 (1.7) F = 6.1 (1.6)	M = 5.1 (2.2) F = 3.9 (2.6)
SPACE	*SCENERY*	M = 6.5 (1.7) F = 6.4 (1.5)	M = 4.8 (2.6) F = 4.4 (2.5)
Bbc's Great Barrier Reef	*SCENERY*	M = 6.9 (1.7) F = 7.2 (1.5)	M = 4.5 (2.5) F = 4.4 (2.3)
The Road	*SADNESS*	M = 3.7 (1.8) F = 2.8 (1.6)	M = 4.8 (2.1) F = 4.3 (2.3)
Blood Diamond	*SADNESS*	M = 4.9 (1.6) F = 4.1 (1.6)	M = 4.2 (2.1) F = 4.8 (2.1)
K-19	*SADNESS*	M = 3.7 (1.3) F = 3.3 (1.4)	M = 4.3 (2) F = 4.2 (2.2)

Million Dollar Baby [1]	*SADNESS*	M = 3.4 (1.5) F = 2.7 (1.6)	M = 4.3 (2.1) F = 4.7 (2.5)
Million Dollar Baby [2]	*SADNESS*	M = 3.1 (1.3) F = 2.2 (1.3)	M = 4.7 (2.1) F = 5.1 (2.4)
The Hours	*SADNESS*	M = 2.6 (1.7) F = 3.5 (1.9)	M = 5.7 (2) F = 6.8 (2)
The Champ	*COMPASSION*	M = 3.2 (1.6) F = 2.3 (1.5)	M = 4.4 (2.1) F = 5.1 (2.1)
My Girl	*COMPASSION*	M = 3.4 (1.4) F = 2.2 (1.2)	M = 3.9 (2.1) F = 5.3 (2.3)
Lost	*COMPASSION*	M = 3.4 (1.7) F = 2.7 (1.8)	M = 4.6 (2.1) F = 5.2 (2.2)
Pearl Harbor	*COMPASSION*	M = 3.4 (1.6) F = 2.5 (1.5)	M = 4.8 (2.2) F = 4.7 (2.3)
Armageddon	*COMPASSION*	M = 4.1 (2) F = 3.5 (2)	M = 5.3 (2.2) F = 5.4 (2.3)
The Pursuit Of Happiness	*COMPASSION*	M = 3.2 (1.6) F = 3.3 (2.1)	M = 5.1 (2.1) F = 5.6 (2.3)
The Others	*FEAR*	M = 4.4 (1.8) F = 3.4 (1.4)	M = 4.9 (2.1) F = 5.7 (2.2)
The Sixth Sense	*FEAR*	M = 3.3 (1.8) F = 2.2 (1.4)	M = 5.4 (2) F = 6 (2.3)
Deep Red [1]	*FEAR*	M = 4 (1.6) F = 3.2 (1.6)	M = 4.5 (2.3) F = 5.5 (2.4)
Deep Red [2]	*FEAR*	M = 4.2 (1.7) F = 3.8 (1.5)	M = 4.4 (2.1) F = 4.1 (2.5)
Gothika	*FEAR*	M = 3.3 (1.5) F = 2.5 (1.5)	M = 5.3 (2) F = 6.2 (2.2)
The Silence of The Lambs	*FEAR*	M = 3.7 (1.4) F = 2.8 (1.4)	M = 4.7 (2.1) F = 5.4 (2.4)
Vacancy	*FEAR*	M = 3.7 (1.8) F = 2.6 (1.7)	M = 5.3 (2.2) F = 6.7 (2.3)
Globe Trekker's London City Guide	*NEUTRAL*	M = 5.3 (1.3) F = 5.3 (1.4)	M = 3.3 (1.9) F = 2.9 (2.1)
Globe Trekker's New York City Guide	*NEUTRAL*	M = 5.1 (1.2) F = 5.4 (1.4)	M = 3 (2) F = 2.7 (2.3)
Globe Trekker's Paris City Guide	*NEUTRAL*	M = 5.1 (1.2) F = 5.3 (1.2)	M = 2.6 (1.8) F = 2.6 (2.1)
Italian Documentary: Bronte	*NEUTRAL*	M = 4.5 (1.6) F = 4.9 (1.3)	M = 2 (1.3) F = 2 (1.7)

Italian Documentary: Pietraperzia	*NEUTRAL*	M = 4.7 (1.3) F = 5 (1.2)	M = 2 (1.5) F = 1.9 (1.6)
Italian Documentary: Calamonaci	*NEUTRAL*	M = 4.6 (1.8) F = 4.7 (1.3)	M = 2.2 (1.7) F = 2 (1.6)
Italian Documentary: Quartesolo	*NEUTRAL*	M = 4.5 (1.5) F = 5 (1.2)	M = 1.9 (1.3) F = 2.1 (1.7)

Table 4.1 List of film clips with corresponding mean and standard deviation for valence and arousal, divided by gender.

Procedure

Participants were tested in groups in different session, with each session comprising a group of no more than 40 participants. Participants were separated with an empty seat in order not to invade the privacy of the neighbors. Furthermore, males and females were tested separately, in order to avoid socially related confounds, especially due to the sensitive nature of some clips (i.e. the Erotic category) in which gender differences are known (Costa, Dinsbach, Manstead, & Ricci Bitti, 2001; Maffei, Vencato, & Angrilli, 2015). Each session started with an introductory clip, that comprised four excerpts (not included in the experimental sample) resembling the categories under investigation. The first clips served to make the participants familiar with both the kind of movies they were going to watch and the questionnaire they were requested to complete after each clip. At the end of the trial phase, the experimental clips were presented as a continuous randomized stream of clips with 20 s intervals for the evaluation. Each session lasted for approximately two and a half hours.

Emotional Assessment

After each clip, participants were required to fill an inventory which included several analogue and likert scales, selected in order to cover a broad spectrum of information about their emotional experience. The inventory was divided in three sections: the first included a paper-and-pencil version of the *Self-Assessment Manikin* (Bradley & Lang, 1994), in which participants were asked to rate the pleasantness of the emotional state elicited by the clip and the arousal felt during the viewing. The second section consisted of a Basic Emotions evaluation, in which participants were presented with a list of six basic emotions (Fear, Sadness, Rage, Disgust, Joy and Surprise) plus a Neutral item and they were asked to rate the degree of each emotion felt on a 9-points Likert scale. In the third section of the inventory, participants were asked to evaluate the clip using a list of 11 emotional adjectives, selected in order to encompass a broad span of positive and negative feelings, and to indicate on a 5 point Likert Scale how much of the listed Emotional Adjectives they fitted with. In addition, participants were also requested to indicate if they had previously watched the clip (Familiarity score).

Statistical Analysis

Subjects' responses were collapsed for each film category and were analyzed with a series of repeated-measures ANOVAs. For the analysis of SAM and Emotional Adjectives ratings, ANOVAs were designed with one within-subjects factor (Film category) and one between-subjects factor (Sex). For the analysis of the Basic Emotion evaluation, two within-subjects factor (Film category and Emotion) and one between-subjects factor (Sex) were included. Due to problems in data collection, sample size for three emotional adjectives (Sad, Anxious and Enchanted) and for the Basic Emotion evaluation was 134 (79 women). When appropriate, the reported p-values are corrected with the Greenhouse-Geisser procedure. Significant effects were further explored using Newman-Keuls post-hoc test with a significance level set at $p<0.05$.

In order to analyze the impact of Familiarity (i.e. having seen previously the clip) on perceived Valence and Arousal, we carried out a series of Welch's t-test (Welch, 1947) on valence and arousal ratings using familiarity as a predictor. In order to handle the large difference found on familiarity score for the clips, we tested only a subgroup of clips which have been seen previously by at least 15 participants. With this criterion, 19 clips surpassed the Familiarity threshold and a statistical test was computed on Valence and Arousal ratings by comparing participants who found the clip familiar with those who did not.

4.4 Results

SAM

ANOVA on Valence revealed both Film Category ($F_{(5,860)}$ = 357.97, p<0.0001, η^2_p = 0.67) and Sex ($F_{(1,172)}$ = 19.45, p<0.0001, η^2_p = 0.10) significant main effects. Furthermore, also the interaction of the two factors was significant ($F_{(5,860)}$ = 8.08, p<0.0001, η^2_p = 0.04). Post-hoc analysis of the interaction term revealed significant differences, for both males and female participants, among Erotic, Scenery and Neutral clips and between these categories and the three negative ones (Sadness, Compassion and Fear), which instead were not differentiated by the valence judgments. In both genders, Scenery clips were perceived as more pleasant than the Erotic ones. Furthermore, gender differences were found between judgments on the three negative film categories, with women reporting lower Valence (more unpleasantness) during the viewing of these films compared to men.

ANOVA on the Arousal ratings showed a significant effect of Film Category ($F_{(5,860)}$ = 135.87, p<0.0001, η^2_p = 0.44) and a significant Film Category*Sex interaction ($F_{(5,860)}$ = 7.34, p<0.0001, η^2_p = 0.04). Post-hoc test on the Film main effect showed that Erotic and Fear clips scored highest while Neutral clips scored lowest on arousal ratings. Post-hoc analysis of the interaction revealed a different pattern between the sexes, with men reporting the same significant higher level of arousal for all the affective categories compared with the Neutral one, while women, during Erotic and Fear excerpts, experienced higher arousal levels with respect to Scenery, Neutral and Sadness clips. Also Scenery and Sadness elicited higher arousal than the Neutral category. Finally, men judged Scenery clips as more arousing than women did.

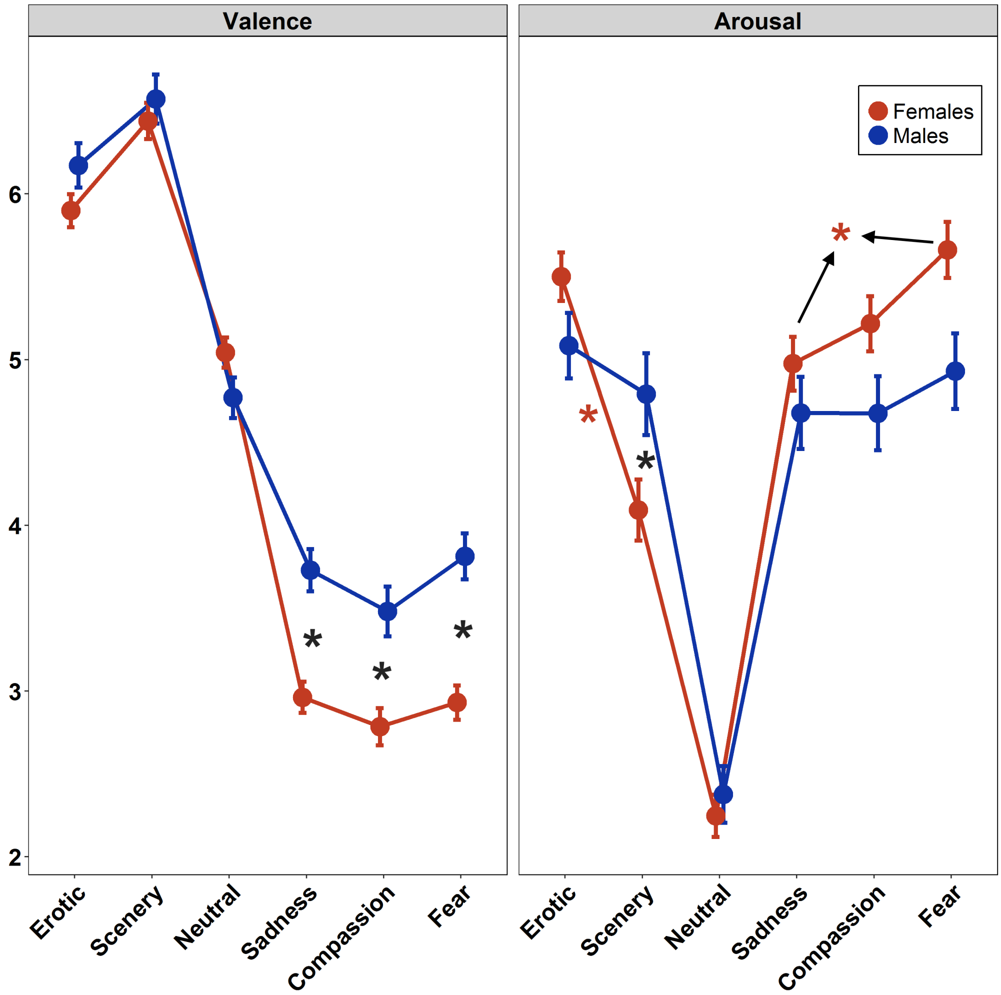

Figure 4.1 Effect of film categories on self-reported valence and arousal. Asterisks indicate significant ($p < 0.05$) post-hoc effect. Bars represent Standard Error (SE)

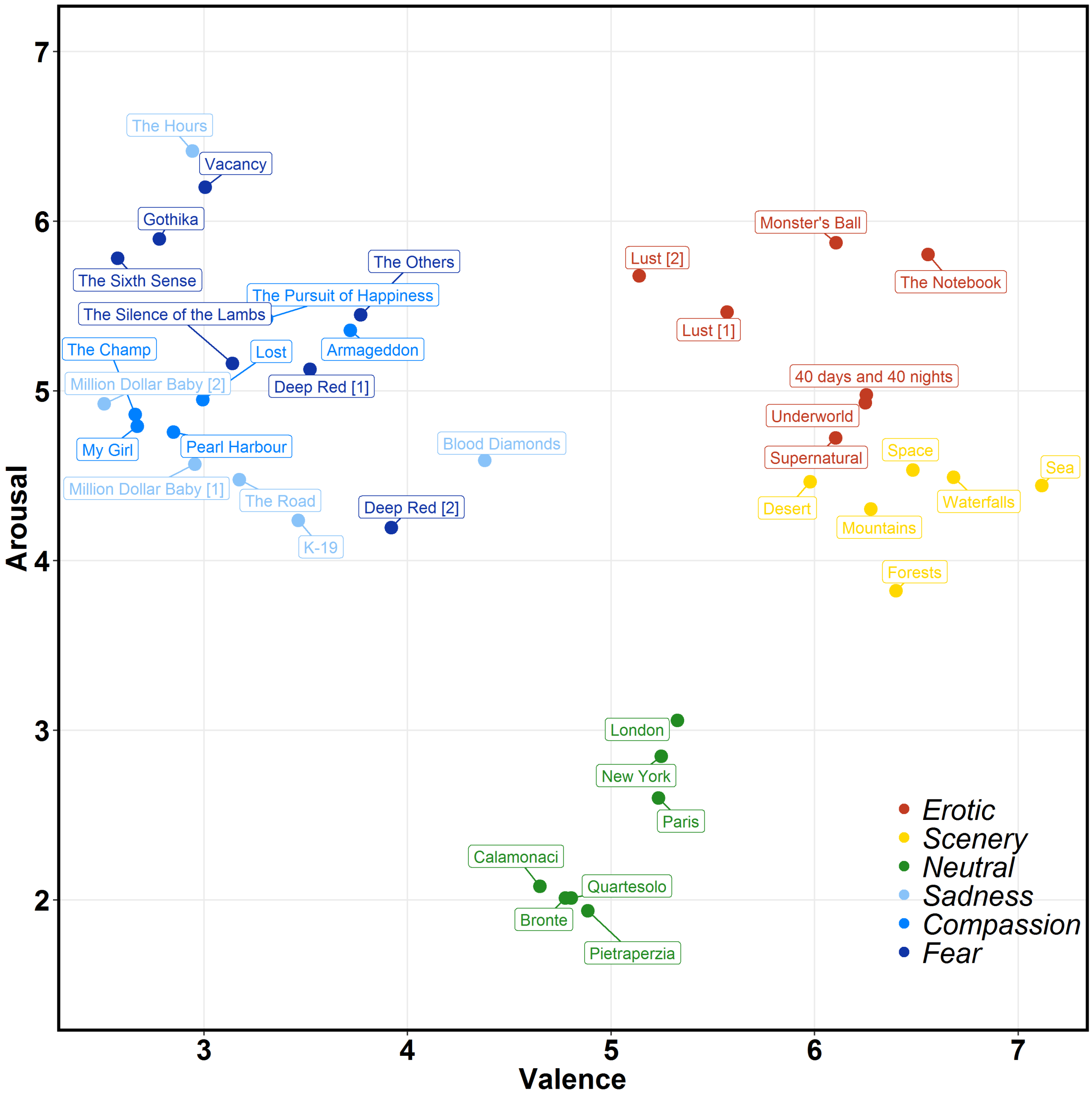

Figure 4.2 Distribution of the 39 film clips in the valence-arousal affective space.

Basic Emotions

ANOVA carried out on Basic Emotion ratings found the Film Category*Emotion ($F_{(30,3990)}$ = 285.45, p<0.0001, η^2_p = 0.68) and the Film Category*Emotion*Sex, $F_{(30,3990)}$ = 11.43, p<0.0001, η^2_p = 0.07) significant interactions. Post-hoc analysis computed on the Film Category*Emotion*Sex interaction revealed several results on the attribution of basic emotions to the six Film categories. Participants showed a weak association of Anger with the whole sample of clips, as they reported relatively small ratings, similar in men and women (Fig. 4.3, first panel from the left).Within this pattern, relatively higher levels of Anger were found, in both genders, in response to Sadness and Compassion films compared with the other ones. The emotion Disgust was weakly associated with the clips (low overall ratings) and mainly in women who evidenced higher levels to Fear and Erotic compared with the other clips (Fig. 4.3, second panel from the left). The emotion Fear was highly associated to Fear clips compared with all other clip categories (Fig. 4.3, third panel from the left) in both genders, but with greater significant levels in women than men. Furthermore, in women fear was also perceived to a larger extent during Sadness and Compassion movies compared with the other pleasant-neutral films. The emotion Joy was associated with higher ratings to both Erotic and Scenery compared to the other clip categories to the same extent in men and women (Fig.4. 3, fourth panel from the left); Scenery excerpts prompted larger Joy ratings than Erotic ones. Neutral clips were evaluated with the greatest Neutral emotion ratings (Fig. 4.3, fifth panel from the left), but relatively high Neutral ratings were attributed by women also to Scenery and Erotic clips. High ratings of emotion Sadness were related to both Sadness and Compassion films, significantly more in women than in men, and more to Compassion than to Sadness clips (Fig. 4.3, sixth panel from the left). Even if the Surprise emotion was associated to overall low ratings, greater levels were found to Fear and Scenery compared with the other films (Fig. 4.3, last panel on the right).

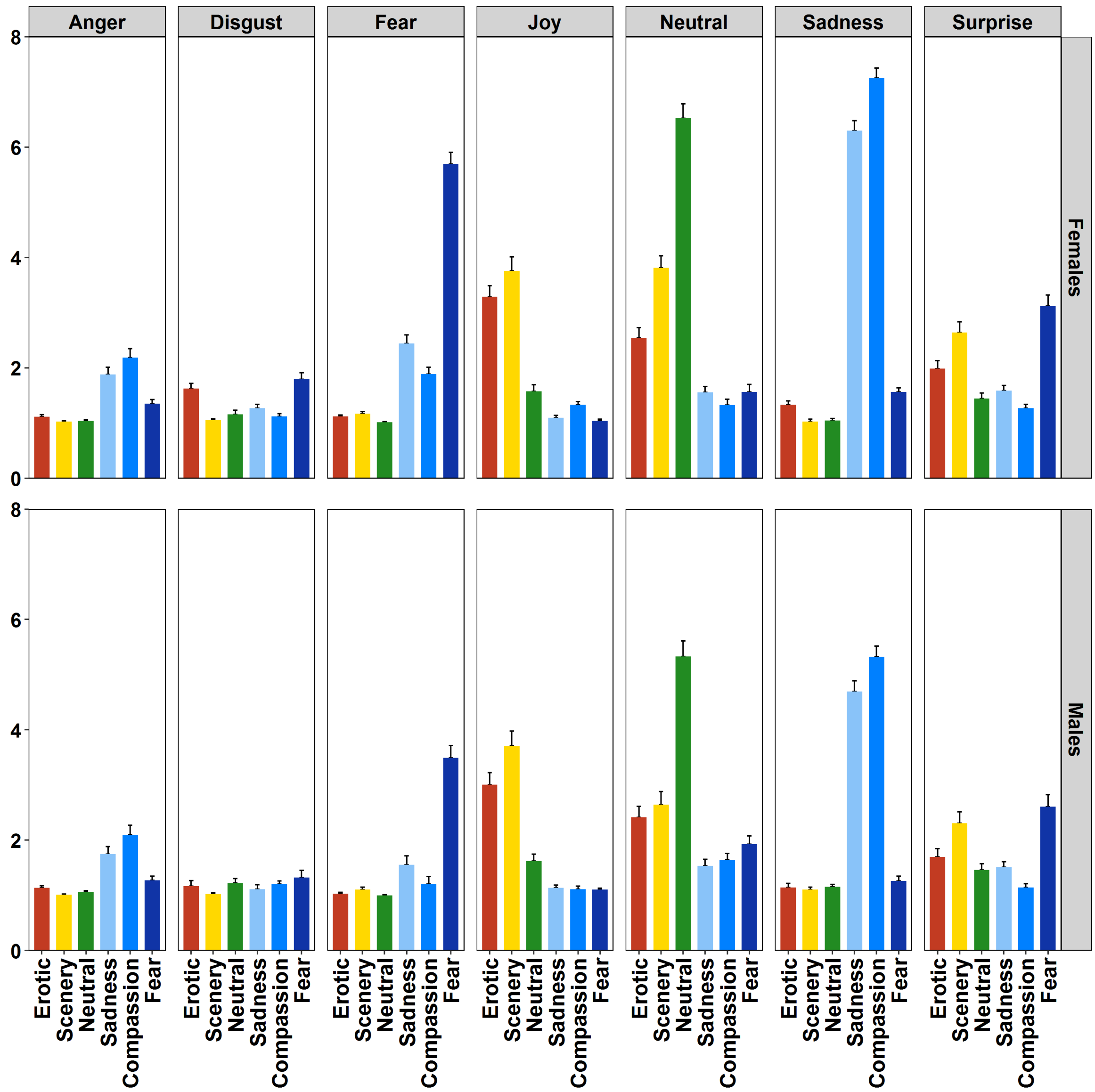

Figure 4.3 Evaluation of the 6 film categories according to the main seven basic emotions. Bars represent SE.

Emotional Adjectives

ANOVAs on the ratings of emotional adjectives showed a significant main effect of film category for all the items, and a significant interaction Film Category*Sex for all but two items, namely Enthusiast and Enchanted (results of the F statistics are reported between parentheses).

The adjectives Anxious, Distressed and Jittery were naturally attributed to the three negative film categories. Indeed, statistical analysis showed that Fear clips received the highest ratings on these three items ($F_{(5,860)}$=11.11, p<0.0001, η^2_p = 0.06, $F_{(5,680)}$=10.49, p<0.0001, η^2_p = 0.07, and $F_{(5,860)}$=9.51, p<0.0001, η^2_p = 0.05, respectively), with women reporting higher levels compared to men (see Fig. 4.4). These adjectives also highlighted differences between Sadness and Compassion clips. Both males (p < 0.05) and females (p < 0.05) reported to feel more Anxious and Distressed in response to Sadness than to Compassion clips. Women also reported to feel more Jittery after presentation of Sadness compared to Compassion excerpts, while this comparison in men was marginally significant (p = 0.07).

Analysis of the item Bored showed that clips included in the Neutral category were rated as being more boring than any other clips ($F_{(5,860)}$=3.41, p=0.004, η^2_p = 0.02), both by men and women.

Erotic clips received significantly high rating on the item Embarrassed ($F_{(5,860)}$=7.26, p<0.0001, η^2_p = 0.04), with female participants reporting feeling more embarrassed when watching these films than males participants.

For the adjective Excited, Erotic films were evaluated as the most exciting category. Men reported more excitement to Erotic clips than women ($F_{(5,860)}$ = 3.29, p=0.005, η^2_p = 0.02). Also Scenery clips were judged as more exciting than the remaining Film categories, again with males assigning higher scores than females.

The adjectives Enthusiast ($F_{(5,860)}$ = 138.38, p<0.0001, η^2_p = 0.45), Enchanted ($F_{(5,680)}$ = 158.58, p<0.0001, η^2_p = 0.54) and Inspired ($F_{(5,860)}$=3.17, p=0.007, η^2_p = 0.02) were clearly associated with Scenery compared with the other clips. Men were more inspired by Scenery films than women.

The adjectives Sad and Touched revealed to be more sensitive to the emotions elicited by the clips comprised in the Sadness and Compassion categories ($F_{(5,680)}$=10.24, p<0.0001, η^2_p = 0.07 and $F_{(5,860)}$=18.37, p<0.0001, η^2_p = 0.10, respectively) compared with the other films.

Women scored higher than males. Analyses also revealed that Compassion clips received higher scores, independent from gender, namely they were described as being more sad and touching compared to the clips included in the Sadness category.

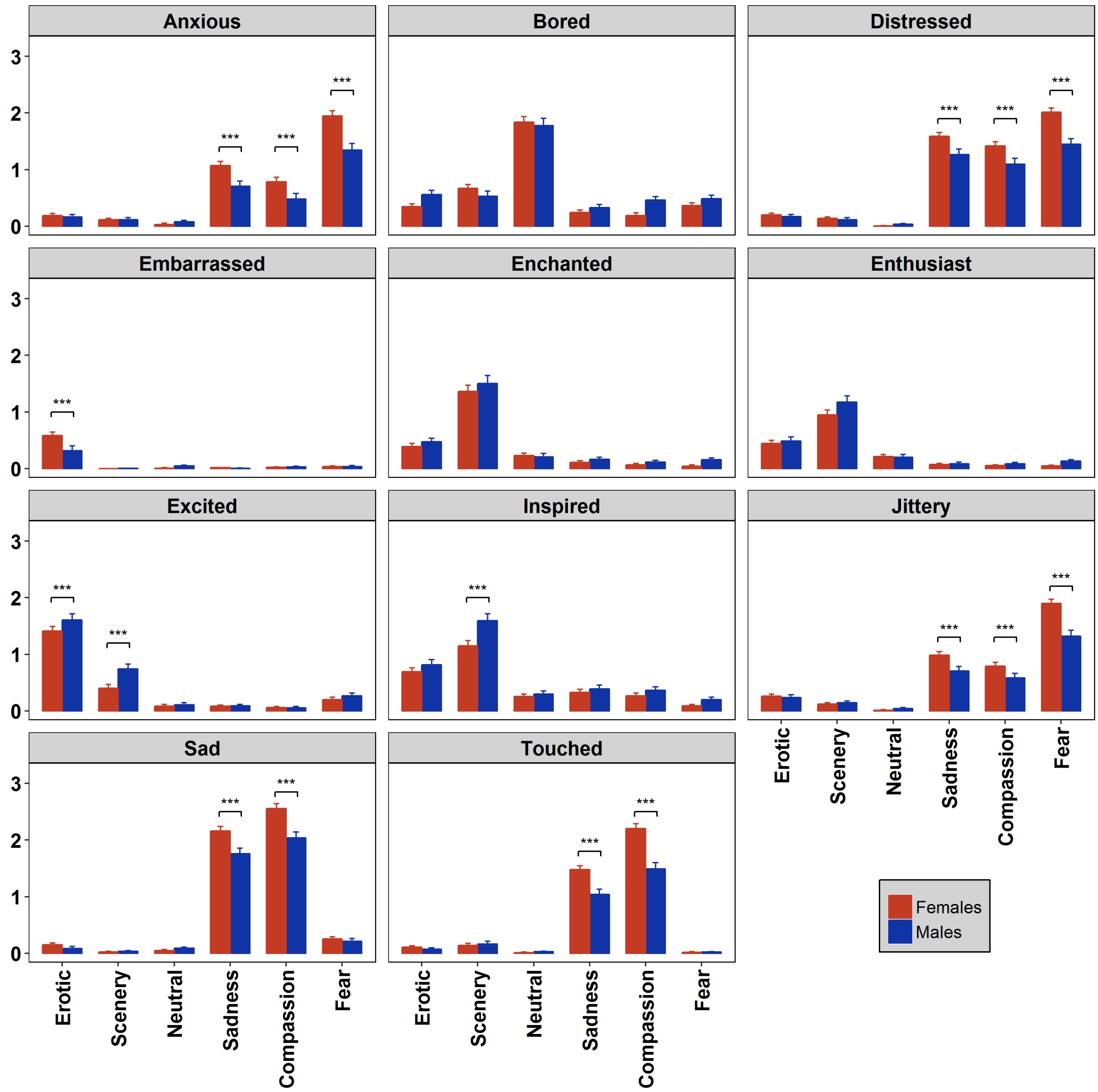

Figure 4.4 Evaluation of the six film categories according to eleven emotional adjectives. Asterisks indicate significant ($p<0.05$) gender differences. Bars represent SE.

Familiarity

Criteria for inclusion in the analysis were met by 19 clips (see Fig. 4.5), with an average of 50.5 participants that already had seen each specific clip (min = 17 participants for *Underworld*, max = 138 for *The Pursuit of Happiness*). Concerning the impact of Familiarity on Valence ratings, the test was significant (p<.05) for three clips, two in the Erotic category, namely *The Notebook* (t(60)= - 2.42), *Underworld* ($t_{(19)}$= -2.25) and within Fear was *The Sixth Sense* ($t_{(122)}$= -2.58). In all the cases, results indicated that participants who had seen the clip previously reported larger ratings (i.e. more pleasantness) on valence scale. Regarding arousal ratings, the test was significant (p<.05) for seven clips, six of which were in the Compassion or Sadness categories. The clips were *The Notebook* ($t_{(74)}$= -2.51) in the Erotic category, *Blood Diamond* ($t_{(50)}$= -2.58), *Armageddon* ($t_{(168)}$= -3.34), *Million Dollar Baby [1]* ($t_{(160)}$= -2.92), *The Pursuit of Happiness* ($t_{(66)}$= -3.84), *Pearl Harbor* ($t_{(164)}$= -2.14) and *K-19* ($t_{(47)}$= -3.48). For all the clips, arousal perceived by participants who already had seen the clip was higher than the arousal reported by participants who did not.

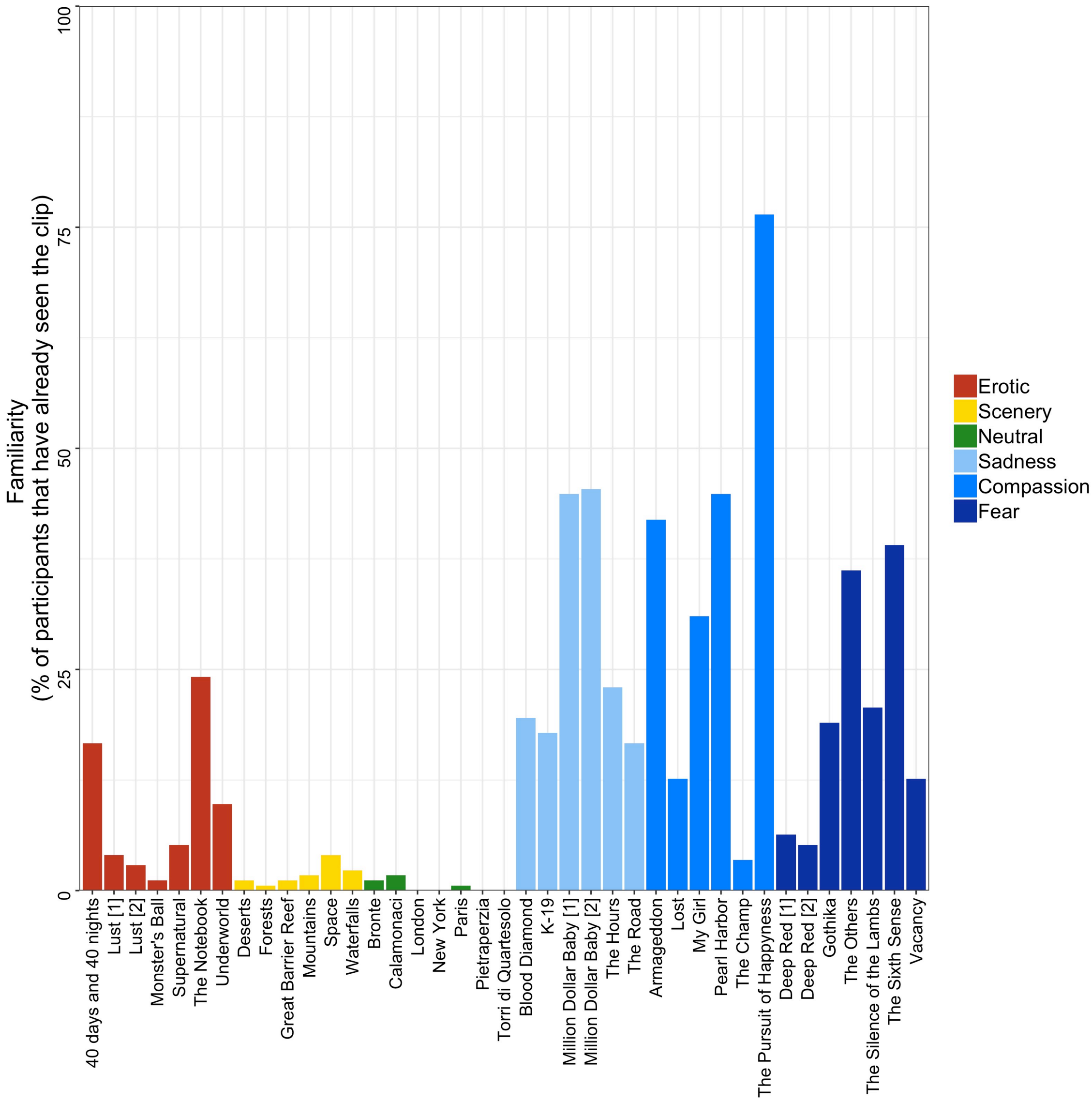

Figure 4.5 Familiarity plot. Percentage (in vertical) of participants who reported to have previously seen the clip. In horizontal axis is represented each of the 39 films.

4.5 Discussion

The present study reports the validation of a new database of film excerpts for experimental emotion induction. In order to provide stimuli suitable for elicitation of either positive and negative affective state, six categories of film clips have been included, namely: Erotic, Scenery, Neutral, Sadness, Compassion, and Fear. Clips were rated on a series of emotional dimensions, assessing also the role of gender and familiarity. We predicted that Fear, Sadness and Compassion clips would have triggered an unpleasant affective state, while

Erotic and Scenery clips would have elicited a positive emotional state. Analysis of valence ratings confirmed our expectation, showing that participants reported higher pleasantness in response to the latter categories of clips compared to the negative and neutral ones. In addition, Joy was the emotion reported with greater intensity in response to both Erotic and Scenery films.

These results confirm the effectiveness of Erotic excerpts to elicit in the viewer a positive emotional state, characterized by an approaching motivational tendency, extending the findings on emotional pictures research (Lang, Greenwald, Bradley, & Hamm, 1993) to the field of emotional film clips. Moreover, analysis of the arousal ratings showed that the arousal elicited by erotic scenes did not differ from the one elicited by fearful excerpts. This is interesting since previous studies rarely measured the levels of arousal characterizing the emotions elicited by their clips, leaving unaddressed the impact of this variable. Results concerning the pleasantness of the affective state induced by viewing nature documentaries support our claim against the inclusion of clips with this content under the label of neutral stimuli. Participants not only judged scenes depicting natural environments as being more pleasant and more arousing compared to urban documentaries, but they also reported feeling more inspired, enthusiast and enchanted when viewing these clips.. Placing Scenery in the positive group of clips in the end was consistent with our results but in past research Scenery was placed in the Neutral emotional group, thus raising some conflicting results. Indeed, Gilman and colleagues (2017) included in their validation a clip extracted from a naturalistic documentary, hypothesizing that it could serve as a neutral stimulus. They found instead that, since it received moderately high ratings in positive emotionality, it did not satisfy the criteria for classifying it as affectively neutral. Carvalho and colleagues (2012) also reported that scenery clips are rated as more pleasant compared to clips depicting object manipulation. The latter category was considered by authors as a true neutral condition. Our results clearly discourage the use of natural scenes as a neutral condition, and highlight their effectiveness as elicitors of positive affect. Ratings of the emotional adjectives further characterize the affective state prompted by this kind of clips, supporting their use in laboratory investigation for inducing aesthetic and contemplative emotional states, but also for studying the psychophysiological effects of the exposure to natural environments (Beute & de Kort, 2014).

When selecting clips for the Fear category, we included only suspenseful excerpts depicting the imminence of threat and danger for the characters, excluding scenes displaying blood and/or mutilations. Although films depicting violent harm and injuries are a very effective method for eliciting fear and anxiety (Carvalho et al., 2012; Schaefer et al., 2010), blood and mutilations prompt in the viewer very specific cognitive, behavioral and physiological reactions (Cisler, Olatunji, Lohr, & Williams, 2009; Palomba et al., 2000; Sarlo et al., 2005), related to the concurrent disgusting nature of this kind of scenes. Our results showed that, even without blood and mutilation, clips included in this category were highly effective in inducing Fear. In addition, these clips prompted the greatest levels of anxiety, jittery and distress, reflecting the thrilling nature of the selected excerpts. In line with our selection criteria, the disgust reported by participants in response to these films was very low.

In this research we also made a distinction among different kind of sadness-eliciting clips. We included film clips depicting characters crying following an important loss in the Compassion category, while clips featuring characters in loneliness, helplessness and desolation were included in the Sadness category. As expected, both these categories were effective at eliciting a negative and highly arousing affective state, whose prevalent emotion was Sadness. Interestingly, participants rated their feelings as being more sad and touched in response to Compassion clips compared to Sadness, while they felt more anxious and distressed in response to Sadness clips than to Compassion. These results support our initial claim that these categories would elicit emotional states partially overlapped but not equivalent. Compassion clips elicited an affective state characterized by being touched and tendency to approach the suffering characters, in line with the idea that viewing another person crying from emotional sufferance would trigger an automatic response mediated by empathic resonance (Jean Decety & Meyer, 2008; Goetz, Keltner, & Simon-Thomas, 2010; Menninghaus et al., 2015), A pattern of response which makes these stimuli suitable for investigation of empathic processing and prosocial behaviors. On the other hand, films included in the Sadness category were able to elicit a sad affective state which was also characterized by distress and anxiety, and this may be useful for experimental induction of depressive mood.

We also explored the impact of familiarity of stimulus material on affective reactions, aiming to replicate previous studies reporting (Gabert-Quillen et al., 2014; Gross & Levenson, 1995) that familiar clips bolster the affective experience of the viewer. Due to an expectation mechanism, familiarity increases the arousal experienced during the viewing of the clips, irrespective of the positive/negative content of the stimuli. Moreover, our results showed that familiarity elicited greater pleasantness on positive clips only, while participants who watched a negative clip for the first time reported greater unpleasantness. Thus, having already watched a film tends to enhance all emotional responses: it seems that the main mechanism underlying this effect is sensitization rather than habituation. Emotions overrule cognitive mechanisms associated with habituation and this makes negative clips, especially the Fear ones, useful in paradigms resembling post-traumatic stress disorder.

Concerning gender differences in emotional responses, men and women showed a substantially similar pattern for emotional categorization of clips (Fig. 4.3), with a few expected results: in line with sex differences found for arousal ratings, women attributed larger ratings than males in the categorization of Fear clips as fear and Sadness-Compassion clips in the sadness category. Instead, several interesting gender differences have been found for the emotional adjectives (Fig. 4.4). After the Erotic clips, women reported feeling more embarrassed than males. This effect was not unexpected since it was previously reported (Costa et al., 2001; Maffei et al., 2015), and it is related to the socially-sensitive and intimate nature of the content of these clips, to which women appear to be more susceptible. Probably this effect is strengthened by the feeling to be under investigation (although in an anonymous setting, participants were tested in groups but tests were anonymous). Men were more excited than women by the Erotic clips. They were also more aroused, excited and inspired than women after the Scenery clips. This result was unexpected and deserves further investigation. We expected women to be in general more sensitive to emotional stimulation including wilderness contents, but perhaps in men the evolutionary gender-specific tendency to explore the environment is stronger and this might be related to the fascination for wild landscapes. With regard to negative clips, women revealed to be more touched and sad than men after the Sadness and Compassion clips. Similarly, they reported also larger ratings of distress, jittery and anxiety compared with men to the three negative clips, Sadness, Compassion and Fear. This is in line with past research on sex differences in emotions using unpleasant slides (Bianchin & Angrilli, 2012; Bradley et al., 2001), but it further specifies the differences with movies of three specific negative categories. An additional explanation for the observed effect of gender on the evaluation of the clips lies in the difference between males and females in processing emotional information involving other people. Indeed, there are many evidences suggesting that social cognitive abilities are influenced by sex, with females showing greater sensitivity to emotional displays through facial expressions (Proverbio, 2017). Moreover, females are also characterized by larger reactivity, at both subjective and physiological levels, to scenes displaying other humans suffering (Proverbio, Adorni, Zani, & Trestianu, 2009), suggesting an overall advantage of females over males in empathic processing of others' negative affect.

In conclusion, the present database revealed to be effective for affect manipulation and elicitation of different emotional states. It was built with the purpose to serve as a flexible tool for researchers, who could select the stimuli needed for their experiments adopting either a categorical or a dimensional perspective. With respect to past databases, we aimed to create new highly homogeneous categories of clips to avoid within-category mixture of contrasting/confounding emotions: Fear was not contaminated with blood-mutilation contents, Neutral did not include wilderness which instead was created as a positive independent category, Sadness was split into Sad and Compassion distinct categories. Erotic, rarely included in past databases, but extensively used as single category in many experiments, was not mixed with other positive categories. A second important feature was the measure of arousal levels to overcome an important limitation of some previous validations. Indeed, many results on emotion-related effects, especially in studies based on psychophysiological methods, may strongly depend on arousal levels unbalanced across different emotion categories. Thus although it is true that different affective states are intrinsically characterized by different levels of arousal, it is also important to control this variable when differences among emotions are under investigation. One interesting feature of our sample is that all categories (excluded the Neutral) induced relative high levels of arousal. In particular, although the highest levels of arousal were reached by some Erotic and Fear clips, it is possible to select a subsample of clips having comparable arousal levels across the main five emotional categories: this allows to study emotional responses induced by different emotional categories by keeping well balanced the arousal level. As a final unique feature, our sample of clips was implemented with the aim of keeping clip duration equal across all categories. The duration was selected in the scale of 2 min which, from one side, permits the induction of most emotions, also those requiring time (e.g., sadness, compassion), from the other side this duration is compatible with the needs of most neuroimaging and psychophysiological paradigms, but also allows, in one experiment, to use more clips from each emotional category to avoid film-specific response related to single long-clip presentation. Future developments of this database include: adding new homogeneous emotional categories (e.g. blood-mutilation, dirt-disgust, etc.); enlarging the sample of participants across different countries, languages and cultures; measuring the central and peripheral physiological correlates of the emotions induced by these clip categories; studying neurological and psychiatric patients with specific deficits in emotional responding.

Chapter 5

STUDY 2: Affective content shapes cortical reactivity to naturalistic stimuli: evidence from oscillatory EEG dynamics and source imaging

5.1 Abstract

Movie clips are an excellent tool to investigate brain activity under ecological conditions. Recent findings revealed that a wide array of brain regions, mostly within the parieto-occipital cortex, are involved in the processing of these complex and rich stimuli, reflecting both low- and high- level features processing. A remarkable feature of movies is their potential as emotion elicitors but, surprisingly, the impact exerted by their affective content on brain activity has been largely under-investigated. In this research, thirty nine participants watched 18 film clips arranged in six categories (Erotic, Scenery, Sadness, Compassion, Fear and Neutral) while their brain activity was recorded using EEG. Analysis of alpha power over central and posterior electrodes showed a strong modulation, with the largest inhibition (indexing greater cortical desynchronization) observed for erotic and fearful clips, reflecting the effect of emotional arousal. Source analysis revealed a common neural generator in the posterior parietal cortex in regions involved in attention and multimodal integration, which showed increased activity for all the emotional clips compared to the neutral ones. Beta activity was instead sensitive to the affective valence of the clips, with a strong activation observed for the three unpleasant categories, whose main generator has been located within the right temporal cortex. This region has been linked to the ability to extract emotional and social features within a continuous narrative , and its activity may also reflect deep nuclei projections boosting the processing of aversive information. These results clearly demonstrate that emotional content modulates the recruitment of brain networks involved in the processing of naturalistic stimuli, and that this modulation is characterized by a functional and spatial

dissociation across different neural oscillatory activities, alpha and beta, encoding the effects of emotional arousal and valence, respectively.

5.2 Introduction

Recent years have been characterized by a growing interest towards the understanding of the brain mechanisms that characterize processing of naturalistic stimuli (Bartels & Zeki, 2004; Hasson, Malach, & Heeger, 2010). This surge has been guided by the need to move beyond the use of simplified artificial stimuli, which have limited usefulness in addressing the functional organization of brain regions that supports interaction between individuals and the external world (Bartels & Zeki, 2004). Nonetheless, neuroscience experiments in real life conditions are still quite difficult to perform, hence experimenters need to find a balance between experimental control and naturalistic stimulation. Fortunately, this conundrum can be overcome using movies, which represent a class of stimuli which provides the best compromise between control and ecology (Rottenberg et al., 2007). Movies are dynamic and multimodal, engaging both visual and auditory systems, and have been shown to elicit predictable and reliable activations in brain networks related to sensory processing, attention and high-order feature integration (Hasson et al., 2010). Interestingly, activity in these regions tends to be highly synchronized across participants (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004), suggesting that coherent activity within these regions, each responding to specific components of the audiovisual scene, contributes to emergence of conscious experience.

Key areas which are consistently activated when participants are required to passively watch a movie are located within the parieto-occipital region of the brain (Bartels & Zeki, 2004; Golland et al., 2007; Hasson et al., 2004; Hasson, Yang, Vallines, Heeger, & Rubin, 2008; Lahnakoski, Salmi, et al., 2012). This cluster of areas includes primary and extrastriate visual cortices together with areas in the posterior parietal cortex, such as the inferior parietal sulcus (IPS) and the superior and inferior parietal lobules (SPL and IPL). Involvement of this wide array of areas reflects the combination of the parcelleted analysis of the different visual features of the scene with higher-order attentional processing and features integration. Visual cortices, both primary and secondary, control the segregated analysis of the elements that comprise the scene, like perception of object, faces and movement (Golland et al., 2007; Lahnakoski, Salmi, et al., 2012). Parietal activity reflects instead the complex process of binding of these features, mediated by attention, which is critical for conscious perception of the information stream (Hasson et al., 2004).

Another cluster of activated regions is usually found within the temporal lobe (Hasson et al., 2004; Lahnakoski, Salmi, et al., 2012). Similarly to visual areas, activity in temporal regions also reflects the combination of low-level processing of auditory information with higher order cognitive integration of this information. Furthermore, activity in the temporal cortex is critical for the elaboration of the social features embedded in the continuous narrative presented with the stimulus (Lahnakoski, Glerean, et al., 2012). The social elements processed in the temporal areas comprise features related to the auditory sensations, like voice and prosody, but are not restricted to this sensory modality, extending to goal perception and intention attribution.

A remarkable feature that characterizes the act of watching a movie is represented by the emotional experience that the movie evokes (Rottenberg et al., 2007). Surprisingly this aspect has not received extensive attention so far in cognitive neuroscience research. The aim of this study is to contribute to this issue showing how activity in the cortical regions involved in processing naturalistic stimuli like movies, is shaped by the manipulation of their affective content.

Emotional experience is usually described using two dimensions, namely valence and arousal. Valence defines the pleasantness/unpleasantness of the feelings evoked by a stimulus, while arousal refers to the degree of activation that it triggers. Both these dimension have been shown to have an impact on brain reactivity to emotional stimuli (Mourão-Miranda et al., 2003; Nummenmaa et al., 2012a). Nummenmaa and colleagues (2012a), using the inter-subject correlation metric on the BOLD response elicited by a series of positive and negative film excerpts, showed that arousal and valence were associated to two different, although partially overlapping, set of brain regions. Arousal was prominently linked to an increased activation in areas within the occipito-parietal region involved in the dorsal attentional network (DAN). On the other hand, valence was inversely related to the activity of mid-brain regions involved in emotional reactivity.

In the present research we investigated the effect of different categories of emotional movies on cortical reactivity by means of electrophysiological measures combined with low-resolution source reconstruction of the scalp activity. We used film clips derived from the E-MOVIE database. A unique strength of this database, compared to other set that are already present in the literature (Gabert-Quillen, Bartolini, Abravanel, & Sanislow, 2015; Gross & Levenson, 1995; Schaefer et al., 2010), is represented by the inclusion of film excerpts of homogeneous durations (2 minutes ±10 seconds), which limits the potential confound represented by stimulus length variability. The clips included in this set are arranged in six different affective categories (Erotic, Scenery, Sadness, Compassion, Fear and Neutral), able to manipulate effectively participants' affect along the appetitive/aversive dimension of emotional experience. We decided to use multiple categories, rather than rely on the general distinction among positive and negative film clips, because we believe that such a broad distinction, may be limited without adding further differentiation among the stimuli. Specifically, it may fail to take into account that movies with very different affective content, albeit falling within the same broad category (positive or negative), could exert on the viewer's physiological activation different effects. Using distinct categories, able to cover the wide spectrum of both positive and negative emotional state, may instead help to overcome this potential limitation and improve the generalizability of the findings.

We decided to focus on electrophysiological responses collected with EEG, since it can provide a direct measure of the brain activity evoked by the movies. In addition, spectral analysis of electrocortical activity allows to investigate the effect of emotions on the oscillatory dynamics of the brain, which have been proved to be sensitive to different feature of the affective experience. Activity in the range of alpha frequency has been repeatedly linked with the effect of the arousal elicited by an emotional stimulus. Using television excerpts Simons and colleagues (2003) showed that amplitude of parietal alpha oscillations was inversely related with clip arousal. Similarly, in a recent paper Dmochowsky and colleagues (2012) showed that parietal alpha power decreased in correspondence to moments of emotional climax of a film clip. This inverse relationship between posterior alpha and arousal, is thought to reflect the increased cortical activity that stems from the attentional engagement prompted by an affectively charged stimulus. Moreover, the topographical distribution of this activity, suggests that it may index activation within the DAN. Based on these evidence, we predicted that film clips belonging to high-arousal emotional categories should elicit larger alpha inhibition, especially in posterior electrodes. In addition, we expected that, according to fMRI studies, the main generator of this activity would be located within occipito-parietal cortical regions involved in the processing of dynamic stimuli.

For what concerns the influence of emotional valence, results from previous studies are less definitive compared to arousal, nonetheless there are some converging evidences that faster oscillatory activity, especially in the beta range, may encode the pleasantness/unpleasantness dimension of a stimulus (Güntekin & Basar, 2007; Güntekin & Başar, 2010; Ray & Cole, 1985). As a consequence, we included in our investigation beta activity in order to explore the relationship between film pleasantness and brain oscillatory pattern within this frequency range.

5.3 Method

Participants

Thirty-nine healthy subjects, 20 males and 19 females (mean age ± S.D.: 20.71 ± 2.17) participated in the present study after giving their written informed consent. Participation to the study was rewarded with course credits. All the participants were screened for the presence of any neurological or psychiatric condition, had normal or corrected to normal vision and normal hearing. Ethics Committee of the Department of General Psychology (University of Padova) approved the study, which was carried out according to the principles expressed in the Declaration of Helsinki.

Stimuli

Eighteen short (2 minutes ± 10 seconds) movie excerpts arranged in six different emotional categories were presented to the participants. Erotic excerpts, portraying heterosexual couples engaged in a sexual act, and Scenery excerpts, portraying stunning views of different natural landscapes (i.e. Coralline Reef, Himalayas) targeted two distinct positive emotional states, the former high arousing while the latter low arousing. Fear excerpts, portraying thrilling scenes of anticipated threat, Sadness excerpts, featuring themes of desperation and helplessness, and Compassion excerpts, depicting scenes of loss, grief and bereavement, were intended to elicit three distinct negative emotional states. Fear excerpts were selected to induce a negative high arousing state; instead Sadness and Compassion excerpts were chosen to elicit a low arousing one. Moreover, the distinctive characteristic of Compassion films was the depiction of crying characters, thought to trigger an automatic emotional response only partially overlapping with the one elicited by the Sadness films, characterized instead by featuring themes of loneliness and hopelessness. Finally, excerpts featuring scenes drawn from urban documentaries, were chosen to elicit an affectively neutral state. The clips were edited, using Adobe Premiere CS5, into a single continuous clip with a resolution of 1280 x 720 pixel. The distribution of the excerpts within the final clip was pseudo-randomized, to avoid that two excerpts belonging to the same category were consecutive. The interval between the excerpts was 110 seconds, so the final length of the clip was 1 hour and 10 minutes. The order of presentation was fixed across all subjects.

Experimental Procedure

Upon arrival, each subject was sat in a comfortable armchair and was given a general description about the experiment, in order to obtain the informant consent. After electrodes placement, the experimental procedure was explained and four practice films (not considered for the analysis) were projected on a 22-inches Full HD screen, in order to acquaint the subject to the procedure. Next, the experimenters gave any additional explanation and the experimental session started.

Self-rating of emotional experience

After each clip, participants were asked to rate their emotional state in order to assess the effect of the clips on their subjective experience. They were asked to rate the valence (1 extremely unpleasant – 9 extremely pleasant) and the arousal (1 extremely calm – 9 extremely aroused) elicited by the clip. In addition, they were asked to describe their feelings during the clip using four emotional adjectives. For each adjective (Distressed, Excited, Jittery, Anxious) they had to indicate how much it described their emotional state during the viewing of the clip, using a 5-point scale ranging from 1 (“Not at All”) to 5 (“Extremely”).

EEG recording and data reduction

Electroencephalographic signal was recorded trough 38 electrodes, 31 mounted on an elastic cap (ElectroCap) according the 10-20 International System, and the residual 7 applied below each eye (IO1, IO2), on the external canthus of each eye (F9, F10), on the mastoids (A1, A2) and nasion (Nz). All the impedances were kept below 5 KΩ. The signal was recorded with a SynAmps RT amplifier and the Curry 7 software (Compumedics Neuroscan, Charlotte, NC, USA), using a sampling rate of 500 Hz and Cz as online reference. EEG was recorded continuously over the whole experimental session, but only the last 30 seconds of each excerpt were considered for the analysis. This choice was due to the nature of the stimuli, all characterized by the concentration of the most emotional scenes in the last minute, and to the nature of the emotion itself, which is a phenomenon that develops over time (Rottenberg et al., 2007). So it was assumed that the maximum effect of the experimental manipulation would be observed in the last 30 seconds of each clip. After collection, EEG data were re-referenced to the average activity of all electrodes and the last 30 seconds of each clip were divided into 14 epochs of 2048 msec. Blinks and eye movements artifact were removed trough the MSEC procedure (Ille, Berg, & Scherg, 2002) using BESA software (v 5.3). Artifact rejection was performed automatically on all the epochs, using amplitude (150 μV threshold) and gradient threshold (100 μV threshold) criteria, included in BESA software. Next, each remaining epoch was visually inspected in search for any residual artifact, marking the epoch when an artifact was revealed, in order to exclude it from the analysis. After data preprocessing the FFT was applied on all artifact-free epochs, in order to obtain the average amplitude spectrum for the six categories considered. Considering the main purpose of the present study, which was to investigate the cortical distribution of emotion-elicited activity, amplitude measures were averaged into 9 clusters comprising two electrodes each: Anterior

Left (F7-F3), Anterior Central (Fpz-Fz), Anterior Right (F8-F4), Central Left (FT7-T7), Central Central (Cz-CPz), Central Right (FT8-T8), Posterior Left (TP7-P7), Posterior Central (Pz-Oz), Posterior Right (TP8-P8). For statistical analysis Alpha and Beta were considered. Alpha band (8-13 Hz) was considered according to an extensive literature that indicates alpha activity as a reliable index of cortical inhibition, and consequently alpha decrease as a valid measure of cortical activation (Bazanova & Vernon, 2014; Klimesch, 1999; Simons et al., 2003). Only an high frequency range for Beta activity was considered, because in several studies low-Beta, ranging from 13 to 20 Hz, was reported to represent a transition from slow frequencies to higher frequencies, rather than a specific rhythm, with its specific functional meaning (Spironelli & Angrilli, 2010).

Finally, standardized low-resolution electromagnetic tomography (sLORETA) (Frei et al., 2001; Pascual-Marqui, 2002) was used to compute the cortical three-dimensional distribution of current density, allowing the identification of the neural sources underlying the activity observed for each emotional category. For each subject and for each condition, average cross-spectral matrices were computed for the same frequency bands considered in the previous analyses. Current density for each frequency band was computed from the cross-spectral matrices using the module included in sLORETA software. Then, the three-dimensional distribution of current density was estimated in a space solution constrained to grey matter in the digitized MNI atlas, divided in 6239 voxels of 5x5x5 mm of size.

Statistical Analysis

Analysis of self-report data was performed using separate repeated-measures ANOVAs for each item, including Film Category as a single within-subject factor. Significant effects were further explored with post-hoc comparisons using the Newman-Keuls tests, considering a significant level of $p < 0.05$.

For each EEG band, a repeated-measures ANOVA was computed, including the following factors: Film Category, Region (Ant-Ct-Post) and Laterality (Left-Ct-Right) as within-subject factors. When appropriate, Greenhouse-Geisser procedure was used and corrected probability values were reported. Significant effects were further explored with post-hoc comparisons using the Newman-Keuls tests, considering a significant level of $p < 0.05$. Statistical analyses were performed using the software STATISTICA (v.6).

Finally, statistical contrasts between source distribution for each emotional category and the neutral for Alpha and Beta frequencies, were performed using the statistical non-parametric mapping (SnPM) approach (Nichols & Holmes, 2002), as implemented in the sLORETA software.

5.4 Results

Self-report emotional evaluation

Analysis of self-reports of affective experience showed a main effect of Film Category for the valence ratings ($F_{(5,185)} = 33.63$, $p<0.05, \eta_p^2 = 0.47$). Post-hoc comparisons revealed that Erotic and Scenery clips were rated as more pleasant compared to all the other clips (all ps < 0.05), while Fear clips were judged as the most unpleasant (all ps < 0.05). Analysis of arousal ratings also revealed a main effect of Film Category ($F_{(5,185)} = 59.70$, $p<0.05, \eta_p^2 = 0.61$), which showed that all the affective clips elicited greater arousal compared to the neutral excerpts (all ps < 0.05), with Fear category eliciting also greater arousal compared to Scenery ($p < 0.05$), Sadness ($p < 0.05$) and Compassion ($p = 0.06$). ANOVAs performed on the ratings of the emotional adjectives revealed a significant main effect for the item Distressed ($F_{(5,180)} = 107.42$, $p<0.05, \eta_p^2 = 0.75$), Excited ($F_{(5,180)} = 56.41$, $p<0.05, \eta_p^2 = 0.61$), Jittery ($F_{(5,180)} = 84.63$, $p<0.05, \eta_p^2 = 0.7$) and Anxious ($F_{(5,185)} = 92.16$, $p<0.05, \eta_p^2 = 0.72$). Post-hoc comparisons showed that Erotic and Scenery clips were judged as the most exciting clips (all ps < 0.05), while participants felt more anxious, jittery and distressed during the clips comprised in the three unpleasant categories Fear, Sadness and Compassion (all ps < 0.05).

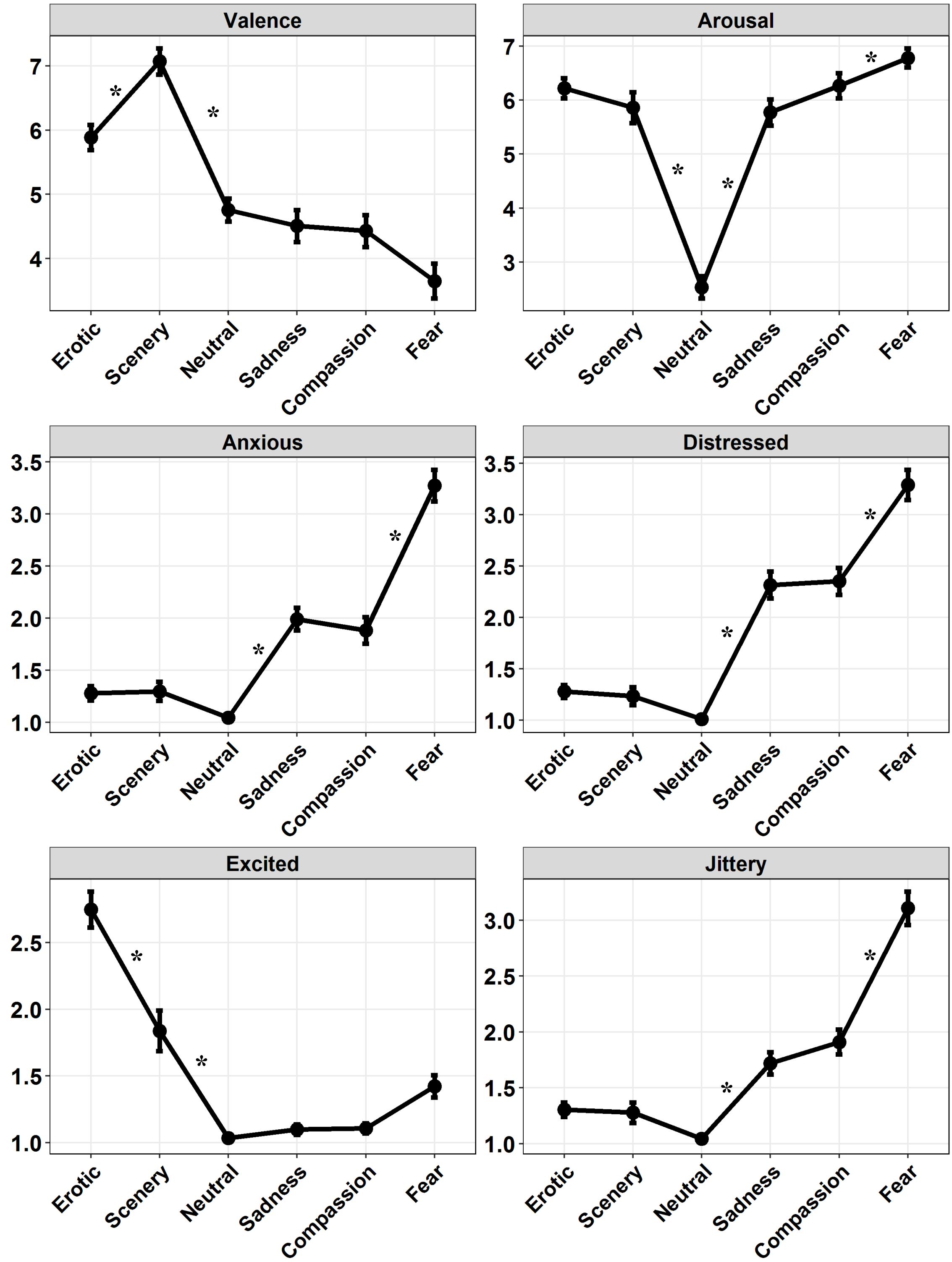

Figure 5.1 Self-report judgments of affective experience. Asterisks represents significant ($p<0.05$) post-hoc effects. Bars represents SE.

Alpha Power

ANOVA performed on alpha band power showed a significant main effect of Film Category ($F_{(5,180)} = 8.51$, $p<0.05$, $\eta_p^2 = 0.19$), a significant main effect of Region ($F_{(2,72)} = 204.47$, $p<0.05$, $\eta_p^2 = 0.85$) and a significant main effect of Laterality ($F_{(2,72)} = 22.81$, $p<0.05$, $\eta_p^2 = 0.38$). Furthermore, a significant three-way interaction Film Category by Region by Laterality ($F_{(20,720)} = 2.89$, $p<0.05$, $\eta_p^2 = 0.07$) was observed. Post-hoc analysis of the significant three-way interaction showed that alpha power was strongly modulated in the central (Cz-CPz) and posterior (Pz-Oz) clusters along the midline, following an arousal gradient. We observed that the low arousing Neutral clips elicited the largest alpha power. Scenery, Compassion and Sadness prompted a decrease in alpha activity, with Sadness eliciting greater inhibition compared to other two (only in the Cz-CPz cluster). Finally, the largest alpha inhibition, indexing greater cortical activation, was observed in response to the most arousing categories, namely Erotic and Fear.

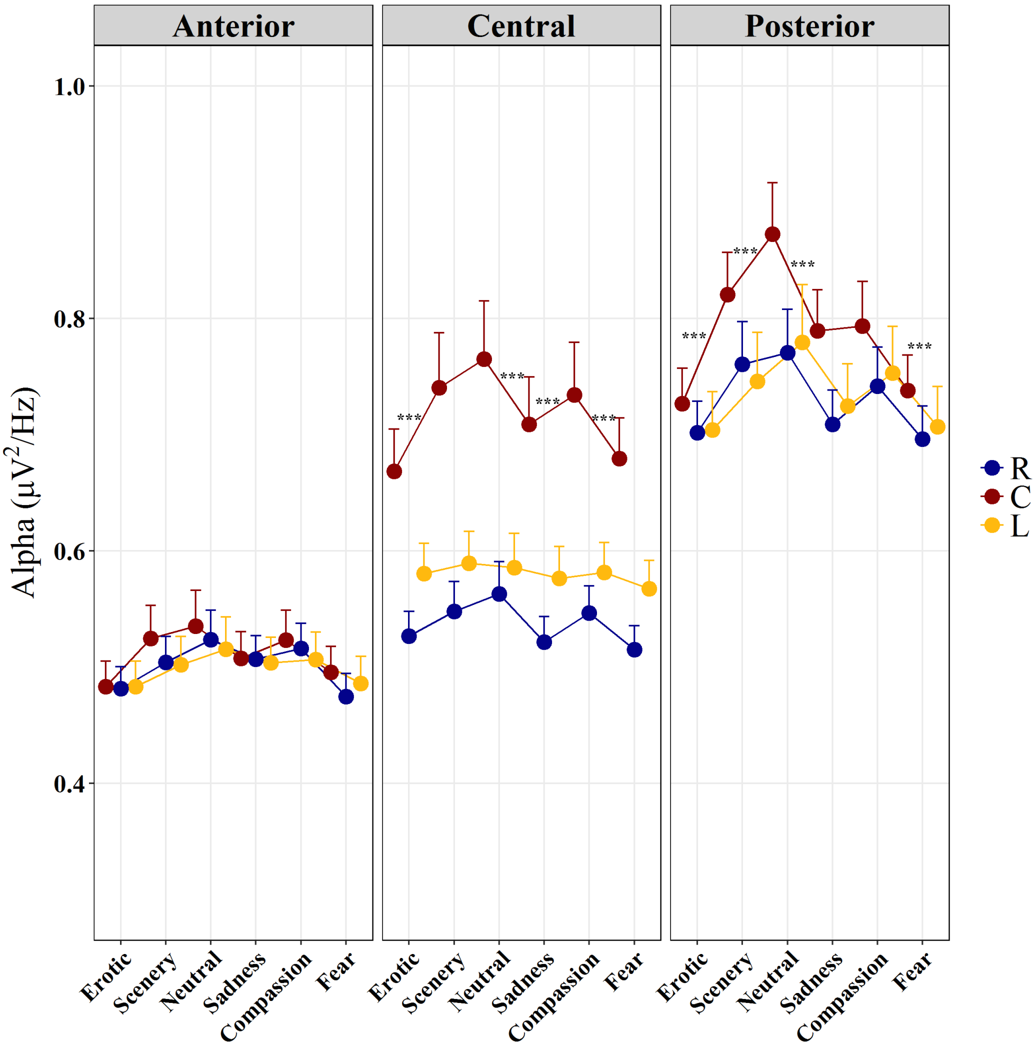

Figure 5.2 Differences in Alpha power among the film categories, in the ROIs considered. Asterisks represents significant ($p<0.05$) post-hoc effects. Bars represents SE.

Beta Power

ANOVA computed on beta band power values showed a significant main effect of Film Category ($F_{(5,180)} = 10.09$, $p<0.05$, $\eta_p^2 = 0.21$), a significant main effect of Region ($F_{(2,72)} = 3.34$, $p<0.05$, $\eta_p^2 = 0.09$) and a significant main effect of Laterality ($F_{(2,72)} = 20.9$, $p<0.05$, $\eta_p^2 = 0.36$). Moreover, the three-way interaction Film Category by Region by Laterality was significant ($F_{(20,720)} = 2.6$, $p<0.05$, $\eta_p^2 = 0.06$). Post-hoc analysis of the three-way interaction revealed that unpleasant film clips elicited the largest beta activation, especially on central and posterior regions, both at left and right sites. At the right central cluster (FT8-T8) beta activation elicited by Fear, Sadness and Compassion excerpts was significantly different from the activation elicited by the other emotional categories, with no difference among them. At the left central cluster (FT7-T7), the analysis showed that activation during Sadness and Compassion was significantly different only from the one occurring during Scenery and Neutral clips, but not from the activation elicited by Erotic excerpts.

Finally, in the posterior regions, for both the left (TP7-P7) and the right cluster (TP8-P8), the pattern of beta activity was identical to the one observed in the right central cluster.

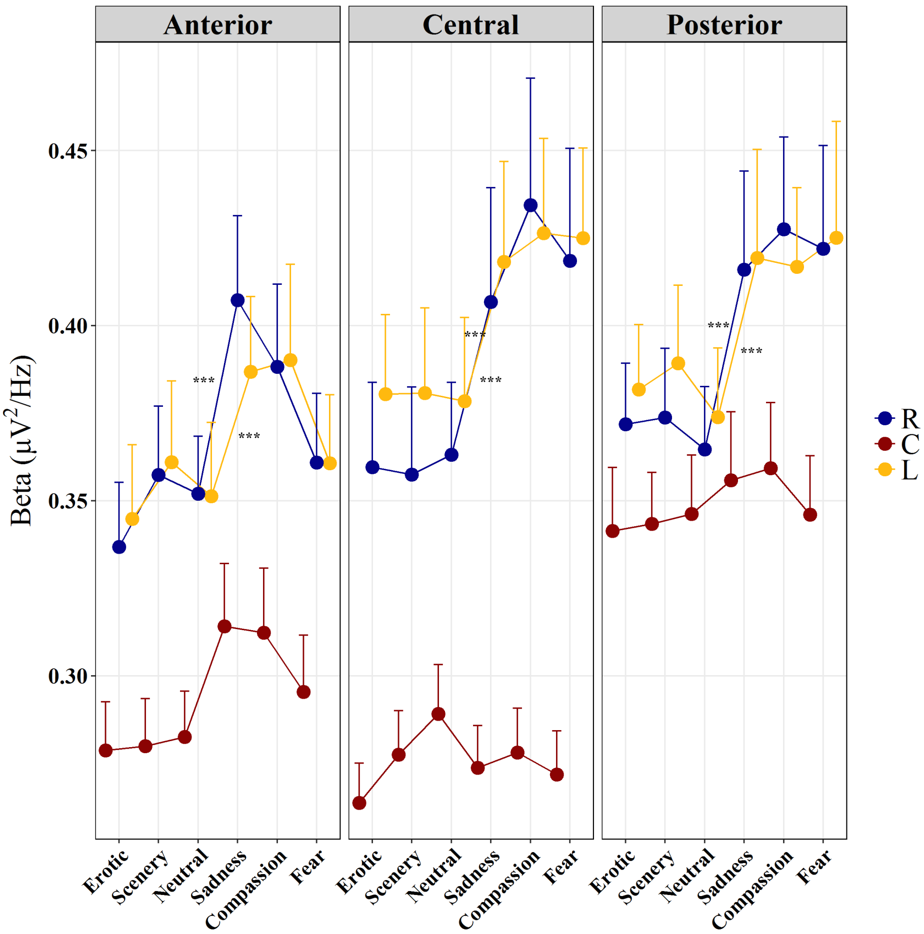

Figure 5.3 Differences in Beta power among the film categories, in the ROIs considered. Asterisks represents significant ($p<0.05$) post-hoc effects. Bars represents SE.

sLORETA Source Analysis

For alpha band, statistical comparisons between source activity elicited by Neutral excerpts and the other film categories, were significant ($p<0.05$), with a greater alpha activity for the Neutral condition in all comparisons. The main generator of this activity was identified in the occipito-parietal regions, with the majority of supra-threshold voxels located in the superior parietal lobule and in the precuneus (BA 7). For the beta band, only the comparisons between Neutral and the three unpleasant categories (Sadness, Compassion and Fear) were significant ($p<0.05$), highlighting a common source of activity located within the right temporal lobe, in the superior and middle temporal gyri (BA 21–22). Contrasts between Neutral and Erotic and Scenery categories, instead, did not reveal any significant difference.

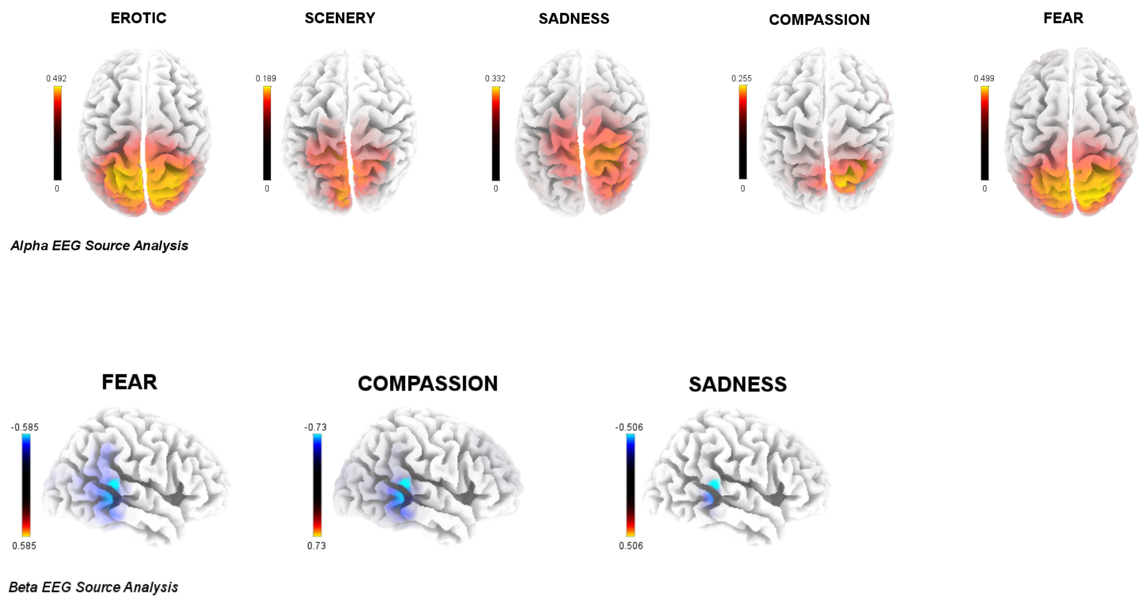

Figure 5.4 Source reconstructed cortical activity for Alpha (top) and Beta (bottom). Activation represents significant sources in the contrasts with the Neutral condition. For Alpha higher source activity indexes larger alpha inhibition in these regions in the emotional condition compared with neutral. For Beta higher source activity reflects larger beta activity in the emotional condition compared with the neutral.

5.5 DISCUSSION

The present research aimed at characterizing the role of emotions in the modulation of brain activity elicited by complex naturalistic stimuli. We presented participants with movie excerpts arranged in six affective categories while recording their cortical activity using EEG. Self-report of affective experience showed a response pattern consistent with previous evaluation of these clips (Maffei et al., 2015), confirming the efficacy of the manipulation. Erotic and Scenery clips were judged as more pleasant and exciting compared to the others, while the three negative categories elicited an unpleasant affective state characterized by increased anxiety and distress, especially for the Fear clips which were also rated as being the most arousing category. For what concerns brain activity, our prediction was that clip content would differentially impact the electrocortical spectral dynamics, especially within the posterior cortices, which were reported to be distinctively recruited by this kind of stimuli (Golland et al., 2007). Our results showed that movie presentation had a strong effect on both alpha, which is a robust indicator of cortical inhibition (Bazanova & Vernon, 2014; Klimesch, 1999), and beta oscillations. We found that Alpha power was strongly modulated as a function of stimulus category, showing an increased cortical activation (i.e. lower alpha power) elicited by all the emotional clips compared to the neutral ones. This pattern strongly suggests an effect of stimulus arousal in the modulation of cortical activity, which appears to be coherent with the self-report ratings. Indeed, our results highlighted a fine distinction among the five affective categories, with the movies belonging to the high-arousal Fear and Erotic categories prompting the largest activation compared to the low arousal ones. These results are consistent with previous electrophysiological evidences which showed that, using both static and dynamic emotional stimuli, alpha power is inversely related with stimulus arousal (Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2002; Simons et al., 2003). In addition, these works reported that this effect is larger over the posterior regions of the scalp, probably reflecting the complex relationship that interrelates arousal and visual attention to emotional stimuli (Dmochowski et al., 2012; Simons et al., 2003). Moreover, fMRI results showed that BOLD signal collected from the extrastriate visual cortices in response to emotional pictures increases compared to the neutral ones, with an arousal gradient (greater BOLD changes for high arousal categories compared to low arousal ones) similar to the one reported in the present results (Sabatinelli et al., 2004).

Interestingly, our findings showed that alpha modulation was larger within the electrodes located above the occipito-parietal cortex. Source analysis identified the main generator of this activation in the parietal cortex, peaking in the superior parietal lobule and precuneus (BA 7), bilaterally. Statistical comparisons across the categories showed that alpha activity in this area was greater, reflecting increased cortical inhibition, in response to the Neutral clips compared to all the affective movies. These results confirmed our initial prediction that manipulating the emotional content of the movies would result in a differential recruitment of the brain regions involved in processing of naturalistic stimuli. Indeed, parietal regions represent a central node in the network activated during the processing of a dynamic movie (Hasson et al., 2004; Pamilo et al., 2012), which is the target of multiple afferent pathways conveying sensory information that become hierarchically more integrated. Consistent with previous reports, we found that activation in these regions is higher during the presentation of emotional arousing videos compared to a neutral one, irrespective of valence (Nummenmaa et al., 2012a). This evidence should be interpreted as the reflection of the neural mechanism underlying the increased deployment of resources toward the processing of an affectively charged stimulus, likely mediated by cortico-subcortical interactions along the visual stream (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Indeed, it is known that visual areas and amygdala are functionally interconnected, and activity in the latter boosts the elaboration of visual information that is emotionally charged. These results in greater attention toward the stimulus and an increased physiological activation in the brain regions involved in visual processing, as well as in supra-modal integration. This mechanism, paired with complex autonomic modifications (i.e. biphasic heart rate response, skin conductance increase) (Bradley, Codispoti, Cuthbert, & Lang, 2001), reflects an adaptive biological strategy evolved to cope with situations that require rapid and effective environment exploration, both negative (i.e. facing a threat) and positive (i.e. detecting a sexual mate).

The same regions responsible for the activity here discussed, have also been included in a complex subset of brain regions called posteromedial cortex, which is a core hub of the default mode network (DMN). A distinctive trait that makes this hub so important is the wide range of bi-directional functional and anatomical connections occurring with both cortical (such as orbitofrontal and anterior cingulate cortices) and subcortical areas, especially insula and amygdala (Hagmann et al., 2008). Despite its name, there are accumulating evidences positing that DMN activity is not restricted to a default, mind-wandering, mental state (Golland et al., 2007; Nummenmaa et al., 2012a; Wilson, Molnar-Szakacs, & Iacoboni, 2008). It rather reflects a more complex psycho-physiological state, which encompasses emotional and social cognition, and appears to be deeply tied with the emergence of the sense of self and conscious experiences (Stawarczyk, Majerus, Maquet, & D’Argembeau, 2011). Our results are consistent with this view of the DMN, and with many evidences positing that brain regions within the DMN are activated also during ecological conditions that do not constrain cognitive activity within an effortful task, like viewing a movie. In addition, they add to this increasing knowledge, providing evidence that the emotional content is preferentially processed in order to making it readily available to consciousness.

For what concerns beta activity, the analysis showed a different pattern. We found that the clips comprised in the three unpleasant categories elicited an increase in beta spectral power, compared to the others, especially in the central and posterior clusters. These results suggest that not only arousal, but also stimulus valence has a role in modulating the cortical dynamics elicited by these movies, showing a functional dissociation across different frequency bands. Moreover, they provide further support for the association between negative affect and cortical activity in the range of beta frequency, which has been consistently reported in previous studies (Güntekin & Basar, 2007; Güntekin & Başar, 2010).

sLORETA analysis traced back the pattern observed at scalp level to the activity of the posterior temporal cortex, with a peak activity located in the superior and middle temporal gyrus (BA 21-22). Interestingly, this activity was more pronounced in the right hemisphere compared to the left, consistent with the asymmetric activation of the right hemisphere in response to negative emotional stimuli (Harmon-Jones et al., 2010). Activity in superior and middle temporal cortices has been reported to be sensitive to a wide range of processes that involve perception and elaboration of social features, including face processing, language comprehension, perception of biological motion and narrative understanding (Allison, Puce, & McCarthy, 2000; Britton et al., 2006; Lahnakoski, Glerean, et al., 2012; Wilson et al., 2008). Our results extend this knowledge, showing a selective activation in response to movie depicting the main characters in an unpleasant social situation. Indeed, we found that activity in STG/MTG regions was enhanced only during the presentation of scenes of social threat (Fear), social exclusion and isolation (Sadness) and emotional sufferance (Compassion), while activity in response to a social positive situation (Erotic) was no different from the neutral condition. This suggest that superior temporal cortex might have a degree of specificity in responding to negative situations that involve a conspecific. This finding is in line with multiple observations across several research fields that showed an asymmetric effect on psychological, as well as physiological, reactivity exerted by stimuli with positive and negative valence, which favors the negative ones (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001). We believe that, in this context, the observed advantage for unpleasant movies reflects a pathway, within the superior temporal cortex, shaped to grant a rapid an effective identification of those social features that indicate an actual or potential threat. From an evolutionary viewpoint this ability is critical for maximizing the chance of survival through the exploitation of social signals, a strategy which is commonly observed in human and other social animals (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003). However, we should acknowledge that the present findings contrast some previous results reported by Britton and colleagues (2006). In their paper, the authors reported that STG was activated in response to both social positive and social negative emotions, and interpreted this finding as the result of the general involvement of STG in processing of social elements of emotional stimuli. Nevertheless, the present experiment has, among several, one critical difference from Britton and colleagues', that is that we analyzed brain activity collected during the last 30 seconds of each clip, while in Britton's the authors considered the activity of the 30 s immediately following the movie. Although, they presented a static frame from the clip to maintain participant's affective state, it is likely that this condition has dampened brain response, possibly reducing the likelihood to observe the difference between the two conditions.

Taken together, the present results return a complex picture of how cortical reactivity is shaped during the presentation of film clips of different emotional categories. The observed functional dissociation across alpha and beta frequency bands, showed that manipulating the content of the movies affects brain dynamics at multiple scales. Emotional arousal was largely reflected in different power of alpha oscillations, while negative valence was encoded in larger beta activity. Moreover, a remarkable feature of the present findings is that they show different activity patterns for emotional categories that are usually confounded. Indeed, we showed that clips depicting natural landscapes, despite being usually considered as an affectively neutral condition (Rottenberg et al., 2007), elicit greater cortical activation compared to urban documentaries. This result is of critical importance for future investigation, since it adds to the increasing number of evidences highlighting that nature-related stimuli are a powerful source of positive affect, able to capture viewer's attention and to elicit distinctive psychophysiological response patterns (Hartig et al., 2003; Ulrich, 1981; Ulrich et al., 1991). Another interesting difference, is the one observed between Sadness and Compassion categories, characterized by an increased activation for the former compared to the latter. These results strongly advocate for the use of multiple categories of stimuli for manipulating participants' affect, rather the rely on a broad distinction among positive and negative stimuli. Indeed, using this finer differentiation could help unveiling the specific neural signatures underpinning similar but not overlapping affective states (i.e. Compassion and Sadness), that are difficult to study within the general dimension of positive-negative affect.

Finally, analysis of electrophysiological dynamics at the source level showed that emotional movies modulate the activation of the brain regions involved in dynamic stimulus processing and multisensory feature integration that lead to conscious experience, showing that the effect of emotions is already present at this stage, in the hierarchy of the neural processing. We believe that these findings may contribute to the understanding of the ubiquitous effect of affective features in the interaction with complex, real-life environments, and invite for further investigation using experimental approaches aiming at effectively mimic conditions close to the everyday emotional experience.

Chapter 6

STUDY 3: Cortical reactivity to emotional movies is shaped by viewer's empathy: Evidence from Gamma EEG activity

6.1 Abstract

Empathy underlies the ability to understand others' emotional state and resonate with them in a coherent response. Despite being a fundamental mechanism, people are characterized by differences in their empathic abilities and the present study seeks to understand how these differences influence emotional reactivity. Forty-one female students, divided in High and Low trait empathy, watched 8 movie clips of four emotional categories (Erotic, Fear, Compassion and Neutral) while subjective evaluation of affective experience and EEG activity were recorded. Analysis of arousal revealed that high trait empathy is characterized by an increased emotional sensitivity compared to low trait empathy. Multilevel modeling of gamma oscillatory activity extended this observation also at cortical level by showing that participants in the HIGH empathy group were characterized by a greater cortical activation to all the emotional categories compared to the neutral, whereas in the LOW empathy group an increased response only to the negative clips was found. Furthermore, participants in the HIGH group also showed a strong correlation between subjective arousal and cortical activity, both at scalp-level and source-level, in response to film clips depicting emotional pain and sufferance. The brain region that showed the greatest activation was located in the right inferior parietal lobe, which is a core region in the network supporting empathic sharing of others' emotions.

Taken together, the present results highlight that higher levels of empathy are associated to greater sensitivity to all emotional stimuli, which is reflected in a larger gamma activity.

Furthermore, scenes designed to elicit empathic reactions and prosocial behavior, are characterized by distinctive cortical processing in people with high levels of empathy.

6.2 Introduction

Empathy is an important psychological construct, which has been the focus of a great amount of researches in the last decades. Despite its popularity, a single, agreed-upon definition of empathy is still far from be achieved (Batson, 2009b), although there is a general consensus about considering empathy not as a unitary ability, but rather as multidimensional construct encompassing different facets, which can be partially dissociated. A generally accepted view posits that it is possible to characterize at least two facets, the one related to the ability to understand other's internal state, usually referred to as cognitive empathy, and another related to the process of sharing others' feeling, usually recognized by human beings as emotional empathy (Davis, 1983).

Cognitive empathy, sometimes referred to as *mentalizing*, includes the cognitive ability to infer the thoughts of other people, as well as the goals of their behaviors and the reasons underlying them (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Singer, 2006). This set of skills constitutes the critical core of social cognition, and it is considered to be defective in people affected by autistic spectrum disorder (ASD) (Blair, 2005; Golan, Baron-Cohen, Hill, & Golan, 2006).

Emotional empathy, on the other hand, entails the process of sharing the affective state of another person (Singer & Lamm, 2009). In cognitive neuroscience the role of affective empathy in mediating the reactivity to others' emotions has been mainly studied considering the relationship between empathy and pain. These studies showed that, in response to the view of another person receiving a painful stimulation, the viewer's brain regions involved in the processing of emotional features associated with painful experience were activated, although the participant did not receive any actual stimulation (Singer et al., 2004). Moreover, individual differences in dispositional empathy modulate this activation, with people characterized by high levels of affective empathy showing the largest activation during the vicarious experience of other's pain (Singer et al., 2004).

Nevertheless, the affective reactivity to others' emotional experience in everyday life is not restricted to physical pain, but extends to a wider range of emotional elicitors, both positive and negative. Indeed, in everyday life it's quite common to share joy as well as fear or sadness, when confronted with these emotions in other people. Surprisingly, compared to empathy for pain, the study of the physiological correlates of these phenomena has received far less attention in the literature, especially for what concerns the role that individual differences of empathic traits play in modulating these affective responses. Moreover, the majority of works investigating how differences in empathy modulate brain correlates of affective reactivity focused on specific cohorts of individuals, characterized by marked abnormalities in their empathic traits, like criminal psychopaths (Blair, 2005; Blair, 2008; Decety, Skelly, & Kiehl, 2013).

The present study aimed at extending the knowledge within this field, investigating how differences in empathic abilities of healthy adults are associated with differences in affective experience and cortical reactions to movie clips, selected to target both pleasant and unpleasant affective states.

To this end, we employed movie clips, which represent one of the best tool available to experimentally manipulate emotions, allowing us to elicit both simple and complex affective states not only with great intensity, but also with great ecology of the emotional experience (Rottenberg et al., 2007). The strong natural appearance of the affect triggered by movies, indeed, relies upon the pivotal role that empathy plays in fostering the transposition of the individual within the fictitious narrative displayed (Coplan, 2006). For this reason, emotional movies are an ideal choice for investigating how differences in empathic abilities modulate individual's emotional reactivity.

The present study addresses two research questions. The first one focuses on ascertaining whether and how people characterized by high empathy traits has different subjective and physiological responses to emotional stimuli, compared to people with low empathy traits. Anecdotal evidence supports the notion that high affective empathy is associated with increased emotional sensitivity. Nevertheless, a systematic investigation of these links has been deficient so far, especially regarding their physiological correlates. The few studies that explicitly investigated differences in emotional reactivity in high and low empathy participants showed that high empathy traits are associated with increased autonomic reactivity (heart rate and skin conductance) to emotional stimuli, regardless of stimulus valence (Mehrabian et al., 1988). Facial mimicry also seems to be modulated by trait level of empathy, with more empathic participants showing larger activation of facial muscles in response to both happy and angry faces (Sonnby-Borgstrom, 2002; Sonnby-Borgström, Jönsson, & Svensson, 2003). This limited information suggests that the role of empathy is independent of stimulus valence, and that individuals with high empathy traits tend to experience stronger emotional activation regardless of the pleasantness/unpleasantness of stimuli. To directly test this hypothesis, in the present study we used various emotional movies with both positive (i.e., Erotic category) and negative (i.e., Fear and Compassion categories) affective content, selected from a newly developed emotional film clip database, that successfully provides a reliable and effective modulation of the viewer's emotional state. Erotic and Fear movies were selected to target two high-arousal states with opposite motivational valence, being appetitive the former, withdrawing the latter. Instead, Compassion clips were included to elicit an empathy-driven affective reaction in the viewer, by showing other people crying and suffering for an emotional pain (i.e., the loss of a relative). Indeed, crying is a behavior evolved to seek help by communicating distress (Hendriks et al., 2008), and seeing another person in tears elicits in the viewer a prosocial motivation toward the other, which is grounded in the empathic resonance with others' sufferance (Vingerhoets, van de Ven, & van der Velden, 2016). We expected that participants characterized by higher levels of dispositional empathy would be characterized by an increased reactivity to all emotional movies, marked by increased cortical activation in the Gamma EEG band. This EEG rhythm has been selected since growing evidences suggest that gamma oscillations are a fundamental mechanism for the neural communication involved in complex multisensory perceptual task (like viewing a movie) as well as high-order cognitive processing (Jerbi et al., 2009), and it has been previously shown to be sensitive to the emotional content of visual stimuli (Martini et al., 2012; Müller, Gruber, & Keil, 2000; Müller, Keil, Gruber, & Elbert, 1999).

The second aim of this study is focused on clarifying how emotional arousal and empathy interact in the modulation of cortical activity elicited by emotional movies. Indeed, several studies showed that processing of film clips involves the recruitment of a complex cluster of brain regions, including both areas engaged by low-level sensory feature processing, and areas active in higher-order cognitive processes, related to attention and multimodal integration (Hasson et al., 2010, 2004). Nummenmaa and colleagues (2012b) showed that activity in this cluster of regions is modulated by the levels of emotional arousal elicited by the clips, increased arousal being associated with greater activation in parietal and occipital cortices. Moreover, these authors reported that the activity in the right temporal lobe (MTG/STS) – considered to be one of the critical regions involved in empathy – was positively correlated with participants' scores on a measure of trait empathic abilities. To increase this knowledge to all the affective categories considered, we explored how the relationship between emotional arousal and brain activity changed as function of dispositional empathy. We predicted that the association between arousal and cortical response to the movie clips would be stronger for participants with high empathy traits compared to those with low empathy traits. We also expected that this relationship would be stronger in parietal and temporal cortical regions, which are typically engaged by empathy and dynamic stimulus processing, such as movie clips.

6.3 Methods

Participants

An initial sample of ninety-four female undergraduates (Mean age = 20.15 years, S.D = 1.69 years), with no history of neurological or psychiatric disease, was recruited for participating in the experiment in exchange for course credits. Participants were asked to fulfill both the Interpersonal Reactivity Index (Davis, 1983) and the Levenson Self Report Psychopathy Scale (Levenson, Kiehl, & Fitzpatrick, 1995), in order to assess dispositional empathy and psychopathic traits, respectively. Starting from a composite score, resulting from the sum of the four IRI subscales (i.e., Empathic concern, Personal Distress, Fantasy and Perspective Taking), we identified two subgroups of participants, the one including participants with high empathy traits (group HE, n = 20) whose scores exceeded the 75° percentile of the IRI score distribution, the other comprising participants with low empathy traits (group LE, n = 21) whose scores were below 25° percentile of the IRI score distribution. As can be seen in Table 6.1, the two groups did not differ in term of primary psychopathy, assessed by the Factor 1 of the LSRPS ($t_{(39)}$=1.49, p=.14). The participants selected took part in the second phase of the experiment, which included the collection of their EEG brain activity during the view of emotional film clips. Ethics Committee of the Department of General Psychology (University of Padova) approved the study, which was carried out according to the principles expressed in the Declaration of Helsinki.

	High Empathy	Low Empathy	
IRI Total score	112.2	87.4	$t_{(39)} = 15.46, p < 0.05$
Fantasy	29.2	21.7	$t_{(39)} = 5.91, p < 0.05$
Empathic Concern	30.4	25.1	$t_{(39)} = 5.21, p < 0.05$
Perspective Taking	27.9	23.3	$t_{(39)} = 4.63, p < 0.05$
Personal Distress	24.7	17.1	$t_{(39)} = 5.13, p < 0.05$
LSRP F1	34.7	32.9	$t_{(39)} = 1.49, p = 0.14$

Table 6.1 Mean scores for the four IRI subscales and the Factor 1 subscale of the LSRPS for High and Low empathy groups.

Stimuli

Participants were presented with eight short film excerpts divided in four different emotional categories, comprising two clips each. Erotic excerpts, portraying heterosexual couples engaged in sexual intercourse, were selected to elicit a positive emotional state, characterized by high arousal and an approaching motivation. Concerning negative emotional state, we selected Fear excerpts, which included thrilling scenes of anticipated threat on one hand, and Compassion excerpts, depicting scenes of grief and loss on the other hand. Fear excerpts were selected to induce a negative, high arousal state, characterized by a withdrawing motivation; instead, Compassion clips, whose distinctive feature was the depiction of characters crying for a bereavement, were chosen for their potential to elicit in the viewer a negative affect characterized by an empathic reaction toward others emotional pain. Thus, this category was specifically included to probe the effect of individual differences in empathy toward the depiction of others emotional, rather than physical, pain. Finally, excerpts featuring scenes drawn from urban documentaries were chosen to elicit an affectively neutral state. The clips were edited, using Adobe Premiere CS5, to match a resolution of 1280 x 720 pixel, and presented to the participants using E-Prime software (v.2). The order of the excerpts was pseudo-randomized, to avoid that two excerpts belonging to the same category were presented consecutively, and fixed across all participants.

Procedure

Upon arrival, every participant received a description of the experiment and its procedures, to give her informed consent to participate in the research. Then, she was sat in a comfortable armchair and electrodes were attached. After electrodes placement, a single practice film (not considered for the analysis) was projected on a 22-inches Full HD screen (16:9 aspect ratio), to acquaint the participant with the procedure. Next, the experimenters gave any additional explanation, if needed, and the experimental session started.

Self-rating of affective experience

To assess the effect of the emotional and neutral clips on their affect, at the end of each clip participants rated their emotional state using the Self-Assessment Manikin (SAM), which asked to judge the valence (1 extremely unpleasant – 9 extremely pleasant) and the arousal (1 extremely calm – 9 extremely aroused) elicited by the movie.

EEG recordings and data reduction

EEG activity was recorded continuously by means of 38 electrodes, 31 mounted on an elastic cap (ElectroCap) according the 10-20 International System, and 7 applied below each eye (IO1, IO2), on the external canthus of each eye (F9, F10), on the mastoids (A1, A2) and in correspondence of the nasion (Nz). The signal was recorded with a SynAmps RT amplifier and the Curry 7 software (Compumedics Neuroscan, Charlotte, NC, USA), using a sampling rate of 500 Hz; all the impedances were kept below 5 KΩ and Cz was used as online reference. EEG activity collected in the final 30 seconds of each excerpt was considered for the statistical analysis. This choice was due to the specific characteristics of the stimuli, all featuring the most emotional scenes in the last minute, and to the specific time course that characterizes the development of emotional experience elicited with movies (Rottenberg et al., 2007). Thus, it was assumed that the maximum effect of the experimental manipulation would be observed in the last 30 seconds of each clip. The EEG data were offline re-referenced to average reference, and the last 30 seconds of each clip were divided into 14 non-overlapping, 2048 msec epochs with 0.488 Hz FFT resolution. Artifacts related to eye movements (blinks and saccades) were removed trough the MSEC procedure (Ille et al., 2002) using BESA software (5.3 version). Then an artifact rejection procedure was performed automatically on all the epochs, with amplitude and gradient thresholds (250 μV and 150 μV/msec, respectively). The remaining epochs were also visually inspected to remove any residual artifacts from the analysis. An average of 85% of epochs were retained for further analyses (Erotic = 87%, Neutral = 83%, Compassion = 81%, Fear = 88%). At the end of data preprocessing, FFT was applied on all artifact-free epochs and the average amplitude spectrum in the Gamma range (35-49 Hz), separately for the four emotional categories. In order to reduce the dimensionality of the data, for statistical purposes activity for each category was averaged into 9 clusters comprising two electrodes each: Anterior Left (F7-F3), Anterior Central (Fpz-Fz), Anterior Right (F8-F4), Central Left (FT7-T7), Central Central (Cz-CPz), Central Right (FT8-T8), Posterior Left (TP7-P7), Posterior Central (Pz-Oz), Posterior Right (TP8-P8). The clustering resulted in a 3 x 3 grid along two dimensions defined Region (Ant-Ct-Pos) and Hemisphere (Left-Ct-Right).

In addition, standardized low-resolution electromagnetic tomography (sLORETA) (Frei et al., 2001; Pascual-Marqui, 2002) was used to identify the distributed source density solutions of Gamma activity observed for each film category at the scalp level. Since sLORETA computes the smoothest possible 3D-distributed current source density solution constrained to gray matter, this approach was particularly suited for our analysis since it does not need an a priori number of known sources. Starting from all of the 2048-ms epochs available from each subject and interval – exactly the same which entered FFT analysis after artifact rejection – a single, 38 × 38 complex-valued, cross- spectral matrix for each participant and condition was computed for the Gamma band. All cross-spectral matrices were then converted in sLORETA transformation matrices to reduce the noise associated with measurement, to minimize the dependence of the source current density on individual subjects, and to eliminate components in the EEG spectra that were common to both groups. This transformation algorithm uses the three-shell spherical head model registered to the Talairach Human Brain Atlas (Talairach and Tournoux, 1988), available as MNI coordinates.

Statistical analysis

For the analysis of both self-report and electrophysiological data we used linear mixed-effects (LME) models. LME models represent an extension of the general linear model, able to encompass classical analytical approaches (i.e., t-test, ANOVA, ANCOVA) within a new and more flexible framework characterized by several strengths. One of the main advantages of LME over classical linear models is the possibility to include in the model both fixed-effects, modeling the source of variation that the experimenter wants to study, and random-effects, that model the sources of variability which have not been explicitly manipulated, but still contribute to explaining the observed data. Typical examples of this "random" factors are inter- and intra-individual variabilities usually found in within-subject experimental designs, that are more effectively handled using LME models compared to a more classical analysis such as repeated-measures ANOVA (Bagiella, Sloan, & Heitjan, 2000; Boisgontier & Cheval, 2016). In addition, another strength of LME models is the possibility to handle easily unbalanced designs and missing observations, which in classical Repeated-Measures ANOVA lead to the removal of the entire subject row, or compel to impute the missing data.

Statistical analysis of self-report affective ratings was performed fitting two separate linear mixed-effects models to valence and arousal responses, considering Film category, Group and their interaction as fixed-effects and including a random intercept for each subject, in order to accommodate for repeated-measurements. Significance of the fixed-effects was evaluated by means of F-test using the Satterthwaite approximation for degrees of freedom (Luke, 2016). Significant effects have been further explored by means of post-hoc pairwise contrasts, corrected for multiple comparisons using false discovery rate (FDR).

Analysis of Gamma activity was performed using linear mixed-effects model adopting a model selection strategy based on the Akaike Information Criterion (AIC) and the Akaike weights (AICw), in order to identify the combination of predictors that best described the data. AIC (Akaike, 1973) is a powerful metric derived from Information Theory which indicates the relative quality of a model, given a set of candidate models (the lowest the AIC the highest the quality of the model, controlling for its complexity), and AIC weights represents, given a set of candidate models, the probability for each one to be the best model (Wagenmakers & Farrell, 2004).

The predictors considered were Film Category, Group, Region and Hemisphere as fixed-effects and a random intercept for each subject. We first estimated the most complex model justified by the experimental design, removed outlier observations (observations with absolute standardized residuals exceeding ±2.5 SD of model standardized residual, < 2% of the dataset) and then derived simpler instances of this model excluding predictors until reaching an intercept-only model. A total of 49 candidate models were estimated and compared. Once identified the best-fitting model (i.e., the model with lowest AIC and largest AICw), we performed an F-test using the Satterthwaite approximation for degrees of freedom in order to test the significance of the predictors. Significant effects have been further explored by means of post-hoc pairwise contrasts, corrected for multiple comparisons using false discovery rate (FDR).

To test the existence of a positive relationship between subjective arousal and cortical activation as a function of individual differences in empathy, Pearson's correlation were computed, separately for each movie category and group, between arousal scores and Gamma power in each ROI. The reported statistical tests are one-sided and probability values are corrected using false discovery rate (FDR), in order to address the problem of multiple comparisons.

In addition, arousal scores were regressed against source reconstructed cortical activity, in order to find, for each category, the cortical regions whose activity was more influenced by subjective emotional arousal in the two groups. Statistical analysis of source activity was performed using the statistical non-parametric mapping (SnPM) approach (Nichols & Holmes, 2002), using 5000 permutation for the estimation of the null distribution of the r statistic. Analysis was performed using the module implemented in the sLORETA software. All results are expressed in Talairach coordinates (Talairach and Tournoux, 1988).

Data manipulation, statistical analyses and figure generation were performed using R (version 3.3.2) (R Core Team, 2016) and the following packages: lme4 (Bates, Mächler, Bolker, & Walker, 2015), lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016), MuMIn (Bartoń, 2016), lsmeans (Lenth, 2016), ggplot2 (Wickham, 2009) and dplyr (Wickham & Francois, 2016).

6.4 Results

Self-Report affective ratings

Analysis of valence ratings showed a main effect of Film category ($F_{(3,156)} = 42.02$, $p < 0.0001$), whereas neither Group main effect ($F_{(1,156)} = 0.79$, *n.s*) nor interaction between Film category and Group ($F_{(3,156)} = 2.01$, *n.s*) were significant. Post-hoc analysis of film effect showed that Fear and Compassion excerpts were rated as the most unpleasant and Erotic clips as the most pleasant (all *p*s < 0.05).

Analysis of arousal scores revealed main effects of Film category ($F_{(3,117)} = 42.02$, $p < 0.0001$) and Group factors ($F_{(1,39)} = 4.84$, $p = 0.03$). Interaction between Film category and Group failed to reach significance, showing only a marginal tendency ($F_{(3,117)} = 2.28$, $p = 0.08$). The Group main effect revealed that HE participants reported to feel more aroused during the viewing of emotional movies, compared to LE participants. In addition, post-hoc contrasts on the Film category main effect revealed that all the affective clips were rated as more arousing compared to the Neutral excerpts (all ps < 0.05), and that Erotic movies were rated less arousing compared to the other two unpleasant categories (all ps < 0.05).

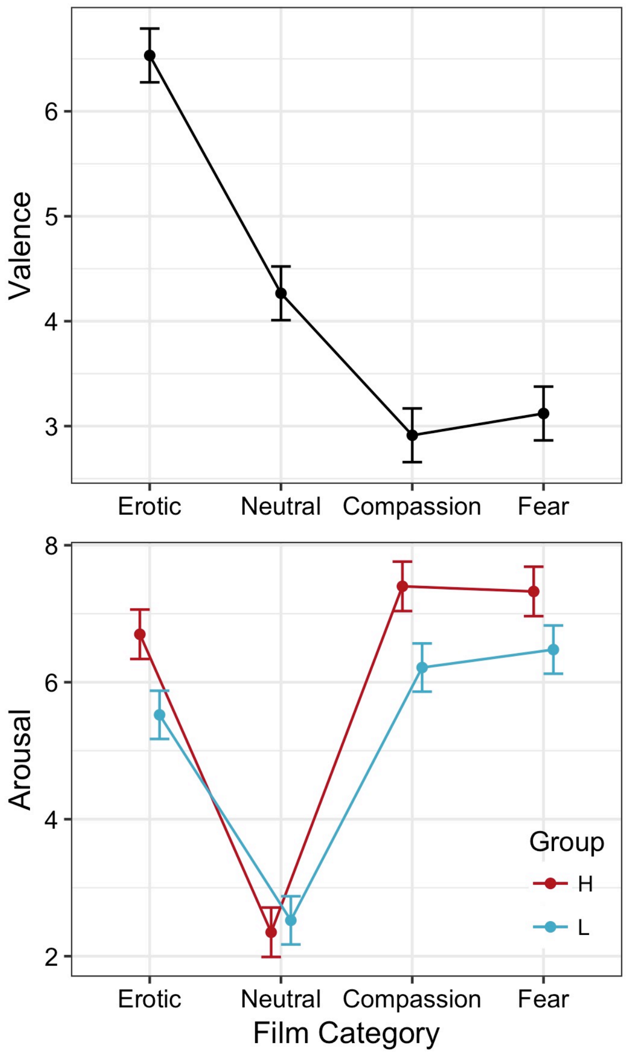

Figure 6.1 Results of SAM analysis. Top Panel shows the effect of film category on valence ratings. Bottom Panel shows the effect of film category on arousal ratings in the two groups. Bars represent SE.

Gamma power

The comparison revealed that the best-fitting model was the one that included as fixed-effect predictors Film Category, Group, Region, Hemisphere, and the interactions between Film Category and Group, Film Category and Region, and Region and Hemisphere. This model was characterized by a ΔAIC score, computed with the second ranked model as a reference, of 5.6 and an AIC weight of 0.87, suggesting strong evidence in favor of this model.

The full list of the models considered, with their associated AIC scores and AIC weights, is listed in Appendix I.

The F-test performed to assess the significance of the predictors included in this model revealed significant main effects of Film Category ($F_{(3,1406)} = 33.96$, $p < 0.0001$), Region ($F_{(2,1406)} = 171.72$, $p < 0.0001$) and Hemisphere ($F_{(2,1406)} = 496.41$, $p < 0.0001$), and significant Film Category by Group ($F_{(3,1406)} = 4.40$, $p = 0.004$), Film Category by Region ($F_{(6,1406)} = 3.69$, $p = 0.001$), and Region by Hemisphere ($F_{(4,1406)} = 145.45$, $p < 0.0001$) interactions.

Post-hoc contrasts performed on the Film Category x Group effect showed that, in HE group, all the emotional movies elicited larger Gamma activity compared to the neutral clips (all ps < 0.05), Erotic movies showing lower cortical activation compared to Compassion (p < 0.05) and Fear (p = 0.05) categories. Instead, cortical activity for LE group was characterized by increased activity in response to Fear and Compassion clips (all ps < 0.05), whereas activity elicited by Erotic excerpts and Neutral clips was not different (p = 0.11).

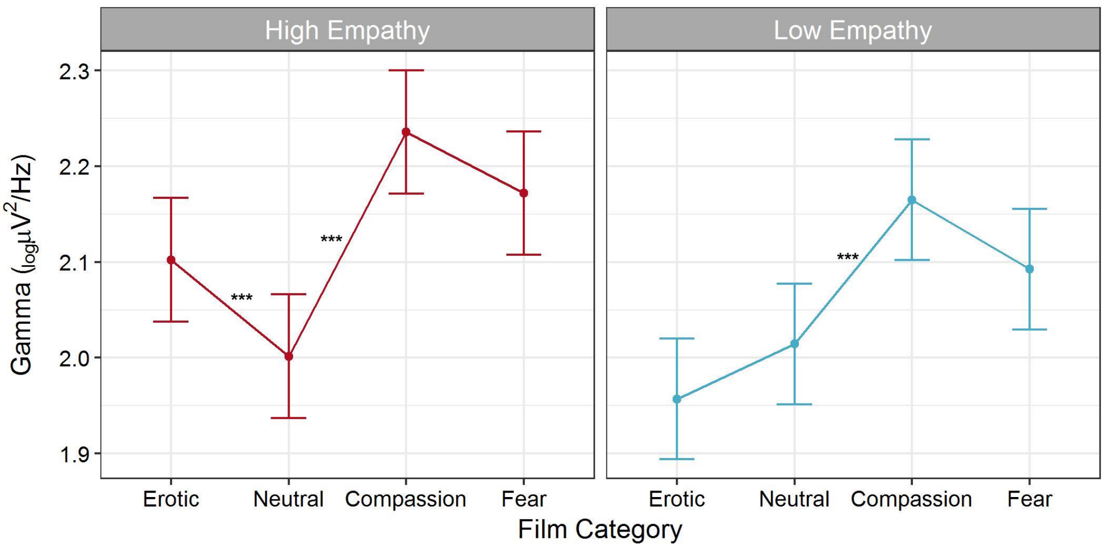

Figure 6.2 Effect of Film category on cortical Gamma power for High and Low Empathy group. Asterisks indicates significant post-hoc effects with p< 0.05. Bars represent SE.

Correlation between Arousal and Gamma power

Pearson's correlations showed a significant positive relationship between arousal scores and Gamma activation in the HE participants during the presentation of Compassion clips. This positive correlation was found in the anterior ROIs over both the right hemisphere (r = 0.59, $t_{(18)} = 3.17$, $p_{corrected} = 0.01$) and the midline (r = 0.44, $t_{(18)} = 2.1$, $p_{corrected} = 0.04$), in the central ROI over the midline (r = 0.47, $t_{(18)} = 2.29$, $p_{corrected} = 0.03$), and in posterior ROIs over both the left (r = 0.65, $t_{(18)} = 3.72$, $p_{corrected} = 0.007$) and the right hemisphere (r = 0.48, $t_{(18)} = 2.33$, $p_{corrected} = 0.03$). A significant correlation was also found in the posterior ROI in the right hemisphere between arousal and Gamma power elicited by Fear excerpts (r = 0.58, $t_{(18)} = 3.1$, $p_{corrected} = 0.02$).

No significant correlations were found instead for the LE group.

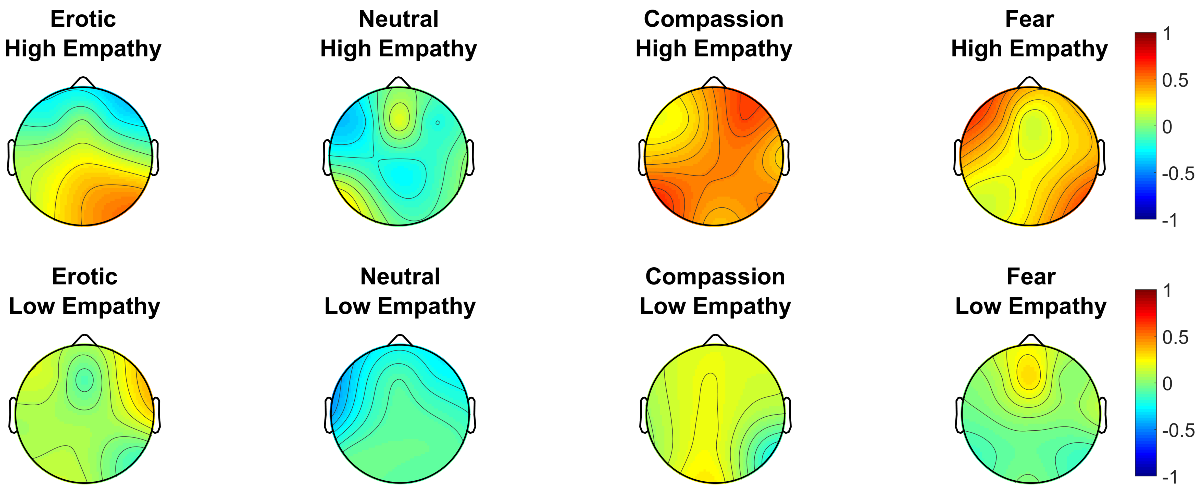

Figure 6.3 EEG topographical map showing the correlation between Gamma power and self-reported Arousal scores in the two groups, for each film category.

Source analysis revealed that the right inferior parietal cortex (Talairach coordinates of the most active voxel: X = 40, Y = -45, Z = 40, $r_{(max)}$ = 0.63, p = 0.007) was the cortical regions which showed the strongest relationship between Gamma activity and arousal in the

HE group for the Compassion movie. No significant effects were found instead for the LE group.

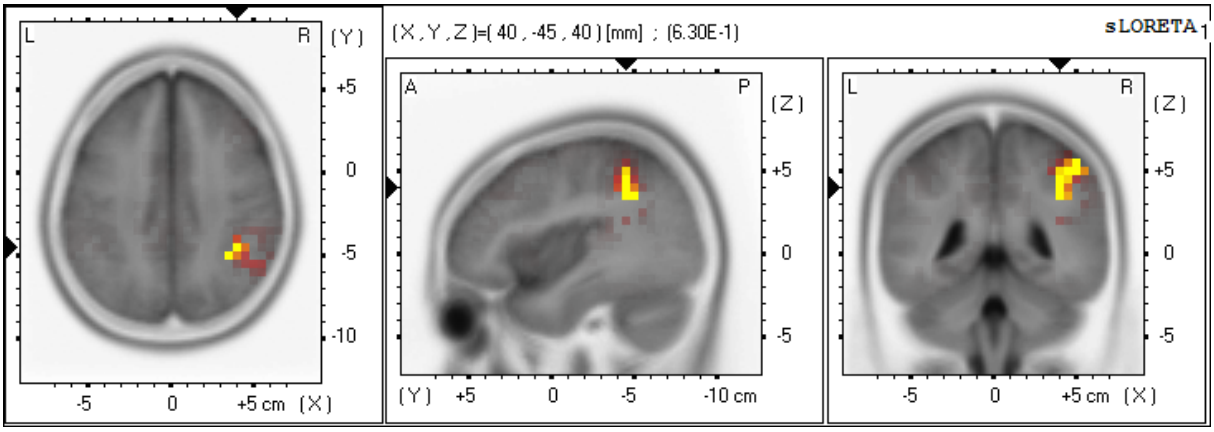

Figure 6.4 sLORETA map showing the cortical regions characterized by the largest correlation between Gamma power and self-reported Arousal in response to Compassion clips in the High Empathy group.

6.5 Discussion

The present study sought to evaluate how individual differences in dispositional empathy modulate subjective experience and cortical reactivity elicited by the presentation of emotional film clips, which were selected to provide a strong and ecological manipulation of the viewer's emotional state (Maffei et al., 2015; Rottenberg et al., 2007). Previous investigation suggested that high levels of empathic abilities appear directly associated with an increased sensitivity to emotional stimuli (Singer et al., 2004; Sonnby-Borgstrom, 2002; Sonnby-Borgström et al., 2003), therefore the main hypothesis of the present study was that emotional arousal elicited by various clips would vary as a function of viewer's empathy traits. The analysis of participants' self-reports of affective state did support this hypothesis, showing that individuals included in the High Empathy group claimed to feel more aroused during the view of emotional excerpts compared to individuals with low empathy traits.

Instead, no evidence was found supporting the presence of a link between empathy levels and emotional valence. Valence analysis revealed just a main effect of film category, which confirmed the efficacy of the experimental manipulation by showing that Erotic movies were rated as more pleasant, and Fear and Compassion clips as more unpleasant, compared to the clips included in the Neutral category. The lack of a clear-cut relationship with valence bolsters the notion that empathy influences sensitiveness to emotional stimulation (Martin, Berry, Dobranski, Horne, & Dodgson, 1996). Indeed, these results suggest that, in the context of emotional experience, empathy acts as a modulator of the threshold for individual emotional reactivity. The higher is a person's dispositional empathy, the more likely would be for her showing an affective response toward the emotional stimulus, irrespective of the pleasantness or the unpleasantness of the stimulus itself.

Considering the analysis carried out to investigate the cortical dynamics underlying emotional movie processing, gamma EEG band has been selected as marker of stimulus affective content. Indeed, the relationship between affect and stimulus content has been previously demonstrated using static visual emotional stimuli, like IAPS slides (Keil et al., 2001; Müller et al., 1999) and emotional faces (Balconi & Lucchiari, 2008), and it has been extended in this study, for the first time, to more dynamic and ecological emotional stimuli, such as film clips. Our analysis revealed that, in the High Empathy group, Gamma activity was increased in response to all the emotional clips compared to the neutral condition, suggesting that in individuals with high dispositional empathy, who are characterized by a greater tendency to get absorbed by the narrative, the emotional content of the clips – irrespective of their pleasantness or unpleasantness – leads to a greater recruitment of resources. The increase of cortical gamma activity found over the scalp likely reflects the cascade of feedback connections from subcortical regions, especially amygdala, which boost the affective content of the visual stimulus and, spreading rapidly all over the cortical surface, maximize its processing (Pessoa & Adolphs, 2010; Vuilleumier et al., 2004). Thus, this result shows, at neural level, how high empathy leads to increased emotional sensitivity, and provides a neurophysiological correlate that marks the role of this trait in shaping the emotional responding.

Results also showed that participants with low empathic abilities, who were expected to display a more flattened cortical response toward the affective clips compared to the high empathy group, were still characterized by an increased activation in response to the negative clips compared to the neutral ones. Although it is possible that, in the present sample, the reduced trait empathy was not so strong to determine a decreased processing of powerful aversive stimuli, like the movies used, this results should be interpreted considering that participants of LE group were not characterized by higher levels of primary psychopathy. Indeed, the scores to the LSRP - F1 showed that the two groups did not differed in term of emotional detachment and primary psychopathy (see Table 6.1). Previous studies that linked a reduced brain responsivity to negative emotional stimuli with low empathic abilities, typically investigated individuals characterized by high levels of psychopathic tendencies, or clinical psychopaths from the incarcerated populations (Blair, 2008; Decety et al., 2013). Although low empathy is an important feature of psychopathy, the abnormal emotional responsivity to unpleasant stimuli that marks individuals with high levels of this personality trait, is the result of the complex interaction among its multiple features, rather than the effect of one feature alone. Considering that the negative film clips here used were characterized by the depiction of emotional scenes highly salient, with a strong evolutionary meaning (physical threat and crying), it's not surprising that they elicited an increased cortical activation also in individuals with low empathy traits. In addition, correlation analyses between cortical activity and self-reported emotional arousal complete the picture, revealing the different mechanisms underlying the processing of negative film clips in the two groups. Correlation analyses carried out considering scalp-level gamma power showed a strong positive relationship between cortical activity and arousal in response to Compassion and, to a lesser extent, Fear clips in the HE group, while no relationship was found in the LE participants. Thus, participants with high empathy traits are more likely to immerge themselves into the movie, thus empathizing with the emotional dynamics displayed on the screen results in the experience of stronger emotional arousal as a consequence of a larger cortical processing of the unpleasant scenes presented in the film excerpts (Nummenmaa et al., 2012b). On the other hand, when dispositional empathy is low, the viewer's engagement in the fictitious story is reduced, and there is no relationship between the degree of brain activation and the emotions experienced: the cortical dynamics just reflect the processing of a stimulus characterized by high salience, without revealing the viewer's empathic emotional responding.

Source-level analysis supports this interpretation, suggesting that the brain region that showed the strongest correlation between Gamma activity and emotional arousal in the HE group was the right inferior parietal lobule, specifically in response to presentation of Compassion movies. This brain region has been consistently reported to be a core hub in the brain network supporting empathy, especially in its affective facet (Shamay-Tsoory, 2011). Indeed, neurons in the IPL are characterized by having mirror-like properties (Chong et al., 2008) and their activation is critical for the ability to share other people's internal state, promoting the matching between the observed action and the viewer's internal representation of it. According to the neurocognitive perception-action model of empathy (De Waal & Preston, 2017; Preston & de Waal, 2002), this process of internal matching of an external perceived cue, extends beyond the context of simple motor actions, encompassing complex motivated behaviors as well, and it is considered the fundamental mechanism that guides empathic sharing of others emotions (De Waal & Preston, 2017). Moreover, the relationship between activity in this region and empathic emotional responding has been previously showed in the context of empathy for pain, revealing that the inferior parietal cortex is a core area in the network activated by the view of other people's physical pain (Lamm, Decety, & Singer, 2011). The present result extends this knowledge providing evidence that IPL is activated by the viewing of another person suffering for an emotional pain, and not only in response to other people experiencing physical pain. In addition, the strong correlation observed suggests that physiological and psychological factors are deeply interweaved, and provides further support to the hypothesis that empathy and arousal do interact in affective response, suggesting that individual differences in empathy traits mediate the relationship between brain activation to others' emotional suffering and subjective experience.

Taken together, these results provide new insights about the complex role played by empathy in shaping emotional reactivity at both subjective and cortical level, showing that individual differences in the ability to empathize modulate how people respond to emotional stimuli, in an ecological setting. Moreover, they revealed that the brain regions that support empathic sharing of observed emotions are activated in response to cues of emotional distress and sufferance in others, and that this activation covaries with the subjective experience in people with high trait empathy.

Finally, it should be acknowledged that these results do not come without limitations. In this study only female participants were investigated to control for potential confounds related with gender differences in emotional reactivity (Bianchin & Angrilli, 2012; Maffei et al., 2015) and in brain activation in empathy-related tasks (Han, Fan, & Mao, 2008; Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008): future studies should focus on male samples to generalize these findings. This is especially important for characterizing the affective reactivity in low empathy individuals, based on the evidence that males generally score lower than females in questionnaire investigating empathy traits (Baron-Cohen & Wheelwright, 2004).

Chapter 7

STUDY 4: PRIMARY PSYCHOPATHIC TRAITS ARE ASSOCIATED WITH REDUCED CORTICAL REACTIVITY TO UNPLEASANT EMOTIONAL MOVIES

7.1 Abstract

The present study investigated the relationship between high trait levels of primary psychopathy, subjective emotional experience and cortical activity in the Gamma band (30 – 49 Hz), during different affective states elicited with ecological emotional stimuli.

Fifty-eight male participants divided in two groups, High and Low primary psychopathy, were selected from a larger sample (n = 271) using the Factor 1 of the Levenson Self-Report Psychopathy Scale. Participants watched 15 two-min clips, divided in five categories (Erotic, Neutral, Scenery, Compassion and Fear) while their EEG activity was recorded from 38 scalp electrodes. Participants reported their emotional experience by evaluating movies on Valence and Arousal dimensions and quantifying how much they felt sad, anxious, touched and excited.

Analysis of the self-report measures revealed that participants in the high compared to low psychopathy felt less anxious in response to Fear clips and less sad and touched by Compassion excerpts. Analysis of Gamma activity showed that negative clips induced larger Gamma power in both groups compared to neutral and positive movies, and that, in the high vs. low psychopathy group, Gamma power in response to Fear movies was reduced. Source analysis revealed that in people with high psychopathic traits there is a reduced cortical activation in a large brain network, comprising regions involved in visual attention and regions involved in affective empathy.

Taken together the present results show that high traits in primary psychopathy are associated to a reduced sensitivity to unpleasant emotional stimuli, which is observed at both the subjective and physiological level. The consistence observed across different response domains highlights the advantages of using strong and ecological emotional stimuli, like movies, to uncover the distinctive psychophysiological markers of the emotional alterations associated to primary psychopathy.

7.2 Introduction

Psychopathy is a severe personality disorder characterized by serious impairment in emotional abilities, accompanied with inappropriate behavioral displays, usually resulting in criminal acts. A distinctive feature of psychopathy, which distinguishes this condition from other psychopathologies, is the absence of overt impairments in social functioning, making psychopaths appear well adjusted in their environment despite their condition (Patrick, 2006). The complexity of the psychopathic phenotype has been conceptualized in different ways (Fowles & Dindo, 2006; Patrick, Fowles, & Krueger, 2009; Vitacco & Jackson, 2005) but all the authors agreed upon distinguishing at least two, partially independent, facets in psychopathy: an affective component usually called *primary psychopathy* or *emotional detachment*, describing the abnormalities in emotional abilities, and a behavioral component capturing the antisocial tendencies, labelled *secondary psychopathy*.

There is a long tradition of studies aiming at characterizing psychopathy from a psychobiological perspective in order to improve both diagnosis, providing objective biomarkers for this disorder, and treatment, guiding the development of better and targeted therapeutic approaches. A finding consistently reported across studies is that psychopathic individuals have a strong impairment in their ability to process aversive stimuli, especially fear-inducing material (Anderson & Kiehl, 2012). Indeed, incarcerated psychopathic criminals do not show the characteristic potentiation of the startle reflex, which usually occurs when processing aversive stimuli (Patrick, 1994). Moreover, fMRI investigations revealed that psychopathic offenders in response to aversive emotional stimuli are characterized by a reduced activation of both amygdala and orbitofrontal cortex, two key brain regions in the network supporting the processing of affective features of external stimuli (Anderson & Kiehl, 2012). Finally, psychopathic individuals fail to show conditioned fear responses (Birbaumer et al., 2005). Taken together, these findings support the idea that impairment in fear-processing is a core element of the psychopathic phenotype.

Another core characteristic of psychopathy is the lack of empathy, especially in its affective facet, which makes psychopaths impaired in the spontaneous tendency to share others emotional state, leading to the distinctive callousness that characterize their behaviors (Blair, 2018). This empathy deficit has been observed across a wide range of measures like questionnaires, behavioral tasks and physiological activity. Psychopathic individuals systematically report lower levels of emotional empathy compared to non-psychopathic inmates and healthy controls, and are characterized by a reduced tendency to exhibit prosocial behaviors (which are deeply linked to affective empathy). For what concerns the neural correlates of this lack of empathy, Decety and colleagues (2013a; 2013b) showed that psychopaths have a reduced cortical response to the view of another person receiving physical pain and that activity in brain regions involved in empathy for pain is inversely correlated with measures of emotional detachment. Interestingly, Meffert and colleagues (2013) reported that the reduced brain engagement in response to the view of emotional interactions occurs more prominently when psychopathic individuals have no instructions, showing instead a relatively normal brain response when instructed to empathize with the presented scene. These evidence remark that lack of empathy is a core element in the psychopathic syndrome, and support the idea that the critical impairment lies in the spontaneous empathic engagement toward emotionally charged scenes, while psychopathic individuals are still able to empathize when the context requires them to do it.

To date, an important limitation of research on psychopathy is represented by the limited number of studies focusing on psychopathic traits in non-incarcerated individuals. The investigation of psychophysiological underpinnings of psychopathic traits in non-forensic samples is extremely relevant for the characterization of psychopathy as a dimensional construct in the general population (Seara-Cardoso & Viding, 2014). Moreover, only through this kind of investigations it would be possible to effectively characterize the affective component of psychopathy disentangled from the violent anti-social behavioral component, since this latter dimension is utterly prominent in criminal psychopaths, but it is not in community samples.

The present study aims at overcoming this issue, investigating participants with high and low traits of primary psychopathy, selected from a relatively large sample of healthy individuals according to their scores on a psychopathy inventory, that were presented with emotional film clips while their brain activity was recorded using EEG. The use of emotional film clips represents an important innovation in this field of research in which static pictures are usually treated as the golden standard of emotion elicitation. Indeed, the use of film clips has repeatedly proved to be more effective for experimental induction of emotions compared to static pictures (Rottenberg et al., 2007; Westermann et al., 1996), since movies are dynamic stimuli that, stimulating the participant trough different sensory domains (visual and auditory), lead to greater engagement. Moreover, the use of emotional movies allows the induction of both simple and complex affective states and, considering that film viewing is a common leisure activity for the majority of the individuals, increases the ecological validity of the experimental paradigm. Finally, experiencing emotions while viewing movies is grounded in the empathic transposition of the viewer in the narrative displayed (Coplan, 2006), thus film excerpts represent the ideal choice for probing empathy in an experimental context.

Different categories of emotional clips (Erotic, Scenery, Compassion, Fear and Neutral) have been used, covering the whole span of the positive/appetitive-negative/aversive dimension, in order to characterize how psychopathic traits affect emotional reactivity. We predicted that primary psychopathy would be related to a reduced experience of negative affect in response to unpleasant movies. Specifically, we hypothesized that individuals with high levels of psychopathic traits would show a reduced emotional reactivity to film clips depicting threatening scenes (Fear), and that this reduction would be reflected in a reduced cortical processing of the stimuli. Moreover, we expected that primary psychopathy, due to its inherent association with lack of empathic concern and disregard for others, would impact also the activity elicited by the presentation of scenes depicting other people crying for an emotional sufferance (i.e. death of a relative). No difference instead was expected in response to pleasant material.

7.3 Methods

Participants

Two-hundred and seventy-one male students from University of Padova were recruited using flyers and online advertisements for completing the Levenson's Self-Report Psychopathy scale (LSRPS), a 26-item self-report questionnaire specifically developed to assess psychopathic traits in non-forensic population. Its structure comprises two factors, the *primary psychopathy* scale which consists of 16 items targeting the affective-interpersonal dimension of psychopathy, and the *secondary psychopathy* scale which includes 10 items targeting the behavioral dimension of psychopathy (impulsivity and anti-social tendencies).

Based on the distribution of the scores to the Primary Psychopathy subscale, we selected 60 participants divided in two group; the High Psychopathy (HP) group comprised participants who scored above the 85^{th} percentile of the distribution, the Low Psychopathy (LP) group comprised instead participants who scored below the 15^{th} percentile of the distribution. This final group of participants (HP mean age = 21.8 yrs, sd = 2.2, LP mean age = 22.4 years, sd = 1.9) took part in the psychophysiological experiment in the laboratory, in exchange for 26 €. The study received approval from the Ethics Committee of the Department of General Psychology (University of Padova), and all the procedures were carried out according to the principles expressed in the Declaration of Helsinki.

Stimuli

Fifteen short film excerpts were selected in order to experimentally manipulate participants' emotional state. The clips were arranged in five categories (3 clips x category), two positive (Erotic and Scenery) and two negative (Fear and Compassion) plus a Neutral condition. Erotic clips included non-pornographic scenes depicting heterosexual couple engaging in sexual intercourse, and were selected to induce a positive and appetitive high arousal affective state. Scenery clips included scenes selected from natural documentaries displaying stunning natural landscapes, which proved to elicit in the viewer a positive affect, despite previous use of pictures of natural environment as neutral stimuli. Compassion clips, included scenes depicting the main character suffering and crying for an emotional pain (i.e. grieving for the loss of a loved person), which were designed to probe in the viewer an affective reaction grounded on the empathic sharing of others emotional pain. Fear clips comprised excerpts depicting thrilling and suspense scenes in which the main character was threatened, in order to elicit in the viewer a negative affective state characterized by fear and anxiety. Finally, the Neutral condition included clips selected from urban documentaries in order to elicit in the viewer a neutral, low-arousal, affective state.

All the clips were were edited, using Adobe Premiere CS5, to match a resolution of 1280 x 720 pixel, and presented to the participants using E-Prime software (v.2). The order of the excerpts was pseudo-randomized, to avoid that two excerpts belonging to the same category were presented consecutively, and fixed across all subjects.

Procedure

Upon arrival, each participant gave his informed consent to participate in the experiment after receiving a detailed description of all the procedures. Then, he was sat in a comfortable armchair and experimenter started electrodes placement. Before starting with the experiment, a single practice film (not considered for the analysis) was projected on a 22-inches Full HD screen (16:9 aspect ratio), in order to acquaint the participant to the procedure. Next, the experimenters gave any additional explanation, if requested, and the session started.

Self-rating of affective experience

At the end of each clip, participant's emotional state was assessed using the Self-Assessment Manikin (SAM), asking to rate the valence (1 extremely unpleasant – 9 extremely pleasant) and the arousal (1 extremely calm – 9 extremely aroused) elicited by the movie. In addition, participants were asked to rate their affect using a series of emotional adjectives (Sad, Touched, Anxious, Anguished, Excited) using a five points Likert scale (0 not at all – 4 extremely).

EEG recordings and data reduction

Cortical activity was collected continuously by means of 38 electrodes connected to a SynAmps RT amplifier. Thirty-one electrodes were mounted on an elastic cap (ElectroCap) according the 10-20 International System, and the remaining 7 were applied below each eye (IO1, IO2), on the external canthus of each eye (F9, F10), on the mastoids (A1, A2) and in correspondence of the nasion (Nz). The signal was digitalized at 500 Hz and stored for further processing using the Curry 7 software (Compumedics Neuroscan, Charlotte, NC, USA). All the impedances were kept below 5 KΩ and Cz was used as online reference.

EEG data were preprocessed using MATLAB and the EEGLab and Brainstorm toolboxes. Activity was high-pass filtered (0.1 Hz), re-referenced to the average of all the channels and submitted to ICA (Independent Component Analysis) in order to extract artefactual components related with eye activity (blinks and saccades) to remove from the data. After components rejection, the last 30 seconds of each clip was considered for further processing and divided into fourteen epochs lasting 2048 msec. This choice was based on the consideration that the effect of the experimental manipulation would peak in the final part of the excerpts, due to the specific characteristics of the stimuli (all featuring the most emotional scenes in the last minute) and to the specific time course that characterizes the development of emotional experience elicited with movies (Rottenberg et al., 2007). Epochs with activity in any channel exceeding an amplitude threshold of ± 100 μV were automatically rejected. Then, remaining epochs were visually inspected for residual artifacts. An average of 84% of epochs were retained for further analyses (Erotic = 85%, Scenery = 82%, Neutral = 85%, Compassion = 87%, Fear = 80%). Spectral power was quantified in the artifact-free epochs using FFT and the average power spectrum in the Gamma range (35-49 Hz), normalized over the entire spectrum, was computed for the five categories.

For statistical analysis, data dimensionality was reduced averaging cortical activity for each category into 9 clusters comprising two electrodes each, arranged in a 3 x 3 grid along two dimensions defined Region (Ant-Ct-Pos) and Hemisphere (Left-Ct-Right). The clusters were defined as follows: Anterior Left (F7-F3), Anterior Central (Fpz-Fz), Anterior Right (F8-F4), Central Left (FT7-T7), Central Central (Cz-CPz), Central Right (FT8-T8), Posterior Left (TP7-P7), Posterior Central (Pz-Oz), Posterior Right (TP8-P8).

In addition, standardized low-resolution electromagnetic tomography (sLORETA) (Frei et al., 2001; Pascual-Marqui, 2002) was used to identify the source density distribution of Gamma activity observed at the scalp level. Since sLORETA computes the smoothest possible 3D-distributed current source density solution constrained to gray matter, this approach was particularly suited for our analysis since it does not need an a priori number of known sources. Starting from all of the epochs available from each subject and category (the same considered for FFT analysis) a single, 38 × 38 complex-valued, cross- spectral matrix for each participant and condition was computed for the Gamma band. All cross-spectral matrices were then converted in sLORETA transformation matrices to reduce the noise associated with measurement, to minimize the dependence of the source current density on individual subjects, and to eliminate components in the EEG spectra that were common to both groups. This transformation algorithm uses the three-shell spherical head model registered to the Talairach Human Brain Atlas (Talairach and Tournoux, 1988), available as MNI coordinates.

Statistical analysis

For the analysis of both self-report and electrophysiological data we used linear mixed-effects (LME) models. LME models represent a new and flexible extension of the general linear model, characterized by multiple advantages. One of the main strengths of LME over classical linear models is the possibility to include in the model both fixed-effects, modeling the source of variation under investigation, and random-effects, that model the sources of variability not explicitly manipulated, that still contribute to the observed data. Two classic examples of random effects that are usually modeled using LME models are inter- and intra-individual variabilities usually found in within-subject experimental designs. This makes LME models more effective compared to the widely used repeated-measures ANOVA (Bagiella, Sloan, & Heitjan, 2000; Boisgontier & Cheval, 2016). Moreover, another advantage of LME models is the possibility to deal easily with missing observations and unbalanced designs, which are instead a critical issue in classical Repeated-Measures ANOVA, usually forcing the experimenter to remove the entire subject row (leading to a significant loss of data) or to rely on imputation methods.

Statistical analysis of self-report affective ratings was performed fitting a linear mixed-effects models separately for each item included in the self-report evaluation. The fixed-effects considered were Film category, Group and their interaction and, in order to accommodate for repeated-measurements, the models included a random intercept for each subject. An F-test using the Satterthwaite approximation for degrees of freedom (Luke, 2016) was used to test the significance of the fixed effects. Significant effects have been explored using post-hoc pairwise contrasts, corrected for multiple comparisons using false discovery rate (FDR).

Analysis of Gamma activity was performed adopting a model selection approach based on the Akaike Information Criterion (AIC) and the Akaike weights (AICw), in order to identify the combination of predictors that best described the data. AIC (Akaike, 1973) is a powerful metric derived from Information Theory which indicates the relative quality of a model, given a set of candidate models (the lowest the AIC the highest the quality of the model, controlling for its complexity), and AIC weights represent, given a set of candidate models, the probability for each one to be the best model (Wagenmakers & Farrell, 2004).

The predictors considered were Film Category, Group, Region and Hemisphere, together with their interactions, as fixed-effects and a random intercept for each subject. First the most complex model was estimated, then outlier observations (observations with absolute standardized residuals exceeding ±2.5 SD of model standardized residual, < 2% of the dataset) were removed, and finally simpler instances of this model were derived excluding predictors until reaching an intercept-only model. Once identified the best-fitting model (i.e. the model with lowest AIC and largest AICw), we performed an F-test using the Satterthwaite approximation for degrees of freedom in order to test the significance of the predictors. Significant effects have been further explored by means of post-hoc pairwise contrasts, corrected for multiple comparisons using false discovery rate (FDR).

Finally, statistical contrasts between the two groups were performed on the source reconstructed gamma activity for each emotional category using the statistical non-parametric mapping (SnPM) approach (Nichols & Holmes, 2002), as implemented in the sLORETA software (Pascual-Marqui, 2002).

Data manipulation, statistical analyses and figure generation were performed using R (version 3.3.2) (R Core Team, 2016) and the following packages: lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2016), MuMIn (Bartoń, 2016), lsmeans (Lenth, 2016), ggplot2 (Wickham, 2009) and dplyr (Wickham & Francois, 2016).

7.4 Results

Self-Report affective ratings

Analysis of SAM ratings revealed a main effect of Film Category for both Valence ($F_{(4,232)} = 74.31$, $p < 0.0001$) and Arousal ($F_{(4,232)} = 50.38$, $p < 0.0001$), while neither the Group main effect nor the Film Category x Group interaction were significant.

Post-hoc analysis performed on the significant Film Category effect for the Valence, revealed that positive film categories (Erotic and Scenery) were rated as more pleasant compared to all the other excerpts (all $p_{FDR} < 0.05$), with the Scenery clips rated as the most pleasant.

Post-hoc analysis of the film Category effect for Arousal ratings showed that all the emotional clips were judged as more arousing compared to the neutral excerpts (all $p_{FDR} < 0.05$). Within the emotional clips, the ones included in the positive categories were rated as more arousing compared to the ones comprised in the negative categories. Moreover, Fear movies were perceived as more arousing compared to Compassion movies, while no difference were found between Erotic and Scenery clips.

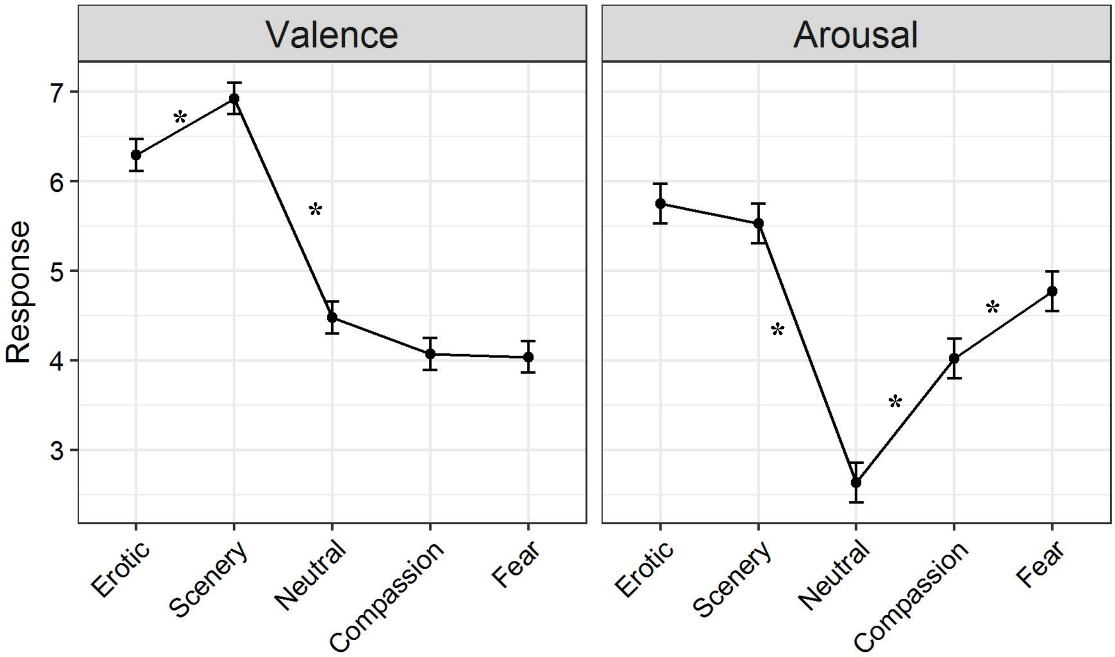

Figure 7.1 Results of SAM ratings. Asterisks represents significant (p< 0.05) post-hoc effects. Bars represent SE.

For what concerns emotional adjectives, a significant Film Category x Group interaction was found for the item Sad ($F_{(4,232)} = 5.63$, $p = 0.0002$), Touched ($F_{(4,232)} = 7.49$, $p < 0.0001$), Anxious ($F_{(4,232)} = 4.99$, $p = 0.0007$) and Anguished ($F_{(4,232)} = 5.37$, $p = 0.0003$), while for the item Excited only the Film category effect was significant ($F_{(4,232)} = 105.63$, $p < 0.0001$).

Post-hoc analysis performed on the Film Category x Group interactions revealed that participants in the HP group felt lower levels of negative emotions compared to the LP participants. Specifically, they felt less anxious in response to Fear clips ($p_{FDR} < 0.05$) and less anguished in response to both Fear and Compassion clips (all $p_{FDR} < 0.05$). Moreover, they reported to feel less sad and touched by Compassion clips (all $p_{FDR} < 0.05$).

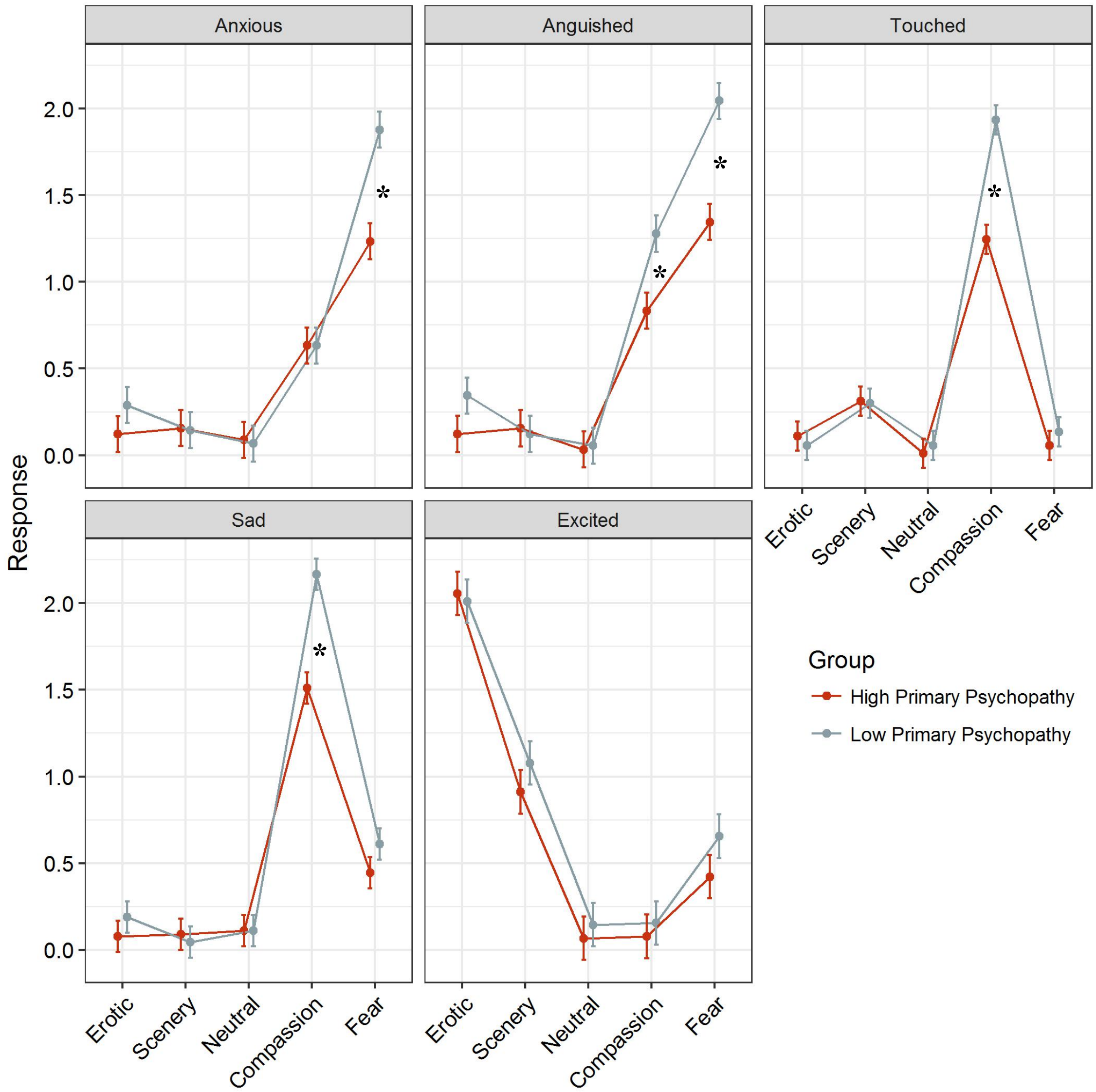

Figure 7.2 Results of adjectives ratings. Asterisks represents significant ($p< 0.05$) post-hoc effects. Bars represent SE.

Gamma power

The best-fitting model, according to the models comparison, included as fixed-effect predictors Film Category, Group, Region, Hemisphere, and the interactions between Film Category and Group, Film Category and Hemisphere, Region and Hemisphere, and Group, Hemisphere and Region. This model was characterized by a ΔAIC score, calculated with respect to the second ranked model, of 2.83 and an AIC weight of 0.73, which indicates good evidence in favor of this model.

The full list of the models compared, with their associated AIC scores and AIC weights is listed in Appendix II.

The F-test performed to assess the significance of the predictors included in the model showed a significant main effect of Film Category ($F_{(4,2501)} = 34.81$, $p < 0.0001$), Region ($F_{(4,2501)} = 178.83$, $p < 0.0001$) and Hemisphere ($F_{(4,2501)} = 1011.93$, $p < 0.0001$) and significant interactions Film Category x Group ($F_{(4,2501)} = 2.77$, $p = 0.02$), Film Category x Hemisphere ($F_{(4,2501)} = 3.71$, $p = 0.0002$), Group x Hemisphere ($F_{(4,2501)} = 10.78$, $p < 0.0001$), Group x Region ($F_{(4,2501)} = 3.56$, $p = 0.02$), Region x Hemisphere ($F_{(4,2501)} = 154.35$, $p < 0.0001$) and Region x Group x Hemisphere ($F_{(4,2501)} = 3.92$, $p = 0.003$).

Post-hoc pairwise comparisons performed on the Film Category x Group interaction revealed that in both groups gamma power was increased in response to the negative clips (Fear and Compassion) compared to the positive and the neutral (all $p_{FDR} < 0.05$), and that cortical activity elicited by Fear movies was reduced in the HP group ($p_{FDR} < 0.05$). No difference were observed between positive and neutral clips in the HP group, while in the LP participants gamma power in response to Scenery clips was larger than the activity elicited by both Erotic and Neutral movies ($p_{FDR} < 0.05$).

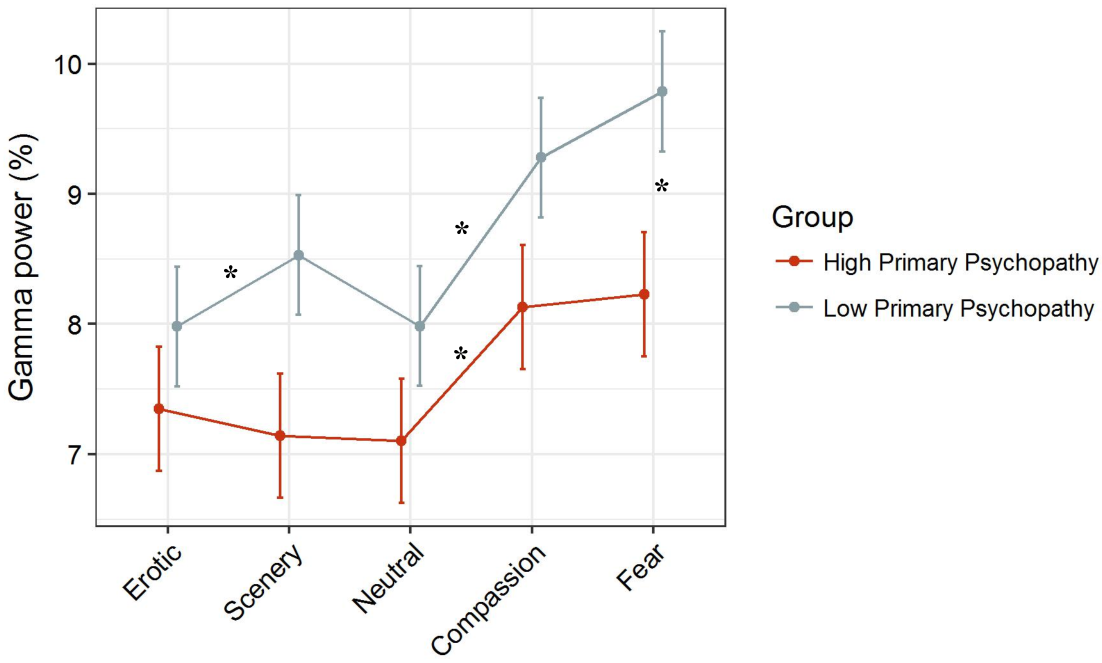

Figure 7.3 Results of Gamma analysis. Asterisks represents significant (p< 0.05) post-hc effects. Bars represent SE.

sLORETA Source Analysis

Non-parametric, permutation-based, contrasts between current source density in the two groups revealed that, in response to the excepts comprised in the Fear category, HP participants were characterized by a reduced cortical activity in several brain areas located in parieto-occipital regions, including the right cuneus and lingual gyrus (BA 19) and the inferior parietal lobules (BA 39-40) of both hemispheres, and in the right frontal lobe (BA 9). No significant differences were observed for the other film categories.

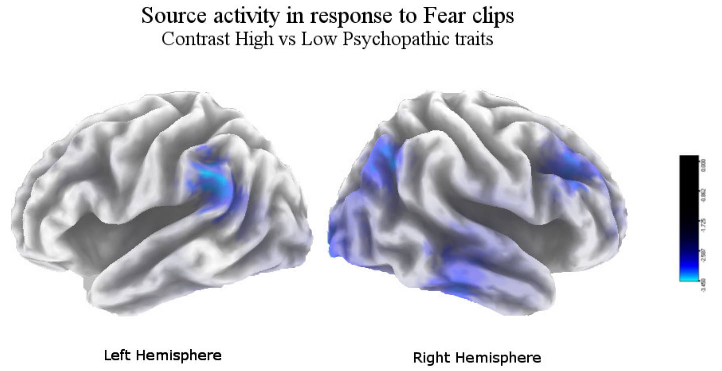

Figure 7.4 Source reconstructed activity for Fear movies. The image shows areas of significant deactivation in the High Psychopathy group during fearful movies presentation.

7.5 Discussion

The present work aimed at characterize subjective and cortical reactivity elicited by emotional stimuli with different emotional content in healthy individuals with high and low trait of primary psychopathy, selected from a large community sample according to their scores to the Levenson's Self-Report Psychopathy scale (LSRPS). In order to elicit a strong emotional induction, we used a series of film clips derived from a recently developed emotional film database covering the whole spectrum of positive and negative emotions. Moreover, in order to probe a detailed affective manipulation sensitive to the personality dimension investigated, we provided a fine distinction within the negative emotional stimuli, including a category of clips displaying frightening and suspenseful scenes (Fear) and a category depicting characters crying out of despair (Compassion). According to psychobiological models of psychopathy developed on forensic sample, we made two major predictions. We first hypothesized that emotional reactivity to threatening, fear-eliciting, clips would be different in the two groups, with individuals characterized by high levels of primary psychopathy showing a reduced physiological activation together with a blunted emotional experience compared with individuals who did not show traits of primary psychopathy. The second prediction was that individuals with high psychopathic tendencies would also show a reduced activation in response to the view of other people suffering, consistently with the idea of psychopathic behavior as driven by an impairment in affective empathy, that is the ability to share others emotional state.

Analysis of self-report of emotional experience showed strong support to both these hypothesis. Indeed, participants in the HP group reported to feel negative affect, in response to unpleasant clips, to a lesser extent compared to participants in LP group. Specifically, in response to the Fear movies individuals with high trait of emotional detachment reported to feel less anxious and less anguished. This result is coherent with findings on criminal psychopaths, and extend previous studies on healthy individuals with psychopathic traits, supporting the centrality of the affective-interpersonal dimension, rather than the behavioral one, in mediating the negative relationship between reduced experience of negative emotions and psychopathic personality (Del Gaizo & Falkenbach, 2008).

The present results also showed that participants in the HP group felt less sad, touched and anguished in response to Compassion movies. This evidence replicates in healthy individuals a pattern that has been previously observed in studies on criminal psychopaths, that is an impairment in processing facial expression of sadness and a reduced negative affect toward people experiencing this emotional state. This points toward the idea that the spontaneous tendency to empathize with others is reduced also in healthy individuals with psychopathic tendencies, not only in criminal psychopaths, bolstering the claim that impairment in empathic sharing of affect, specifically others' emotional sufferance, is a core element of the affective component of psychopathy. Moreover, it suggests that this pattern of affective reactivity might be targeted as potential predictor of emotional detachment in the general population.

For what concerns the analysis of the cortical dynamics elicited by the emotional movies, the results clearly showed that psychopathic traits affect how the clips are processed, especially the ones with an aversive emotional content. Gamma band was selected for investigating cortical dynamics because it is an oscillatory brain activity involved in the processing of complex and dynamic visual stimuli (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Kaiser & Lutzenberger, 2005), which has been previously demonstrated to be sensitive to their emotional content (Balconi & Lucchiari, 2008; Müller et al., 1999).

We found that the movies comprised in the negative categories (Fear and Compassion) elicited in both groups larger cortical activity compared with the clips in the other categories, and that, within this general pattern, gamma band power in response to threatening videos was reduced in participants with high levels of psychopathic traits, compared to participants without psychopathic tendencies. This result supports the initial hypotheses, showing at neurophysiological level, that primary psychopathy is related to abnormalities in processing of aversive and threatening stimuli. Considering the relationship that characterizes gamma oscillatory activity and emotional arousal, the present pattern might reflect a cortical correlate of the reduced emotional activation in response to threatening cues. Moreover, source analysis showed that in HP participants the reduced activation involves a distributed cluster of brain regions, mostly in the right hemisphere, suggesting that the reduced processing of fear-inducing material is the result of the complex interaction of different brain networks. Indeed, sLORETA analysis showed a reduced activation in the extra-striate visual cortex, maximal in the right lingual gyrus, which is a region critically involved in visual processing, the activity of which in the gamma range is modulated by attentional engagement (Tallon-Baudry, Bertrand, Hénaff, Isnard, & Fischer, 2005), and in the cuneus, which is also involved in visual attention and is sensitive to the interaction between attention and emotional information conveyed by the processed stimulus (Sander et al., 2005). HP participants also showed a reduced activity in the inferior parietal lobule, bilaterally, that, considering the pivotal role played by this cortical area in the ability to understand others affective states, might be interpreted as an evidence in support of the claim for a reduced tendency in HP individuals to spontaneously empathize with affectively relevant scenes showing other people threatened and scared.

The reduced activation of specific regions in the right hemisphere in HP individuals, namely dorsal prefrontal and inferior temporal cortices, fits well with the literature indicating the key role of the right hemisphere and especially of the right prefrontal cortex and right amygdala in emotional activation to aversive stimuli (Damasio, 2010). Indeed, neurological patients with localized brain lesions, inhibited responses to aversive stimuli but without cognitive impairments demonstrated how the right prefrontal cortex and amygdala are specifically involved in emotional processing of unpleasant conditions (Angrilli et al, 1996, 1999, 2008).

Taken together this pattern of results suggest that the observed blunted affectivity in response to aversive films in individuals with emotional detachment might stem from the interaction between a reduced engagement of visual attention toward the emotionally charged scene and the reduced emotional processing, which in turn would lead to an impaired ability to empathize with the actions displayed on screen. Thus, the threat embedded in the stimulus is not adequately processed resulting in a reduced experience of fear and negative emotionality, as indexed by the self-report judgments. This interpretation is also in line with recent findings on incarcerated psychopaths showing the negative relationship between Factor 1 scores and functional connectivity within the occipito-parietal networks involved in visual attention and empathic understanding (Espinoza et al., 2018).

For what concerns Compassion movies, analysis of cortical dynamics did not support the hypothesized reduced cortical reactivity in HP group. This may suggest that, at least at the physiological level, possessing high levels of trait of emotional detachment does not necessarily imply a reduced processing of stimuli depicting others sufferance, which instead might be a feature characterizing only individuals with the full psychopathic syndrome. Thus, the reactivity when viewing other people in distress might be discriminative between the "successful" psychopath and pathological individuals. Indeed, the former seems to be able to appropriately elaborate powerful social cues of distress (i.e. crying) even if experiencing less negative affect (as showed by self-report judgments), consistently with findings that showed that non-criminal psychopaths without history of criminal records have a preserved reactivity to unpleasant emotional stimuli involving social distress (Hall & Benning, 2006).

In conclusion, the present study provided new evidence that the affective dimension underlying psychopathy, construed as a general dimension in the personality space of the healthy individual, is characterized by a distinctive pattern of psychophysiological response toward aversive emotional elicitors, which closely resemble the pattern of activity observed in the criminal psychopath. Analysis of cortical dynamics suggests that a complex interaction between areas involved in low-level attentional mechanisms and areas involved in high-level empathic processes might be responsible for the reduced processing of fearful stimuli, which prompt individuals with high levels of primary psychopathy to feel numb toward them. Future studies should focus on the explicit characterization of the functional connectivity patterns during movie processing in order to provide further support for this conclusion.

Finally, it is interesting to note that in this study we found a coherent response across different domains (physiological and subjective), which is rarely the norm and might be the result of the use of a stronger emotion elicitation technique, compared with previous studies using low intensity static pictures (Mauss, McCarter, Levenson, Wilhelm, & Gross, 2005).

Chapter 8

General Discussion

8.1 Summary of the findings

The aim of the present project was to explore the neural underpinnings of affective states by means of a new and ecological approach represented by emotional film clips. The basic concept behind this work is that a thorough understanding of emotion as a fundamental psychophysiological process cannot be grasped if the tools used to model experimentally this process are an oversimplified representation of the everyday life. Indeed, the major limitation of most affective neuroscience studies is that mood induction and manipulation are accomplished by means of stimuli, usually static images, which are generally not able to induce a strong affective experience in the participants. Considering that movies represent an excellent alternative for emotional induction, the efficacy of which has been repeatedly showed, and that current standardized databases suffer from various flaws that might jeopardize their effectiveness in psychophysiological experiments (like extremely variable durations), the first purpose of this work has been the development of a new set of film clips for emotional induction, the first of its kind ever developed in Italian language. The analysis presented in the Study 1 showed that the E-MOVIE database satisfies all the necessary characteristics for being used in affective neuroscience experiments. First, all the clips in E-MOVIE have a comparable duration with a very narrow variability (± 10 seconds), lasting long enough to accommodate the development of the affective response of the viewer while still allowing the use of multiple clips in the same experiment. Second, it provides new categories of film clips (Erotic, Scenery) and a better characterization of categories included in other studies (i.e. Fear without depicting blood, distinction between Sadness-eliciting and Compassion-eliciting clips). Finally, the standardization has been carried out without an *a* *priori* commitment to a dimensional view or a categorical view of emotions, providing normative ratings useful for both perspectives. Thus, its applications are expected to be as wide as possible.

In Study 2, the most effective subset of the clips included in E-MOVIE has been used to explore the effect of the emotions elicited by the view of these movies on cortical dynamics. Results showed that different brain oscillations seem to reflect distinct features of the emotional experience. Alpha activity, which is a relatively slow rhythm whose inhibition indexes cortical activation, revealed to be sensitive to the arousal dimension of the affective reactions prompted by the movies. High Beta activity, which instead is a faster brain rhythm, was modulated by the unpleasantness of the clip content. Analysis of source activity showed that these two rhythms were driven by activity in different brain regions. Arousal modulation largely depends on activity in parietal regions involved in attention, high-order multimodal integration, and that are central in the network supporting self-reference (DMN). Temporal regions in the right hemisphere were instead modulated by the negative valence of the clips.

After the implementation of the stimuli set and the characterization of its neural correlates, this work aimed at investigating the complex interrelationship between emotional responses and individual differences in empathy, especially its affective component. Study 3 investigated how people characterized by high dispositional empathy differ in their response to emotional movies from individuals characterized by low trait empathy. Results showed that high empathy is generally associated with an increased susceptibility to emotional stimuli, reflected in increased perceived arousal and larger cortical activity during film presentation. Moreover, in response to Compassion clips, designed to probe through the depiction of crying individuals an empathic reaction in the viewer, those who had high empathy showed an enhanced brain activity in the inferior parietal lobe, crucial for the ability to empathize with others, that covaried with the intensity of their experience, a result which suggests that trait empathy might acts as a mediator between physiological and subjective responses to compassion-eliciting stimuli. Finally, Study 4 aimed at providing a better characterization of how a personality trait associated with lack of emotional empathy influences emotional responses. Results showed that people with high traits of primary psychopathy are characterized by a diminished response to unpleasant emotional stimuli, especially threat and compassion movies, at both experiential and neural level. Source analysis showed that in response to fearful movies, detached individuals were characterized by a reduced activity in a large brain network comprising both regions crucial for visual attention and areas necessary for empathic sharing, suggesting that their impaired affective response might result from the complex interaction between areas involved in low-level and high-level feature processing. Moreover, the observed reduction of brain activity in right frontal regions in people with high psychopathic tendencies in response to unpleasant movies further supports that these areas represent a core hub for emotional processing and emotional experience.

Taken together, the results here presented confirm and extend what has been showed about brain processing of dynamic and ecological stimuli like movies, providing new evidence about the role played by the affective content of the clips, which is a feature that has been largely neglected in the literature so far. The first critical advance provided is the generalization of previous fMRI findings about the cortical regions involved in movie processing to the EEG technique. We consistently observed across three studies that the presentation of movies engages large portion of the cortex, in line with a large corpus of fMRI studies (Golland et al., 2007, Hasson et al., 2004, 2010, Lahnakoski et al., 2012), mostly in the parieto-occipital and temporal cortices. This evidence give support to the EEG as a valid approach for the investigation of brain dynamics that involve large-scale networks, like the ones that seem to be involved in movie processing, which is extremely relevant considering the costs associated with fMRI studies compared to EEG ones, despite the poorer spatial resolution of EEG as a brain imaging tool (but see the Limitations section for this issue). Moreover, EEG carries a large amount of multidimensional information related with the modulation of the signal both in time and frequency, which can add new insights about the complex mechanisms underlying processing of ecological scenes, like the role of their affective and motivational content. This leads to the second major advance provided by the experiments presented in this work, that is the demonstration that the role of the different building blocks of emotion (i.e. valence and arousal) can be isolated at different frequencies. The effect of arousal is reflected in a relatively slow brain rhythm like alpha, while the effect of the valence is reflected in fast brain oscillations (beta and gamma) featuring a gradient that sees greater high frequency power related with negative affect. The functional specialization of alpha activity for emotional arousal reflects the tie that bonds alpha power modulation with the degree of attentional engagement (Klimesch, 1999, 2012). Indeed, scenes charged with a strong affective content which are perceived as very arousing will also be scenes able to capture to a large extent the viewer's attention. Therefore, the observed modulation of alpha as a function of the arousal of the movies reflects these mechanisms. For what concerns the relationship between valence and high frequency EEG activity, especially in the right temporal regions as observed in Study 2, in line with previous reports this functional specificity might be interpreted as the fingerprint of the synchronized firing of neuronal assemblies in both cortical and subcortical regions that respond to the affective features embedded in the visual stimuli (Müller et al., 2001). Converging evidence from anatomical animal studies and human lesion studies suggest that the neurophysiological mechanism underlying these effects should be searched in the wide range of bidirectional connections that subcortical nuclei, especially amygdala, have with large portions of the cortex (John P. Aggleton, 1993; Phelps & LeDoux, 2005). By means of this connectivity subcortical nuclei rapidly extract from the sensory stream its motivational significance and then trough feedforward projections modulate activity of cortical regions, especially in those associative areas deputed to higher-order processing (Phelps & LeDoux, 2005). Indeed, amygdala lesions compromise the ability to extract emotional information from visual stimuli (Vuilleumier et al., 2004), impairing the emergence of psychophysiological responses usually associated with emotional stimuli (Angrilli et al., 1996). The reported modulation of the activity in the right temporal cortex and in the posteromedial cortex is in line with this interpretation according to anatomical data showing that amygdala projects to both PMC and STG/MTG (Aggleton, Burton, & Passingham, 1980; Parvizi, Van Hoesen, Buckwalter, & Damasio, 2006), and functional data derived from both electrophysiology and fMRI showing that varying the emotional content of the stimulus modulates activity in these regions (Heinzel et al., 2005; Krolak-Salmon et al., 2004). Moreover, the observed right dominance for the temporal activation provides further support with the idea that the right hemisphere is preferentially involved in the elaboration of negative emotional information.

The studies presented in this work also provide new insights into the relationship between empathic abilities and emotional processing and responding, adopting a new approach to the study of this relationship. Indeed, previous studies relied almost exclusively on the empathy-for-pain paradigm which fails to take into account that the influence of empathy (and individual differences in empathy) on emotional processing extends well beyond seeing another person in pain. Emotional movies, on the other hand, are an ideal tool to study empathy, considering that empathic sharing the feeling of the actors is the necessary condition for experiencing emotions from a movie (Coplan, 2006). Their use allowed to uncover that individual differences in empathy does not influence only the experience of negative emotions, but that positive and arousing affective states also are more blunted in individuals with low empathic abilities. This is extremely relevant considering that the major trend in empathy-related studies is to consider empathy as a construct that plays a role only in negative emotions (i.e. distress, concern for others). Instead, empathy has an influence also in the modulation of positive states (Morelli, Lieberman and Zaki, 2015) and acknowledging this will definitely lead to a better understanding of the role played by empathic abilities in emotions. Finally, the results from Study 3 and especially from Study 4 show that individual differences in empathy and psychopathic traits shape how the brain process movies, highlighting the involvement of multiple brain networks. Indeed, an important contribution of this work lies in showing that empathy affects interplay between these regions when processing emotional stimuli, a result that provides the ground for future investigation targeting explicitly how individual differences in personality and emotions influence the complex balance between brain networks during the elaboration of rich and ecological stimuli.

8.2 Limitations

The results presented in this thesis should be interpreted in light of several limitations. First, the results of Study 2, 3 and 4 are based on source activity estimated from medium density EEG recordings. Methodological studies showed that accuracy of source estimation increases with the increase of the spatial sampling of the activity over the scalp with larger number of sensors (Song et al., 2015). Thus, it might be argued that the validity of these findings should be confirmed in experiments using high-density EEG and/or fMRI. On the other hand, it should be acknowledged that the cortical sources identified across the three studies are strongly consistent with previous fMRI investigations on brain activity elicited by movie watching, with and without emotion manipulation (Hasson et al., 2004; Nummenmaa et al., 2012a; Pajula et al., 2012), suggesting that activity in this regions might be reliably estimated even with a relatively low number of sensors. A second limitation of the present work might be represented by the fact that basic visual perceptual characteristics of the movies used in the three EEG experiments have not been explicitly controlled or modeled in the analyses. Controlling for basic visual features (i.e. spatial frequencies, visual complexity, visual salience) has been carried out with more consolidated paradigms using emotional images (De Cesarei et al., 2017). The main advantage of this approach is that it allows to disambiguate the contribution of basic visual features of a stimulus from its affective and motivational characteristics. Unfortunately, due to the inherent dynamicity that characterizes movie clips, addressing this issue is not as straightforward as it is for static images. Nevertheless, the main purpose of these investigations was to lay down a foundation, on top of which more detailed investigations could tackle these aspects. Finally, the influence of gender in modulating the interaction between affective reactivity and empathy has not been considered in a perfectly balanced experimental design. Indeed, Study 3 and Study 4 were conducted on two separate samples of female and male participants, respectively. This inevitably left the questions regarding the role played by sex differences in this interaction unanswered, considering the well-known differences between males and females in both empathy and emotional reactivity (Bianchin & Angrilli, 2012; Maffei et al., 2015; Rueckert & Naybar, 2008; Schulte-Rüther et al., 2008).

8.3 Conclusions and Future directions

The results presented in this thesis provide a solid foundation for a new approach to the study of emotional reactivity using ecological and naturalistic affective stimuli. The effort to refine emotional states usually considered overlapping, allowed to highlight that the sadness elicited by the view of others sufferance (Compassion category in the present work) has a unique affective profile, at both subjective and physiological levels, that distinguishes it from the affective state elicited by the sense of helplessness (Sadness category). Moreover, these results further support the idea that wilderness is not affectively neutral, but rather represent a source of positive affect, inviting to be cautious in the evaluation of studies that consider natural landscapes as neutral condition. They also provide new perspectives about the complex interaction between emotional empathy and emotional reactions, adopting a new paradigm that can help overcoming the inherent limitations of the dominant approach to the study of empathic sharing of others' emotions. Finally, these results add to the growing field of research about psychopathic traits in normal individuals, suggesting a potential network of brain regions involved in mediating the blunted affectivity that define these individuals.

Future works should focus on further characterizing the psychophysiological profile of the reactions elicited by these emotional movies, specifically exploring their autonomic correlates and how they link with the observed cortical activations. Indeed, bodily reactions, especially cardiovascular, are a crucial element of affective experience which are studied either as a phasic phenomena or as tonic, trait-like, characteristic of the individual. The use of emotional movies might help to characterize in detail the cardiovascular dynamics that occur during the rise (and fall) of an emotional reaction, allowing to explore both slow changes over an entire clip and fast changes elicited by specific scenes (Kreibig, Wilhelm, Roth, & Gross, 2007). Moreover, cardiovascular activity could help to further disambiguate Compassion from Sadness, according to findings that suggest that the act of crying, as well as, the view of others crying, and in general empathic and prosocial reactions, are deeply tied with parasympathetic control over heart dynamics (Gross et al., 1994; Stellar, Cohen, Oveis, & Keltner, 2015; Vingerhoets, Cornelius, Van Heck, & Becht, 2000).

For what concerns the interaction between empathy and emotions, future works should definitely overcome the current limit represented by lack of analysis on gender differences, putting effort in quantifying the contribution of this factor in the modulation of the relationship between empathy and affect.

Finally, future works should also focus on using physiological reactivity to emotional stimuli as an independent variable able to predict individual differences in empathy and empathy-related behaviors (i.e. tendency to help others), in order to minimize the impact of the inherent construct bias that the choice of one questionnaire over others has in studies that address blurred and not-easy-to-define concepts like empathy.

References

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*, 67–82.

Aggleton, J. P. (1993). The contribution of the amygdala to normal and abnormal emotional states. *Trends in Neurosciences*, *16*(8), 328–333. https://doi.org/10.1016/0166-2236(93)90110-8

Aggleton, J. P., Burton, M. J., & Passingham, R. E. (1980). CORTICAL AND SUBCORTICAL AFFERENTS TO THE AMYGDALA OF THE RHESUS MONKEY (MACACA MULATTA). *Brain Research*, *190*, 347–368. https://doi.org/10.1186/1472-6904-8-8

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & B. F. Csaki (Eds.), *Second International Symposium on Information Theory* (pp. 267–281). Budapest: Academiai Kiado.

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

Anderson, A. K., Christoff, K., Panitz, D., De Rosa, E., & Gabrieli, J. D. E. (2003). Neural correlates of the automatic processing of threat facial signals. *The Journal of Neuroscience*, *23*(13), 5627–5633. https://doi.org/10.4324/9780203496190

Anderson, N. E., & Kiehl, K. A. (2012, January). The psychopath magnetized: Insights from brain imaging. *Trends in Cognitive Sciences*. NIH Public Access. https://doi.org/10.1016/j.tics.2011.11.008

Angrilli, A., Mauri, A., Palomba, D., Flor, H., Birbaumer, N., Sartori, G., & Di Paola, F. (1996). Startle reflex and emotion modulation impairment after a right amygdala lesion. *Brain*, *119*(6), 1991–2000. https://doi.org/10.1093/brain/119.6.1991

Balconi, M., & Lucchiari, C. (2008). Consciousness and arousal effects on emotional face processing as revealed by brain oscillations. A gamma band analysis. *International Journal of Psychophysiology*, *67*(1), 41–46. https://doi.org/10.1016/j.ijpsycho.2007.10.002

Banissy, M. J., Kanai, R., Walsh, V., & Rees, G. (2012). Inter-individual differences in empathy are reflected in human brain structure. *NeuroImage*, *62*(3), 2034–2039.

https://doi.org/10.1016/J.NEUROIMAGE.2012.05.081

Baron-Cohen, S., & Wheelwright, S. (2004). The Empathy Quotient: An Investigation of Adults with Asperger Syndrome or High Functioning Autism, and Normal Sex Differences. *Journal of Autism and Developmental Disorders*, *34*(2).

Barrett, F. S., Grimm, K. J., Robins, R. W., Wildschut, T., Sedikides, C., & Janata, P. (2010). Music-Evoked Nostalgia: Affect, Memory, and Personality. *Emotion*, *10*(3), 390–403. https://doi.org/10.1037/a0019006

Barrett, L. F., & Russell, J. A. (1999). The Structure of Current Affect: Controversies and Emerging Consensus. *Current Directions in Psychological Science*, *8*(1), 10–14.

Bartels, A., & Zeki, S. (2004a). Brain dynamics during natural viewing conditions—A new guide for mapping connectivity in vivo. https://doi.org/10.1016/j.neuroimage.2004.08.044

Bartels, A., & Zeki, S. (2004b). Functional Brain Mapping during Free Viewing of Natural Scenes. *Human Brain Mapping*, *21*(2), 75–85. https://doi.org/10.1002/hbm.10153

Bartels, A., & Zeki, S. (2004c). The chronoarchitecture of the human brain - Natural viewing conditions reveal a time-based anatomy of the brain. *NeuroImage*, *22*(1), 419–433. https://doi.org/10.1016/j.neuroimage.2004.01.007

Bartels, A., & Zeki, S. (2004d). The neural correlates of maternal and romantic love. *NeuroImage*, *21*(3), 1155–1166. https://doi.org/10.1016/j.neuroimage.2003.11.003

Bartoń, K. (2016). MuMIn: Multi-Model Inference. R package.

Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *International Journal of Psychophysiology*, *39*(2–3), 241–248. https://doi.org/10.1016/S0167-8760(00)00145-8

Bassett, D. S., & Sporns, O. (2017). Network neuroscience. *Nature Neuroscience*, *20*(3), 353–364. https://doi.org/10.1038/nn.4502

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Batson, C. D. (2009a). These things called empathy: Eight related but distinct phenomena. In J. Decety & W. Ickes (Eds.), *The social neuroscience of empathy* (pp. 3–15). The MIT Press. https://doi.org/10.7551/mitpress/9780262012973.003.0002

Batson, C. D. (2009b). These things called empathy: Eight related but distinct phenomena. In *The social neuroscience of empathy* (pp. 3–15). https://doi.org/10.7551/mitpress/9780262012973.003.0002

Baumeister, R. F., Bratslavsky, E., Finkenauer, C., & Vohs, K. D. (2001). Bad Is Stronger Than Good. *Review of General Psychology*, *5*(4), 323–370. https://doi.org/10.1037//1089-2680.5.4.323

Bazanova, O. M., & Vernon, D. (2014). Interpreting EEG alpha activity. *Neuroscience & Biobehavioral Reviews*, *44*, 94–110. https://doi.org/10.1016/J.NEUBIOREV.2013.05.007

Bechara, a, Damasio, H., & Damasio, a R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, *10*(3), 295–307. https://doi.org/10.1093/cercor/10.3.295

Begeer, S., Gevers, C., Clifford, P., Verhoeve, M., Kat, K., Hoddenbach, E., & Boer, F. (2011). Theory of Mind Training in Children with Autism: A Randomized Controlled Trial. *Journal of Autism and Developmental Disorders*, *41*(8), 997–1006. https://doi.org/10.1007/s10803-010-1121-9

Besel, L. D. S., & Yuille, J. C. (2010). Individual differences in empathy: The role of facial expression recognition. *Personality and Individual Differences*, *49*(2), 107–112. https://doi.org/10.1016/J.PAID.2010.03.013

Beute, F., & de Kort, Y. A. W. (2014). Salutogenic effects of the environment: Review of health protective effects of nature and daylight. *Applied Psychology: Health and Well-Being*, *6*(1), 67–95. https://doi.org/10.1111/aphw.12019

Bianchin, M., & Angrilli, A. (2012). Gender differences in emotional responses: A psychophysiological study. *Physiology & Behavior*, *105*(4), 925–932. https://doi.org/10.1016/j.physbeh.2011.10.031

Birbaumer, N., Veit, R., Lotze, M., Erb, M., Hermann, C., Grodd, W., & Flor, H. (2005). Deficient Fear Conditioning in Psychopathy. *Archives of General Psychiatry*, *62*(7), 799. https://doi.org/10.1001/archpsyc.62.7.799

Blair, R. J. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition*, *14*(4), 698–718. https://doi.org/10.1016/j.concog.2005.06.004

Blair, R. J. R. (2008). Fine cuts of empathy and the amygdala: Dissociable deficits in psychopathy and autism. In *Quarterly Journal of Experimental Psychology* (Vol. 61, pp. 157–170). SAGE PublicationsSage UK: London, England. https://doi.org/10.1080/17470210701508855

Blair, R. J. R. (2018). Traits of empathy and anger: Implications for psychopathy and other disorders associated with aggression. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, *373*(1744). https://doi.org/10.1098/rstb.2017.0155

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion (Washington, D.C.)*, *1*(3), 276–98.

Bradley, M. M., Codispoti, M., Sabatinelli, D., & Lang, P. J. (2001). Emotion and motivation II: sex differences in picture processing. *Emotion (Washington, D.C.)*, *1*(3), 300–319. https://doi.org/10.1037/1528-3542.1.3.300

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, *25*(1), 49–59.

Bradley, M. M., & Lang, P. J. (2000). Affective reactions to acoustic stimuli. *Psychophysiology*, *37*(2), 204–215.

Bradley, M. M., & Lang, P. J. (2007). The International Affective Digitized Sounds (2nd Edition; IADS-2): Affective ratings of sounds and instruction manual. Gainesville, FL: University of Florida.

Britton, J. C., Phan, K. L., Taylor, S. F., Welsh, R. C., Berridge, K. C., & Liberzon, I. (2006). Neural correlates of social and nonsocial emotions: An fMRI study. *NeuroImage*, *31*(1), 397–409. https://doi.org/10.1016/j.neuroimage.2005.11.027

Carvalho, S., Leite, J., Galdo-Álvarez, S., & Gonçalves, Ó. F. (2012). The emotional movie database (EMDB): A self-report and psychophysiological study. *Applied Psychophysiology Biofeedback*, *37*(4), 279–294. https://doi.org/10.1007/s10484-012-9201-6

Chong, T. T. J., Cunnington, R., Williams, M. A., Kanwisher, N., & Mattingley, J. B. (2008). fMRI Adaptation Reveals Mirror Neurons in Human Inferior Parietal Cortex. *Current Biology*, *18*(20), 1576–1580. https://doi.org/10.1016/j.cub.2008.08.068

Christov-Moore, L., Simpson, E. A., Coudé, G., Grigaityte, K., Iacoboni, M., & Ferrari, P. F. (2014). Empathy: Gender effects in brain and behavior. *Neuroscience and Biobehavioral Reviews*, *46*, 604–627. https://doi.org/10.1016/j.neubiorev.2014.09.001

Cisler, J. M., Olatunji, B. O., Lohr, J. M., & Williams, N. L. (2009). Attentional bias differences between fear and disgust: Implications for the role of disgust in disgust-related anxiety disorders. *Cognition & Emotion*, *23*(4), 675–687. https://doi.org/10.1080/02699930802051599

Coan, J. a., & Allen, J. J. B. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, *67*(1–2), 7–49.

https://doi.org/10.1016/j.biopsycho.2004.03.002

Codispoti, M., Surcinelli, P., & Baldaro, B. (2008). Watching emotional movies: Affective reactions and gender differences. *International Journal of Psychophysiology*, *69*(2), 90–95. https://doi.org/10.1016/j.ijpsycho.2008.03.004

Cohen, A. (2001). Music as a source of emotion in film. In P. N. Juslin & J. A. Sloboda (Eds.), *Music and Emotion - Theory and Research* (pp. 249–272). New York, NY, US: Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780199230143.003.0031

Coplan, A. (2006). Catching Characters' Emotions: Emotional Contagion Responses to Narrative Fiction Film. *Film Studies*, *8*(Summer 2006), 26–38. https://doi.org/https://doi.org/10.7227/FS.8.5

Costa, M., Dinsbach, W., Manstead, A. S. R., & Ricci Bitti, P. E. (2001). Social presence, embarrassment, and nonverbal behavior. *Journal of Nonverbal Behavior*, *25*(4), 225–240. https://doi.org/10.1023/A:1012544204986

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*(2), 189–195. https://doi.org/10.1038/nn1176

Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*. https://doi.org/10.1016/0278-2626(92)90065-T

Davidson, R. J. (2002). Anxiety and affective style: Role of prefrontal cortex and amygdala. *Biological Psychiatry*, *51*(1), 68–80. https://doi.org/10.1016/S0006-3223(01)01328-2

Davidson, R. J. (2004). What does the prefrontal cortex "do" in affect: Perspectives on frontal EEG asymmetry research. *Biological Psychology*, *67*(1–2), 219–233. https://doi.org/10.1016/j.biopsycho.2004.03.008

Davis, M. H. (1983). Measuring Multidimensional Approach of Empathy. *Journal of Personality and Social Psychology*, *44*(1), 113–126.

De Cesarei, A., Loftus, G. R., Mastria, S., & Codispoti, M. (2017). Understanding natural scenes: Contributions of image statistics. *Neuroscience and Biobehavioral Reviews*, *74*, 44–57. https://doi.org/10.1016/j.neubiorev.2017.01.012

De Waal, F. B. M., & Preston, S. D. (2017). Mammalian empathy: Behavioural manifestations and neural basis. *Nature Reviews Neuroscience*, *18*(8), 498–509. https://doi.org/10.1038/nrn.2017.72

Decety, J., Chen, C., Harenski, C., & Kiehl, K. A. (2013). An fMRI study of affective perspective taking in individuals with psychopathy: imagining another in pain does not evoke empathy. *Frontiers in Human Neuroscience*, *7*, 489. https://doi.org/10.3389/fnhum.2013.00489

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: A social developmental neuroscience account. *Development and Psychopathology*, *20*(04), 1053. https://doi.org/10.1017/S0954579408000503

Decety, J., Skelly, L. R., & Kiehl, K. A. (2013). Brain response to empathy-eliciting scenarios involving pain in incarcerated individuals with psychopathy. *JAMA Psychiatry*, *70*(6), 638–45. https://doi.org/10.1001/jamapsychiatry.2013.27

Del Gaizo, A. L., & Falkenbach, D. M. (2008). Primary and secondary psychopathic-traits and their relationship to perception and experience of emotion. *Personality and Individual Differences*, *45*(3), 206–212. https://doi.org/10.1016/J.PAID.2008.03.019

Dimberg, U., Andréasson, P., & Thunberg, M. (2011). Emotional empathy and facial reactions to facial expressions. *Journal of Psychophysiology*, *25*(1), 26–31. https://doi.org/10.1027/0269-8803/a000029

Dmochowski, J. P., Sajda, P., Dias, J., & Parra, L. C. (2012). Correlated components of ongoing EEG point to emotionally laden attention - a possible marker of engagement? *Frontiers in Human Neuroscience*, *6*, 112. https://doi.org/10.3389/fnhum.2012.00112

Ekman, P. (1992). An argument for basic emotions. *Cognition & Emotion*, *6*(3), 169–200. https://doi.org/10.1080/02699939208411068

Ekman, P., & Cordaro, D. (2011). What is Meant by Calling Emotions Basic. *Emotion Review*, *3*(4), 364–370. https://doi.org/10.1177/1754073911410740

Ekman, P., & Friesen, W. (1976). *Pictures of Facial Affect*. Palo Alto (CA): Consulting Psychology Press.

Espinoza, F. A., Vergara, V. M., Reyes, D., Anderson, N. E., Harenski, C. L., Decety, J., … Calhoun, V. D. (2018). Aberrant functional network connectivity in psychopathy from a large (N = 985) forensic sample. *Human Brain Mapping*, *39*(6), 2624–2634. https://doi.org/10.1002/hbm.24028

Feldman Barrett, L., & Bliss-Moreau, E. (2009). Affect as a psychological primative. *Advances in Experimental Social Psychology*, *41*(08), 167–218. https://doi.org/10.1016/S0065-2601(08)00404-8.Affect

Felnhofer, A., Kothgassner, O. D., Schmidt, M., Heinzle, A. K., Beutl, L., Hlavacs, H., & Kryspin-Exner, I. (2015). Is virtual reality emotionally arousing? Investigating five emotion inducing virtual park scenarios. *International Journal of Human Computer Studies*, *82*, 48–56. https://doi.org/10.1016/j.ijhcs.2015.05.004

Floresco, S. B. (2015). The Nucleus Accumbens: An Interface Between Cognition, Emotion, and Action. *Annual Review of Psychology*, *66*(1), 25–52. https://doi.org/10.1146/annurev-psych-010213-115159

Fowles, D. C., & Dindo, L. (2006). A Dual-Deficit Model of Psychopathy. In *Handbook of psychopathy.* (pp. 14–34). New York, NY, US: Guilford Press.

Frei, E., Gamma, A., Pascual-Marqui, R., Lehmann, D., Hell, D., & Vollenweider, F. X. (2001). Localization of MDMA-Induced Brain Activity in Healthy Volunteers Using Low Resolution Brain Electromagnetic Tomography (LORETA). *Hum. Brain Mapping*, *14*, 152–165.

Gabert-Quillen, C. A., Bartolini, E. E., Abravanel, B. T., & Sanislow, C. A. (2015a). Ratings for emotion film clips. *Behavior Research Methods*, *47*(3), 773–787. https://doi.org/10.3758/s13428-014-0500-0

Gabert-Quillen, C. A., Bartolini, E. E., Abravanel, B. T., & Sanislow, C. A. (2015b). Ratings for emotion film clips. *Behavior Research Methods*. https://doi.org/10.3758/s13428-014-0500-0

Gilman, T. L., Shaheen, R., Nylocks, K. M., Halachoff, D., Chapman, J., Flynn, J. J., … Coifman, K. G. (2017). A film set for the elicitation of emotion in research: A comprehensive catalog derived from four decades of investigation. *Behavior Research Methods*, 1–22. https://doi.org/10.3758/s13428-016-0842-x

Goetz, J., Keltner, D., & Simon-Thomas, E. (2010). Compassion: an evolutionary analysis and empirical review. *Psychological Bulletin*, *136*(3), 351–374. https://doi.org/10.1037/a0018807.Compassion

Golan, O., Baron-Cohen, S., Hill, J. J., & Golan, Y. (2006). The “Reading the Mind in Films” Task: Complex emotion recognition in adults with and without autism spectrum conditions. *Social Neuroscience*, *1*(2), 111–123. https://doi.org/10.1080/17470910600980986

Golland, Y., Bentin, S., Gelbard, H., Benjamini, Y., Heller, R., Nir, Y., … Malach, R. (2007). Extrinsic and Intrinsic Systems in the Posterior Cortex of the Human Brain Revealed during Natural Sensory Stimulation. *Cerebral Cortex*, *17*(4), 766–777. https://doi.org/10.1093/cercor/bhk030

Gross, J. J., Fredrickson, B. L., & Levenson, R. W. (1994). The psychophysiology of crying. *Psychophysiology*, *31*(5), 460–468. https://doi.org/10.1111/j.1469-8986.1994.tb01049.x

Gross, J. J., & Levenson, R. W. (1995). Emotion elicitation using films. *Cognition & Emotion*, *9*(1), 87–108. https://doi.org/10.1080/02699939508408966

Güntekin, B., & Basar, E. (2007). Emotional face expressions are differentiated with brain oscillations. *International Journal of Psychophysiology*, *64*(1), 91–100. https://doi.org/10.1016/j.ijpsycho.2006.07.003

Güntekin, B., & Başar, E. (2010). Event-related beta oscillations are affected by emotional eliciting stimuli. *Neuroscience Letters*, *483*(3), 173–178. https://doi.org/10.1016/J.NEULET.2010.08.002

Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C. J., Van Wedeen, J., & Sporns, O. (2008). Mapping the structural core of human cerebral cortex. *PLoS Biology*, *6*(7), 1479–1493. https://doi.org/10.1371/journal.pbio.0060159

Hall, J. R., & Benning, S. D. (2006). The “Successful” Psychopath: Adaptive and Subclinical Manifestations of Psychopathy in the General Population. In C. J. Patrick (Ed.), *Handbook of psychopathy,* (2nd ed., p. 459–478.). New York, NY, US: Guilford Press.

Han, S., Fan, Y., & Mao, L. (2008). Gender difference in empathy for pain: An electrophysiological investigation. *Brain Research*, *1196*, 85–93. https://doi.org/10.1016/j.brainres.2007.12.062

Harmon-Jones, E., & Allen, J. J. B. (1998). Anger and Frontal Brain Activity: EEG Asymmetry Consistent With Approach Motivation Despite Negative Affective Valence, *74*(5), 1310–1316.

Harmon-Jones, E., Gable, P. a., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology*, *84*(3), 451–462. https://doi.org/10.1016/j.biopsycho.2009.08.010

Harmon-Jones, E., Harmon-Jones, C., & Summerell, E. (2017). On the Importance of Both Dimensional and Discrete Models of Emotion. *Behavioral Sciences*, *7*(4), 66. https://doi.org/10.3390/bs7040066

Hartig, T., Evans, G. W., Jamner, L. D., Davis, D. S., & Gärling, T. (2003). Tracking restoration in natural and urban field settings. *Journal of Environmental Psychology*, *23*(2), 109–123. https://doi.org/10.1016/S0272-4944(02)00109-3

Hasson, U., Malach, R., & Heeger, D. J. (2010). Reliability of cortical activity during natural stimulation. *Trends in Cognitive Sciences*, *14*(1), 40–48. https://doi.org/10.1016/j.tics.2009.10.011

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject Synchronization of Cortical Activity DuringNatural Vision. *Science*, *303*(5664), 1634–1640. https://doi.org/10.1126/science.1089506

Hasson, U., Yang, E., Vallines, I., Heeger, D. J., & Rubin, N. (2008). A hierarchy of temporal receptive windows in human cortex. *The Journal of Neuroscience*, *28*(10), 2539–50. https://doi.org/10.1523/JNEUROSCI.5487-07.2008

Hein, G., & Singer, T. (2008). I feel how you feel but not always: the empathic brain and its modulation. *Current Opinion in Neurobiology*, *18*(2), 153–158. https://doi.org/10.1016/J.CONB.2008.07.012

Heinzel, A., Bermpohl, F., Niese, R., Pfennig, A., Pascual-Leone, A., Schlaug, G., & Northoff, G. (2005). How do we modulate our emotions? Parametric fMRI reveals cortical midline structures as regions specifically involved in the processing of emotional valences. *Cognitive Brain Research*, *25*(1), 348–358. https://doi.org/10.1016/j.cogbrainres.2005.06.009

Hendriks, M. C. P., Croon, M. a, & Vingerhoets, A. J. J. M. (2008). Social reactions to adult crying: the help-soliciting function of tears. *The Journal of Social Psychology*, *148*(1), 22–41. https://doi.org/10.3200/SOCP.148.1.22-42

Hendriks, M. C. P., & Vingerhoets, A. J. J. M. (2006). Social messages of crying faces: Their influence on anticipated person perception, emotions and behavioural responses. *Cognition & Emotion*, *20*(6), 878–886. https://doi.org/10.1080/02699930500450218

Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *Journal of Clinical Neurophysiology : Official Publication of the American Electroencephalographic Society*, *19*(2), 113–24. https://doi.org/10.1097/00004691-200203000-00002

Jerbi, K., Ossandón, T., Hamamé, C. M., Senova, S., Dalal, S. S., Jung, J., … Lachaux, J. P. (2009). Task-related gamma-band dynamics from an intracerebral perspective: Review and implications for surface EEG and MEG. *Human Brain Mapping*, *30*(6), 1758–1771. https://doi.org/10.1002/hbm.20750

Johnsen, S. Å. K., Rydstedt, L. W., & Rydstedt, L. W. (2013). Active Use of the Natural Environment for Emotion Regulation. *Europe's Journal of Psychology*, *9*(4), 798–819. https://doi.org/10.5964/ejop.v9i4.633

Kaiser, J., & Lutzenberger, W. (2005). Human gamma-band activity: A window to cognitive processing. *NeuroReport*, *16*(3), 207–211. https://doi.org/10.1097/00001756-200502280-00001

Kaplan, S. (1995). The restorative benefits of nature: Toward an integrative framework. *Journal of Environmental Psychology*, *15*(3), 169–182. https://doi.org/10.1016/0272-4944(95)90001-2

Keil, A., Muller, M., Gruber, T., Wienbruch, C., Stolarova, M., & Elbert, T. (2001). Effects of emotional arousal in the cerebral hemispheres: a study of oscillatory brain activity and event related potentials. *Clinical Neurophysiology*, *112*(2001), 2057–2068.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, *29*, 169–195.

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*, 14–41. https://doi.org/10.1016/j.biopsycho.2010.03.010

Kreibig, S. D., Wilhelm, F. H., Roth, W. T., & Gross, J. J. (2007). Cardiovascular, electrodermal, and respiratory response patterns to fear- and sadness-inducing films. *Psychophysiology*, *44*(5), 787–806. https://doi.org/10.1111/j.1469-8986.2007.00550.x

Krolak-Salmon, P., He, M., Vighetto, A., Bertrand, O., Thomas, A., & Lyon, C. B. (2004). Early Amygdala Reaction to Fear Spreading in Occipital, Temporal, and Frontal Cortex: A Depth Electrode ERP Study in Human. *Neuron*, *42*, 1–12.

Kurdi, B., Lozano, S., & Banaji, M. R. (2017). Introducing the Open Affective Standardized Image Set (OASIS). *Behavior Research Methods*, *49*(2), 457–470. https://doi.org/10.3758/s13428-016-0715-3

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). lmerTest: Tests in Linear Mixed Effects Models.

Lahnakoski, J. M., Glerean, E., Salmi, J., Jääskeläinen, I. P., Sams, M., Hari, R., & Nummenmaa, L. (2012). Naturalistic fMRI Mapping Reveals Superior Temporal Sulcus as the Hub for the Distributed Brain Network for Social Perception. *Frontiers in Human Neuroscience*, *6*, 233. https://doi.org/10.3389/fnhum.2012.00233

Lahnakoski, J. M., Salmi, J., Jääskeläinen, I. P., Lampinen, J., Glerean, E., Tikka, P., & Sams, M. (2012). Stimulus-Related Independent Component and Voxel-Wise Analysis of Human Brain Activity during Free Viewing of a Feature Film. *PLoS ONE*, *7*(4), e35215. https://doi.org/10.1371/journal.pone.0035215

Lakatos, K., Toth, I., Nemoda, Z., Ney, K., Sasvari-Szekely, M., & Gervai, J. (2000). Dopamine D4 receptor (DRD4) gene polymorphism is associated with attachment disorganization in infants. *Molecular Psychiatry*, *5*(6), 633–637. https://doi.org/10.1038/sj.mp.4000773

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage*, *54*(3), 2492–2502. https://doi.org/10.1016/j.neuroimage.2010.10.014

Landis, C. (1924). Studies of emotional reactions. I. 'A preliminary study of facial expression.". *Journal of Experimental Psychology*, *7*(5), 325–341.

https://doi.org/10.1037/h0076072

Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology*, *84*(3), 437–450. https://doi.org/10.1016/J.BIOPSYCHO.2009.10.007

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1999). *International affective picture system (IAPS): Instruction manual and affective ratings. Technical Report A-2*. Gainesville, FL: University of Florida. https://doi.org/10.1016/j.epsr.2006.03.016

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology*, *30*(3), 261–273. https://doi.org/10.1111/j.1469-8986.1993.tb03352.x

Lang, P. J., Kozak, M. J., Miller, G. A., Levin, D. N., & McLean, A. (1980). Emotional imagery: conceptual structure and pattern of somato-visceral response. *Psychophysiology*, *17*(2), 179–192. https://doi.org/10.1111/j.1469-8986.1980.tb00133.x

LeDoux, J. (2003). The emotional brain, fear, and the amygdala. *Cellular and Molecular Neurobiology*. https://doi.org/10.1023/A:1025048802629

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, *69*(1), 1–33. https://doi.org/10.18637/jss.v069.i01

Levenson, M. R., Kiehl, K. A., & Fitzpatrick, C. M. (1995). Assessing Psychopathic Attributes in a Noninstitutionalized Population. *Journal of Personality and Social Psychology*, *68*(1), 151–158. https://doi.org/10.2224/sbp.2006.34.3.221

Lindquist, K. A., Satpute, A. B., & Gendron, M. (2015). Does Language Do More Than Communicate Emotion? *Current Directions in Psychological Science*, *24*(2), 99–108. https://doi.org/10.1177/0963721414553440

Luke, S. G. (2016). Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods*, *49*(4), 1494–1502. https://doi.org/10.3758/s13428-016-0809-y

Lundqvist, D., Flykt, A., & Öhman, A. (1998). The Karolinska Directed Emotional Faces - KDEF, CD ROM from Department of Clinical Neuroscience, Psychology section. *Karolinska Institut, ISBN 91-630-7164-9*. https://doi.org/10.1017/CBO9781107415324.004

Maffei, A., Vencato, V., & Angrilli, A. (2015). Sex differences in emotional evaluation of film clips: Interaction with five high arousal emotional categories. *PLoS ONE*, *10*(12). https://doi.org/10.1371/journal.pone.0145562

Marchewka, A., Zurawski, L., Jednoróg, K., & Grabowska, A. (2014). The Nencki Affective Picture System (NAPS): Introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior Research Methods*, *46*(2), 596–610.

https://doi.org/10.3758/s13428-013-0379-1

Marsh, A. A., & Blair, R. J. R. (2008). Deficits in facial affect recognition among antisocial populations: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, *32*(3), 454–465. https://doi.org/10.1016/J.NEUBIOREV.2007.08.003

Martin, R. A., Berry, G. E., Dobranski, T., Horne, M., & Dodgson, P. G. (1996). Emotion Perception Threshold: Individual Differences in Emotional Sensitivity. *Journal of Research in Personality*, *30*(2), 290–305. https://doi.org/10.1006/JRPE.1996.0019

Martini, N., Menicucci, D., Sebastiani, L., Bedini, R., Pingitore, A., Vanello, N., … Gemignani, A. (2012). The dynamics of EEG gamma responses to unpleasant visual stimuli: From local activity to functional connectivity. *NeuroImage*, *60*(2), 922–932. https://doi.org/10.1016/j.neuroimage.2012.01.060

Mauss, I. B., McCarter, L., Levenson, R. W., Wilhelm, F. H., & Gross, J. J. (2005). The tie that binds? Coherence among emotion experience, behavior, and physiology. *Emotion*, *5*(2), 175–190. https://doi.org/10.1037/1528-3542.5.2.175

Mauss, I. B., & Robinson, M. D. (2009). Measures of emotion: A review. *Cognition & Emotion*, *23*(2), 209–237. https://doi.org/10.1080/02699930802204677

Meffert, H., Gazzola, V., Den Boer, J. A., Bartels, A. A. J., & Keysers, C. (2013). Reduced spontaneous but relatively normal deliberate vicarious representations in psychopathy. *Brain*, *136*(8), 2550–2562. https://doi.org/10.1093/brain/awt190

Mehrabian, A., Young, A. L., & Sato, S. (1988). Emotional empathy and associated individual differences. *Current Psychology*, *7*(3), 221–240. https://doi.org/10.1007/BF02686670

Mennella, R., Patron, E., & Palomba, D. (2017). Frontal alpha asymmetry neurofeedback for the reduction of negative affect and anxiety. *Behaviour Research and Therapy*, *92*, 32–40. https://doi.org/10.1016/J.BRAT.2017.02.002

Menninghaus, W., Wagner, V., Hanich, J., Wassiliwizky, E., Kuehnast, M., & Jacobsen, T. (2015). Towards a psychological construct of being moved. *PloS One*, *10*(6), e0128451. https://doi.org/10.1371/journal.pone.0128451

Mourão-Miranda, J., Volchan, E., Moll, J., De Oliveira-Souza, R., Oliveira, L., Bramati, I., … Pessoa, L. (2003). Contributions of stimulus valence and arousal to visual activation during emotional perception. *NeuroImage*, *20*(4), 1955–1963. https://doi.org/10.1016/j.neuroimage.2003.08.011

Müller, M. M., Gruber, T., & Keil, A. (2000). Modulation of induced gamma band activity in the human EEG by attention and visual information processing. *International Journal of*

Psychophysiology, *38*(3), 283–299. https://doi.org/10.1016/S0167-8760(00)00171-9

Müller, M. M., Keil, A., Gruber, T., & Elbert, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band EEG activity. *Clinical Neurophysiology*, *110*(11), 1913–1920. https://doi.org/10.1016/S1388-2457(99)00151-0

Mulligan, K., & Scherer, K. R. (2012, October 26). Toward a working definition of emotion. *Emotion Review*. SAGE PublicationsSage UK: London, England. https://doi.org/10.1177/1754073912445818

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*(1), 1–25. https://doi.org/10.1002/hbm.1058

Nummenmaa, L., Glerean, E., Viinikainen, M., Jaaskelainen, I. P., Hari, R., & Sams, M. (2012a). Emotions promote social interaction by synchronizing brain activity across individuals. *Proceedings of the National Academy of Sciences*, *109*(24), 9599–9604. https://doi.org/10.1073/pnas.1206095109

Nummenmaa, L., Glerean, E., Viinikainen, M., Jaaskelainen, I. P., Hari, R., & Sams, M. (2012b). Emotions promote social interaction by synchronizing brain activity across individuals. *Proceedings of the National Academy of Sciences*, *109*(24), 9599–9604. https://doi.org/10.1073/pnas.1206095109

Pajula, J., Kauppi, J.-P., Tohka, J., Spiers, H., Maguire, E., Hasson, U., … Harel, M. (2012). Inter-Subject Correlation in fMRI: Method Validation against Stimulus-Model Based Analysis. *PLoS ONE*, *8*(8), e41196. https://doi.org/10.1371/journal.pone.0041196

Palomba, D., Sarlo, M., Angrilli, A., Mini, A., & Stegagno, L. (2000). Cardiac responses associated with affective processing of unpleasant film stimuli. *International Journal of Psychophysiology*, *36*(1), 45–57. https://doi.org/10.1016/S0167-8760(99)00099-9

Pamilo, S., Malinen, S., Hlushchuk, Y., Seppä, M., Tikka, P., & Hari, R. (2012). Functional Subdivision of Group-ICA Results of fMRI Data Collected during Cinema Viewing. *PLoS ONE*, *7*(7), e42000. https://doi.org/10.1371/journal.pone.0042000

Parvizi, J., Van Hoesen, G. W., Buckwalter, J., & Damasio, A. (2006). Neural connections of the posteromedial cortex in the macaque. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(5), 1563–8. https://doi.org/10.1073/pnas.0507729103

Pascual-Marqui, R. D. (2002). Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. *Methods and Findings in Experimental and Clinical Pharmacology*, *24 Suppl D*, 5–12.

Patrick, C. J. (1994). Emotion and psychopathy: Startling new insights. *Psychophysiology*, *31*(4), 319–330. https://doi.org/10.1111/j.1469-8986.1994.tb02440.x

Patrick, C. J. (2006). Back to the Future: Cleckley as a Guide to the Next Generation of Psychopathy Research. In *Handbook of psychopathy.* (pp. 605–617). New York, NY, US: Guilford Press.

Patrick, C. J., Fowles, D. C., & Krueger, R. F. (2009). Triarchic conceptualization of psychopathy: developmental origins of disinhibition, boldness, and meanness. *Development and Psychopathology*, *21*, 913–938. https://doi.org/10.1017/S0954579409000492

Pessoa, L. (2010). Emotion and Cognition and the Amygdala: From "what is it?" to "what's to be done?". *Neuropsychologia*, *48*(12), 3416–29. https://doi.org/10.1016/j.neuropsychologia.2010.06.038

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a "low road" to "many roads" of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11), 773–782. https://doi.org/10.1038/nrn2920

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the Amygdala to Emotion Processing: From Animal Models to Human Behavior. *Neuron*, *48*(2), 175–187. https://doi.org/10.1016/J.NEURON.2005.09.025

Philippot, P. (1993). Inducing and assessing differentiated emotion-feeling states in the laboratory. *Cognition and Emotion*, *7*(2), 171–193. https://doi.org/10.1080/02699939308409183

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*(6650), 495–498. https://doi.org/10.1038/39051

Pollatos, O., Gramann, K., & Schandry, R. (2007). Neural systems connecting interoceptive awareness and feelings. *Human Brain Mapping*, *28*(1), 9–18. https://doi.org/10.1002/hbm.20258

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *The Behavioral and Brain Sciences*, *25*(1), 1-20; discussion 20-71. https://doi.org/10.1017/S0140525X02000018

R Core Team. (2016). R: A Language and Environment for Statistical Computing. Vienna, Austria.

Ray, W., & Cole, H. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science*, *228*(4700), 750–752.

https://doi.org/10.1126/science.3992243

Reznik, S. J., & Allen, J. J. B. (2018). Frontal asymmetry as a mediator and moderator of emotion: An updated review. *Psychophysiology*, *55*(1). https://doi.org/10.1111/psyp.12965

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews. Neuroscience*, *2*(9), 661–70. https://doi.org/10.1038/35090060

Rottenberg, J., Ray, R. D., & Gross, J. J. (2007). Emotion elicitation using films. Handbook of emotion elicitation and assessment. In *Handbook of emotion elicitation and assessment Series in affective science* (pp. 2–28). https://doi.org/10.1080/02699939508408966

Rueckert, L., & Naybar, N. (2008). Gender differences in empathy: The role of the right hemisphere. *Brain and Cognition*, *67*(2), 162–167. https://doi.org/10.1016/j.bandc.2008.01.002

Sabatinelli, D., Flaisch, C. a T., Bradley, M. M., Fitzsimmons, J. R., & Lang, P. J. (2004). Affective picture perception: gender differences in visual cortex ? *Neuroreport*, *15*(7), 1109–1112. https://doi.org/10.1097/01.wnr.0000126558.41468.3d

Samson, A. C., Kreibig, S. D., Soderstrom, B., Wade, A. A., & Gross, J. J. (2015). Eliciting positive, negative and mixed emotional states: A film library for affective scientists. *Cognition and Emotion*, *30*(5), 827–856. https://doi.org/10.1080/02699931.2015.1031089

Sander, D., Grandjean, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., & Vuilleumier, P. (2005). Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody. *NeuroImage*, *28*(4), 848–858. https://doi.org/10.1016/J.NEUROIMAGE.2005.06.023

Sarlo, M., Buodo, G., Poli, S., & Palomba, D. (2005). Changes in EEG alpha power to different disgust elicitors: The specificity of mutilations. *Neuroscience Letters*, *382*(3), 291–296. https://doi.org/10.1016/j.neulet.2005.03.037

Schaefer, A., Nils, F., Sanchez, X., & Philippot, P. (2010). Assessing the effectiveness of a large database of emotion-eliciting films: A new tool for emotion researchers. *Cognition & Emotion*, *24*(7), 1153–1172. https://doi.org/10.1080/02699930903274322

Scherer, K. R. (2004). Which Emotions Can be Induced by Music? What Are the Underlying Mechanisms? And How Can We Measure Them? *Journal of New Music Research*, *33*(3), 239–251. https://doi.org/10.1080/0929821042000317822

Schienle, A., Stark, R., Walter, B., Blecker, C., Ott, U., Kirsch, P., … Vaitl, D. (2002). The insula is not specifically involved in disgust processing: An fMRI study. *NeuroReport*, *13*(16), 2023–2026. https://doi.org/10.1097/00001756-200211150-00006

Schulte-Rüther, M., Markowitsch, H. J., Shah, N. J., Fink, G. R., & Piefke, M. (2008). Gender differences in brain networks supporting empathy. *NeuroImage*, *42*(1), 393–403. https://doi.org/10.1016/J.NEUROIMAGE.2008.04.180

Schultz, W. (2015). Neuronal Reward and Decision Signals: From Theories to Data. *Physiological Reviews*, *95*(3), 853–951. https://doi.org/10.1152/physrev.00023.2014

Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*(5306), 1593–1599.

Schutter, D. J. L. G. (2009). Antidepressant efficacy of high-frequency transcranial magnetic stimulation over the left dorsolateral prefrontal cortex in double-blind sham-controlled designs: A meta-analysis. *Psychological Medicine*, *39*(1), 65–75. https://doi.org/10.1017/S0033291708003462

Seara-Cardoso, A., & Viding, E. (2014). Functional Neuroscience of Psychopathic Personality in Adults. https://doi.org/10.1111/jopy.12113

Seara-Cardoso, A., Viding, E., Lickley, R. A., & Sebastian, C. L. (2015). Neural responses to others' pain vary with psychopathic traits in healthy adult males. *Cognitive, Affective, & Behavioral Neuroscience*, *15*(3), 578–588. https://doi.org/10.3758/s13415-015-0346-7

Shamay-Tsoory, S. G. (2011). The Neural Bases for Empathy. *The Neuroscientist*, *17*, 18–24. https://doi.org/10.1177/1073858410379268

Shamay-Tsoory, S. G., Aharon-Peretz, J., & Perry, D. (2009). Two systems for empathy: A double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain*, *132*(3), 617–627. https://doi.org/10.1093/brain/awn279

Simons, R. F., Detenber, B. H., Cuthbert, B. N., Schwartz, D. D., & Reiss, J. E. (2003). Attention to Television: Alpha Power and Its Relationship to Image Motion and Emotional Content. *Media Psychology*, *5*(3), 283–301. https://doi.org/10.1207/S1532785XMEP0503_03

Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research. *Neuroscience and Biobehavioral Reviews*, *30*(6), 855–863. https://doi.org/10.1016/j.neubiorev.2006.06.011

Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences*, *1156*, 81–96. https://doi.org/10.1111/j.1749-6632.2009.04418.x

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, *303*(5661), 1157–62. https://doi.org/10.1126/science.1093535

Song, J., Davey, C., Poulsen, C., Luu, P., Turovets, S., Anderson, E., … Tucker, D. (2015). EEG source localization: Sensor density and head surface coverage. *Journal of Neuroscience Methods*, *256*, 9–21. https://doi.org/10.1016/j.jneumeth.2015.08.015

Sonnby-Borgstrom, M. (2002). Automatic mimicry reactions as related to differences in emotional empathy. *Scandinavian Journal of Psychology*, *43*(5), 433–443. https://doi.org/10.1111/1467-9450.00312

Sonnby-Borgström, M., Jönsson, P., & Svensson, O. (2003). Emotional empathy as related to mimicry reactions at different levels of information processing. *Journal of Nonverbal Behavior*, *27*(1), 3–23. https://doi.org/10.1023/A:1023608506243

Spironelli, C., & Angrilli, A. (2010). Developmental aspects of language lateralization in delta, theta, alpha and beta EEG bands. *Biological Psychology*, *85*(2), 258–267. https://doi.org/10.1016/j.biopsycho.2010.07.011

Stawarczyk, D., Majerus, S., Maquet, P., & D'Argembeau, A. (2011). Neural Correlates of Ongoing Conscious Experience: Both Task-Unrelatedness and Stimulus-Independence Are Related to Default Network Activity. *PLoS ONE*, *6*(2), e16997. https://doi.org/10.1371/journal.pone.0016997

Stellar, J. E., Cohen, A., Oveis, C., & Keltner, D. (2015). Affective and Physiological Responses to the Suffering of Others: Compassion and Vagal Activation, *108*(4), 572–585. https://doi.org/10.1037/pspi0000010

Stevens, J. S., & Hamann, S. (2012). Sex differences in brain activation to emotional stimuli: A meta-analysis of neuroimaging studies. *Neuropsychologia*, *50*(7), 1578–1593. https://doi.org/10.1016/j.neuropsychologia.2012.03.011

Stevenson, R. A., & James, T. W. (2008). Affective auditory stimuli : Characterization of the International Affective Digitized Sounds (IADS) by discrete emotional categories. *Behavior Research Methods*, *40*(1), 315–321.

Sutton, S. K., Vitale, J. E., & Newman, J. P. (2002). Emotion Among Women With Psychopathy During Picture Perception. https://doi.org/10.1037//0021-843X.111.4.610

Tallon-Baudry, C., Bertrand, O., Hénaff, M.-A., Isnard, J., & Fischer, C. (2005). Attention Modulates Gamma-band Oscillations Differently in the Human Lateral Occipital Cortex and Fusiform Gyrus. *Cerebral Cortex*, *15*(5), 654–662. https://doi.org/10.1093/cercor/bhh167

Ulrich, R. S. (1981). Natural Versus Urban Scenes: Some Psychophysiological Effects. *Environment and Behavior*. https://doi.org/10.1177/0013916581135001

Ulrich, R. S., Simons, R. F., Losito, B. D., Fiorito, E., Miles, M. A., & Zelson, M. (1991). Stress recovery during exposure to natural and urban environments. *Journal of Environmental Psychology*, *11*(3), 201–230. https://doi.org/10.1016/S0272-4944(05)80184-7

van den Berg, A. E., Koole, S. L., & van der Wulp, N. Y. (2003). Environmental preference and restoration: (How) are they related? *Journal of Environmental Psychology*, *23*(2), 135–146. https://doi.org/10.1016/S0272-4944(02)00111-1

Västfjäll, D. (2001). Emotion induction through music: A review of the musical mood induction procedure. *Musicae Scientiae*, *5*(1_suppl), 173–211. https://doi.org/10.1177/10298649020050S107

Verona, E., Patrick, C. J., & Curtin, J. (2004). Psychopathy and Physiological Response to Emotionally Evocative Sounds. *Article in Journal of Abnormal Psychology*, *113*(1), 99–108. https://doi.org/10.1037/0021-843X.113.1.99

Vingerhoets, A. J. J. M., Cornelius, R. R., Van Heck, G. L., & Becht, M. C. (2000). Adult crying: A model and review of the literature. *Review of General Psychology*, *4*(4), 354–377. https://doi.org/10.1037/1089-2680.4.4.354

Vingerhoets, A. J. J. M., van de Ven, N., & van der Velden, Y. (2016). The social impact of emotional tears. *Motivation and Emotion*, *40*(3), 455–463. https://doi.org/10.1007/s11031-016-9543-0

Vitacco, M. J., & Jackson, R. (2005). Testing a Four-Factor Model of Psychopathy and Its Association With Ethnicity, Gender, Intelligence, and Violence. *Article in Journal of Consulting and Clinical Psychology*. https://doi.org/10.1037/0022-006X.73.3.466

Volkow, N. D., Wang, G.-J., & Baler, R. D. (2010). Reward, dopamine and the control of food intake: implications for obesity. *Trends in Cognitive Sciences*, *15*, 37–46. https://doi.org/10.1016/j.tics.2010.11.001

Volkow, N. D., Wise, R. A., & Baler, R. (2017). The dopamine motive system: Implications for drug and food addiction. *Nature Reviews Neuroscience*, *18*(12), 741–752. https://doi.org/10.1038/nrn.2017.130

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*(11), 1271–1278. https://doi.org/10.1038/nn1341

Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights.

Psychonomic Bulletin and Review. https://doi.org/10.3758/BF03206482

Wager, T. D., Kang, J., Johnson, T. D., Nichols, T. E., Satpute, A. B., & Barrett, L. F. (2015). A Bayesian Model of Category-Specific Emotional Brain Responses. *PLOS Computational Biology*, *11*(4), e1004066. https://doi.org/10.1371/journal.pcbi.1004066

Welch, B. L. (1947). The generalization of `Student's' problem when several different population variances are involved. *Biometrika*, *34*(1/2), 28–35. https://doi.org/10.1093/biomet/34.1-2.28

Westermann, R., Stahl, G., & Hesse, F. W. (1996). Relative effectiveness and validity of mood induction procedures: a meta-analysis. *European Journal of Social Psychology*, *26*, 557–580. https://doi.org/10.1002/(SICI)1099-0992(199607)26:4<557::AID-EJSP769>3.0.CO;2-4

Weymar, M., & Schwabe, L. (2016). Amygdala and Emotion: The Bright Side of It. *Frontiers in Neuroscience*, *10*, 224. https://doi.org/10.3389/fnins.2016.00224

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wickham, H., & Francois, R. (2016). dplyr: A Grammar of Data Manipulation.

Wierzba, M., Riegel, M., Pucz, A., Leśniewska, Z., Dragan, W. Ł., Gola, M., … Marchewka, A. (2015). Erotic subset for the Nencki Affective Picture System (NAPS ERO): cross-sexual comparison study. *Frontiers in Psychology*, *6*, 1336. https://doi.org/10.3389/fpsyg.2015.01336

Wilson, S. M., Molnar-Szakacs, I., & Iacoboni, M. (2008). Beyond superior temporal cortex: Intersubject correlations in narrative speech comprehension. *Cerebral Cortex*, *18*(1), 230–242. https://doi.org/10.1093/cercor/bhm049

Zaki, J., & Ochsner, K. N. (2012). The neuroscience of empathy: progress, pitfalls and promise. *Nature Neuroscience*, *15*(5), 675–680. https://doi.org/10.1038/nn.3085

Zentner, M., Grandjean, D., & Scherer, K. R. (2008). Emotions evoked by the sound of music: characterization, classification, and measurement. *Emotion*, *8*(4), 494–521. https://doi.org/10.1037/1528-3542.8.4.494

Appendixes

Appendix I

Region	Category	Group	Hemisphere	Region X Category	Region X Hemisphere	Category X Group	Category X Hemisphere	$_{log}$Likelihood	AIC_c	ΔAIC	AIC_{weight}
x	x	x	x	x	x	x		-348.76	746.36	0	0.8981
x	x		x	x	x			-355.68	751.95	5.5981	0.0547
x	x	x	x	x	x			-355.33	753.31	6.9535	0.0278
x	x	x	x	x	x	x	x	-346.99	755.3	8.9444	0.0103
x	x	x	x		x	x		-359.73	755.93	9.5732	0.0075
x	x		x	x	x		x	-353.92	760.83	14.473	0.0006
x	x		x		x			-366.66	761.62	15.2616	0.0004
x	x	x	x	x	x		x	-353.57	762.2	15.8457	0.0003
x	x	x	x		x			-366.31	762.95	16.5963	0.0002
x	x	x	x		x	x	x	-357.98	764.81	18.4521	<0.00001
x	x		x		x		x	-364.92	770.43	24.0744	<0.00001
x	x	x	x		x		x	-364.57	771.78	25.426	<0.00001
x			x		x			-414.85	851.89	105.529	<0.00001
x		x	x		x			-414.49	853.2	106.8449	<0.00001
x	x	x	x	x		x		-592.18	1224.94	478.5881	<0.00001
x	x		x	x				-597.16	1226.7	480.3426	<0.00001
x	x	x	x			x		-599.61	1227.51	481.1538	<0.00001
x	x	x	x	x				-596.78	1227.98	481.6278	<0.00001
x	x		x					-604.62	1229.4	483.0454	<0.00001

x	x	x	x					-604.24	1230.67	484.3102	<0.00001
x	x	x	x	x		x	x	-590.91	1234.8	488.4424	<0.00001
x	x		x	x			x	-595.88	1236.48	490.1203	<0.00001
x	x	x	x			x	x	-598.34	1237.27	490.9178	<0.00001
x	x	x	x	x			x	-595.5	1237.78	491.4223	<0.00001
x	x		x				x	-603.36	1239.09	492.7356	<0.00001
x	x	x	x				x	-602.97	1240.37	494.017	<0.00001
x			x					-639.48	1293.03	546.678	<0.00001
x		x	x					-639.09	1294.28	547.9237	<0.00001
	x	x	x			x		-708.44	1441.09	694.7346	<0.00001
	x		x					-712.72	1441.54	695.1834	<0.00001
	x	x	x					-712.29	1442.71	696.3534	<0.00001
	x	x	x			x	x	-707.34	1451.17	704.8098	<0.00001
	x		x				x	-711.62	1451.54	705.184	<0.00001
	x	x	x				x	-711.2	1452.73	706.3702	<0.00001
			x					-743.06	1496.17	749.8099	<0.00001
		x	x					-742.63	1497.32	750.9597	<0.00001
x	x							-885.94	1787.99	1041.6304	<0.00001
x	x	x				x		-882.47	1789.16	1042.801	<0.00001
x	x	x						-885.54	1789.21	1042.8498	<0.00001
x	x			x				-880.64	1789.57	1043.2087	<0.00001
x	x	x		x				-880.23	1790.81	1044.4487	<0.00001
x	x	x		x		x		-877.19	1790.87	1044.5122	<0.00001
x								-910.14	1830.33	1083.97	<0.00001
x		x						-909.73	1831.53	1085.1698	<0.00001
	x							-959.23	1930.52	1184.167	<0.00001
	x	x						-958.79	1931.65	1185.2922	<0.00001

	x	x				x		-956.1	1932.36	1185.9988	<0.00001
								-981.31	1968.64	1222.2815	<0.00001
		x						-980.86	1969.74	1223.3862	<0.00001

List of the models included in the model selection in Study 3, ranked according to AIC scores (from lowest to highest). Each row represents a different model, with “X” indicating the predictors included.

Appendix II

Category	Group	Hemisphere	Region	Category x Group	Category x Hemisphere	Category x Region	Group x Hemisphere	Group x Region	Hemisphere x Region	Category x Group x Hemisphere	Category x Group x Region	Category x Hemisphere x Region	Group x Hemisphere x Region	Category x Group x Hemisphere x Region	$_{log}$Likelihood	AICc	ΔAIC	AICweight
x	x	x	x	x	x		x	x	x				x		-6114.9	12302.8	0.0	0.7
x	x	x	x		x		x	x	x				x		-6120.4	12305.6	2.8	0.2
x	x	x	x	x	x	x	x	x	x				x		-6109.3	12308.1	5.3	0.1
x	x	x	x	x	x		x	x	x						-6122.7	12310.2	7.4	< 0.001
x	x	x	x		x	x	x	x	x				x		-6114.8	12310.9	8.1	< 0.001
x	x	x	x	x	x		x		x						-6126.1	12313.0	10.2	< 0.001
x	x	x	x		x		x	x	x						-6128.2	12313.0	10.2	< 0.001
x	x	x	x	x	x		x	x	x	x			x		-6111.7	12313.0	10.2	< 0.001
x	x	x	x	x	x	x	x	x	x						-6117.1	12315.6	12.8	< 0.001
x	x	x	x		x		x		x						-6131.6	12315.7	13.0	< 0.001
x	x	x	x	x			x	x	x				x		-6129.6	12315.8	13.1	< 0.001
x	x	x	x	x	x	x	x	x	x			x	x		-6097.2	12317.3	14.5	< 0.001
x	x	x	x		x	x	x	x	x						-6122.6	12318.3	15.5	< 0.001
x	x	x	x				x	x	x				x		-6135.0	12318.4	15.6	< 0.001
x	x	x	x	x	x	x	x	x	x	x			x		-6106.1	12318.4	15.7	< 0.001
x	x	x	x	x	x	x	x		x						-6120.6	12318.5	15.7	< 0.001
x	x	x	x	x	x	x	x	x	x		x		x		-6106.6	12319.3	16.6	< 0.001
x	x	x	x		x	x	x	x	x			x	x		-6102.7	12319.9	17.1	< 0.001
x	x	x	x	x	x		x	x	x	x					-6119.6	12320.4	17.7	< 0.001
x	x	x	x		x	x	x		x						-6126.1	12321.1	18.4	< 0.001
x	x	x	x	x		x	x	x	x				x		-6124.1	12321.3	18.5	< 0.001
x	x	x	x	x			x	x	x						-6137.4	12323.2	20.4	< 0.001
x	x	x	x	x	x		x		x	x					-6123.0	12323.2	20.5	< 0.001
x	x	x	x			x	x	x	x				x		-6129.5	12323.8	21.1	< 0.001
x	x	x	x	x	x	x	x	x	x			x			-6105.2	12324.9	22.1	< 0.001
x	x	x	x				x	x	x						-6142.7	12325.8	23.0	< 0.001
x	x	x	x	x	x	x	x	x	x	x					-6114.0	12325.9	23.1	< 0.001
x	x	x	x	x			x		x						-6140.8	12325.9	23.2	< 0.001
x	x	x	x	x	x	x	x	x	x		x				-6114.5	12326.8	24.0	< 0.001
x	x	x	x		x	x	x	x	x			x			-6110.6	12327.5	24.7	< 0.001
x	x	x	x	x	x			x	x						-6133.4	12327.5	24.7	< 0.001
x	x	x	x	x	x	x	x	x	x	x		x	x		-6094.0	12327.8	25.0	< 0.001
x	x	x	x	x	x	x	x		x			x			-6108.7	12327.8	25.0	< 0.001
x	x	x	x				x		x						-6146.1	12328.5	25.7	< 0.001
x	x	x	x	x	x	x	x	x	x		x	x	x		-6094.4	12328.6	25.9	< 0.001

x	x	x	x	x		x	x	x	x						-6132.0	12328.7	26.0	< 0.001
x	x	x	x	x	x	x	x		x	x					-6117.6	12328.8	26.0	< 0.001
x	x	x	x	x	x	x	x	x	x	x	x		x		-6103.4	12329.7	26.9	< 0.001
x	x	x	x		x			x	x						-6138.8	12330.2	27.4	< 0.001
x	x	x	x	x	x				x						-6136.8	12330.2	27.4	< 0.001
x	x	x	x		x	x	x		x			x			-6114.2	12330.4	27.6	< 0.001
x	x	x	x			x	x	x	x						-6137.3	12331.2	28.5	< 0.001
x	x	x	x	x		x	x		x						-6135.4	12331.6	28.8	< 0.001
x	x	x	x	x		x	x	x	x		x		x		-6121.4	12332.5	29.7	< 0.001
x	x	x	x		x				x						-6142.2	12332.8	30.1	< 0.001
x	x	x	x	x	x	x		x	x						-6127.9	12332.9	30.1	< 0.001
x		x	x		x				x						-6143.8	12333.9	31.2	< 0.001
x	x	x	x			x	x		x						-6140.7	12334.0	31.2	< 0.001
x	x	x	x	x	x	x	x	x	x	x		x			-6102.0	12335.4	32.6	< 0.001
x	x	x	x		x	x		x	x						-6133.3	12335.5	32.7	< 0.001
x	x	x	x	x	x	x			x						-6131.3	12335.7	32.9	< 0.001
x	x	x	x	x	x	x	x	x	x		x	x			-6102.5	12336.2	33.5	< 0.001
x	x	x	x	x	x	x	x	x	x	x	x				-6111.3	12337.2	34.4	< 0.001
x	x	x	x		x	x			x						-6136.7	12338.3	35.5	< 0.001
x	x	x	x	x	x	x	x		x	x		x			-6105.6	12338.3	35.6	< 0.001
x	x	x	x	x	x	x	x	x	x	x	x	x	x		-6091.2	12339.1	36.4	< 0.001
x		x	x		x	x			x						-6138.3	12339.4	36.6	< 0.001
x	x	x	x	x		x	x	x	x		x				-6129.3	12339.9	37.1	< 0.001
x	x	x	x	x				x	x						-6147.9	12340.2	37.4	< 0.001
x	x	x	x	x	x	x		x	x			x			-6115.9	12342.2	39.5	< 0.001
x	x	x	x					x	x						-6153.2	12342.7	39.9	< 0.001
x	x	x	x	x					x						-6151.3	12342.9	40.1	< 0.001
x	x	x	x	x	x	x		x	x		x				-6125.2	12344.1	41.3	< 0.001
x	x	x	x		x	x		x	x			x			-6121.4	12344.7	42.0	< 0.001
x	x	x	x	x	x	x			x			x			-6119.5	12345.1	42.3	< 0.001
x	x	x	x						x						-6156.5	12345.3	42.5	< 0.001
x	x	x	x	x		x		x	x						-6142.5	12345.8	43.0	< 0.001
x		x	x						x						-6158.1	12346.4	43.6	< 0.001
x	x	x	x	x	x	x	x	x	x	x	x	x			-6099.3	12346.8	44.0	< 0.001
x	x	x	x		x	x			x			x			-6124.8	12347.6	44.8	< 0.001
x	x	x	x			x		x	x						-6147.8	12348.2	45.4	< 0.001
x	x	x	x	x		x			x						-6145.9	12348.5	45.7	< 0.001
x		x	x		x	x			x			x			-6126.4	12348.6	45.8	< 0.001
x	x	x	x			x			x						-6151.2	12350.9	48.1	< 0.001
x		x	x			x			x						-6152.8	12352.0	49.2	< 0.001
x	x	x	x	x	x	x		x	x		x	x			-6113.2	12353.6	50.8	< 0.001
x	x	x	x	x		x		x	x		x				-6139.9	12356.9	54.1	< 0.001
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	-6088.5	12367.9	65.2	< 0.001
	x	x	x				x	x	x				x		-6201.9	12444.2	141.5	< 0.001
	x	x	x				x	x	x						-6209.3	12450.8	148.0	< 0.001
	x	x	x				x		x						-6212.5	12453.1	150.3	< 0.001

	x	x	x					x	x						-6219.3	12466.7	163.9	< 0.001
	x	x	x						x						-6222.4	12469.0	166.2	< 0.001
		x	x						x						-6224.0	12470.1	167.3	< 0.001
x	x	x	x	x	x		x	x							-6398.4	12853.3	550.6	< 0.001
x	x	x	x		x		x	x							-6402.9	12854.2	551.5	< 0.001
x	x	x	x	x	x		x								-6401.0	12854.5	551.7	< 0.001
x	x	x	x		x		x								-6405.5	12855.3	552.6	< 0.001
x	x	x	x	x	x	x	x	x							-6393.8	12860.6	557.9	< 0.001
x	x	x	x	x			x	x							-6410.4	12861.1	558.3	< 0.001
x	x	x	x		x	x	x	x							-6398.3	12861.5	558.7	< 0.001
x	x	x	x				x	x							-6414.8	12861.8	559.0	< 0.001
x	x	x	x	x	x	x	x								-6396.5	12861.9	559.1	< 0.001
x	x	x	x	x			x								-6413.0	12862.2	559.4	< 0.001
x	x	x	x		x	x	x								-6401.0	12862.6	559.9	< 0.001
x	x	x	x				x								-6417.3	12862.9	560.1	< 0.001
x	x	x	x	x	x		x	x		x					-6395.7	12864.4	561.6	< 0.001
x	x	x	x	x	x		x			x					-6398.3	12865.5	562.7	< 0.001
x	x	x	x	x	x			x							-6406.9	12866.4	563.6	< 0.001
x	x	x	x		x			x							-6411.4	12867.2	564.5	< 0.001
x	x	x	x	x	x										-6409.5	12867.5	564.7	< 0.001
x	x	x	x		x										-6414.0	12868.3	565.5	< 0.001
x	x	x	x	x		x	x	x							-6405.9	12868.5	565.7	< 0.001
x	x	x	x			x	x	x							-6410.3	12869.1	566.3	< 0.001
x		x	x		x										-6415.6	12869.5	566.7	< 0.001
x	x	x	x	x		x	x								-6408.5	12869.6	566.9	< 0.001
x	x	x	x			x	x								-6412.9	12870.2	567.5	< 0.001
x	x	x	x	x	x	x	x	x		x					-6391.1	12871.8	569.0	< 0.001
x	x	x	x	x	x	x	x	x			x				-6391.6	12872.7	569.9	< 0.001
x	x	x	x	x	x	x	x			x					-6393.8	12873.0	570.2	< 0.001
x	x	x	x	x	x	x		x							-6402.4	12873.7	570.9	< 0.001
x	x	x	x	x				x							-6418.8	12874.0	571.2	< 0.001
x	x	x	x		x	x		x							-6406.9	12874.5	571.7	< 0.001
x	x	x	x					x							-6423.2	12874.6	571.8	< 0.001
x	x	x	x	x	x	x									-6405.0	12874.9	572.1	< 0.001
x	x	x	x	x											-6421.4	12875.0	572.2	< 0.001
x	x	x	x		x	x									-6409.5	12875.6	572.8	< 0.001
x	x	x	x												-6425.8	12875.6	572.9	< 0.001
x		x	x		x	x									-6411.1	12876.8	574.0	< 0.001
x		x	x												-6427.4	12876.8	574.1	< 0.001
x	x	x	x	x		x	x	x			x				-6403.7	12880.4	577.7	< 0.001
x	x	x	x	x		x		x							-6414.4	12881.3	578.6	< 0.001
x	x	x	x			x		x							-6418.8	12881.9	579.1	< 0.001
x	x	x	x	x		x									-6417.0	12882.5	579.7	< 0.001
x	x	x	x			x									-6421.3	12883.0	580.2	< 0.001
x	x	x	x	x	x	x	x	x		x	x				-6388.8	12883.9	581.1	< 0.001
x		x	x			x									-6423.0	12884.2	581.4	< 0.001

x	x	x	x	x	x	x		x			x				-6400.2	12885.8	583.0	< 0.001
x	x	x	x	x		x		x			x				-6412.2	12893.3	590.5	< 0.001
	x	x	x				x	x							-6469.6	12963.3	660.5	< 0.001
	x	x	x				x								-6472.1	12964.2	661.4	< 0.001
	x	x	x					x							-6477.7	12975.5	672.7	< 0.001
	x	x	x												-6480.1	12976.3	673.6	< 0.001
		x	x												-6481.7	12977.5	674.8	< 0.001
x	x	x		x	x		x								-6531.1	13110.6	807.8	< 0.001
x	x	x			x		x								-6535.3	13110.9	808.1	< 0.001
x	x	x		x			x								-6542.2	13116.7	813.9	< 0.001
x	x	x					x								-6546.4	13116.9	814.1	< 0.001
x	x	x		x	x		x			x					-6528.6	13122.0	819.2	< 0.001
x	x	x		x	x										-6539.1	13122.7	819.9	< 0.001
x	x	x			x										-6543.3	13122.9	820.1	< 0.001
x		x			x										-6545.0	13124.2	821.4	< 0.001
x	x	x		x											-6550.2	13128.6	825.8	< 0.001
x	x	x													-6554.3	13128.7	825.9	< 0.001
x		x													-6556.0	13130.0	827.2	< 0.001
	x	x					x								-6596.7	13209.5	906.8	< 0.001
	x	x													-6604.4	13220.9	918.1	< 0.001
		x													-6606.1	13222.1	919.4	< 0.001
x	x		x												-7041.0	14102.2	1799.4	< 0.001
x			x												-7042.6	14103.3	1800.5	< 0.001
x	x		x					x							-7039.7	14103.4	1800.7	< 0.001
x	x		x	x											-7038.2	14104.5	1801.8	< 0.001
x	x		x	x				x							-7036.8	14105.8	1803.0	< 0.001
x	x		x			x									-7038.0	14112.3	1809.5	< 0.001
x			x			x									-7039.6	14113.4	1810.6	< 0.001
x	x		x			x		x							-7036.6	14113.5	1810.7	< 0.001
x	x		x	x		x									-7035.2	14114.7	1812.0	< 0.001
x	x		x	x		x		x							-7033.7	14116.0	1813.2	< 0.001
x	x		x	x		x		x			x				-7032.3	14129.4	1826.7	< 0.001
	x		x												-7074.3	14160.6	1857.9	< 0.001
			x												-7075.9	14161.8	1859.0	< 0.001
	x		x					x							-7073.0	14162.0	1859.2	< 0.001
x	x														-7120.1	14256.2	1953.5	< 0.001
x															-7121.7	14257.5	1954.7	< 0.001
x	x			x											-7117.3	14258.8	1956.0	< 0.001
	x														-7151.9	14311.9	2009.1	< 0.001
															-7153.6	14313.1	2010.3	< 0.001

List of the models included in the model selection in Study 4, ranked according to AIC scores (from lowest to highest). Each row represents a different model, with “X” indicating the predictors included.