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The psychological and neural mechanisms of anger and its regulation.

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Civilization began the first time an angry person cast a word instead of a rock.

Sigmund Freud

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Chapter 1 Introduction

Emotions and affective neuroscience

Affective neuroscience is a relatively new discipline characterized by an unique potential: it can be considered the "royal road to put theories of emotion to the test" (Sandler, 2013). Indeed, the study of emotions in the past has been confused and fragmented. In 1928 Claparede wrote "the psychology of affective processes is the most confused chapter in all psychology"; then, behaviorism put the mind in a "black box", and emotions in those years were absolutely out of question. Only with the cognitive revolution (1970-1990) the content of the mind, and in part also emotions, started to be considered; in the affective domain, a particular interest was given to the critical role of cognition in modulating the emotion (Arnold, 1960; Lazarus, 1966; Schachter & Singer, 1962). This led to the establishment of two important mechanisms that involve cognition in emotional processes, which are the appraisal, involved in the emotion elicitation, and labeling, involved in the emotion categorization. In particular, nowadays appraisal theories play an important role in affective neuroscience.

Appraisal is a term coined by Arnold (1960), referring to the evaluation of a situation that plays a key role in the following elicitation of an emotion or an affective response. In particular, Schachter (1964) proposed that cognition is an antecedent of emotion. However, this seems to not always be the case.

The importance of emotions regardless of cognition emerged with the emotional revolution, which reached its peak only in the 90s, after Zajonc (1980) argued against Schachter's idea (1964) that cognition is necessary for emotion. Indeed, Zajonc argued that "Affective reactions can occur without extensive perceptual and cognitive encoding, are made with greater confidence than cognitive judgments, and can be made sooner".

This hypothesis is supported by a fundamental discovery in the field of affective neuroscience that is the pathway through which fear is encoded in the brain. Indeed, LeDoux (1996) not only found that the amygdala is a fundamental structure involved in the experience of fear, but it can be considered a stage of a double way on which the brain relies to process this emotion. There is a "Low Road" that

starts from external stimuli and sense organs, passes through the thalamus and reaches the amygdala that immediately reacts in order to produce behaviors and actions that allow us to express our emotion. This is a pathway that does not need higher cognition, is faster and allows us to immediately respond to environmental stimuli in particular when they are characterized by danger. Indeed, this rapid processing is responsible for fear conditioning. However, there is also a "High Road" that starts from external stimuli, passes through the thalamus but before reaching the amygdala includes a further step: the passage through the cortex, that allows us to be more conscious of the stimuli in the environment, and to make inferences about them.

This model can make the theory of Schachter and the theory of Zajonc coexist together (beyond the debates that are still present nowadays), given that sometimes our brain can process emotions without the necessity of a higher cognition to be involved, while other times cognition has a fundamental role in the emotional experience.

However, this is only an example of the potential role of affective neuroscience in the understanding of our emotions. Indeed, the hope is that this interdisciplinary field "will be able to constrain such varied models of emotion by bridging the gaps among different disciplinary approaches to emotion" (Sandler, 2013). According to this ambitious perspective, this thesis aims to improve at least in part, from a cognitive and an affective perspective, our knowledge on the mechanisms of anger: an emotion that is still poorly understood.

Anger

Anger can be defined as an intense emotional state involving a strong uncomfortable and hostile response to a perceived provocation, hurt or threat (Videbeck, Sheila L., 2006). On one hand, anger can be considered the fuel of life, since it helps us to reach our goals, overcome obstacles and define our boundaries in our relationships with others. On the other hand, although anger has an adaptive role in physical survival (Cannon, 1929) and in social relations (Keltner et al., 2006; Novaco, 1976), the importance of understanding anger and its regulation is unequivocal. Unbalanced and excessive anger is prevalent not only in numerous psychopathological and personality disorders, but also in medical conditions, such as cardiovascular disease or chronic pain (Novaco, 2010; Williams, 2010;

Fernandez & Turk, 1995). Indeed, anger can have a huge impact upon our ability to have happy lives.

Nevertheless, anger has been considered as the forgotten emotion. Although violence is prevalent in our society, and many researchers and clinicians focus on the problem of violence and aggressive behavior, little is heard about the emotion that frequently precedes such behavior.

During the experience of anger, a person is characterized by a cluster of physiological (both sympathetic and parasympathetic reactions such as an increase in respiration, blood pressure, heart rate, skin and body temperature and skin conductance – Stemmler, 2010-), cognitive (a negative cognitive appraisal of circumstances characterizing rumination, that can intensify and prolong the angry experience) and behavioral (physical or verbal aggression) attributes which are directly related to the temporal dynamics of anger.

The temporal dynamics of anger consists in different steps involved in the process of the experience of anger. The first step is the presence of a provocative event that in turn elicits the feelings and the appraisal associated with the experienced situation and emotion. Then, high-order thoughts can lead to further processes whose outcome is the occurrence of some regulation strategies on one hand, or the behavioral expression of anger on the other hand, i.e., aggression (Gilam, 2015).

Further, when anger is not regulated or suppressed, the temporal dynamics are characterized by an escalating property from annoyances and irritations that accumulate over time, to behavioral responses that can vary from mild request to strong angry outbursts. Berkowitz (1990) proposed a cognitive-neoassociationistic model to explain how the initial negative affect characterizing an aversive occurrence can result in angry feelings and aggression (or, on the other hand, in escaping from the unpleasant stimulation). According to this model, there is an association between negative affect and anger-related feelings due to the link with a person's particular thoughts, memories and physiological reactions resulting in the actual experience of this emotion.

Indeed, anger does not emerge only from specific situations but from the way in which individuals subjectively evaluate situations or events. This is conceptualized in the appraisal theory, according to which this process involves a cognitive evaluation that can determine the elicitation and the

differentiation of emotions, evaluating a relevant event in a particular way based on past experiences, personality, and current motivations (Wranik and Scherer, 2010).

To sum up, anger emerges from a conjunction of specific feelings, cognitions and physiological reactions associated with the urge to injure some target, that are eventually further object of appraisal and higher order processes that can up-regulate or down-regulate the emotion (Berkowitz & Harmon-Jones, 2004; Grecucci et. al. 2012).

Finally, another important component of emotion in the dimensional models on arousal and valence is the "core affect", that is the primary emotional reaction to a situation or event (Russell, 2003). According to this model, anger is characterized by strong, negative valence and high activation values.

The elicitation of anger in life

Different authors tried to classify different situations that can elicit anger, and three main categories have been identified (Gilam, 2015). The first involves the presence of a threat (real or imagined), such as physical or psychological pain, representing the most basic form of anger as the instinctive survival response, which triggers the fight reaction of the fight-flight system. The second involves the frustration elicited by a goal obstruction, while the third involves the perception of a personal offence or humiliation due to unfair treatment, violation of social norms, rejections and criticism.

This distinction, especially regarding the second and third points, is coherent with the model on the elicitation of anger in social contexts of Tripp and Bies (Bies & Tripp, 2004; Aquino, Tripp, & Bies, 2006). According to their model, an angry response is elicited by some sort of offense, real or perceived.

Interestingly, they distinguished between three categories of offense that elicit anger and revenge in social contexts: (a) goal obstruction; (b) violation of rules, norms, and promises; and (c) status and power derogation.

Goal obstructions represent the basic expression of anger, as an instrumental action (Lewis, 2010); in social contexts, this category includes situations in which one prevents the achievement of another's goals and the prevention can lead to anger and acts of revenge in response. In particular, goal

obstruction can lead to frustration, and that frustration can lead to an aggressive response like revenge.

The second category includes the violation of rules, norms, or promises. It is evident that this kind of offense elicits a socialized aspect of anger, which is learned during development (Lewis, 2010). In social contexts, this category includes situations in which a person gets angry when formal rules are violated in order to obtain special benefits or avoid common burdens (Bies & Tripp, 1996).

The last category includes the derogation of personal status and/or power, and could be related to the consequences of shame (Lewis, 2010). This category includes actions that diminish another's reputation or power, such as destructive criticism, public mockery intended to embarrass a subordinate or coworker, or when the person is wrongly accused (Bies & Tripp, 1996). These situations can elicit anger by motivating victims to regain status and power through attacking those who harmed them.

In addition, some key factors can modulate the amount of anger experienced and eventually expressed by people. These include the motivational relevance, the external attribution of blame and the copying potential. Indeed, anger seems to increase when (a) the obstructed goal is personally significant because it violates a basic need of the person; (b) someone or something is blamed for the negative unfair or illegitimate event; (c) the person perceives the ability (or the power) to deal successfully with the eliciting event (Berkowitz & Harmon-Jones, 2004).

However, also other factors can influence the outcomes of anger (its expression with aggression or its suppression and/or regulation). In order to better understand the outcomes, it is important to consider the approach vs. withdrawal tendencies that are elicited in the presence of a stressors in life. In the next paragraph some models will be considered.

Approach vs. withdrawal and the outcomes of anger

According to the internal-conflict model of hostility (Miller, 1948) during aversive events, there is the coexistence of both fear/anxiety-based withdrawal and anger derived approach inclinations, and the self-regulation of the latter can depend not only by controlled internal regulation, but sometimes also by externally fear-induced anger suppression. This means that aggressive tendencies can be

optimally regulated through effective strategies and emotional control, or can be suppressed due to the prevalence of a higher withdrawal inclination (more linked to emotions such as anxiety) rather than an approach one.

Indeed, anger has been defined as an approaching emotion; accordingly, its uniqueness is given by the fact that anger is the only negative emotion characterized by an approaching motivation rather than a withdrawal one (Berkowitz & Harmon-Jones, 2004). Given this tendency to approach, the typical behavioral outcome of anger is aggression, since anger usually leads to the activation of behaviors, even violent ones (Parrott & Giancola, 2007), aimed to restore a condition that has been interrupted or blocked.

In particular cases, when anger is uncontrollable and leads to rapid aggression, it seems to involve a "low road" in the brain; otherwise, a further cognitive component can support the elicitation of this emotion (Alia-Klein et al., 2019). This is particularly true when social rules come into play. Indeed, in order to limit its destructive potential, anger must be regulated and controlled according to the majority of cultures in the world (Matsumoto, Yoo & Chung, 2010). For this reason, aggression is no longer the unique response to anger: given the social need to avoid the expression of anger, this emotion can lead not only to approaching behaviors, but also to withdrawal and suppression, especially in social conditions (Breen & Kashdan, 2011). However, both approach and withdrawal tendencies can be associated with a regulated, goal-directed outcome or a dysregulated response after anger provocation. Indeed, it has been suggested that in the second case, an approaching tendency would represent aggression, while a withdrawal tendency associated with a dysregulated response would represent rumination (Gardner and Moore, 2008). According to this point of view, clinical anger is characterized by an exaggerated sensitivity to the experience of emotion, which has become strongly associated with personal danger through chronic early aversive environments. These conditions lead to a hostile anticipation of the world, involving different biases that lead to an exaggerated interpretation of life situations. According to this hypothesis, the angry individual is consumed with issues related to interpersonal safety (both physical and psychological) in response to a world perceived as dangerous and uncontrollable. This is elaborated in the Anger Avoidance Model (Gardner and Moore, 2008), according to which the problem is not the emotion of anger per se. Instead, what is most problematic is the belief that emotions (and anger in particular) are intolerable. The consequence is an inflexible overgeneralized use of avoidance through overt (behavioral) and

covert (cognitive) responses in a desperate effort to reduce, eliminate, or otherwise control the emotion of anger and maintain personal safety. This desperate effort to control this emotion is finally characterized by a dysfunctional internalization of anger (i.e., rumination) or by externalized avoidance (i.e., aggression).

Individual Differences in Anger: The State and Trait Anger Expression Inventory (STAXI, Spielberger)

Another line of research started to take into account individual differences in anger. Even if there is still poor evidence regarding this aspect especially when considering the neural mechanisms of anger, the most used questionnaire in literature is the State and Trait Expression Inventory of Spielberger (STAXI, Spielberg, 1988). This includes different subscales: State Anger, Trait Anger, Anger-In, Anger-Out and Anger Control.

State Anger refers to the transitory emotional state, more or less intense, that is elicited by a specific situation or in a specific moment (i.e., when the questionnaire is presented).

According to the *appraisal-tendency framework* (Lerner and Keltner, 2000; 2001), anger is experienced as a sense of certainty and individual control along with other-responsibilities (Lazarus, 1991; Smith & Ellsworth, 1985), and it can influence the appraisal of future events. Indeed, the event-related appraisals can persist beyond the eliciting situations, becoming automatic lenses for interpreting subsequent events (Litvak et al., in Potegal et al., 2009). In other words, when anger is frequently elicited in the individual's life, it can be automatically evoked even during the interpretation of new low provocative environmental cues. This means that an "emotion schema" (see the *differential emotions theory* Izard et al., 2007; Schultz et al., in Potegal et al., 2009) is frequently activated, leading to a change in the individual's emotional functioning. Indeed, when a *schema* frequently occurs, it can crystallize into stable individual traits (Clark et al., 1994; Rothbart and Bates, 1998; Goldsmith et al., 2000; Schultz et al., in Potegal et al., 2009), such as trait anger.

This process can explain a shift from state anger (a transitory emotional state marked by subjective feelings) to trait anger (a long-lasting individual difference in frequency and duration of anger episodes; Spielberger, 1988).

Other two scales of the STAXI, Anger-In and Anger-Out, refers to the possible reactions that can follow an angry state. The first consists in the extent to which people hold things in or suppress this emotion (i.e. the internalization of anger), while the second consists in the extent to which people express their anger outwardly in a poorly controlled manner (i.e., the externalization of anger). Finally, Anger Control refers to the ability of people to monitor and control the physical and verbal expression of anger, and the ability to calm down.

The neural bases of anger

Potegal and Stemmler (2010) hypothesized a neural circuit involved in anger processing, from the perception of triggering stimuli to the subjective experience of anger. According to their point of view, posterior and middle temporal cortices are involved in processing verbal and visual triggers, which evokes memory of related events and other relevant information processed in more anterior temporal areas. This mutual interaction would shape perceptions of anger-provoking situations, leading to the initial appraisal of anger. Finally, this information is anteriorly transmitted to the ventromedial and orbitofrontal cortex. In particular, the latter "integrates anger-provoking perceptions, e.g. combining the insulting verbal comment with the visual sneer, and weights inhibitory factors[...], empathy with the offender and his relative social status". The combined result determines eventual angry aggressive responses.

However, in literature the study of the neural mechanisms of anger is still fragmentized due to the fact that different studies relied on different paradigms. In addition, these paradigms are usually characterized by some limitations (see next section for more details). Therefore, the next chapter will focus on the results of a meta-analysis that will try to organize the literature evidence associated with anger and its neural correlates. Instead, the neural mechanisms underlying the individual differences of anger will be exposed in chapter 3 and chapter 4.

The measurement of anger in literature

As outlined in the last paragraph, anger has been studied through many different kinds of paradigms in literature, especially when considering its neural correlates. For example, in the past different stimuli were used to elicit the experience of anger in participants: racism images (Harmon-Jones et

al., 2006), news reports (Newhagen, 1998), video or movie clips (Gross and Levenson, 1995), insults and critiques by the experimenter (Eckhardt and Cohen, 1997; Stemmler, 1997; Mauss et al., 2005; Lobbestael et al., 2008), punishment (Taylor, 1967) and mental imagery (Ray et al., 2008). Further, even the presentation of angry faces (or voices) has been used to study anger, especially when considering its neural correlates (d'Alfonso et al., 2000; Sorella et al., 2021).

However, all of these paradigms show some limitations. At first, the presentation of an angry face doesn't necessarily elicit the experience of anger in the participant. Indeed, as it will be explored in chapter 2, they are two different processes.

Secondly, many of the experiments involving an insult or a critique do not allow for repetition of the trial/situation, excluding the possibility of repetitive measure. On the other hand, other tasks that used trials' repetition involve the elicitation of anger as a secondary feature; indeed, they mainly rely on a different task such as a game or a provocation that can produce a confounding factor in the measurement of the subsequent anger, especially when the neural correlates of this emotion are under investigation.

Finally, imagery techniques produce variable and not controllable stimuli across participants.

Therefore, in this thesis a new paradigm will be presented, with the attempt to overcome the described limitations. In particular, this paradigm will be used to evaluate the regulation of anger.

Anger Regulation

While having an adaptive role in physical survival (Cannon, 1929) and in social relations (Novaco, 1976), the importance of anger (down) regulation is unequivocal. Unbalanced and excessive anger is prevalent in numerous psychopathological conditions, such as in Post-Traumatic Stress Disorder and various personality disorders (Novaco, 2010), as well as in other medical conditions, such as in cardiovascular disease (Williams, 2010) and chronic pain (Fernandez & Turk, 1995). However, also some regulation strategies can be dangerous. For example, over-controlled anger has been associated with depression and anxiety. Indeed, anger, and especially the way we manage our anger, can have a huge impact upon our ability to have happy lives. For these reasons, another aim of my doctorate project consists in studying emotion regulation of anger.

Gross (1998) defined emotion regulation as "the processes by which individuals influence which emotions they have, when they have them, and how they experience and express these emotions". It may be automatic or controlled, implicit or explicit and may modulate the emotion at any stage. The most investigated strategy is cognitive reappraisal, in which one changes or reinterprets how he thinks about the emotional situation. Another widely investigated strategy is suppression, which aims to inhibit the affective response and the consequent behaviors (Gross, 2014). Reappraisal seems to be more adaptive than suppression, since it has been shown to increase positive emotions (Cameron & Overall, 2018), while the use of suppression is more associated with psychopathology (Aldao et al., 2010). Accordingly, even studies on anger show that reappraisal seems to be more effective than suppression in diminishing the experienced emotion (Memedovic et al., 2010; Szasz et al., 2011), while the latter seems to be useless, leading to cognitive and social consequences (Chervonsky & Hunt, 2017). However, anger and its regulation are much less studied when compared to a general regulation of negative emotions (Gross, 1998b; Sheppes et al., 2011). In particular, no standardized study has been proposed to understand which stimuli can be used to evoke anger, and how to study its regulation and the possible outcomes of anger experience.

Aims and hypotheses

This thesis aims to better understand the neural and psychological mechanisms underlying anger and its regulation.

In the first study (Chapter 2) the specific aim is to summarize the literature evidence on the neural mechanisms of anger, in particular considering and distinguishing between the two main processes investigated in literature: the perception of an angry stimulus and the subjective experience of anger. In particular, I expect that while perceptual brain regions such as the amygdala would be associated with the former, the activity in areas linked to the subjective evaluation of the situation, such as the insula and the vIPFC, would be associated with the latter. Moreover, in order to understand whether there is a brain area responsible for a comprehension and conceptualization of anger independently from the process through which it is elicited (i.e. its perception or its experience), a conjunction analysis will be performed. Indeed, while different meta-analyses tried to summarize the processes linked to emotion perception or emotion experience, there is still no evidence on a possible evidence of a common brain area involved in both processes.

In Chapter 3 and Chapter 4, instead, the brain connectivity associated with individual differences in anger and its outcomes will be examined. In particular, in Chapter 3 a multivariate approach will be used to extract structural and functional brain networks, whose possible association with trait anger and anger control will be evaluated. In particular, the main hypothesis of this chapter is that a structural network would be associated with trait anger, given that it is a more stable individual difference related to the interpretation of external stimuli in the environment and the following elicitation of anger. On the other hand, since the control of anger is a less stable and improvable individual difference, I expect an association of this aspect with a functional network. In particular, the DMN seems to be involved in affective processes and control of the emotions especially in social contexts, when anger is usually elicited.

In Chapter 4, the individual differences in two different aspects of anger will be evaluated in relation to the frontal asymmetry hypothesis. Indeed, in the past higher left frontal versus right frontal activity has been associated with positive vs. negative emotions or approach vs. withdrawal behaviors. Since anger is a negative emotion, such as anxiety and sadness, but is characterized by an approach rather than a withdrawal motivation when compared to others, its study in the context of the frontal asymmetry hypothesis is crucial. In particular, I expect that the frontal asymmetry could be related to

an affective response, rather than a simple emotion or behavior. According to this hypothesis, I expect to find that left frontal connectivity will be associated with the externalization of anger (anger-out scale) while the right frontal connectivity will be associated with the internalization of anger (anger-in scale).

Finally, Chapter 5 and Chapter 6 will focus on the regulation of anger from a psychological perspective. In particular, two emotion regulation strategies will be evaluated: a cognitive strategy based on reappraisal and a behavioral strategy based on suppression. In particular, in Chapter 5 it will be evaluated an effect of the emotion intensity on the choice of a specific strategy that the person would apply in different simulated situations. According to the evidence on other emotions, the expectation is that when anger is more intense, it will lead to higher usage of suppression; instead, when more cognitive resources will be available, and so when anger intensity is lower, a higher probability of choosing reappraisal to regulate anger would be highlighted.

In Chapter 6 the effect of a mindfulness training on the regulation of anger will be investigated. According to the literature evidence, I expect that mindfulness can improve emotion regulation both through bottom-up and top-down mechanisms. Therefore, on one hand I expect that after mindfulness training the intensity of anger experienced in the same situation will be reduced, as an effect of a bottom-up mechanism. On the other hand, I expect that, after the mindfulness course, the usage of reappraisal would increase when compared to suppression, as an effect of a top-down mechanism. Finally, in the last chapter I will try to summarize the evidence evaluated in this thesis in order to integrate the different results.

Chapter 2

Study 1 - Common and specific neural features of the perception and the experience of anger: a Meta-analytic study¹

As outlined in chapter 1, the neural bases of anger are still under investigation. Even if some scholars tried to understand the neural mechanisms underlying this emotion, the literature still lacks of a comprehensive view. Indeed, different studies relied on extremely different paradigms. For example, some studies relies on social games in which the provocation can elicit a certain amount of anger; others relies on imagery techniques in which the experience of anger is recalled or induced through imagination; others simulate a provocation of the experimenter during a performance-based task. Finally, even the presentation of an angry stimulus, such as a face or a voice, was used to investigate the neural correlates of this emotion. However, it is evident that these processes are different, leading to heterogeneous results especially when considering fMRI evidence.

To solve this problem and to organize the literature evidence, in this chapter a meta-analysis on the neural correlates of anger was performed. The main analysis relies on the distinction of the two main kinds of mechanisms used to investigate this emotion: the perception of an angry stimulus and the elicitation of a subjective experience of anger. Moreover, not only separate analyses were performed, but also a conjunction analysis in order to identify a possible brain area that is responsible for a general understanding, or conceptualization, of anger independently from the process that can elicit this emotion in the brain. Finally, also secondary analyses were performed in order to understand further differences between tasks among the two main categories.

¹ This chapter has been adapted from Sorella et al., 2021

Introduction

Anger is a core emotional experience often aroused during interpersonal situations that leads people to suffer or perceive that they suffer a pain. (DiGiuseppe & Tafrate, 2007).

Although negative in valence, anger departs from other unpleasant emotions characterized by an avoidance inclination, as it is associated with an approach inclination (Berkowitz & Harmon-Jones, 2004) that leads us to respond to difficult situations in daily life. Anger can be elicited in different situations; for example, the presence of a threat (real or imagined), such as physical or psychological pain, can elicit the most basic form of anger as the instinctive survival response, which triggers the fight reaction of the fight-flight system. In interpersonal contexts, anger seems to be elicited by three specific situations: (1) goal obstruction, (2) the violation of rules, norms and promises, or (3) status and power derogation (Bies & Tripp, 2004; Aquino, Tripp, & Bies, 2006; Gilam and Handler, 2015).

Overall, anger can be considered a complex negative emotion that emerges from a conjunction of specific feelings, cognitions and physiological reactions associated with the urge to injure some target; then, these reactions are eventually further object of appraisal and higher order processes that can up-regulate or down-regulate the emotion (Berkowitz, 1990; Berkowitz & Harmon-Jones, 2004; Grecucci et. al. 2012).

In literature investigators that tried to study the neural bases of anger relied on different paradigms; although some interesting reviews tried to clarify this heterogeneity of studies (see for example Gilam and Hendler, 2015; Alia-Klein et al., 2019), the literature lacks a meta-analytic approach. Indeed, the majority of studies on the neural bases of anger relied on the presentation of angry stimuli, such as a face or a voice; on the other hand, interactive games and imagination have been used to elicit the experience of this emotion in participants (Gilam, 2015). As the author suggested, "perceiving anger in faces or voices is not necessarily experiencing anger though such stimuli may serve as a social signal of threat". However, when considering the neural bases of anger, the two concepts are often confused and not well distinguished in literature. For this reason, I decided to differentiate between these two main kinds of mechanisms involved in literature to study the neural correlates of anger: the perception of an angry stimulus, such as a face or a voice, and the experience of this emotion elicited throughout an imaginative paradigm or an interactive game (Gilam, 2015).

Anger perception (AP) has been investigated through the processing of a stimulus characterized by anger, such as a face or a voice. Angry faces can be categorized as "negative" or "threatening" stimuli that could elicit an aggressive or a withdrawal response after the attribution of hostile intentions to others (Penton-Voak et al. 2013; Springer et al., 2007). Interestingly, there seems to be some individual differences according to which an angry or hostile stimulus can be interpreted with an aggressive or a withdrawal response. In particular, according to the *hostile-attribution bias*, individuals characterized by higher levels of aggressiveness tend to attribute higher hostility to social stimuli (Nasby er al., 1980). Regardless of these individual differences in their interpretation, when angry faces are compared to neutral, happy and even fearful faces, they elicit a heightened startle response, suggesting a threatening categorical distinction associated with a defensive physiological activity and withdrawal response (Springer et al., 2007; Dunning et al., 2010).

Physiological activity during the perception of angry faces and voices also includes heightened heart rate acceleration, skin conductance response and forehead temperature (Dimberg, 1987; Aue et al., 2011; Banks et al., 2012).

From a neural point of view, the presentation of angry faces elicits neural activity in different regions of the lateral PFC, the entorhinal cortex and occipito-temporal areas (Lindquist et al., 2012).

Further, the superior temporal cortex is particularly involved in anger perception not only during the processing of social signals, such as an angry face, voice or gesture, but also during the interpretation of contextual information used to understand others' behaviors (Seok and Cheong, 2019; Baldwin, 1992; McArthur & Baron, 1983).

Further, the activity of the amygdala seems to be more controversial during anger perception: although its activation is much more related to fearful faces exposure, it has been found also after the presentation of angry faces, especially when considering idiosyncratic personality differences and arousal (Passamonti et al., 2008; Lindquist et al., 2012). In particular, angry faces seem to be interpreted as more provocative by individuals with higher levels of appetitive motivation, influencing the activity of the amygdala (Passamonti et al., 2008): increased amygdala activation was more characteristic of individuals with higher levels of "behavioral activation system", while individuals with higher levels of "behavioral activation system" showed increased activity in the dorsal anterior cingulate, a region involved in the perception of fear and threat (Beaver et al., 2008).

Interestingly, Buades-Rotger and colleagues (2016) showed that the STG mediates the relation between the amygdala reactivity and aggression after the presentation of an angry face. This could be linked to the higher hostility associated with other's intentions due to an angry facial expression. Lastly, the ventral prefrontal cortex, in particular when considering the right hemisphere, has been found to be responsible for the recognition and classification of emotional stimuli, including anger (Jastorff et al., 2015; Lieberman et al., 2007; Adolphs, 2002; Hornak et al., 1996; Blair et al., 1999).

On the other hand, the experience of anger is usually elicited in literature throughout an imaginative paradigm or an interactive game (Gilam, 2015). The first method consists in asking the participant to recall an autobiographical episode or to imagine a situation in which he or she experiences anger (Gilam and Hendler, 2015). The second method usually involves a social interaction with an opponent; for example, widely used paradigms consist in classic economic games such as the Ultimatum or the Dictator game (Guth et al., 1982; Sanfey et al., 2003; Grecucci et al., 2013a,b,c; 2015; Gilam et al., 2018; De Panfilis et al., 2019; Grecucci et al., 2020), usually based on unfair monetary offers; other kinds of paradigms involve games based on provocation (Taylor Aggression Paradigm, Taylor, 1967), or exclusion (Radke et al., 2018; Chester et al., 2018b; Dewall et al., 2011). Physiological activity during the experience of anger includes heightened heart rate, skin conductance responses, respiratory rate, and muscle activity that represent the arousal characteristic of this emotion (Potegal et al., 2010; Kreibig, 2010), allowing the individual to be ready to respond toward the cause of harm, according to the approach motivation underlying this emotion (Harmon-Jones, 2004). Regarding the neural bases of anger experience, on one hand, paradigms based on imagination of an experience characterized by anger showed brain activation in the PFC, the medial temporal lobe, the anterior insula, the orbitofrontal cortex, the IFG, the amygdala and the putamen/caudate (Denson et al., 2009; Blair, 2011; Fabiansson et al., 2012; Lindquist et al., 2012; Gilam and Handler, 2015). On the other hand, paradigms based on interpersonal games characterized by the elicitation of anger showed brain activation in dACC, insula, ventrolateral, dorsolateral and dorsomedial PFC, precuneus, temporal pole, TPJ, and visual regions including the FFG (Wagels et al., 2019; Weidler et al., 2019; Repple et al., 2017; Feng et al., 2015).

Of these brain activations, the ventral PFC cortex seems to play a key role in the regulation of anger, with a distinction between the ventrolateral and the ventromedial regions; while the former seems to

be responsible for selecting context-appropriate responses and inhibiting context-inappropriate responses, the latter seems to be responsible for a situational evaluation, especially when considering possible outcomes linked to the elicitation of anger (Gilam and Hendler, 2015; Ochsner and Gross, 2014).

On the contrary, the insula seems to be responsible for the subjective experience of anger. Indeed, its activity is not only linked to arousal and visceral sensations (Ochsner and Gross, 2014; Lindquist et al., 2012; Penfield and Faulk, 1955), but is also modulated by both up and down regulation of this emotion (Emmerling et al., 2016; Grecucci et al., 2012; 2013 a,b): its activity is decreased when anger is downregulated (Grecucci et al., 2013 b,c), while it is increased during angry retaliation and rumination (Denson et al., 2009; Emmerling et al., 2016). Since the insula is part of the salience network, probably involved in the detection of painful and emotional situations in life (Gilam and Hendler, 2015), it can represent the "core affect" of anger in the brain: the primary emotional reaction to a situation or event, characterized by a strong negative valence and high activation arousal (Russell, 2003; Wager and Barrett, 2017).

In particular, while the insula seems to be linked to the affective meaning of anger when considering emotional arousal, the ventral PFC is linked to the affective meaning of anger when considering the conceptual information about specific outcomes (Roy et al., 2012).

Then, the dACC seems to be associated with the control and modification of behavioral responses during challenging situations (Gasquoine, 2013), explaining its activation in both anger induction and aggression studies. Otherwise, mPFC, PCC, temporal poles, and the TPJ activity is related to the mentalizing system during self-generated or induced anger, reflecting the interpersonal nature of angering events (Denny et al. 2012). Indeed, it has been argued that in order to experience anger, humans need to attribute the intention to do harm to another person (Berkowitz and Harmon-Jones, 2004). This is in line with the fact that unfair offers proposed by a computer during interpersonal games (such as the TAP or the Ultimatum games) are less refused and activate less the bilateral anterior insula when compared to human unfair offers (Sanfey et al., 2003).

Finally, during the second phase of these interpersonal paradigms, it is usually possible to measure the aggressive behavior through refusals of unfair offers.

Thalamic, limbic and brainstem regions seem to reflect the activity of the threat detection network, with a critical role in reactive aggression (Siever, 2008). Further, aggression seems to be related also

to vmPFC, whose activity (in particular in the OFC) is negatively correlated with aggressive responses (Beyer, 2015), while more dorsal areas of the ACC positively correlated with aggressive behavior. In addition, it is also possible to study how emotion regulation influences the consequent behavior of accepting the offer and financially benefit from them, instead of aggressively react, identifying brain areas related to emotion regulation. For example, the reappraisal regulation during unfair offers involves the anterior region of the dIPFC (Grecucci & Sanfey, 2013; Grecucci et al., 2013).

To conclude, taking into account the relation between anger perception and anger experience can be particularly interesting. Indeed, in the previous studies on anger perception, the emotion category is stereotypically represented "within" the stimuli, while in anger experience studies the emotion is not represented by the stimulus itself but it is actually evoked within the participant. Interestingly, it has been proposed that language and conceptualization can play a key role in the categorization of the emotion, during both its perception and experience. This process can be more or less explicit, according to different situations and points of view; indeed, according to some models emotion can simply refer to the explicitation of the emotion category; otherwise, according to other models, emotions are constructed through implicit categorizations, which involve the conceptualization of individual sensations from the world or the body (Fugate and Barrett, 2014).

For example, Berkowitz (1990) proposed a cognitive-neoassociationistic model to explain how the initial negative affect characterizing an aversive occurrence can be linked to particular thoughts, memories and physiological reactions associated with this emotion. Indeed, anger does not emerge from specific circumstances but from the way that individuals subjectively evaluate situations or events. This is conceptualized also in the appraisal theory, according to which this process involves a cognitive evaluation that can determine the elicitation and the differentiation of emotions, considering the relevant life situations in a particular way based on past experiences, personality, and current motivations (Wranik & Scherer, 2010). Regardeless of the theory considered and of the modality (i.e. perception or experience), it is evident that this process of conceptualization is shared and fundamental to detect and interpret sensory information coming from the self or from others, leading to the categorization of a specific emotion, such as anger. To note, with the term "conceptualization" I do not mean a specific and complex mechanism, but a simple "understanding" of the affective

experience that is necessary to consciuously understand what is happening in the self or in others during the presence of anger. Then, this process of understanding or conceptualization can lead to further processes, such as empathy, emotional reactions, appraisals, ...

Nevertheless, this process of conceptualization can represent the common mechanism for understanding the affective process involved during both anger perception and experience (for a review on this topic see Fugate and Barrett, 2014). Indeed, there is evidence on shared mechanisms between self and other affective processes (Decety and Sommerville, 2003; de Vignemont and Singer, 2006; Keysers and Gazzola, 2006), and some meta-analytic approaches have started to investigate the neural bases of these common mechanisms through conjunction analyses (see for example Lamm et al., 2010).

Therefore, in this study I propose a model according to which there can be differences during anger processing, that emerge from the specific process through which anger is elaborated (its perception or its experience), but also a common higher process, characteristic of categorization and appraisal, that is shared and necessary to evaluate the situation, understand the emotion and act on the basis of the context of the emotional situation.

Indeed, the previous models as well as the constructionist one assign a causal role to the conceptualization of the emotion: according to Barrett (2006), "people experience an emotion when they conceptualize an instance of affective feeling. In this view, the experience of emotion is an act of categorization, guided by embodied knowledge about emotion. [...] We experience an instance of emotion in ourselves, or see it in others, when we conceptualize an ongoing, basic affective state via the process of categorization ".

Thus, besides looking for distinct and specific mechanisms for anger perception and anger experience, I also expect to find common regions to capture the aspects of categorization, necessary to understand anger.

Methods

In order to find studies investigating the neural underpinnings of anger, we conducted a research on PubMed (<u>https://www.ncbi.nlm.nih.gov/pubmed/</u>) using the terms ((anger) OR(angry) OR

(basic emotions) OR (frustration) OR (aggression)) AND ((fMRI) OR (PET) OR (positron emission tomography) OR (functional magnetic resonance imaging) OR (functional MRI)), and setting a range of dates between January 1st 1995 and January 28th 2019. This research identified 1839 studies.

Subsequently, we refined our research by applying the following criteria:

1) paper originally published in English;

2) fMRI or PET studies including task-related whole brain analyses. Studies reporting region of interest (ROI) analyses, resting-state fMRI analyses, diffusion tensor imaging (DTI) or voxel-based morphometry (VBM) were excluded;

3) participants were healthy adults: in case of studies involving neurological or psychiatric patients, children or adolescents, we considered only contrasts involving healthy controls, if reported;

4) Studies investigating the neural underpinnings of anger were included into two different sets. Specifically, we included studies contrasting angry stimuli vs. neutral ones (faces and voices) or the induction of an angry/frustrated condition vs. neutral condition. Studies failing to report this information were excluded.

This method allowed us to identify 35 studies for the anger perception set (297 foci, 778 total subjects, 430M, mean age 26.23±8.97) and 26 studies for the anger experience set (310 foci, 724 total subjects, 407M, mean age 24.88±6.90). The most used paradigm in the anger perception condition was the presentation of emotional vs. neutral stimuli, in a visual condition (angry vs. neutral faces) or in an auditory one (angry vs. neutral prosody).

Therefore, besides the smaller number of studies, as additional analyses we included also the separate conditions when considering anger perception from a visual² (222 foci, 25 experiments, 599 subjects) versus an auditory³ (75 foci, 10 experiments, 174 subjects) modality.

In the anger experience condition, the most used paradigms were different interpersonal games with an opponent (Taylor Aggression Paradigm, Ultimatum Game, Cyberball Paradigm) or the imagination of a situation characterized by anger (with scripts, vignettes or recollection of autobiographical memories).

² Anger perception – faces included: Rymarczyk , 2018; Chan , 2016; Mccloskey ,2016; Ihme, 2014; Beaver, 2008; Wheaton ,2014; Pawliczek ,2013; Passamonti ,2012; Jehna ,2011; 2011b; Hurlemann ,2008; Lee,2006; Rauch ,2007; Britton ,2006; Sato , 2004; Chakrabarti ,2006; Kilts ,2003; Sprengelmeyer ,1998; Lassalle ,2017; Morawetz ,2016; Wabnegger ,2015; Weisenbach ,2012; Jollant ,2008; Chiao ,2008; Blair , 1999.

³ Anger perception – voices included: Sander,2005; Grandjean,2005; Ceravolo, 2016; Smith, 2015; Fruhholz, 2014; Maurage, 2013; Ethofer,2009; Mothes-Lash,2011; Castelluccio,2015; Mitchell, 2016.

Therefore, besides the smaller number of studies, as additional analyses we included also the separate conditions when anger is elicited during interpersonal games⁴ (174 foci, 16 experiments, 521 subjects) or during imaginative paradigms⁵ (104 foci, 8 experiments, 139 subjects).

Finally, among the interpersonal games set of studies, 11 of them⁶ (88 foci, 11 experiments, 318 subjects) also investigated an aggressive reaction following provocation.

⁴ Anger experience – games included: Weidler,2019; Chester,2018; Repple, 2018; Repple,2017; Skibsted,2017; Buades,2017; Vieira, 2013; Dougherty,2004; Lotze, 2006; Radke, 2018; Chester, 2018; Dewall, 2012; Gilam,2018; Emmerling,2016; Dambacher, 2015; Kramer, 2007.

⁵ Anger experience – imagine included: Dougherty,2004; Oaten,2018; Minamoto,2014; Marci,2007; Damasio,2000; Dougherty,1999; Kimbrell,1999; Pietrini, 2000.

⁶ Anger experience - aggression included: Weidler, 2019; Repple, 2018; 2017; Skibsted, 2017; Buades, 2017; Emmerling, 2016; Dambacher, 2015; Kramer, 2007; Lotze, 2006; Pietrini, 2000; Chester, 2018.

Table 2.1. Overview of the 35 studies on anger perception and the 26 studies on anger experience included in the metaanalysis. Adapted from Sorella et al., 2021.

| Anger Perc | ception Studies | | | | | |
|------------|------------------|-----------------|--------------|-------------|-----------------|---------------|
| N° paper | Author | Subjects | Age | fMRI or PET | Stimuli | Contrast |
| 1 | Rymarczyk,2018 | 46 (21F, 26M) | 23.7+-2.5 | fMRI | face perception | angry>neutral |
| 2 | Lassalle,2017 | 21M | 19.70+-7.74 | fMRI | face perception | angry>neutral |
| 3 | Chan, 2016 | 54 hc (38.9% M) | 23+-2.4 | fMRI | face perception | angry>neutral |
| 4 | Morawetz, 2016 | 60(30F) | 30.48+-11.10 | fMRI | face perception | angry>neutral |
| 5 | Mccloskey, 2016 | 20(12M) | 32.8 | fMRI | face perception | angry>neutral |
| 6 | Wabnegger, 2015 | 22 (11M) | 51.8+-9.8 | fMRI | face perception | angry>neutral |
| 7 | Wheaton, 2014 | 24 (54.2%F) | 25+-5.6 | fMRI | face perception | angry>neutral |
| 8 | Ihme, 2014 | 48 (23F) | 24+-3 | fMRI | face perception | angry>neutral |
| 9 | Pawliczek, 2013 | 33M | 22.3+-2 | fMRI | face perception | anger>neutral |
| 10 | Weisenbach, 2012 | 17M | 31.2+-14.2 | fMRI | face perception | anger>neutral |
| 11 | Passamonti, 2012 | 30(17F) | 25.1+-3.2 | fMRI | face perception | angry>neutral |
| 12 | Jehna, 2011 | 15 (5M) | 30.3+-10.6 | fMRI | face perception | angry>neutral |
| 13 | Jehna, 2011b | 30(21F) | 36.3 ± 14.3 | fMRI | face perception | angry>neutral |

| 14 | Chakrabarti,2006 | 26(13M) | 23.4+-4.23 | fMRI | face perception | angry>neutral |
|----|--------------------|----------|-------------------------|------|------------------|---------------|
| 15 | Hurlemann, 2008 | 14(7) | 25.4+-2.4 | fMRI | face perception | anger>neutral |
| 16 | Chiao, 2008 | 14M | students | fMRI | face perception | angry>neutral |
| 17 | Jollant, 2008 | 16M | 34.3+-9.8 | fMRI | face perception | angry>neutral |
| 18 | Beaver, 2008 | 22(13F) | 26.2+-7.6 | fMRI | face perception | angry>neutral |
| 19 | Lee,2006 | 18(9F) | 26 | fMRI | face perception | angry>neutral |
| 20 | Rauch,2007 | 20(10M): | 25.3+-2.1; 24.5+-3.1 | fMRI | face perception | angry>neutral |
| 21 | Britton,2006 | 12(6F) | 21.4+-2.2 | fMRI | face perception | angry>neutral |
| 22 | Sato,2004 | 10(5F) | 24.4+-7.8 | fMRI | face perception | anger>neutral |
| 23 | Kilts, 2003 | 13(9M) | 24.5(22-26 range) | PET | face perception | angry>neutral |
| 24 | Blair,1999 | 13M | 25.3 | PET | face perception | angry>neutral |
| 25 | Sprengelmeyer,1998 | 6(2M) | 23.5+-1.3 | fMRI | face perception | angry>neutral |
| 26 | Castelluccio, 2015 | 8(3M) | 22.68+-3.84 | fMRI | voice perception | angry>neutral |
| 27 | Mitchell, 2016 | 27(14F) | 21.5+-3.89 | fMRI | voice perception | angry>neutral |
| 28 | Ceravolo, 2016 | 17(8M) | 24.29+-4.87 | fMRI | voice perception | angry>neutral |
| 29 | Smith, 2015 | 17(10M) | 26.5+-5.95 | fMRI | voice perception | angry>neutral |

| 30 | Fruhholz, 2014 | 15(8F) | 23.67+-3.5 | fMRI | voice perception | angry>neutral |
|----|--------------------|---------|------------|------|------------------|---------------|
| 31 | Maurage, 2013 | 12 (5F) | 23.4+-4.21 | fMRI | voice perception | angry>neutral |
| 32 | Mothes-Lasch, 2011 | 24(16F) | 22.7+-1.49 | fMRI | voice perception | angry>neutral |
| 33 | Ethofer, 2009 | 24(12M) | 26.3 | fMRI | voice perception | angry>neutral |
| 34 | Sander, 2005 | 15(7M) | 24.4+-4.6 | fMRI | voice perception | angry>neutral |
| 35 | Grandjean,2005 | 15(7F) | | fMRI | voice perception | angry>neutral |

| Anger Experi | ence Studies | | | | |
|--------------|--------------|----------|------------------------------|--|---|
| N°paper | Author, year | Subjects | Age | Task and Stimuli | Contrast |
| 1 | Weidler,2019 | 52M | 24.86+-3.92 | Taylor Aggression Paradigm (modified) | Parametric modulation : provocation intensity |
| 2 | Gilam,2018 | 25(15F) | 26.16+-3.63 | Anger Infused Ultimatum Game | Unfair>Fair offers (High provocation > Low provocation) |
| 3 | Repple, 2018 | 42(22M) | F24.77 (2.8); M27.45(9.3) | Taylor Aggression Paradigm | High provocation > Low provocation |

| 4 | Chester,2018 | 61 | 18-22 | Taylor | High provocation > |
|----|-----------------|-----------|-------------|-------------------|----------------------|
| | | (27.87%M) | | Aggression | Low provocation |
| | | | | Paradigm | |
| | | | | 6 | |
| 5 | Repple, 2017 | 29M | 23.6+-3.2 | Taylor | Aggression after |
| | | | | Aggression | high provocation > |
| | | | | Paradigm | aggression after low |
| | | | | | provocation |
| 6 | Skibsted, 2017 | 19 (8M) | 24.6+-2.9 | Point | Provocation event > |
| | | | | subtraction | Monetary Response |
| | | | | aggression | (High provocation > |
| | | | | paradigm | Low provocation) |
| 7 | Buades-Rotger, | 36F | 22+-4 | provocative | High provocation > |
| | 2017 | | | fight or avoid | Low provocation |
| | | | | task | |
| 8 | Emmerling, 2016 | 15 | 22.33+-2.35 | provoking, | High provocation |
| | | | | aggressive | and aggression > |
| | | | | reaction, | Low provocation |
| | | | | retailation (340) | |
| | | | | | |
| 9 | Dambacher, 2014 | 15M | 22.33+-2.35 | Taylor | Provocation > No |
| | | | | Aggression | provocation |
| | | | | Paradigm | |
| | | | | (modified) | |
| 10 | Minamoto, 2014 | 35(11F) | 23.05+-2.53 | frustration (ego | Ego blocking > |
| | | | | blocking) | Neutral condition |
| | | | | | |
| | | | | | |
| | | | | | |

| 11 | Pawliczek, 2013 | 40M | 22.4+-2.2 | frustration | Unsolvable > Solvable conditions |
|----|-----------------|---------------------------------|--|----------------------------------|--|
| 12 | Vieira,2013 | 17 (12F) | 21.24+-2.05 | Ultimatum Game | Linear regression: Unfair > Fair |
| 13 | Lotze,2007 | 16M | 28.6+-6.5 | provocation | Parametric: receiving aversive stimuli (provocation) |
| 14 | Kramer,2007 | 15(11F/20, 5 sbj removed) | 22.9+-2.2 | Taylor Aggression Paradigm | High provocation > Low provocation |
| 15 | Dougherty,2004 | 10 (5F) | 33.90+- 11.85 | Autobiographic al scripts | Anger>Neutral |
| 16 | Abler,2005 | 12 (6F) | 21-33 | frustration | Frustration > No frustration |
| 17 | Radke,2018 | 80(40F) | males: M = 24.38 years, SD = 3.37, females: M = 24.69 years, SD = 3.85 | Cyberball task | social exclusion>inclusion |
| 18 | Chester,2018 | 60(38F) | 20.28+-2.77 | Cyberball task | Reject>Accept (High provocation > Low provocation) |

| 19 | Dewall,2011 | 25(16F) | | Cyberball task | Exclusion > Inclusion (High provocation > Low provocation) |
|----|----------------|----------|----------------------------------|--|---|
| 20 | Park, 2016 | 16M | 50.06+-6.10 (31-61) | induction: audio-visual film clips | Anger > Neutral conditions |
| 21 | Oaten, 2018 | 20(9M) | 22.2+-2.8 | Vignettes | Anger > Neutral conditions |
| 22 | Pietrini, 2000 | 15 (8M) | 22+-2 | Imagery | Aggression>Neutral |
| 23 | Damasio, 2000 | 11F+ 12M | 24-42 | imagery | Anger > Neutral conditions |
| 24 | Dougherty,1999 | 8M | 25+-4.4 | imagery | Anger > Neutral conditions |
| 25 | Marci, 2007 | 10 (5M) | 33.9+-11.9 | autobiographica l memory | Anger > Neutral conditions |
| 26 | Kimbrell,1999 | 8f+10M | 31.25+-8.9F; 34.75+- 11.6M | recall | Anger > Neutral conditions |

Statistical analyses

Analyses were conducted using the software GingerALE v2.4.6 (http://brainmap.org/). The activation likelihood estimation method, implemented in the software (Eickhoff et al., 2009; 2012; Turkeltaub et al., 2012), uses probability theory to define the spatial convergence of foci reported in the selected studies. Specifically, a Gaussian blur with an empirically-derived full-width half maximum (dependent on the number of participants included in the study) is applied to each focus from a single

study. Then, all the foci from a single study are represented in a modeled activation map and voxelwise ALE scores are computed combining all the individual maps. To distinguish between true convergence of foci from random noise a permutation test is applied. We adopted the method described by Turkeltaub et al. (2012) that minimizes within-study effects, preventing the summation of foci of the same experiment that are placed close to each other. For each set of studies we performed the meta-analysis applying a cluster-level family-wise error correction using an uncorrected *p*-value < .001 for individual voxels, 1000 permutations and a cluster-level threshold of *p* < .05, as suggested by Eickhoff and collaborators (2016).

In addition, we performed contrast analyses to compare the two different sets of studies, in order to evaluate similarities (conjunction) characterizing the perception and the experience of anger. Contrast analyses were performed subtracting one of the outputs of the previous analyses (ALE images) to the other (i.e., Perception vs. Experience, Experience vs. Perception). Since the two sets of studies differ in the sample size, GingerALE software computes a simulation of data randomly pooling the original data and then creating two new sets of the same size of the original datasets. For each new dataset, an ALE image is created and then subtracted to the other. These simulated images are compared with the real observed data. After 1000 permutations, a voxelwise P-value image reveals for each voxel, where the real data is located in the distribution of all the possible values (for that specific voxel). Values are converted into z-scores. Contrast analyses results are presented with a threshold of p < .001 uncorrected and a cluster size > 200 mm³, since input data for these contast analyses were already corrected for multiple comparsons, as in previous studies (Eickoff et al., 2012, Laird et al., 2005; Zmigrod et al., 2016). Results are visualized using Mango (http://ric.uthscsa.edu/mango/mango.html).

Results

Anger Perception

The meta-analysis on anger perception revealed four significant clusters (See Figure 2.1 and Table 2.2). Two clusters were located bilaterally in the amygdala and in the left rhinal cortex, while the other

two were located in the right hemisphere at the level of the inferior and the lateral orbito-frontal gyri and the superior temporal gyrus.

In particular, the visual perception of anger revealed four significant clusters at the level of the left amygdala and insula, right fusiform gyrus, right amygdala and right middle occipital gyrus. On the other hand, the auditory perception of anger revealed four significant clusters at the level of the left superior and transverse temporal gyrus, the right inferior frontal gyrus, the right caudate and the right superior temporal gyrus.

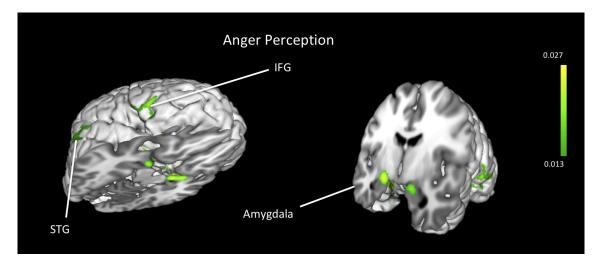


Figure 2.1 The neural bases of anger perception. The meta-analysis on anger perception (the perception of angry faces or voices) shows brain activity in the bilateral amygdala, the right superior temporal gyrus and the right inferior frontal gyrus. Adapted from Sorella et al., 2021.

| Analysis | Cluster | x | X | <u>z</u> | ALE | Brodmann | Label (Nearest Gray Matter within 5mm) |
|------------------|---------|-----|-----|----------|-------|----------|--|
| Anger Perception | 1 | -18 | -8 | -10 | 0.036 | | Left Amygdala |
| | 1 | -24 | -2 | -10 | 0.032 | | Left Amygdala |
| | 1 | -30 | 8 | -12 | 0.017 | 13 | Left Inferior Frontal Gyrus |
| | 2 | 58 | -30 | 10 | 0.025 | 42 | Right Superior Temporal Gyrus |
| | 2 | 48 | -36 | 4 | 0.017 | 22 | Right Superior Temporal Gyrus |
| | 3 | 48 | 26 | 8 | 0.029 | 45 | Right Inferior Frontal Gyrus |
| | 4 | 20 | -4 | -14 | 0.024 | | Right Amygdala |

 Table. 2.2 The neural bases of anger perception.
 Adapted from Sorella et al., 2021.

Anger Experience

The meta-analysis on anger experience revealed two significant clusters (See Figure 2.2 and Table 2.3). These clusters were located bilaterally at the level of the anterior insula and the lateral orbitofrontal cortex, but the one on the right hemisphere included also the right inferior frontal gyrus.

In particular, the elicitation of anger through interpersonal games revealed six significant clusters respectively located in the right inferior frontal gyrus and insula, left insula, right cingulate gyrus, left insula, right medial frontal gyrus and thalamus. The elicitation of anger through imagination revealed one significant cluster in the right superior and middle temporal gyrus.

Finally, as an extra analysis we considered the aggressive response in interpersonal games. This revealed activity in five clusters (uncorrected p<0.001) respectively located in the left postcentral gyrus, the anterior cingulate, the right temporo-parietal junction, the left putamen and the right anterior insula. However, when correcting at a cluster-level threshold of 0.05 (as the previous analyses), only the left postcentral gyrus remained significant.

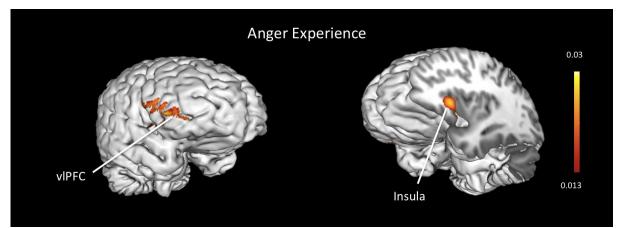


Figure 2.2 The neural bases of anger experience. The meta-analysis on anger experience (elicited through imagination or interpersonal games) shows brain activity in the bilateral ventrolateral prefrontal cortex and bilateral anterior insula. Adapted from Sorella et al., 2021.

| | | ~ | · | ~ | | | |
|------------------|---|-----|----|----|-------|----|--|
| | | | | | | | |
| Anger Experience | 1 | -32 | 22 | 2 | 0.027 | 13 | Left Insula |
| | 1 | -40 | 24 | 2 | 0.024 | 47 | Left Inferior Frontal Gyrus, lateral Orbitofrontal Gyrus |
| | 2 | 40 | 28 | 4 | 0.028 | 13 | Right Insula |
| | 2 | 44 | 18 | 12 | 0.019 | 45 | Right Inferior Frontal Gyrus, lateral Orbitofrontal Gyrus |
| | 2 | 38 | 12 | 10 | 0.017 | 13 | Right Insula |

 Table. 2.3 The neural bases of ancer experience. Adapted from Sorella et al.. 2021.

 Analysis
 Cluster
 X
 X
 Z
 ALE
 Brodmann
 Label (Nearest Gray Matter within 5mm)

Contrast

The conjunction analysis (see Figure 2.3 and Table 2.4) showed that both anger experience and anger perception share the activation of one cluster located within the right inferior frontal gyrus, surrounding the horizontal ramus.

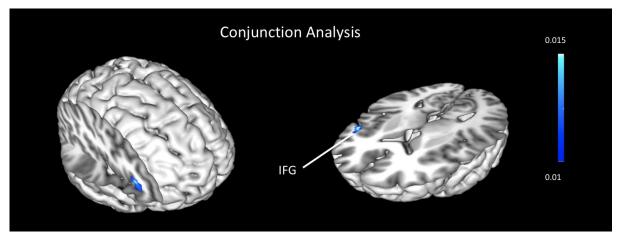


Figure 2.3 The neural bases of anger perception and experience. The meta-analysis on the conjunction between anger perception and experience shows brain activity in the right inferior frontal gyrus. Adapted from Sorella et al., 2021.

| Table. 2.4 Th Analysis | | ral bas ^{Cluster} | es of a | anger po ¥ | ercept Z | ALE | Brodmann | Adapted from Sorella et al., 2021. Label (Nearest Gray Matter within 5mm) |
|---------------------------|------|-------------------------------|---------|---------------|-------------|-------|----------|--|
| Conjunct (Perceptio | n & | 1 | 46 | 22 | 10 | 0.018 | 45 | Right Inferior Frontal Gyrus |
| Experien | ice) | 1 | 44 | 26 | 4 | 0.017 | 13 | Right Inferior Frontal Gyrus |

Discussion

The current meta-analysis aims to clarify the role of different brain regions that have been linked to anger in literature. Indeed even if anger is a primary emotion universally experienced, it has been investigated with different experimental paradigms that sometimes did not lead to similar results. Actually, some experiments studied the effects of viewing or hearing angry stimuli (such as faces or voices), while others tried to elicit anger as an experienced emotion; for example, social interactive games with an opponent are widely used paradigms to elicit anger, due to the proposal of an unfair offer, an insult or a social exclusion. Otherwise, other paradigms involve the elicitation of anger through the imagination or the retrieval of autobiographical episodes characterized by this emotion (Gilam, 2015).

Given the different paradigms in literature, two separate ALE meta-analyses on anger perception and anger experience were performed, in order to find quantitative evidence of their specific neural bases. Nevertheless, beside the distinct processes, both anger perception and anger experience may rely on a common mechanism underlying the conceptualization of this emotion (Barrett et al., 2006). Therefore, we also performed a conjunction analysis to identify the possible brain areas that are involved during both the perception and the experience of anger. Finally, we performed secondary analyses on the specific different paradigms used in the perception and in the experience of anger, and the possible aggressive response that follows this second kind of experiment.

Anger perception results show activation in the bilateral amygdala, in the left rhinal cortex, in the right ventrolateral PFC and the right superior temporal gyrus. While temporal areas have been linked to emotion detection, such as the detection of an angry movement, more frontal areas such as the inferior frontal gyrus have been linked to emotion categorization (Jastorff et al., 2016). Instead, the role of the amygdala is more ambivalent. The amygdala is associated with the perception of emotional stimuli, such as fearful faces. However, it has been found an activation of the amygdala also after the presentation of angry faces, when considering personality differences and arousal (Passamonti et al., 2008; Lindquist et al., 2012). In particular, the amygdala seems to be involved in the perception of angre by participants with high levels of appetitive motivation (Beaver et al., 2008).

Therefore, it may depend on how an angry face is considered as a provocative or a threatening stimulus (Öhman, 2002), and this could depend on personality traits that should be taken into account in future studies.

As expected, ventral PFC activity also emerged, probably related to a more conscious recognition, understanding and categorization of the perceived emotion (Jastorff et al., 2015; Lieberman et al., 2007; Adolphs, 2002; Hornak et al., 1996; Blair et al., 1999).

The meta-analysis on anger experience, instead, shows bilateral activation of the ventrolateral PFC and the anterior insula.

The anterior insula is associated with core affect, such as when motivational states associated with subjective feelings and goals are elicited (Wager & Barrett, 2017). In addition, its activity correlates with the perceived ability to reappraise the emotion after interpersonal provocation (Grecucci et al., 2013). Therefore, its function when anger is aroused can be traced to the affective assessment of motivational relevance and potential outcomes, by increasing this emotion as the subjective relevance of the situation increases, or by decreasing it when anger-regulation is needed. Indeed, the insula is an important area of present affective awareness, integrating signals between bottom-up interoceptive and top-down predictive mechanisms (Gu et al., 2013). Therefore, the function of the insula can be related to the core affect of the emotion (Russell, 2003; Lindquist et al., 2012; Wager and Barrett, 2017).

On the other hand, the inferior frontal gyrus has been linked to the control of the emotional experience; in particular, while the left IFG seems to control the impact of emotion on goal-directed behavior, the right IFG seems more involved in the control of the subjective feelings (Dolcos et al., 2006) and in the processing of emotional stimuli (Naamura et al., 1999). Furthermore, the vIPFC seems to play a key role in both the generation and the regulation of emotions, probably modulating the meaning of the emotional experience relying on processes of appraisal and/or reappraisal (Wager et al., 2008). Indeed, this area has been found to be involved not only in anger rumination (Denson et al., 2009; Fabiansson et al., 2012) and in anger experience (Tonnaer et al., 2017), but also in the inhibition and regulation of emotions (Aron et al., 2014; Wager et al., 2008; Chester et al., 2018b).

Finally, some brain regions seem to be involved in both anger perception and experience, such as the ventrolateral PFC (Potegal et al., 2010). In 1907, it was suggested that seeing an emotional face in others triggers a similar facial expression in the observer, as an effect of facial expressions. Thus, feelings related to one's own face may trigger the experience of the same feelings in the observer. Also according to James (1884), it could be that this sharing of perceived and experienced emotions is necessary for emotional understanding and empathy processes (Jabbi and Keysers, 2008).

Accordingly, the right inferior frontal gyrus emerged in the conjunction analysis as the only area that is activated in both anger perception and anger experience. Therefore, we can hypothesize that this brain region could be responsible for a higher conceptualization of anger and of its meaning in the situation, needed in order to decide what to do during both the perception and the experience of anger.

However, past neuroimaging studies and meta-analyses on emotions focused on the perception of emotional stimuli (Fusar-Poli et al., 2009) or on the experience of the induced emotions (Kirby et al., 2015), without making comparisons between the two. A key question of this chapter is: *do they share some mechanisms*? Understanding whether emotion perception and emotion experience share some mechanisms at a brain level, is of fundamental importance for advancing knowledge on affective processes.

For the first time, we aim to offer a more complete view of the neurological studies on anger by analyzing anger perception and anger experience in order to detect not only differences, but especially possible similarities. Accordingly, the conjunction analysis showed that the right inferior frontal gyrus is involved during both anger perception and anger experience.

Indeed, both categorization of the perceived emotional stimuli (Cunningham et al., 2003; Nomura et al., 2003; Lieberman et al., 2007) and appraisal or reappraisal of the experienced emotion (Grecucci et al., 2013b;c; Buhle et al., 2013) elicit brain activity in the right IFG; accordingly, it has been proposed that "it is possible that reappraisal and affect labeling rely on some of the same neural machinery, as reappraisal typically engages propositional thought about emotional stimuli" (Lieberman et al., 2007).

Further, the rIFG has been linked to emotional labeling (Lieberman et al., 2007; 2011), reappraisal (Grecucci et al., 2013a,b,c) and ruminative processes (Fabiansson et al., 2012; Gilam et al., 2017).

Therefore, I propose that the rIFG might be responsible for a first linguistic conceptualization of this emotion (perceived or experienced) needed to understand the bottom-up sensory information.

Barrett (2006), indeed, wrote: "People experience an emotion when they conceptualize an instance of affective feeling. In this view, the experience of emotion is an act of categorization, guided by embodied knowledge about emotion. [...] We experience an instance of emotion in ourselves, or see it in others, when we conceptualize an ongoing, basic affective state via the process of categorization".

This can lead to the following modulation of cognition (e.g. reappraisal or rumination) or behavior (e.g. inhibition).

Finally, another meta-analysis on different emotions found that all of them showed activation in the right IFG, suggesting a possible involvement of affective conceptualization, or more in general an interaction of higher cognitive and affective functions in this brain area (Kirby et al., 2015). Future studies are needed to explore the role of this area in other emotions, considering their perception and their experience at the same time. Here, I hypothesize that this area would allow what was defined as "anger conceptualization", referring to different processes such as anger labeling, needed to recognize the specific perceived emotion, and appraisal, needed to understand the emotional context of the experience situation.

Aggression

To conclude, on the basis of these results and of the reviewed literature, I propose a model on the brain mechanisms characterizing anger.

At first, the perception of a triggering stimulus evokes neural activity in perceptual areas such as the amygdala, whose response is associated with salience (Lindquist et al., 2012), the STG, involved in stimulus processing (Potegal et al., 2010), and the right ventro-lateral PFC, involved not only in the perception of emotional stimuli, but also in its categorization (Lieberman et al., 2007); this would allow the conscious perception of the provoking situation. Then, the experience of anger shows activation in the insula and in the ventrolateral PFC, bilaterally. This activity, especially regarding the frontal asymmetry in the lateral PFC, could involve an evaluation of the possible outcomes of approach vs. avoide the situation (Harmon-Jones, 2004; Lacey et al., 2020), besides the conscious appraisal of the emotion (Wager et al., 2008). The conjunction analysis shows a common activation between anger

perception and anger experience in the right ventro-lateral PFC. We can hypothesize that this area would allow a conceptualization of anger in both perception and experience situations.

Finally, even with a few studies and an uncorrected threshold, we performed an analysis on aggression that showed brain activity in the cingulate, the insula and the inferior parietal cortex. Interestingly, no frontal activity emerged during aggression. We think that the reason would be that aggression impulses and anger originate in perceptual areas, during the first phases of provocation, and then PFC activity would allow the eventual evaluation and regulation of behavior. This is coherent with the hypothesis of a "low road" of anger that does not necessarily involve higher cognitions (Alia-Klein et al., 2020), since the initial appraisal of anger in the temporal lobe can induce angry/aggressive acts even without passage through the frontal lobe, especially when provocation leads to a reactive immediate response. Indeed, the orbitofrontal cortex seems to integrate anger-provoking perceptions from temporal input, and to exert inhibitory control of aggression; actually, reductions of OFC output and frontal dysfunction result in unregulated and disinhibited aggression (Potegal and Stemmler, 2010). Further, it has been found that both temporal and frontal damage can lead to anger expression and aggressivity; however, while temporal involvement leads to unwarred and poorly directed anger, frontal involvement can lead to directed responses toward the source (Potegal et al., 2010).

Further, posterior cingulate and insula activity have been found to increase during the up-regulation of anger (Grecucci, 2013), and in association with the inferior parietal cortex, these brain areas are associated to agency and the self in interaction with the external world, blame and punishment (Young et al., Krueger & Hoffman; Farrer & Frith).

Conclusions

These data suggest that while the perception of the stimulus and the impulse of reactive aggression are linked to perceptual and interoceptive areas such as the amygdala, the cingulate and the insula, the evaluation and the regulation of the situation and the possible outcomes rely more on the PFC. However, literature evidence on the regulation of anger is still at the beginning and a meta-analytic approach was not applicable. In addition, individual differences in anger and its outcomes have also been poorly investigated. To overcome these limitations of the literature, the next chapter will explore

the individual differences related to anger, in particular considering trait anger and the control of this emotion.

Chapter 3

Study 2 - Trait anger and its control are differently coded in the brain: Structural and Resting-state evidence⁷

Emotion regulation is crucial to people's daily life, since its deficits can be problematic. Indeed, anger dysregulation leads to psychological, physical and relational problems, making the study of anger the focus of several neuroimaging studies. However, there is still poor evidence when anger and its control are considered as individual differences and personality traits rather than taskrelated measures.

Therefore, while in the previous chapter the neural bases of anger were sum up relying on a meta-analysis of task-based fMRI paradigms, in this chapter the aim is to understand the neural networks underlying the individual differences related to anger. Specifically, findings on the relationship between structural and functional neural networks on the one hand, and trait anger and anger control on the other will be shown.

Introduction

Trait Anger and Anger Control

Anger can be defined as an intense emotional state characterized by a strong unpleasant and hostile response to a perceived provocation, hurt or threat (Videbeck, Sheila L., 2006). According to the *appraisal-tendency framework* (Lerner and Keltner, 2000; 2001), anger is experienced as a sense of certainty and individual control along with other-responsibility (Lazarus, 1991; Smith & Ellsworth, 1985), and it can influence the appraisal of future events by influencing perceptions, decisions, and behaviors. Such event-related appraisals can persist beyond the eliciting situation, becoming an

⁷ This chapter has been adapted from Sorella et al., 2021b

automatic lens for interpreting subsequent events (Litvak et al., in Potegal et al., 2009). In other words, when anger has been frequently aroused in a person's life history, it may be automatically evoked even when low provocation and low evaluation are associated with the occurring event. Such "emotion schemas" (see the *differential emotions theory* lzard et al., 2007; Schultz et al., in Potegal et al., 2009) change an individual's emotional functioning: when they frequently occur, they crystallize into stable individual differences (Clark et al., 1994; Rothbart and Bates, 1998; Goldsmith et al., 2000; Schultz et al., in Potegal et al., 2009), or what we define as trait anger.

Accordingly, extensive research often distinguishes between state and trait emotions. According to Spielberger (1988, p. 1), state anger relates to a transitory emotional state marked by subjective feelings. On the other hand, trait anger relates to long-lasting individual differences in frequency and duration of anger episodes, due to the more frequent activation of anger-related appraisal system (Lerner and Keltner, 2000; 2001) and emotional schemas (Izard et al., 2007; Schultz et al., in Potegal et al., 2009).

High trait anger can lead to irrational and biased cognitions, such as catastrophizing, overgeneralization and dichotomous thinking (Eckhardt et al., 1998; 2002; Zillman et al., 1994; Schultz et al., in Potegal et al., 2009) that can affect not only individual but also interpersonal wellbeing. While state and trait anger correlate (Bettencourt et al., 2006; Deffenbacher et al., 1996), instruments such as the State-Trait Anger Expression Inventory (STAXI; Spielberger, 1988), can be used to differentiate the two.

However, given that state anger in laboratory settings is usually low and not sufficiently differentiated among participants, beside trait anger we decided to focus our analyses on another STAXI scale: anger control, which implies the capacity to control the experience of anger, calming down and monitoring the outcomes of this emotion.

Anger control capacity is surely one of the most important aspects connected with this emotion, given its clinical and societal relevance. A poor control of anger is associated with a tendency to both react with anger to hostile stimuli and to behave aggressively to reach instrumental goals (Dodge and Coie, 1987). Research has shown that poor anger control is associated with several negative outcomes, such as a greater frequency of aggressive reactions in studies conducted in both laboratories (Bettencourt et al., 2006) and ecological settings, e.g. working and domestic environment (Deffenbacher et al., 2001). Beside psychological and interpersonal consequences

(Baron et al., 2007), high anger levels and its poor control can also have physiological drawbacks such as higher incidence of cardiovascular diseases (Smith et al., 2004), tobacco use (Spielberger et al., 1995) and excessive alcohol intake (Litt et al., 2000). Moreover, extreme levels of anger and aggressive outbreaks also characterize different psychiatric diseases, such as Borderline Personality disorder (De Panfilis et al., 2019; Kernberg, 2012), Antisocial Personality Disorder (Kolla et al., 2016), and the intermittent explosive disorder (Coccaro et al., 2014). Given this evidence, the study of the mechanisms that underlie and regulate anger is crucial.

The Integrative Cognitive Model (Wilkowski and Robinson, 2008) attempts to understand the relationship between trait anger and anger control ability, and their influence on anger-related negative outcomes. In particular, this model argues that trait anger is linked to more automatic processes of hostile interpretation of situations (for reviews, see Crick & Dodge, 1994; Verhoef et al., 2019). However, in order to explain anger outcomes, a more controlled form of cognition must also be considered, i.e., a capacity for effortful control (Eisenberg et al., 2004). This ability can override automatic tendencies toward anger reactivity and aggression that characterize trait anger in different ways: by changing the biased hostile interpretation (reappraisal of the situation), by distracting individuals from hostile thoughts or by suppressing aggressive behaviors (Wilkowski and Robinson, 2008; Wilkowsi and Robinson, 2010).

Thus, this model suggests that final anger outcomes depend on two different levels of cognition, one more automatic and related to trait anger, and the other more effortful and related to anger control. Therefore, I hypothesized on the one hand that there is a relationship between trait anger and structural features in the brain, possibly related to more automatic processes, and on the other hand a relationship between anger control and functional connectivity, possibly related to more effortful and situation-dependent cognition. However, an alternative and less expected outcome could also include a possible relationship between trait anger and functional connectivity on one side, and anger control and structural connectivity on the other side. In order to examine also this possibility, a control analysis would be performed in which these relationships will be taken into account.

To sum up, according to the main hypothesis of this study, trait anger would be associated with structural features while anger control would be associated with functional features in the brain; on the other hand, a less expected result would show a significant relationship between structural features and anger control on one side, and functional features and trait anger on the other side.

Beyond the confirmed hypothesis, any insight on which brain circuits are involved in these processes could contribute to shed some light on the neurocognitive mechanisms that characterize and regulate trait anger, and pave the way to new forms of neuroscience-based psychological treatments.

The neural bases of trait anger and anger control

According to Wilkowski and Robinson (2007), the neural mechanisms of anger control and trait anger may be respectively explained as an effortful control of frontal brain regions over more automatic subcortical activity.

For example, resting state studies showed that the strength of functional connectivity between amygdala and contralateral orbitofrontal cortex is inversely associated with trait anger (Fulwiler et al., 2012). The psychological constructionist view considers the amygdala as a part of a distributed network involved in the detection of exteroceptive sensory information when motivationally salient (Lindquist et al., 2012), given that when the amygdala is injured, the automatic allocation of attention to aversive stimuli (Anderson and Phelps 2001) and socially relevant stimuli (Kennedy and Adolphs 2010) is impaired. Indeed, the amygdala reactivity is linked to trait anger (Carrè et al., 2012).

However, high trait anger individuals are not only characterized by attentional bias toward negative stimuli, but also by excessive ways of interpreting events in life as more negative, aversive and hostile (Nasby et al., 1980). Indeed, individuals with high trait anger are prone to hostile interpretations of relevant situational input (Wilkowski and Robinson, 2010). Hostile attributions have been associated not only with the amygdala (Anderson and Phelps 2001), but also with other brain areas such as the temporo-parietal junction (Giardina et al., 2011; Quan et al., 2019; Carlson et al., 2012) and medial brain areas related to emotional conceptualization (Lindquist et al., 2012). In particular, the posterior cingulate cortex is associated with certainty (Luttrell et al., 2016) that is one of the main features characterizing high levels of anger (Lerner and Keltner, 2000).

Otherwise, frontal brain regions have been proposed to effortfully control anger, probably topdown regulating subcortical brain regions (Wilkowski and Robinson, 2007). In particular, the connectivity between the amygdala and the top-down control capacity of the prefrontal cortices increased during the induced control of anger after an insult (Denson et al., 2013). Accordingly, the above cited study of Fulwiler and collaborators showed a positive correlation of anger control and the

functional connectivity between the amygdala and the contralateral orbitofrontal cortex (Fulwiler et al., 2012).

On the other hand, increased resting-state amygdala-paralimbic connectivity and decreased amygdala-medial prefrontal cortex connectivity was found in violent offenders after anger provocation (Siep et al., 2018), suggesting that a lack of medial prefrontal cortex regulation can lead to reactive aggression. Indeed, this area is involved in anger control (Gilam et al., 2015; Jacob et al., 2018; Gilam et al., 2018).

However, previous connectivity studies usually focused on specific a priori defined brain regions (e.g. ROI studies), such as in the case of the amygdala. In a different way, the aim of this study is to put forward a more inclusive approach, trying to understand the neural networks of trait anger and the capacity to control it through a whole brain perspective.

Therefore, the relation between trait anger and anger control was respectively explored at structural and functional levels. To this aim morphometric features and resting state activity of 71 healthy individuals were taken into consideration. The goal was to understand whether trait anger and anger control capacity are associated respectively with specific cortical features (i.e. gray matter density) and patterns of connectivity (i.e. the frequency of activation of a network) in the brain.

Since trait anger is considered a stable individual tendency, the expectation is to find evidence of gray matter changes at the structural level. Furthermore, considering that trait anger is characterized by the perception of environmental cues as hostile, the hypothesis is to find gray matter changes in a network involving perceptual brain regions linked to emotional processing, such as paralimbic and temporal areas. However, besides the perception of events in life, trait anger can also influence their conceptualization, therefore involving medial brain areas (Lindquist et al., 2012) such as the posterior cingulate cortex that is associated with the certainty characterizing anger (Luttrell et al., 2016).

On the other hand, anger control is expected to be related to functional networks. Indeed, when considering the ability to regulate anger, what is important is not the overall level of control, but *when* it is recruited and employed (Wilkowski & Robinson, 2007). As the authors pointed out, time is an important factor for anger control; for example, low-trait anger individuals were capable of attenuating the biasing effects of hostile primes but only when they had sufficient time. Therefore, the hypothesis is that specific time-related features of functional connectivity, rather than structural

features, can be related to anger control. In particular, the temporal variability and frequency indexes of resting state networks will be taken into account. These are innovative measures that are still poorly investigated in literature. Indeed, connectivity studies usually rely on measures such as the strength of connections between specific brain regions. However, these features cannot evaluate the change over time of these connectivity patterns (Calhoun et al., 2014; Chang et al., 2010). In addition, they rely on predefined regions of interest, without considering the possible involvement of other brain regions. To overcome these limitations, this study takes into account the temporal variability and frequency of whole brain networks. Indeed, previous studies showed that these features can vary on the basis of different conditions, such as age and gender (Allen et al., 2011), cognitive states (Garrett et al., 2013), empathy and awareness (Stoica and Depue, 2020) and mental illness (Garrity et al. 2007).

Among different networks, two networks seem to play a key role in regulating several cognitive and emotional functions: the Default Mode Network (DMN) (Sripada et al., 2014; Pan et al., 2018) and the Executive Network (Alia-Klein et al., 2020). Indeed, both of them include medial prefrontal brain regions, which plays a key role in the regulation of anger, as mentioned before. However, this region could be considered in interaction with other brain areas, such as the medial regions of the DMN. The possible underlying mechanism can be internal mentalization (imaginative constructions of hypothetical events), by which the DMN could suppress limbic and paralimbic areas responsible for emotional processes and reactivity (Harris and Friston, 2010; Buckner et al., 2008). In addition, alterations of the DMN have been also associated with anger expression in individuals with ADHD (Hasler et al., 2017) and to criminal psychopathic tendencies (Pujol et al., 2012), suggesting that this network could be particularly involved in the regulation of violent acts. For these reasons, temporal features of the DMN at rest are expected to positively correlate with anger control capacity.

Methods

Participants

For this study we took advantage of data coming from the MaxPlanck Institute sample (MPI-S) dataset (OpenNeuro database, accession number ds000221), which contains behavioural, physiological and neuroimaging data from healthy subjects. For the purpose of this study we selected

the participants for which the scores from the State-Trait Anxiety Inventory (STAXI), a self report measure to assess both trait anger and anger control (Spielberger, et al 1988) were available. The questionnaire is composed of 44 items which form six scales: State Anger, Trait Anger, Anger-Out, Anger-In and Anger Control. The structural T1-weighted image and a 15-minute eyes-open resting-state fMRI session, entered the analyses. The final sample included 71 subjects (M= 42 F= 29) ranging from 20 to 30 years (age was indicated as between 20 and 25 years or between 25 and 30 years).

Data acquisition

Neuroimaging data were acquired on a 3T Siemens Magnetom Verio Scanner. For our analyses, we considered T1-weighted images, acquired using a MP2RAGE sequence (TR=5000 ms, TE=2.92 ms, TI1=700 ms, TI2=2500 ms, flip angle 1=4°, flip angle 2=5°, voxel size=1.0 mm isotropic, duration=8.22 - min), and the 15 minutes resting state data (voxel size = 2.3 mm isotropic, FOV = 202 x 202 mm2, imaging matrix = 88 x 88, 64 slices with 2.3 mm thickness, TR = 1400 ms, TE = 39.4 ms, flip angle = 69°, echo spacing = 0.67 ms, bandwidth = 1776 Hz/Px, partial fourier 7/8, no pre-scan normalization, multiband acceleration factor = 4, 657 volumes, duration = 15 min 30 s.).

The structural analysis: Source-based Morphometry

In order to analyze structural images through the Independent Component Analysis, we performed Source-based morphometry (SBM). This is a data-driven multivariate alternative to the voxel-based morphometry (VBM), which allows identifying "source networks", i.e. groups of spatially distinct regions in the brain with common covariation among participants (Xu et al. 2009). Indeed, this approach utilizes the Independent Component Analysis (ICA) to identify patterns of covariation of gray matter in different independent areas, detecting and decomposing the mixed signals coming from whole brain structural images . The multivariate nature of this approach makes it more efficient than other structural analyses since it reduces the noise while acting as a spatial filter (Gupta et al., 2018), and highlights source networks, considering the interrelationships between voxels rather than a voxel-by-voxel comparison (Grecucci et al., 2016; Pappaianni et al., 2017; Sorella et al., 2019).

Before applying ICA, images were processed with SPM12 (<u>http://www/http://www.fil.ion.ucl.ac.uk/spm/software</u>), using the toolbox CAT12 (<u>http://www.neuro.uni-jena.de/cat/</u>) for images segmentation.

A data quality check was performed in order to identify any distortion such as head-motion or stripes. Then, images were reoriented according to the origin, and segmented in gray matter, white matter and cerebrospinal fluid through CAT12. For the purposes of the study we only took into account the grey matter images. The registration was computed through Diffeomorphic Anatomical Registration using Exponential Lie algebra (DARTEL) tools for SPM12, rather than using traditional approaches. The last step of the preprocessing consisted in the normalization to MNI space with spatial smoothing (full-width at half maximum of Gaussian smoothing kernel [8, 8, 8]).

After the preprocessing steps, the ICA has been applied to the data, allowing us to identify independent sources in the brain. The ICA has been performed with the Group ICA fMRI Toolbox (GIFT, <u>http://mialab.mrn.org/software/gift</u>), using the sMRI modality which applies the ICA to structural images.

The Infomax algorithm has been used to maximize the recognition of IC from images' signal information (Bell and Sejnowski, 1995; Lee et al., 1999), while the ICASSO toolbox (http://research.ics.aalto.fi/ica/icasso/) was used to investigate the reliability of the ICA algorithm (RandInit mode, with 100 repetitions).

Finally the ICA converted GM volumes of each component into numerical vector; indeed, it returned a n x m matrix (n subjects in rows and m components in columns), which represent how a specific component is expressed in each participant (Pappaianni et al., 2017).

After obtaining the components we performed statistical analyses to determine which networks are linked to anger. In particular, we performed the Pearson correlation between each component and the scores of trait anger of the STAXI. Surf-ice software was used to visualize the networks of interest (https://github.com/neurolabusc/surf-ice).

The rs analysis: Connectivity ICA networks

Preprocessing steps were done through the default processing pipeline (https://www.nitrc.org/frs/?group_id=279) for volume-based analysis. It includes the following steps: functional realignment and unwarping, translation and centering, functional outlier detection

(conservative settings), functional direct segmentation and normalization (2mm resolution), structural translation and centering, structural segmentation and normalization (2 mm resolution), functional and structural smoothing (spatial convolution with Gaussian kernel 8 mm).

Then, CONN includes a component-based noise correction method (CompCor) for the physiological and other noise source reduction. This step applies linear regression and band-pass filtering in order to remove unwanted motion, physiological, and other artifactual effects from the BOLD signal before computing connectivity measures. Then, data were checked through Quality Assurance plots. Given that we did not want to restrict our analyses to a priori seeds/ROIs, investigating possible connectivity differences related to trait anger across the entire brain, we selected voxel-to-voxel analysis, specifically the group-ICA one. Through the Independent Component Analysis we identified 20 networks (default settings) of highly functionally-connected areas. This analysis is based on Calhoun's group-level ICA approach (Calhoun et al., 2001), including the following steps: variance normalization pre-conditioning, subject concatenation of BOLD signal data along temporal dimension, group-level dimensionality reduction, fastICA for estimation of independent spatial components, and GICA1 backprojection for individual subject-level spatial map estimation (Whitfield-Gabrieli and Nieto-Castanon, 2012; Nieto-Castanon, 2020).

Among the 20 networks, the 8 correspondent ones to well-known resting-state networks in literature (Soman et al., 2020) were selected through the CONN Spatial match to template function. In particular, this function allows to automatically identify which of the data-driven networks correspond to the following ones: the Default Mode Network, the Sensori-Motor Network, the Visual Network, the Salience Network, the Dorsal Attention Network, the Fronto Parietal Network, the Language Network and the Cerebellar Network. In particular, this function computes the correlation between each group-level spatial map and CONN's default networks.

Usually, resting state analysis is based on a ROI-to-ROI approach or a seed-based analysis, in which the average BOLD time course of voxels within a ROI is correlated with the voxels of another ROI or all the other voxels in the brain (see for example, chapter 4). Instead, this study relies on an alternative approach that is based on networks' features rather than on the connectivity between different voxels. Indeed, in the ICA-based approach the connectivity between voxels is used to identify different networks maximizing their statistical independence. Then, some features of the BOLD signal

timeseries associated with these networks are considered. Specifically, through the function ICA.Temporal.Components, the variability and frequency (center of mass in spectral power) of the timeseries that are computed for each subject were taken into account. In particular, the temporal variability is defined as the fluctuation of neural activity overtime, while the temporal frequency is defined as the distribution of neural activity fluctuations over various frequencies,

Finally, the possible relationship between the temporal variability or the temporal frequency of the identified networks and anger control scores of the 71 subjects was tested through correlation coefficients.

In addition, to better explore the relationship between trait anger, anger control and the significant networks, I relied on both correlational analysis and Bayesian statistics. The former was used to visualize the relationship between these variables, while the latter was used to compare the model that better predicts each significant network. In particular, a Bayesian Linear Regression will be performed for each network.

Results

Structural Results: SBM ICA

Through Source-based Morphometry, the Independent component analysis automatically identified 8 components, which have been regressed with trait anger scores. All of them showed an Iq>0.9, that indicates a highly stable ICA decomposition.

The analysis showed a positive significant correlation between Independent Component 3 (IC 3, Iq =0.97) and trait anger (r= 0.3386, p=0.004), even after correcting for gender (r=0.327, p=0.0058) or age (r=0.339, p=0.0041). Results remained significant after correcting for the number of components identified by the ICA (Bonferroni corrected p critic = 0.006). The IC 3 included portions of the Fusiform gyrus, different parts of the Cerebellum, the Temporal pole, the Lingual gyrus, the Visual Association Area, the Posterior Cingulate cortex and the Inferior Parietal lobule. See Table 3.1 and Figure 3.1.

The other 7 components were not significantly correlated with trait anger (r=-0.007,p=0.954; r=-0.178, p=0.137; r=-0.040;p=0.740; r=0.070,p=0.563; r=-0.079,p=0.511; r=0.147,p=0.220; r=0.112,p=0.352). ⁸

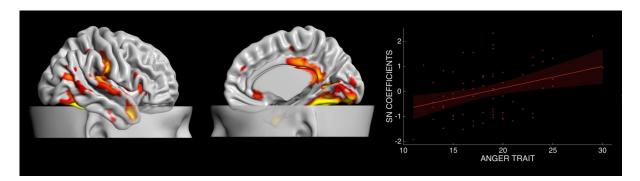


Figure 3.1 The structural network. The structural network, represented on the left, includes portions of the Temporal pole, the Posterior Cingulate cortex and the Inferior Parietal lobule, the Lingual gyrus, the Visual Association Area, Fusiform gyrus, and parts of the Cerebellum. The plot on the right shows the significant positive correlation between the structural network's (SN) coefficients of gray matter density and the scores of trait anger for each individual (r= 0.3386, p=0.004). Adapted from Sorella et al., 2021b.

| ICA | Volume | random effects: Max Value (x, y, z) | Brodmann | Label (Nearest Gray Matter within 5mm) |
|-----------|---------|--|----------|--|
| Network 3 | (cc) | | | |
| | 4.8/6.7 | 5.6 (-33, -55, -16)/6.3 (36, -56, -16) | 19,20,37 | Fusiform Gyrus |
| | 2.4/5.9 | 5.3 (-30, -52, -16)/6.2 (34, -52, -16) | 19,20,37 | Fusiform Gyrus |
| | 0.8/3.0 | 4.7 (-36, -55, -14)/6.0 (39, -53, -16) | 19,20,37 | Fusiform Gyrus |
| | 0.3/1.0 | 4.1 (-43, -68, -23)/5.1 (48, -52, -25) | • | Cerebellum-Tuber |
| | 0.1/0.2 | 4.4 (-39, -55, -16)/5.8 (34, -66, -13) | 19,20,37 | Fusiform Gyrus |
| | 0.1/0.0 | 4.0 (-22, -56, 8)/- | 23 | Posterior Cingulate Cortex |
| | 0.1/0.0 | 3.9 (-37, -70, -23)/- | • | Cerebellum-Uvula |
| | 0.0/2.7 | -/5.7 (43, -50, -38) | * | Cerebellar Tonsil |
| | 0.0/0.9 | -/4.7 (36, -69, -39) | * | Cerebellum-inferior semi-lunar lobule |
| | 0.0/0.8 | -/5.0 (4, -84, -10) | 18 | Lingual Gyrus |
| | 0.0/0.3 | -/5.0 (21, 3, -37) | 38 | Parahippocampal gyrus |
| | 0.0/0.2 | -/4.0 (36, -75, -34) | * | Cerebellum-pyramis |
| | | | | |

Table 3.1 The structural network. Tha table shows, from left to right, the volumes, the coordinates, theBrodmann areas and the name of the areas included in the structural network. Adapted from Sorella et al.,2021b.

⁸ To exclude a possible relation between structural connectivity and anger control, we also computed this analysis as a control condition. No significant correlations emerged with any of the 8 components (r=-0.103,p=0.394; r=-0.126, p=0.295; r=-0.092;p=0.445; r=0.021,p=0.862; r=0.020,p=0.867; r=-0.206,p=0.085; r=0.072,p=0.550; r=0.035, p=0.772).

| 0.0/0.1 | -/4.4 (1, -83, -7) | 18 | Visual Association Area |
|---------|---------------------|----|--------------------------|
| 0.0/0.1 | -/3.8 (53, -16, 27) | 40 | Inferior Parietal Lobule |
| 0.0/0.1 | -/3.7 (36, -39, 39) | 40 | Inferior Parietal Lobule |
| 0.0/0.1 | -/3.6 (46, 10, -26) | 38 | Temporal Pole |

Functional Results: CONN ICA

We identified 20 functional networks through the Independent Component Analysis. Among them, we selected the temporal frequency of the 8 principal resting state networks that have been regressed with anger control scores, that are the Default Mode Network (ICA14), the Sensori-Motor Network (ICA19), the Visual Network (ICA15), the Salience Network (ICA3), the Dorsal Attention Network (ICA18), the Fronto Parietal Network (ICA17), the Language Network (ICA12) and the Cerebellar Network (ICA 1).

The analysis showed a positive significant correlation between the Default Mode Network frequency and anger control (r= 0.36, p = 0.002), even when correcting for sex (r=0.33, p=0,006) or age (r=0,35, p=0,004). Results remain significant after correcting for the number of components identified by the ICA (Bonferroni corrected p critic = 0.006). See Table 3.2 and Figure 3.2. None of the other networks showed significant correlation with anger control, when considering the variability (ICA1: r<0.01, p=0.95; ICA3: r =0.10, p=0.48; ICA12: r=0.17, p=0.19; ICA14: r=0.14, p=0.27; ICA15: r<0.01, p=0.61; ICA17: r=0.22, p=0.07; ICA18: r<0.01, p= 0.64; ICA19: r=0.20, p=0.11) or the frequency (ICA1: r<0.01, p=0.80; ICA3: r <0.01, p=0.55; ICA12: r<0.01, p=0.20; ICA15: r<0.01, p=0.67; ICA17: r<0.01, p=0.94; ICA18: r<0.01, p=0.95) of each network.

⁹ To exclude a possible relation between functional connectivity and trait anger, we also computed this analysis as a control condition. The analysis showed no significant correlations with trait anger when considering the variability (ICA1: r=0.25, p=0.033; ICA3: r <0.01, p=0.730; ICA12: r<0.01, p=0.970; ICA14: r=0.1, p=0.544; ICA15: r<0.01, p=0.811; ICA17: r=0.1, p=0.359; ICA18: r=-0.25, p= 0.039; ICA19: r=-0.141, p=0.242), or the frequency (ICA1: r=-0.25, p=0.042; ICA3: r <0.01, p=0.719; ICA12: r<0.01, p=0.693; ICA14: r=-0.283, p=0.021; ICA15: r<0.01, p=0.973; ICA17: r<0.01, p=0.982; ICA18: r=0.1, p= 0.433; ICA19: r<0.01, p=0.723) of each network after Bonferroni correction.

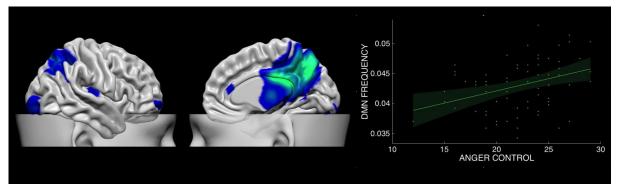


Figure 3.2 Default Mode Network. The functional network represented on the left shows the data-driven network (IC14) that correspond to the Default Mode Network. The plot on the right shows the significant positive correlation between the DMN temporal frequency and the anger control scores for each individual (R^2 = 0.13, p = 0.002). Adapted from Sorella et al., 2021b.

Table 3.2 Default Mode Network. Tha table shows, from left to right, the coordinates, the Brodmann areas and the name of the areas included in the functional network. Adapted from Sorella et al., 2021b.

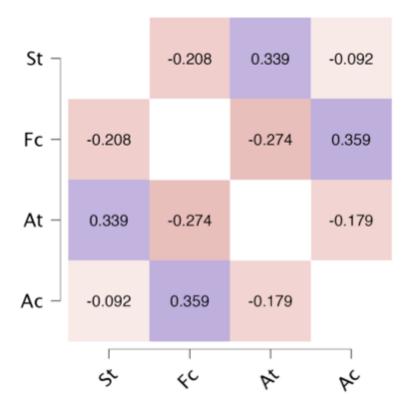
| Default Mode | Max Value (x, y, z) | Brodmann | Label |
|--------------|---------------------|----------|---------------------------------------|
| Network | | | |
| | +10 -66 +38 | 7 | Posterior Cingulate |
| | +38 +38 -6 | 47 | Ventral PFC |
| | +42 -80 -34 | * | Cerebellum |
| | -40 -78 -32 | * | Cerebellum- |
| | -22 +58 +2 | 10, 32 | Anterior Cingulate |
| | +28 -90 -10 | 18 | Visual association cortex |
| | -28 -94 -10 | 18 | Visual association cortex |
| | +6 +34 +16 | 32 | Anterior Cingulate |
| | +0 -90 +32 | 32 | Cerebellum-inferior semi-lunar lobule |
| | +42 -60 -52 | 19 | Visual extrastriate cortex |
| | +56 -20 -10 | 22 | Superior Temporal Gyrus |
| | -44 -52 -44 | • | Cerebellum |
| | -32 +8 +58 | 6 | Premotor Cortex |
| | -14 +12 -10 | • | Putamen |
| | -60 -40 +50 | 40 | Parietal Lobule |
| | +62 -40 +50 | 40 | Parietal Lobule |
| | -30 +44 +44 | 9 | Medial Prefrontal Cortex |
| | +14 +12 -10 | • | Nucleus Accumbens |
| | +6 -84 -42 | • | Cerebellum |

Further relationships between variables

To better explore the relationship between trait anger, anger control and the structural and functional networks, I relied on both correlational analysis and Bayesian statistics. The former was used to visualize the relationship between these variables, while the latter was used to compare the model that better predicts respectively the structural and functional networks. In particular, a Bayesian Linear Regression was performed for each network, and the other variables (trait anger, anger control and the other network) were considered as covariates.

Results of the correlational analysis show a relationship not only between trait anger and the structural network on one side, and anger control and the functional network on the other side, but also a negative relationship between the functional network and trait anger (see Figure 3.3 and Table 3.3).

Figure 3.3 Pearson's r heatmap of the correlations between trait anger (At), anger control (Ac), the structural (St) and functional (Fc) networks. Each value represents the Pearson's correlation coefficient between two measures among structural coefficients, functional coefficients, trait anger and anger control. P-values are represented in the following table.



| Variable | | St | Fc | At | Ac |
|----------|-------------|--------|--------|--------|----|
| 1. St | Pearson's r | | | | |
| | p-value | _ | | | |
| 2. Fc | Pearson's r | -0.208 | | | |
| | p-value | 0.082 | _ | | |
| 3. At | Pearson's r | 0.339 | -0.274 | — | |
| | p-value | 0.004 | 0.021 | — | |
| 4. Ac | Pearson's r | -0.092 | 0.359 | -0.179 | _ |
| | p-value | 0.444 | 0.002 | 0.135 | _ |

Table 3.3 Pearson's Correlations between trait anger (At), anger control (Ac), the structural (St) and functional (Fc) networks. The Pearson's correlation coefficient and the p-value between each couple of measures among structural coefficients, functional coefficients, trait anger and anger control, are represented in the table.

Results of the Bayesian Linear Regression are displayed in table 3.4 and 3.5, where the posterior probabilities (P(M|data)) of the models can be used to select the best one.

Regarding the structural network, the best model includes only trait anger as covariate.

Regarding the functional network, the best model includes all the variables (trait anger, anger control and also the structural network) as covariates.

This means that while structural features in the brain are associated with trait anger, the functional features also reflect an effect of the other variables.

Table 3.4 Bayesian Linear Regression of the structural network with trait anger (At), anger control (Ac) and the functional network (Fc) as covariates. Each row of the first column represents a different model in which one or more variables are included, while the following columns represent the prior (P(M)) and the posterior (P(M|data)) probability of the model, the Bayes Factor of the specific model when compared to the others (BF_M) or to the null model (BF₁₀) and the R-squared. Then, the prior and posterior probability, the BF, the mean, the SD and the Credible Interval for each variable are represented in the following part.

Model Comparison - St

| Models | P(M) | P(M data) | BF _M | BF 10 | R ² |
|--------------|-------|-----------|-----------------|-------|----------------|
| At | 0.083 | 0.368 | 6.410 | 1.000 | 0.115 |
| At + Ac + Fc | 0.250 | 0.181 | 0.661 | 0.163 | 0.129 |
| At + Fc | 0.083 | 0.172 | 2.287 | 0.467 | 0.129 |
| Null model | 0.250 | 0.112 | 0.377 | 0.101 | 0.000 |
| At + Ac | 0.083 | 0.110 | 1.361 | 0.299 | 0.116 |
| Fc | 0.083 | 0.034 | 0.390 | 0.093 | 0.043 |
| Ac | 0.083 | 0.012 | 0.131 | 0.032 | 0.008 |
| Ac + Fc | 0.083 | 0.011 | 0.127 | 0.031 | 0.044 |

Posterior Summaries of Coefficients

| | | | | | | | | 95% C | 95% Credible | |
|------------|-----------|---------|--------------|--------------|--------------|-----------|--------|---------|--------------|--|
| | | | | | | | | Inte | erval | |
| Coefficien | t P(incl) | P(excl) | P(incl data) | P(excl data) | BF inclusion | Mean | SD | Lower | Upper | |
| Intercept | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 1.972e -9 | 0.114 | -0.239 | 0.206 | |
| At | 0.500 | 0.500 | 0.831 | 0.169 | 4.914 | 0.059 | 0.037 | 0.000 | 0.117 | |
| Ac | 0.500 | 0.500 | 0.314 | 0.686 | 0.457 | -7.720e-4 | 0.016 | -0.039 | 0.039 | |
| Fc | 0.500 | 0.500 | 0.398 | 0.602 | 0.662 | -10.496 | 21.037 | -61.529 | 16.422 | |
| | | | | | | | | | | |

Table 3.5 Bayesian Linear Regression of the functional network with trait anger (At), anger control (Ac) and the structural network (St) as covariates. Each row of the first column represents a different model in which one or more variables are included, while the following columns represent the prior (P(M)) and the posterior (P(M|data)) probability of the model, the Bayes Factor of the specific model when compared to the others (BF_M) or to the null model (BF₁₀) and the R-squared. Then, the prior and posterior probability, the BF, the mean, the SD and the Credible Interval for each variable are represented in the following part.

Model Comparison - Fc

| Models | P(M) P(| M data) | BF _M | BF 10 | R ² |
|--------------|----------------|---------|-----------------|-------|----------------|
| At + Ac + St | 0.250 | 0.363 | 1.709 | 1.000 | 0.187 |
| At + Ac | 0.083 | 0.241 | 3.499 | 1.995 | 0.175 |
| Ac | 0.083 | 0.173 | 2.293 | 1.426 | 0.129 |
| Ac + St | 0.083 | 0.142 | 1.818 | 1.173 | 0.160 |
| Null model | 0.250 | 0.031 | 0.097 | 0.086 | 0.000 |
| At | 0.083 | 0.027 | 0.305 | 0.223 | 0.075 |
| At + St | 0.083 | 0.013 | 0.150 | 0.111 | 0.090 |
| St | 0.083 | 0.010 | 0.106 | 0.079 | 0.043 |

Posterior Summaries of Coefficients

| | | | | | | | | 95% Cr | edible |
|------------|-----------|---------|--------------|--------------|--------------|-----------|-----------|------------|-----------|
| | | | | | | | | Inter | val |
| Coefficien | t P(incl) | P(excl) | P(incl data) | P(excl data) | BF inclusion | Mean | SD - | Lower | Upper |
| Intercept | 1.000 | 0.000 | 1.000 | 0.000 | 1.000 | 0.043 | 4.777e -4 | 0.042 | 0.044 |
| At | 0.500 | 0.500 | 0.645 | 0.355 | 1.815 | -1.211e-4 | 1.328e -4 | -4.006e -4 | 4.708e -5 |
| Ac | 0.500 | 0.500 | 0.919 | 0.081 | 11.296 | 2.988e -4 | 1.457e -4 | 0.000 | 5.323e -4 |
| St | 0.500 | 0.500 | 0.528 | 0.472 | 1.118 | -2.666e-4 | 4.278e -4 | -0.001 | 2.298e -4 |
| | | | | | | | | | |

Discussion

Anger is an essential emotion that helps us respond to perceived provocations, hurts or threats (Sorella et al., 2021). In this study two important aspects of anger were explored through self-reported measures: trait anger defined as a stable personality tendency, and anger control capacity, or the ability individuals have to regulate its expression. Specifically, the hypothesis is that trait anger, as a stable tendency that influences the perception of the world as hostile, relates to structural connectivity; on the other hand, the ability to control anger is not such a stable tendency since it is characterized by the specific time at which it is recruited and employed (Wilkowski and Robinson, 2007); therefore I hypothesized a relation of this measure to a more variable parameter, that is functional connectivity. Confirming the predictions, a structural network was found to be significantly associated with trait anger, while a functional neural signature was significantly associated with anger control capacity. The structural network involves posterior brain areas such as temporal regions, the posterior cingulate and the cerebellum. At a functional level, a correlation between the frequency of the Default Mode Network and anger control scores emerged in the second analysis.

The structural neural correlates of trait anger

Morphometric analysis showed that trait anger significantly correlates with a structural network including the bilateral fusiform gyrus (anterior and posterior regions), the right temporal pole, the right ventromedial temporal area, the posterior cingulate, and the cerebellum. While the involvement of the temporal and medial brain areas was expected, involvement of the fusiform gyrus and cerebellum was less predictable. Nevertheless, some evidence may explain their involvement. Furthermore, unlike functional neuroimaging studies, this one considers gray matter, highlighting possible differences with the literature.

It has been proposed that a mutual interaction between posterior and anterior temporal areas can be responsible for the interaction between visual and verbal environmental triggers and semantic memories of past experiences, leading to anger provoking perceptions (Potegal and Stemmler, 2009). Accordingly, the structural analysis includes different temporal regions that may underlie these processes.

In literature a link between the fusiform gyrus and emotional valence has been observed (Mattek et al., 2020), in particular when considering anger during mental imagery (Drexler et al., 2000). In addition, the right anterior fusiform plays a key role in associative semantic knowledge (Mion et al., 2010). In fact, this process might be related to the induction of anger when the belief (stored in our semantic system) that the individual has been treated unfairly is evoked (Smedslund, 1993; Fernandez and Wasan, 2009).

Mnemonic and emotional processes also involve medial temporal areas in the brain (Grecucci et al., 2010; 2013a,b; Harris and Friston, 2010); for example, higher activations of these regions have been associated with primitive thought and emotion (Pietrini et al., 2000; Dougherty et al., 2004) and to the recollection of distressing memories and emotions in patients with post-traumatic stress disorder (Bremner et al., 1999; Shin et al., 2004, 2006; Hopper et al., 2007).

Indeed, temporal areas are also typically involved in mentalizing and emotional processing, and they can play a crucial role in anger-related experiences. For example, when temporal areas are injured through lobectomy, anger-related behaviors can be reduced; in particular, after this practice social withdrawal is observed in monkeys and reduced aggression and rage is observed in both monkeys and humans (Fenwick, 1989; Olson et al., 2007; Potegal and Stemmler, in Potegal et al., 2009).

In addition, previous research showed that the temporal pole in particular, which also emerged in this analysis, plays a key role during anger self-induced paradigms or inequality games (Dougherty et al., 1999; Kimbrell et al., 1999; Damasio et al., 2000; Olson et al., 2007; Klimeki et al., 2018; Foster and Harrison, 2002; Grecucci et al., 2013a,b) and its alteration is indeed linked to aggressive and/or violent individuals (Bufkin and Luttrell, 2005; Potegal and Stemmler, in Potegal et al., 2009). This process could be explained by associations of perceptions and emotions; indeed, when anger-related social signals are used to interpret others' behaviors (Sorella et al., 2021), the temporal pole seems to play a key role in binding complex perceptual inputs to visceral affective responses, leading to the emergence of personal affective semantic memories (Olson et al., 2007).

This evidence suggests that different temporal regions may be responsible for a link between perceptions, memories, and emotions that in high trait anger individuals is characterized by greater hostility likely related to higher gray matter density.

A further step characterizing trait anger, besides the perception of events as hostile, regards a more explicit conceptualization of them. Since the activity of the posterior cingulate cortex is linked to the conceptualization of self-relevant stimuli (Rameson et al., 2010; Ochsner et al., 2005), in particular when characterized by social and contextual focus (Johnson et al., 2006), the hostility characterizing high trait anger individuals could be explicitly conceptualizations of these individuals (Lerner and Keltner, 2000). Accordingly, high certainty has been previously linked to the posterior cingulate (Luttrell et al., 2016), and meta-analytic evidence revealed that this area is involved in anger perception and the recall of anger-inducing life experiences (Murphy et al., 2003; Phan et al., 2002).

Regarding the cerebellum, it has been found that this area plays a key role for negative emotions such as anger and disgust, in particular when emotional control linked to goal-directed behaviour is needed in social contexts (Schraa-Tam, C. K et al 2012).

In addition, there is also evidence on the involvement of this area in both perceptual and aggressive mechanisms associated with anger (Klaus and Schutter, 2021; Adamaszek, M., et al 2017). Furthermore, Klaus and Schutter (2021) found that the cerebellum is functionally connected with the default mode network. Therefore, this network could modulate the cerebellar activity with a regulatory role, as explained in the following section.

The functional neural correlates of anger control

Functional analysis showed that individual differences in anger control significantly correlate with the DMN. This finding extends the evidence of previous results, since this is the first study that considers the relation between anger control and the frequency of activation of the DMN rather than the role of its areas or the strength of its connections. Indeed, even if this measure is not yet widely used, it has been linked to physiological activity (Yuen et al., 2019), age, gender (Allen et al., 2011) and mental illness (Garrity et al., 2007).

Our results are in line with literature evidence, which shows that alterations of the DMN are linked to anger in both clinical and non-clinical populations. For example, anger expression is linked to inter-hemispheric DMN asymmetry (in particular in the inferior parietal lobule and in the medial frontal gyrus) in ADHD individuals characterized by the dysregulation of this emotion (Hasler et at 2017). In addition, alterations of the FC in the DMN characterize criminal psychopathic individuals (Pujol et al., 2012). This evidence suggests that the DMN is involved not only in anger-related behaviors but also in the regulation of violent acts.

Other evidence comes from studies that focused on non-clinical population, which found that impaired connectivity between DMN regions might lead to negative affective states such as anger. For example, the connectivity of DMN, in particular of the dorsal regions, negatively correlates with anger (Dong et al., 2017). Another study showed that a change in mood followed the modulation of the DMN through acute tryptophan depletion (which reduces serotonin levels), and in particular low-frequency spontaneous BOLD activity in the superior parietal lobule is linked to self-reported scores of anger and hostility (Kunisato et al., 2011).

Another finding suggests that the anterior cingulate cortex could be involved in the control of anger; in particular, it has been shown that during a frustration task, males with high trait aggression were characterized by a decreased activation of this area (Pawliczek et al., 2013).

In addition, medial frontal regions of the DMN show greater connectivity with temporal areas during social and moral emotions, such as embarrassment and guilt, rather than during basic emotion, such as anger (Burnett and Blakemore, 2009; Li 2014). This is in line with evidence that moral emotions can regulate and mediate anger and aggression (Colasante et al., 2015; Stuewig et al., 2008). Therefore, the DMN can induce a self-referential process that in the case of experiencing anger can regulate and control this emotion. This is also consistent with the fact that abnormalities of the DMN are associated with withdrawal emotions as in depression (Grimm et al., 2009; Sheline et al., 2009), probably underlying a withdrawal from the external world and a pathological self-focus (Harris and Friston, 2010). One hypothesis is that the DMN is linked to a modulation of withdrawal and approach motivation, and this can influence the regulation of high trait anger, an emotion characterized by an approach motivation. However, future studies are needed to better understand the relation between DMN and withdrawal vs. approach motivation in different emotional experiences.

The relation between anger and the structural and functional networks

In this study, evidence for a structural network associated with trait anger, and a functional network associated with anger control capacity was highlighted. This is in line with the expectations, since trait anger is a fairly stable personality trait; and, our results show that the more gray matter density in

posterior perceptual, mnestic, and paralimbic brain regions, the higher trait anger, which is characterized by higher attribution of salience and hostility to negative events in life. On the other hand, functional results show a relation between anger control capacity and the frequency of the DMN during resting-state activity. Indeed, the DMN is involved in social behavior and mood control (Raichle, 2015).

Finally, we also found a significant inverse relationship between the functional network and trait anger. Indeed, Bayesian analyses showed that while the structural network is best predicted only by trait anger, the functional one is best predicted by all the other variables (in the following order: anger control, trait anger and the structural network). Therefore, our hypothesis on the distinction between structural features and trait anger on one side, and functional features and anger control on the other side, is partially supported. In particular, the unique relationship between the structural network and trait anger is confirmed. However, these additional analyses suggest that the functional network associated with anger control could also exert a regulatory influence on both the structural network associated with trait anger, and trait anger itself (since there is a negative relationship between these variables).

These findings are also in line with the dual-component model of belief (Sugiura et al., 2015), according to which belief representations are primarily perceptual in nature and supported by posterior cortices, while more prefrontal brain areas, such as those included in the DMN, are involved in the evaluation of the formed representations of life events. My hypothesis is that the DMN, and in particular frontal regions' functional connectivity with limbic and perceptual brain areas, can reduce the effect of hostile interpretations through an effortful control (Wilkowski and Robinson, 2010) and through a more conscious evaluation of the automatic representations of beliefs (Sugiura et al., 2015). Indeed, the DMN is also linked to the monitoring of potential alternative courses of action (Allegra et al., 2018), where a modulation of the inferences and thoughts about other's belief and intention (Schilbach et al., 2008; Laird et al., 2011; Li, 2014) could play a key role in the control of anger.

Indeed, different studies suggest that the activation of the DMN suppresses activity in lower systems (Harris and Friston, 2010). Accordingly, on one hand a high goal directed inclination and a high external causality attributed to others' behaviors characterize high trait anger; on the other hand, a reduction in goal directed motivation and a higher social understanding and representation of others'

mental states are linked to DMN activity (Gusnard and Raichle, 2001; Greicius et al., 2003; Samson et al., 2004; Li, 2014).

Other evidence supporting this hypothesis shows that some areas of the DMN can influence an inhibition of activity in other areas included in the structural network linked to trait anger. Indeed, many studies show that the medial prefrontal cortex can suppress limbic activation of subcortical, paralimbic and temporal areas (Hariri et al., 2000; Milad and Quirk, 2002; Rosenkranz and Grace 2002; Rosenkranz et al., 2003; Phillips et al., 2003; Phelps et al., 2004; Etkin et al., 2006; Milad et al., 2006; Harris and Friston, 2010). In addition, also the anterior cingulate seems to have a suppressive effect on the amygdala (Stein et al., 2007). In fact, primitive thought and distressing memories and emotions are enhanced when the medial prefrontal cortex activity decreases and the medial temporal activity increases (Bremner et al., 1999; Pietrini et al., 2000; Dougherty et al., 2004; Shin et al., 2004, 2006; Hopper et al., 2007), while an opposite pattern of activation is associated with a regulation of these experiences (Pietrini et al., 2000; Beauregard et al., 2001; Lanius et al., 2002; Reinders et al., 2003, 2006; Dougherty et al., 2004; Harris and Friston, 2010).

Although other studies are needed to better understand the relation between the suppressive actions of the DMN on brain regions structurally related to trait anger, our results are in line with previous evidence and, moreover, expand it by considering individual differences related to the anger control ability and the frequency of activation of the DMN.

Finally, some observations should be made. In particular, unexpectedly we did not found prefrontal areas associated with trait anger, and the medial prefrontal involvement in the DMN seems to be restricted. Therefore, differently from literature evidence, this study shows a reduced involvement of the prefrontal cortex in anger-related features. On one hand, the absence of frontal areas in the structural network associated with trait anger could be explained by different speculations; the first regards the method, since structural features in the brain are less studied and could not involve prefrontal regions that emerged in functional ones (see Chapter 2 for more details about functional neuroimaging evidence on anger). The second speculation regards the fact that trait anger, as outlined before, seems to involve an alteration in the perception of stimuli, which are characterized by higher levels of hostility in high trait anger individuals. Therefore, the lack of prefrontal involvement could suggest that trait anger is encoded in the brain as an automatic perceptual

mechanisms that do not rely on higher cognition (i.e. prefrontal brain areas). Finally, another explanation could be that the development of prefrontal cortices is not yet completed in the younger participants, and this couls also explain the lack of PFC involvement in these results.

On the other hand, unexpectedly, also the functional results seem to show a reduced involvement of the medial PFC. However, the reason could be explained by the methodology used. Indeed, in this study the DMN was defined automatically through the data features, and not through the usage of a predefined mask. This process leads to the fact that the DMN identified by the ICA mainly involved posterior brain regions. However, also other studies relying on the same methodology found similar effects (see, e.g. Motoyama et al., 2019). Indeed, in multivariate analyses posterior regions of the DMN seem to be more robust than anterior ones (Kim and Lee, 2011).

Conclusions

The study of how trait anger and anger control capacity are related to our brain connectivity has been poorly addressed by affective neuroscience. Beside the theoretical relevance of such results, clinicians can greatly benefit from the understanding of the functional and structural bases of anger to develop neuroscience-based psychological treatments to modulate through pharmacology or neurostimulation methods the areas emerged in the present study. Such treatments can be used to improve anger regulation in populations suffering from anger dyscontrol, and help them "turn off the fuse" in their daily life. However, the internalization (anger-in scale) and externalization of anger (anger-out) are two fundamental aspects of this emotion that also needs to be taken into account, especially when considering possible treatments. For example, a neuroscience-based treatment for depression consists in the stimulation of the left prefrontal cortex with transcranial direct current stimulation (tDCS), since it was found that depressive symptoms and negative emotions such as anxiety are associated with higher right vs. left frontal activity. However, even if anger is a negative emotion, it is characterized by approach motivation. Indeed, it seems that this emotion is associated with higher left vs. right frontal activity. Therefore, the next chapter will focus not only on the evidence of this frontal asymmetry and its implications, but also on new evidence linking this hypothesis to frontal connectivity and anger. In particular, the internalization and the externalization of anger will be taken into account, two individual differences still unexplored from a neuroscientific perspective.

Chapter 4

Study 3 - Testing the Prefrontal Asymmetry hypothesis of Anger: a connectivity study¹⁰

In the previous chapter, it was shown that trait anger and anger control are associated with two networks in the brain, a structural network for the former and a functional network for the latter. However, other two individual differences' scales must be considered in the study of the neural bases of anger: the externalization and the internalization of this emotion. In particular, given the previous evidence on the frontal asymmetry hypothesis, we expected that the externalization of anger would be associated with left frontal connectivity while the internalization of anger would be associated with the right frontal connectivity. The results will be discussed in the next sections, in particular considering the literature's evidence on the frontal asymmetry.

Introduction

Anterior cortical regions play an important role in emotional behavior and experience. In particular, the asymmetry of the frontal cortex seems to play a key role in different affective domains (Davidson, 1992).

Studies on brain injuries showed that damage to the left anterior PFC is associated with depressive symptoms (such as apathy, loss of interest and pleasure in objects and people, difficulty in voluntary actions), while damage to the right anterior PFC is associated with mania symptoms (Robinson et al., 1984).

¹⁰ This chapter has been adapted from Consolini et al., under review

Therefore, Davidson and colleagues proposed that the left anterior cortex is specialized for approach processes while the right is specialized for withdrawal processes (Davidson, 1984; 1987; 1988; Davidson et al., 1990; Davidson & Tomarken, 1989; Davidson, 1992).

Indeed, he argued that the left frontal region is involved in intention, self-regulation and planning (Luria, 1973), and more generally to the sense of *willingness* and approach-related behavior.

On the other hand, the right anterior cortex is more frequently associated with negative emotions and withdrawal.

This frontal asymmetry seems to be implicated in particular when individual differences in affective styles are taken into account. For example, individuals with higher scores on the Beck Depression Inventory showed less left frontal activation when compared to individuals with lower scores (Henriques and Davidson, 1991).

Interestingly, it seems that these differences are also detectable in 2 ½ years old children. Indeed, behaviorally inhibited children (those who spend the majority of their time near their mothers, without playing or interacting with new environmental stimuli in a peer play situation) showed higher right frontal activation while uninhibited children showed higher left frontal activation in an EEG study (Davidson, 1992).

Based on this evidence, the frontal asymmetry hypothesis has been linked in particular to positive and negative emotions. Indeed, the *affective-valence hypothesis* was proposed, which associated positive emotions with higher left frontal activity and negative emotions with higher right frontal activity (Davidson, 1984).

However, the study of anger has disproved this hypothesis. Indeed anger is a negative emotion, but its uniqueness when compared to other negative emotions such as sadness and anxiety, consists in the fact that anger is characterized by an approach motivation rather than a withdrawal motivation. Interestingly, the experience of anger has been associated with higher left frontal activity (Harmon-Jones, 2004).

Therefore, scholars have proposed that the frontal asymmetry is not specifically linked to emotional valence but is more associated with behavioral motivation, according to the *motivational-direction model* (Harmon-Jones, 2004). In particular, a component of the Reinforcement Sensitivity Theory (Gray, 1970), that is the Behavioral Activation/Inhibition system, has been associated with the frontal asymmetry hypothesis (Sutton & Davidson, 1997; Watson et al., 2016). This scale measures

approach (Behavioral Activation System, BAS scale) and avoidance behaviors (Behavioral Inhibition System, BIS scale) (Carver & White, 1994; Leone et al., 2002). Interestingly, these scales have been associated respectively with higher left (Amodio et al., 2008; Coan & Allen, 2003; Gable & Poole, 2014; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997; Watson et al., 2016) or right (Sutton & Davidson, 1997; Watson et al., 2016; but see Harmon-Jones & Allen, 1997 for opposite results) frontal activity.

Finally, another emerging hypothesis modified the concepts related to the frontal asymmetry according to the revised Reinforcement Sensitivity Theory (RST, Gray and McNayghton, 2000); in particular, this theory replaced the BIS with two systems: on one hand, the Fight Flight Freeze System (FFFS), activated by aversive stimuli and responses to threat, and on the other hand the revised Behavioral Inhibition System (r-BIS), that is activated by conflicts that arises from motivations linked to the BAS and the FFFS, and represent a superordinate motivational system involved in the motivational control that mediates approach and avoidance conflicts or suppresses motivational responses (Gray and McNaughton, 2000). Therefore, it has been proposed that the right frontal activity is not specifically linked to withdrawal motivation or behavior, but to this r-BIS system. This system is indeed involved in an effortful control or suppression of motivation, especially when associated with approach behaviors (Lacey et al., 2020; Gable et al., 2018). This hypothesis has been supported (Lacey et al., 2020) not only by the failure of different studies to link withdrawal motivation with greater right frontal activity (Amodio et al., 2008; Berkman and Lieberman, 2010; Coan and Allen, 2003; Coan et al., 2001; De Pascalis et al., 2013; Wacker et al., 2008) summarized in a meta-analysis (Garrison et al. 2018), but also by studies linking the stimulation of the right frontal cortex with higher response inhibition and weaker risky decision making (Fecteau et al., 2008: Jacobson et al., 2011; Stramaccia et al., 2015).

However, individual differences associated with anger have been less studied in the context of the frontal asymmetry hypothesis, when compared to both other emotions such as sadness (and depression) and anxiety, and behavioral systems.

Anger is an intense emotional experience characterized by hostile interpretations of environmental stimuli, especially in social contexts (Sorella et al., 2021b). After the experience of anger, this emotion can lead to opposite behavioral responses: some people can be characterized by the tendency to

express anger outwardly with physical or verbal reactions, in line with approach motivation that characterizes anger (Harmon-Jones, 2004); instead, other people can be characterized by the tendency to internalize anger and suppress its instincts (Smits & Kuppens, 2005). Interestingly, it has been proposed that these tendencies are linked to the approach and avoidance motivational systems: the tendency to express anger would be related to the approach system, whereas the tendency to internalize anger would be related to the approach system, whereas the tendency to internalize anger would be related to the avoidance system (Carver & Harmon-Jones, 2009; Smits & Kuppens, 2005; Smits et al., 2004).

In particular, the BAS and BIS scales can be associated with the approach or withdrawal reactions to provocative stimuli that follow the elicitation of anger (Gray, 1990; Heponiemi et al., 2003; Smits & Kuppens, 2005).

Nonetheless, there is poor evidence that deepens the relationship between individual differences in anger-related behaviors and the prefrontal asymmetry activity, given that the majority of studies focused on provocative paradigms that tried to elicit this emotion in experimental settings.

For example, EEG studies showed that the externalization of anger increases the left prefrontal activity after an anger-induction task (e.g. negative evaluation of a writing task) (Harmon-Jones & Sigelman, 2001), whereas suppression of this emotion is related to increased right prefrontal activity (Carver & Harmon-Jones, 2009; Harmon-Jones & Gable, 2018; Kelley et al., 2017), such as when anger is suppressed in interracial contexts (Zinner et al., 2008).

This pattern is also confirmed by stimulatory techniques that can modulate the prefrontal asymmetry, heightening the left or the right prefrontal activity and measuring the consequences linked to angry behaviors. For example, anodal transcranial direct current stimulation (tDCS) of the left dorsolateral PFC produced higher anger and more aggressive behaviors during a social interaction game (the Taylor Aggression Paradigm) (Hortensius et al., 2012), while the stimulation of the right dorsolateral PFC increased rumination, which is associated with anger suppression and inhibition (Kelley et al., 2013).

However, very few studies took into account individual differences in anger behaviors. For example, Harmon-Jones and colleagues (1998) found that anger scores (Buss and Perry Aggression Questionnaire; Buss et al., 1992) were positively associated with greater left (than right) cortical activity. In this way the authors concluded that also dispositional anger was linked to the prefrontal asymmetry.

However, the questionnaire used in this study (Buss and Perry Aggression Questionnaire) measured anger with sentences more linked to its expression rather than its experience (e.g. "When frustrated, I let my irritation show" or "some of my friends think I'm a hothead"). Instead, another questionnaire takes into account the individual differences distinguishing between various facets of anger: the State-Trait Anger Expression Inventory (STAXI) proposed by Spielberger (1999). Indeed this questionnaire not only measures individual differences in trait anger, but also effectively distinguishes between the tendency to externalize anger (anger-out scale) or internalize it (anger-in scale). For this reason, this questionnaire has been taken into account in the present study.

In addition, a limitation of the previous studies is the poor specificity of the techniques used (such as EEG or tDCS), not allowing the identification of specific brain regions, and their interaction, that are associated with the tendency to externalize or internalize anger. Therefore, we decided to rely on resting-state functional connectivity (rs-FC) to perform our study. Indeed, relying on rs-FC and self-report data rather than task-based measurements has been considered a more reliable alternative (Elliott et al., 2020; Poldrack et al., 2017).

Therefore, the aim of this study is to investigate the relationship between individual differences in the experience of anger, and in particular in the externalization and internalization of anger-related behaviors measured through the STAXI, and the frontal asymmetry hypothesis.

Moreover, for this aim, we rely for the first time on a rs-FC approach in order to better understand not only the role of the frontal asymmetry but also the role of specific brain regions and their connectivity patterns.

On the basis of the previous literature, if the frontal asymmetry is more associated with emotional reactions, I expect that the externalization of anger would be associated with left rs-FC patterns (Hewig et al., 2004), while the internalization of anger would be associated with right ts-FC patterns (Zinner et al., 2008; but see Hewig et al., 2004). This view would be particularly in line with the hypothesis that links the frontal asymmetry with the revised Reinforcement Sensitivity Theory (Lacey et al., 2020), given that the internalization of anger can be interpreted as an effortful inhibition and internalization of the approach motivation associated with anger (Spielberger, 1988).

A second scenario, also in line with the association of the left frontal connectivity with the externalization of anger and the right frontal connectivity with the internalization of anger, would rely

on the standard motivational-direction model. However, in this case I would expect an association between the BAS, the externalization of anger and the left frontal connectivity on one side, and an association between the BIS (the standard scale linked to withdrawal motivation), the internalization of anger and the right frontal connectivity on the other side.

Therefore, the second aim of this study is to understand whether the frontal asymmetry is more explained by individual differences in emotional reactions (anger out and anger in scales, which explain the tendencies to express or suppress and control anger) or by individual differences in classic behavioral motivations (BAS and BIS scales, which explain the tendencies to behaves in line with approach or withdrawal motives).

Indeed, individual differences in BAS could be associated with both higher left frontal activity and the externalization of anger, and individual differences in BIS can be associated with both higher right frontal activity and the internalization of anger. However, another possibility is that the behavioral systems and the reactions to anger are independent constructs and the asymmetry in rs-FC patterns can be specific for one of them. To this aim, we also tested the correlation between anger out and BAS on one side, and anger in and BIS on the other side.

Finally, both hypotheses on behavioral motivations (the Reinforcement Sensitivity Theory and the revised one) poorly considered the previous studies that associate depression to higher right frontal activity when compared to the left one at rest (Henriques and Davidson, 1991). To better understand this point, we decided to test a possible correlation between the Beck Depression Inventory (BDI, Beck et al., 1961) and both the anger-in scale of the STAXI and the BIS scale. Indeed, in line with previous hypotheses we could expect positive correlations of the BDI with anger-in and BIS.

Methods¹¹

Participants:

For our study we capitalized on the data derived from the MPI-Leipzig Mind Brain-Body dataset (OpenNeuro Dataset, <u>http://openneuro.org</u>, RRID:SCR_005031, accession number ds000221), made available by an extended cross-sectional project conducted at the Max Planck Institute (MPI) of Human Cognitive and Brain Sciences in Leipzig, Germany and approved by the ethics committee of

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the University of Leipzig (097/15-ff) (Mendes et al., 2019). This open-access database comprises behavioral and MRI data from a sample of 318 participants.

Participants were recruited through online and poster advertisement and had to give the informed consents in order to participate in the project, furthermore they were informed of a monetary refund obtainable at the end of the research. Prior to the effective participation in the research project, subjects were screened for past and present psychiatric and neurological disorder and had to be considered medically eligible to undergo magnetic resonance sessions; also, they had to fulfil the MRI safety requirements of the MPI-CBS (Mendes et al., 2019). For the current research, 71 healthy subjects (M = 42; F = 29) with mean age of 26.02 (\pm 3.53) were selected on the basis of the following criteria: availability of both structural and resting-state functional Magnetic Resonance Imaging (rs-fMRI) images, age between 20 and 40 years of age (age was indicated in a 5 years bin, where the middle value was used for calculations), and availability of the STAXI and BIS/BAS questionnaires' scores (see next section for more details).

Behavioral data:

To study the individual differences behind externalizing or internalizing anger the scores from the Anger-Out and Anger-In scales of the STAXI (Spielberger, 1999) were taken into account. Anger-Out measures the inclination to direct anger outwards (e.g externalizing anger; items included in this scale are: "Faccio cose come sbattere le cose" or "Dico delle cattiverie"), and Anger-In measures the tendency to internalize anger and to suppress or inhibit it (items included in this scale are: "Rimugino dentro e non ne parlo con nessuno" or "Mi sento bollire dentro ma non lo manifesto") (Spielberger, 1999). Mean scores for Anger-In was of 15.87 (±4.32), and for Anger-Out was of 12.03 (±3.1).

To measure differences in motivational systems, the BIS/BAS questionnaire (Carver & White, 1994) was taken into account. The BIS scale aims at investigating the motivational incentives behind behavioral avoidance and inhibition such as concerning about the possibility that something risky may happen (items included in this scale are: "Di solito, quando penso che mi succederà qualcosa di spiacevole divento ansioso/a" or "Mi sento preoccupato/a quando penso di aver fatto qualcosa in modo inadeguato"); on the other hand, BAS scale provides a measure of the reward sensitivity and of the desire to achieve goals, from which we activate approach behaviors (items included in this scale

are: "Normalmente quando voglio qualcosa faccio tutto quello che posso per ottenerla" or "Agisco spesso in base all'impulso del momento").

. The mean scores of BIS was of 20.62 (±2.95), and for BAS of 37.69 (±3.73).

MRI data acquisition:

A high-resolution structural scan and four rs-fMRI scans were collected on a 3T Siemens Magnetom Verio scanner (Magnetom Verio, Siemens Healthcare, Erlangern, Germany) for each participant (Mendes et al., 2019). Two gradient echo field maps, two pairs of spin echo images with reversed phase encoding direction and a low-resolution structural image using a FLAIR sequence for clinical screening were additionally captured (Mendes et al., 2019).

The structural – T1 weighted – acquisitions were obtained using the MP2 RAGE sequence (Marques et al., 2010), with the following parameters: TR = 5000 ms; TE = 2.92 ms; TI1 = 700 ms; TI2 = 2500 ms; flip angle₁ = 4 °; flip angle₂ = 5 °; voxel size = 1,0 mm isotropic; duration = 8.22 min (Mendes et al., 2019).

The rs-fMRI images were recorded utilizing GE-EPI sequence and they set these criteria: voxel size = 2,3 mm isotropic; FOV = 202 x 202 mm2; imaging matrix = 88 x 88,64 slices with 2,3 mm thickness; TR = 1400 ms; TE = 39,4 ms; flip angle = 69 °; echo spacing = 0,67 ms; bandwidth = 1776 Hz/Px, partial Fourier 7/8, no pre-scan normalization, multiband acceleration factor = 4, 657 volumes, duration = 15.30 min) (Mendes et al., 2019).

Pre-processing

All images were pre-processed with CONN toolbox (Connectivity Toolbox, https://www.nitrc.org/projects/conn, RRID:SCR 009550;) running through MatLab R2019a (MATLAB, http://www.mathworks.com/products/matlab/, RRID:SCR 001622, MathWorks, Inc., Natick, MA, USA) and SPM12 (SPM, https://www.fil.ion.ucl.ac.uk/spm/software/spm12/, RRID:SCR 007037;) software. The default pipeline was executed with the following steps: functional realignment and unwarping, translation and centering, functional outlier detection (conservative settings), functional direct segmentation and normalization (2mm resolution), structural translation and centering, structural segmentation and normalization (2 mm resolution), functional and structural smoothing (spatial

convolution with Gaussian kernel 8 mm). Then, a component-based noise correction procedure (CompCor) was run during the denoising step; in this way, the artefactual sources generated from head movements or physiological effects (e.g., respiration rate) were removed.

Finally, the quality of the data was checked through Quality Assurance plots showing the homogeneity of the global activation.

Functional connectivity analyses

To examine the rs-FC across multiple brain regions in relation to the behavioral data, a Multivariate ROI-to-ROI Connectivity (mRRC) matrices analysis was conducted using CONN toolbox. This analysis was adopted to study multivariate models predicting each voxel BOLD signal from all the ROIs simultaneously. Mean time-series of each ROI were extracted from the pre-processed data. Subsequently, a ROI-to-ROI analysis was performed in CONN, where a bivariate correlation was computed between the time courses of the selected ROIs. To test the hypothesis of a frontal asymmetry, we included all the frontal regions considered by CONN: inferior frontal gyrus (IFG); lateral PFC; frontal eve field (FEF); rostral PFC, anterior cingulate (AC); medial PFC; IFG pars opercularis and pars triangularis; middle frontal gyrus (MFG); superior frontal gyrus (SFG); frontal pole (FP); orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC). CONN's default atlas - FSL Harvard-Oxford Atlas - generated the set of ROIs (Whitfield-Gabrieli & Nieto-Castanon, 2012). Correlation coefficients underwent Fisher's r-to-z transformation to ensure the normality of the distribution. Finally, a General Linear Model was performed as second level analysis to examine the relation between the rs-FC values previously obtained and the Anger-Out, Anger-In and BIS/BAS scales' scores. Results were considered significant at a level threshold of p < 0.05 false discovery rate (FDR) corrected. CONN software was also used to visualize ROI-to-ROI connectivity.

Results¹²

Brain activity

The degrees of association (rs-FC values) between each pair of regions (source-seed selected to enter the ROI-to-ROI analysis) per subject were extracted. Then, to obtain an account of the connectivity modulation by the STAXI behavioral measures, the association between the scales' scores and the rs-FC values was evaluated. As predicted, a left frontal rs-FC pattern was significantly associated with Anger-Out, whereas a right frontal rs-FC pattern was significantly associated with Anger-In. Specifically, the results revealed a rs-FC pattern including the left IFG pars opercularis and the left FEF (T(66)=-3.50; p= 0,019) (part of the vIPFC and dIPFC respectively), as significantly modulated by Anger-Out (see Figure 4.1 for more details). This finding demonstrates the left lateralized modulation returned by the outward expression of anger. Moreover, results revealed several rs-FC patterns including right lateralized regions of the dIPFC and vIPFC, that were significantly modulated by Anger-In (see Figure 4.1 for more details). Specifically, we found a relationship between the right rostral PFC, and the right OFC (T(66)=-4.13; p= 0.001), the right IFG pars triangularis (T(66)=-3.71; p= 0.003), the right SFG (T(66)=-3.40; p= 0.007), the right MFG (T(66)=-3.21; p= 0.008), the right IFG (T(66)=-3.24; p= 0.008), the right lateral PFC (T(66)=-3.15; p=0.008), the right FP (T(66)=-4.21; p= 0.001) and the right IFG pars opercularis (T(66)=-2.87; p=0.016). The right lateral PFC resulted connected with the ACC (T(66)=-3.80;p= 0.007), the AC (T(66)=-3.52; p= 0.009) and the right rostral PFC (T(66)=-3.15; p=0.019); the left rostral PFC was related to the right IFG pars opercularis (T(66)=-3.09; p= 0.048), the right FP (T(66)=-2.82; p= 0.048), the right MFG (T(66)=-2.77; p=0.048), the right lateral PFC (T(66)=-2.66; p=0.048) and the right OFC (T(66)=-2.63; p=0.048); the ACC was connected with the right FP (T(66)=-3.82; p=0.004), the right lateral PFC (T(66)=-3.80; p=0.004), the right MFG (T(66)=-3.68; p= 0.004) and the right SFG (T(66)=-2.94; p = 0.026); then, the AC was found to be related to the right lateral PFC (T(66)=-3.52; p=0.011), the right FP (T(66)=-3.47; p= 0.011), the right MFG (T(66)=-3.05; p= 0.025) and the right OFC (T(66)=-2.88; p= 0.031). These findings demonstrate a predominant right lateralized pattern modulated by internalizing anger. See Figure 4.1 for more details. No significant rs-FC pattern for the BIS/BAS scales was visible (FDR p < 0.05).

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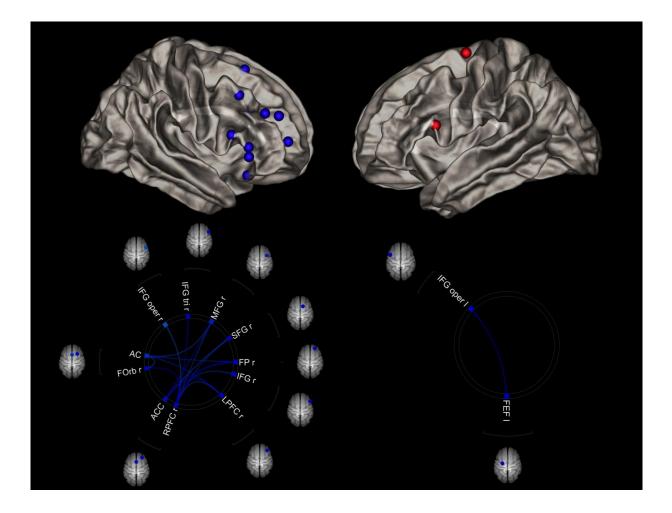


Figure 4.1 The frontal functional patterns of anger internalization and externalization. Functional patterns of brain areas associated with the internalization of anger (on the left) and the externalization of anger (on the right), respectively involving right versus left frontal regions. In particular, anger-in scores were significantly associated with the connectivity of the right frontal orbital and rostral areas, the AC, the right IFG, MFG and SFG. On the other hand, anger-out scores were significantly associated with the left FEF and IFG. Adapted from Consolini et al., under revision.

Additional results

Additionally, to further explore a possible relation between externalizing and internalizing anger on one hand, and approach and withdrawal motives on the other hand, we computed the correlations between Anger-Out and BAS scales that returned to be not significant (r= 0.0156, p= 0.8973), and the correlation between Anger-In and BIS scales, again not significant (r= 0.1732, p= 0.1485). Finally, we found a significant positive correlation between the Anger-In scale and the BDI (r=0.3744, p= 0.0013).

Discussion

Anger and the frontal asymmetry hypothesis

This study aims to investigate the relationship between the frontal asymmetry hypothesis and the individual differences in the experience of anger, and in particular of the externalization and internalization of anger-related behaviors measured through the STAXI.

At first, differences in the frontal left and right activity were conceptualized in the *affective-valence hypothesis*, which consisted in the fact that higher left frontal activations were associated with positive emotions while higher right frontal activations were associated with negative emotions, such as sadness and anxiety (Davidson, 2004; 1992; 1984).

However, the study of anger, a negative emotion characterized by an approach motivation rather than a withdrawal one as other negative emotions, has confutated this hypothesis. Indeed, anger is associated with higher levels of left frontal activity (Harmon-Jones, 2004). Therefore, this hypothesis was updated with the *motivational-direction model*, which associates higher levels of left frontal activity to approach motivations and behaviors, and higher levels of right frontal activity to withdrawal ones (Harmon-Jones, 2004; Van Honk and Schutter, 2006).

The aim of this study is to better clarify the role of rs-FC in the frontal asymmetry hypothesis, in particular distinguishing between patterns of behavioral tendencies and patterns of affective reactions. To this aim, we relied on two questionnaires: the Anger-Out and Anger-In scales of the STAXI (Spielberger, 1999) and the Behavioral Activation System (BAS) and Behavioral Inhibition System (BIS) scales of the BIS/BAS questionnaire (Carver & White, 1994). Individual differences in the STAXI show that higher scores in the Anger-Out scale are associated with the tendency to express angry reactions toward provoking stimuli externalizing anger, while higher scores in the Anger-In scale are associated with the tendency to inhibit angry reactions toward provoking stimuli, internalizing this emotion and suppressing its aggressive motives. On the other hand, individual differences in the BIS/BAS questionnaire show that higher scores in the BAS scale are associated with the tendency to express and the BIS/BAS questionnaire show that higher scores in the BAS scale are associated with the tendency to the express behaviors linked to the appetitive motives' regulation, while higher scores in the BIS scale are

associated with the tendency to behave avoiding aversive events and detecting anxious stimuli in the environment (Gray, 1990; Leone et al., 2002).

In the past, higher levels of left frontal activity have been associated with tendencies to behave in line with both the Behavioral Activation System (Amodio et al., 2008; Coan & Allen, 2003; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997; Watson et al., 2016) and some aspects of anger externalization (d'Alfonso et al., 2000; Hortensius et al., 2012), while higher levels of right frontal activity have been associated with tendencies to behave in line with both a Behavioral Inhibition System (Sutton & Davidson, 1997; Watson et al., 2016) and the internalization or suppression of anger (Zinner et al., 2008).

However, it is still not clear whether the frontal asymmetry is more associated with behavioral tendencies or emotional reactions, given the heterogeneity of previous results. In addition, the previous studies usually took into account experimental paradigms, while individual differences of self-report scales that clearly distinguish between these features were poorly considered, especially when dealing with anger.

This study shows for the first time that individual differences in emotional reactions elicited by anger are associated with rs-FC frontal asymmetry patterns, while this was not the case for behavioral tendencies.

Furthermore, the specific brain areas involved in this hypothesis have not been defined yet, since the majority of studies relied on low specificity measures such as EEG and tDCS.

On the contrary, this study relies on a methodology that allows the identification of brain regions whose connectivity is associated with the tendency to externalize and internalize anger.

In particular, the former was found to be related to the left frontal connectivity between the IFG pars opercularis of the vIPFC and the left FEF area of the dIPFC, while the latter was found to be related to different patterns of connectivity especially in the right frontal brain area. This lateralized pattern involved the right rostral and lateral PFC, the right OFC, the right inferior, middle and superior FG and the AC.

Instead, no frontal connectivity pattern was found to be associated with the BIS/BAS scale.

These findings suggest that the frontal asymmetry hypothesis could be more specifically associated with emotional reactions and motivational control rather than behavioral activation tendencies, at least when considering the rs-FC patterns of frontal brain regions.

In particular, in line with recent evidence (see Lacey et al., 2020), our results suggest that the frontal asymmetry is not simply associated with approach and withdrawal tendencies. In particular, our findings seem to be more coherent with a new hypothesis that links higher left frontal activity to approach motivation and higher right frontal activity to an effortful control of motivation (Lacey et al., 2020). Indeed, the externalization of anger can be considered the expression of the automatic behavior associated with anger experience, and we found that this emotional reaction is linked to left frontal connectivity. On the other hand, the internalization of anger can be considered the inhibition of the natural impulses that characterize anger, which is indeed internalized and suppressed. We found that this emotional reaction, which can be also considered as an effortful control of this natural motivation, is linked to right frontal connectivity.

This and previous evidence confutated the affective valence hypothesis based on the fact that left frontal activity is associated with positive emotions while right frontal activity is associated with negative emotions (Davidson, 1984). Nevertheless, this hypothesis was particularly supported by the fact that patients with depressive symptoms showed higher right frontal activity in different contexts (Pizzagalli et al., 2002; Henriques and Davidson, 1991). However, the new hypotheses on approach motivation and its control (respectively linked to left vs. right frontal activity) poorly took into account the evidence on the association between depression and the frontal asymmetry. In order to better understand this point, also the Beck Depression Inventory was considered, finding a positive correlation with the internalization of anger (anger-in scale of the STAXI).

Depression is known to be a disorder associated with high levels of rumination, which is the tendency to recycle, repeat, and reiterate negative and intrusive thoughts. Interestingly, this pattern of thinking seems to be more associated with cognitive inhibition, when compared to both perceptual and behavioral inhibition (Introzzi et al., 2016).

Interestingly, anger rumination has been also associated with right frontal regions (Fabiansson et al., 2012). Indeed, higher right frontal activity induced by the tDCS, is not only linked to a decrease in aggression (Dambacher et al., 2015) but also to increased rumination on the angering event: it was

found that the same stimulation parameters combined with interpersonal insults and the impossibility of an aggressivity response, produces more ruminative thoughts in the experimental condition than in control (Kelley et al., 2013). These data and the correlation between the BDI and the internalization of anger suggest that the higher levels of right frontal activity characterizing these patients could be associated in particular with ruminative processes, also when considering the emotion of anger and its internalization.

The frontal connectivity patterns associated with the externalization and internalization of anger

Regarding our results, anger out was associated with rs-FC of the left FEF and IFG pars opercularis. This is in line with previous studies. Indeed, the left IFG has been associated with the experience of anger (Sorella et al., 2021) also when considering individuals characterized by high trait anger (Tonnaer et al., 2017). In addition, the stimulation of this area with tDCS has been found to increase aggression, and so the externalization of anger, after the induction of frustration (Gallucci et al., 2020). Instead, the FEF is a region associated not only with oculomotor coordination, but also with visual attention (Brooks and List, 2006). In particular, it has been proposed that individuals with high levels of trait anger or hostility are characterized by biases in the attentional domain, since attention directed toward negative and hostile stimuli seems to be higher (Sorella et al., 2021; 2021b; Walters et al., 2016; Wilkowski and Robinson, 2008). In addition, the FEF receives input from the Supplementary Eye Field (SEF), which is involved in goal-directed behavior receiving information about the environment and value from regions such as the OFC and the amygdala (Stuphorn, 2015).

Therefore, these regions of the left PFC could be linked to the attentional bias characterized by hostility and/or goal-directed motivations that lead to the externalization and expression of anger.

On the other hand, rs-FC was modulated by the internalization of anger when considering a pattern of different brain regions: the rostral and lateral PFC, the OFC, the FP, the SFG, the MFG, the IFG and the AC. According to previous studies, the ventrolateral areas in particular seems to be involved in ruminative processes after the elicitation of anger (Fabiansson et al., 2012; Gilam et al., 2017), showing that these areas can be responsible for an effortful control of this emotion through its internalization. Furthermore, in Chapter 2 of this thesis it has been proposed that the activity of the

right IFG in particular could be linked to a process of conceptualization of anger that can be followed by the regulation of this emotion through different processes. These processes can involve emotional labeling, that has been shown to produce the regulation of the emotion (Lieberman et al., 2007; Lieberman, 2011), interpersonal reappraisal in particular during interpersonal games that can elicit anger (Grecucci et al., 2013a, b, c), inhibition of the behavior (Aron et al., 2014) and top-down regulation of subcortical structures such as the amygdala (Morawetz et al., 2016). Therefore, during the internalization of anger, these processes could be involved resulting in the reduction or the inhibition of this emotion.

Instead, the dIPFC, which includes the SFG and MFG, may be involved in processes characterized by higher levels of cognition, such as reappraisals and more explicit emotion regulation strategies (Buhle et al., 2014; Grecucci et al., 2013b, c, Messina et al., 2021; Ochsner & Gross, 2005). These involve, for example, the suppression of anger expression and aggressive behaviors; indeed, the stimulation of the dIPFC has been shown to produce a reduction in behaviors linked to anger externalization (Dambacher et al., 2015).

The OFC is also involved in emotion regulation; in particular, when anger is elicited the orbitofrontal cortex seems to integrate anger-provoking perceptions from temporal input, and to exert inhibitory control of the aggression that follows anger; actually, reductions of OFC output and frontal dysfunction result in unregulated and disinhibited aggression (Potegal and Stemmler, 2010). Further, alterations of the OFC, in particular when considering its connections with the amygdala, have been found in clinical populations characterized by aggressive and antisocial behaviors (Coccaro, 2012; Coccaro et al., 2007; New et al., 2009).

Finally, the AC has a role in the regulation of emotions (Grecucci et al., 2013b, c) and in particular in the regulation of aggressive impulses (Coccaro, 2012; Frankle et al., 2005; New et al., 2002; Rosell & Siever, 2015) and social interactions (Etkin et al., 2011; Lavin et al., 2013; Rigoni et al., 2010; Sanfey et al., 2003), for example when empathy is involved (Gu et al., 2010; Lamm et al., 2010; Lavin et al., 2013; van Veen & Carter, 2002). To summarize, all of these regions seem to play key roles in the regulation of emotions and anger in particular, and results of this chapter also suggest a specific role in the internalization and inhibition of anger.

Conclusions

This study confirms and extends previous results regarding the frontal asymmetry hypothesis. In particular, for the first time rs-FC was applied to understand the link between anger and patterns of frontal connectivity, finding a left pattern associated with anger externalization involving the left FEF and IFG, and a right pattern associated with anger internalization involving the rostral and lateral PFC, the OFC, the FP, the superior, middle and inferior frontal gyri and the AC.

The first hypothesis on the frontal asymmetry, the affective-valence hypothesis, argued that the left frontal activity was associated with positive emotions while the right frontal activity was associated with negative emotions. According to this hypothesis, anger should be associated with higher levels of right frontal activity, but this is not the case.

The second hypothesis on the frontal asymmetry, the motivational-direction model, argued that the left frontal activity was associated with approach motivation while the right frontal activity was associated with withdrawal motivation. According to this hypothesis, anger has been associated with higher levels of left frontal activity in previous studies. However, no study took into account individual differences in the externalization or internalization of anger. For the first time, this study shows that the externalization of anger is associated with patterns of left frontal connectivity, while the internalization of anger is associated with patterns of right frontal connectivity. This is in line with a recent update of the motivational-direction model, based on the revised Reinforcement Sensitivity Theory. In particular, according to this innovative hypothesis, the left frontal activity is associated with approach motivation but the right frontal activity is not simply associated with withdrawal motivation but with an effortful control of motivation. Given that anger is characterized by an approach motivation, the fact that we found that its internalization is associated with right frontal connectivity confirms that this area is linked with the inhibition and control of the early and automatic motivation associated with anger. In addition, it was found that the internalization of anger is also associated with depressive symptoms, giving a possible explanation on the reason why depression has been associated with higher right frontal activity: not only for the prevalence of negative emotions such as sadness and anxiety (as postulated by the affective-valence hypothesis), but also, and probably more specifically, for the tendency to ruminate and suppress natural instincts that characterize this disorder.

Future studies are needed to better understand this process and the potential implications in the treatment of disorders characterized by excessive levels of anger externalization or internalization.

However, in order to better understand which is the optimal way to regulate anger, a new paradigm should be developed. Indeed, there are different paradigms used to evaluate anger and aggression in literature, such as social games (see chapter 2 for more details), but there are no validated ones specifically developed to investigate anger and its regulation. To exceed this limit, in the next chapter a new paradigm to study anger and its regulation will be presented. In particular, different stimuli were developed and validated in order to specifically evoke an experience of anger in the participants. Then, the aim of the next chapter is to understand whether different ways to regulate anger will be used on the basis of the intensity of this emotion. Indeed, there is evidence in literature that threatening images lead to regulating them with a specific strategy according to the intensity of the elicited emotion. In particular, cognitive strategies seem to be applicable only when the intensity of the emotion is lower, given the need of available resources in order to engage a new cognitive process. However, anger has never been taken into account when considering this effect. Therefore, the next chapter will explore the role of anger intensity in emotion regulation.

Chapter 5

Study 4: The role of reappraisal and suppression in the regulation of anger

This chapter aims to understand when specific regulatory strategies of emotions are used in people's life to regulate anger. In particular, two specific strategies will be evaluated: reappraisal and suppression. The first is a cognitive strategy in which the meaning of the event that elicits anger is actively evaluated with a new meaning that usually allows one to experience a lower level of anger. Instead, suppression is a behavioral strategy in which the reactive response to anger (e.g. aggression) is actively suppressed in order to avoid its possible consequences. In the next section, these two strategies will be discussed and evaluated, in particular when considering the intensity of anger elicited in different (simulated) social situations.

Introduction

Emotion regulation refers to the modulation of the type of emotion a person experiences, when it is experienced or expressed, and how it evolves over time. This process is characterized by three core features: the activation of a goal linked to the modification of the emotion-generative process, the engagement of the processes needed to achieve this modification, that can be explicit or implicit, and the impact of these processes on the emotional dynamics (Gross, 2014).

The most prevalent model in this field is the Process Model of Emotion Regulation (Gross, 1998). This model is based on the Modal Model of emotions, according to which the dynamics of emotions consist in a sequence of steps. At the beginning there is a psychologically relevant situation, internal or external; then, the attention can be oriented toward this situation in different ways, leading in turn to different kinds of appraisals. The appraisal represents the individual evaluation of the situation's meaning. Finally, there is an emotional response that can also lead to environmental changes. This

process of situation-attention-appraisal-response can reoccur many times, where the final response of a cycle can lead to a subsequent environmental change that represents the initial "situation" of a new cycle.

The Process Model of emotion regulation considers each of these steps of the emotion generation process as a possible target for regulation. Specifically, there are five different points in the emotion generation process at which individuals may apply a different type of regulatory process. Regarding the situation that elicits the emotion generation process, one can regulate the emotion through either a (1) situation selection process or a (2) situation modification process. These regulatory strategies refer, respectively, to actions that make the situation more (or less) likely to happen, or that can actively modify the situation, in order to modulate the generation of the emotion that can be associated with that particular context. Instead, the (3) attentional deployment is a regulatory strategy that involves directing the attention in a particular way in order to modulate the emotion, and it is linked to the "attentional" step involved in the emotion generation process. Then, the appraisal of the situation can be targeted by regulatory strategies that involve a (4) cognitive change. This step involves a modification of the appraisal (that is defined as "reappraisal") linked to the situation itself or to the ability of the individual to cope with that situation, in order to alter the emotional significance, and thus, the emotional experience. Finally, there can be a (5) response modulation in the latest step of the emotion-generative process, which involves the direct influence of the experiential, behavioral or physiological components of the emotional response.

From this model, different regulatory strategies have been compared in literature. Two kinds of strategies have been particularly explored, especially when considering their consequences: reappraisal and suppression.

Reappraisal can be defined as a change in the personal attribution and significance of a situation, in order to modulate the emotional process elicited by that situation. Therefore, this is a cognitive change that can be applied during the appraisal step of the emotion generation process. On the other hand, suppression is a behavioral form of regulation that consists in the decreasing of the emotion-expressive behavior. Therefore, this step happens late in the process of emotion generation, after the occurrence of the cognitive components characteristic of appraisal and/or reappraisal.

Several researchers demonstrated that these two regulatory strategies can have different consequences from affective, cognitive and social perspectives. In particular, from an affective perspective, suppression leads to decreased positive but not negative emotional experience, and this could be related to the fact that suppression also leads to increased amygdala activity (Goldin et al., 2008) and sympathetic activity (Gross, 2014; Demaree et al., 2006; Harris et al., 2001; Richards and Gross, 2000; Gross, 1998; Gross and Levenson, 1993; 1997; Stepper and Strack, 1993). From a cognitive perspective, suppression leads to a worse memory performance (Johns et al., 2008; Richards et al., 2003; Richards and Gross, 1999; 2000; 2006; Gross, 2014) whereas from a social perspective it leads to less positive and emotionally close relations with others (English et al., 2013; Gross & John, 2003; Srivastava et al., 2009; Gross, 2014).

On the other hand, reappraisal leads to more positive outcomes (Gross, 2014), since it is linked to decreased levels of negative emotions (Gross, 1998; Feinberg et al., 2012; Lieberman et al., 2011; Ray et al., 2010; Wolgast et al., 2011; Szasz er al., 2011) and reduced amygdala activation (Goldin et al., 2008; Ochsner & Gross, 2008; Ochsner et al., 2004). Therefore, even if the effects can vary on the basis of the contexts, reappraisal seems to be preferable. In addition, when reappraisal is compared to suppression, it is associated with better interpersonal functioning and well-being (Gross and John, 2003).

Given that many studies investigated the effect of these regulatory strategies by asking participants to apply them, there is little evidence on the antecedents that lead people to choose one specific strategy to regulate their emotions in life. In other words, *When do we tend to prefer one strategy over the other?* To answer this question, Sheppes and colleagues (2011) developed the emotion regulation choice paradigm, in which after the presentation of emotional stimuli participants can choose the strategy they would use to regulate the emotion. Relying on this paradigm, they found that for low-intensity stimuli the preferred strategy is reappraisal, while for high-intensity stimuli the preferred strategy is distraction. Distraction is a regulatory strategy linked to the attentional deployment stage and involves the disengagement from negative emotions, for example by producing neutral thoughts (Sheppes et al., 2011). This finding can be explained by the fact that reappraisal, being a cognitive strategy, requires the availability of cognitive resources needed to change the significance and the interpretation of the situation. Indeed, it has been found that working memory abilities influence not

only the capacity to avoid the expression of negative emotions, but also the ability to use reappraisal (Schmeichel et al., 2008).

Differently from other projects that compared distraction and reappraisal, in this research I aim to compare the cognitive strategy based on reappraisal with suppression, a behavioral strategy that has a later influence on the emotion-generative process. In addition, previous evidence also suggests that when reappraisal and suppression are compared, the usage of the former requires higher levels of cognitive resources in particular when the emotional intensity is higher (Ortner et al., 2016; Szczygieł and Baryła, 2019). However, in this research I decided to rely on the emotion regulation choice paradigm in which, differently from previous studies, participants can choose the preferred regulatory strategy for each emotional stimulus. In particular, a new paradigm that includes the simulation of different interpersonal situations that can elicit anger is presented, in order to understand whether the emotional intensity influences the choice of the regulatory strategy. On the basis of the reviewed literature, I expect that when the intensity of anger is lower, reappraisal can be successfully chosen to regulate the emotion. On the other hand, when anger intensity is higher, I expect that the lower availability of the cognitive resources lead people to choose suppression, given the difficulty to rely on the remaining cognitive resources in order to regulate a more intense emotional state.

Furthermore, in order to evaluate the consequence of the usage of reappraisal vs. suppression, I compared the mean level of anger in the following trial. In particular, I distinguished the mean level of anger when the participant chose reappraisal vs. suppression in the previous trial. Finally, to better understand whether these consequences on anger level are more linked to the previous regulatory strategy applied or to the previous level of anger's intensity experienced in the antecedent trial, I applied a General Linear Model. In particular, I expect that after the usage of reappraisal, the mean level of anger experienced in the following trial would be lower when compared to the usage of suppression. However, if the first hypothesis is true, reappraisal is used when anger intensity is lower. Therefore, both the chosen strategy and the level of anger could influence the level of anger in the following trial. Therefore, in the GLM I will evaluate not only whether the effect of the chosen regulatory strategy, but also that of the level of anger in the previous trial, can influence the level of anger experienced in the following trial.

Methods

This study involved 67 participants (55F, mean age = $23,30\pm2,54$), who performed a new study developed to investigate the experience of anger and its regulation (Mattevi et al., 2019). The task is based on the emotion regulation choice paradigm of Sheppes and colleagues (2011) in which participants are presented with stimuli and then they choose a regulatory strategy that they would apply to regulate the elicited emotion (see Figure 5.1).

The task consisted in 60 trials and each of them included the fixation point (1000ms), the presentation of a stimulus (5000ms), the evaluation of the level of anger experienced (7 point Likert Scale) and the choice of a regulatory strategy (Reappraisal, Suppression or nothing).

The stimuli were created in a previous phase (see next section), and 30 provocative target stimuli and 30 neutral stimuli were selected for the present research. Each of them included a verbal stimulus describing a situation and a neutral face used to simulate the agent of the interpersonal event. Images were taken from the Chicago Face Database (CFD; Ma, et al., 2015).

A paired-samples t-test was conducted to compare the mean level of anger for each participant associated with the usage of reappraisal vs. suppression, in order to determine if one strategy is preferred with high vs. low levels of anger.

A paired t-test was conducted to compare the mean level of anger for each participant used in trials that follow the usage of reappraisal vs. suppression, in order to see if the usage of one strategy can influence the following experienced level of anger.

Finally, in case of significant results in both of the previous analyses, a generalized linear model would be applied to determine whether the level of anger in a specific trial vs. the usage of a specific strategy in the same trial (or an interaction between these factors) is more responsible for the level of anger in the following trial.

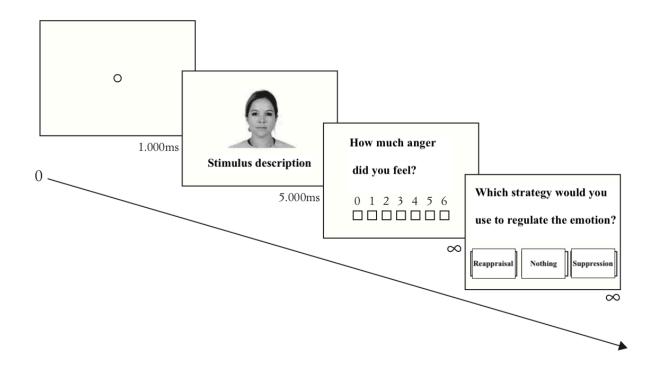


Figure 5.1 Example of a stimulus presentation. The experimental procedure consisted in a fixation point (1000ms) followed by the presentation of the stimulus: a face representing the agent associated with a description of the situation (see Appendix for more details); then, the stimulus was followed by the evaluation of the level of anger experienced (7 point Likert Scale) and the choice of a regulatory strategy (Reappraisal, Suppression or nothing, in different order for different participants). Adapted from Mattevi et al., 2019.

Stimuli creation

At an earlier research stage, 120 stimuli were selected and included in the research paradigm. 60 of them were provocative and elicited anger, while 60 of them were neutral. However, in this study only 30 target stimuli and 30 neutral stimuli were used.

The stimuli were created on the basis of possible situations that can elicit anger based on different questionnaires' items or theories on $anger^{13}$. The stimuli were created on the basis of the model of Tripp and Bies (2010), according to which anger in interpersonal situations can be elicited by three kinds of situations: goal blockage, injustice and humiliation. After the creation of the stimuli, a free nomination task was used to evaluate the stimuli. Following the presentation of each stimulus, the participants (N=53, M=17, mean age= 25,85 ± 3,54) were asked to write the elicited emotion (for example "sadness", "anger" or "nothing" if no emotion was elicited). In a second step, stimuli that

¹³ Anger Control Inventory (ACI; Hoshmand and Austin, 1987); Anger Provoking situations (Törestad, 1990); The Clinical Anger Scale (CAS; Snell et al., 1995); Multidimensional Anger Inventory (MAI; Siegel et al., 1986); Novaco Anger Scale (NAS; Novaco, 1994); The Reaction Inventory (RI; Evans and Stangeland, 1971); Subjective Anger Scale (SAS; Knight et al., 1985).

elicited "anger" (or synonyms such as "rage") most frequently as a response were selected for further evaluation, in which participants were asked to evaluate the level of anger for each stimulus in a scale from 0 to 6. From this task, 45 target stimuli and 45 neutral stimuli were selected for the experiment, in which they were associated with a face (half of them with a male and half of them with a female, randomized). A list of all stimuli is in the appendix. For further information about the creation of the stimuli, see Mattevi et al., 2018; 2019.

Reappraisal

The description of Reappraisal strategy was adapted from Grecucci et al., 2013c:

Reinterpretazione: Il modo in cui valutiamo un evento influisce sul modo in cui lo viviamo: una stessa situazione può risultare più o meno negativa in base a come la percepiamo. Se una persona ci guarda storto per strada potrebbe avercela con noi, evocando emozioni spiacevoli, che possono cambiare se pensiamo invece che le dia semplicemente fastidio il sole negli occhi. Sono entrambe modalità di interpretare l'evento, ma l'effetto di queste due strategie di pensiero è differente.

Se scegli la strategia di reinterpretazione durante il compito dovrai cercare una chiave di lettura della situazione in grado di renderla meno negativa, ovvero tale da giustificare il comportamento della persona implicata e rendere l'effetto meno negativo.

Esempi di questo modo di pensare potrebbero essere "questa persona reagisce così perché è molto stressata", "non ce l'ha davvero con me" o "agisce in buona fede".

Suppression

The description of Suppression strategy was adapted from Szasz et al., 2011:

Soppressione: Capita spesso, soprattutto in presenza di emozioni negative, che non sia possibile o che sia controproducente esprimere apertamente quello che stiamo provando, oppure che non ci vada di far sapere alle altre persone come ci sentiamo. Ad esempio non possiamo prendere a calci un oggetto in un luogo pubblico per sfogare la frustrazione, e può sembrare una cattiva idea scoppiare a piangere su un autobus. In questo caso può aiutare cercare di concentrarsi per trattenere l'emozione e ridurne l'effetto percepito.

Se scegli la strategia di SOPPRESSIONE durante il compito dovrai cercare di inibire la risposta automatica che l'emozione ti porterebbe a mettere in atto, evitando di dare sfogo all'emozione stessa.

Per esempio, se il comportamento della persona in questione ti spingerebbe ad urlargli contro, cerca di trattenerti il più possibile facendo "buon viso a cattivo gioco.

Results

The paired-samples t-test was conducted to compare the mean level of anger for each participant when reappraisal vs. suppression was chosen in target stimuli. There was a significant difference in anger scores when reappraisal (M=3.81, SD=0.93) or suppression (M=4.33, SD=0.93) was chosen to regulate the emotion. t(66) = -5.54, p<0.001.

The assumptions were successfully controlled with the Shapiro test of the means' difference (W=0.99, p=0.787) and the Bartlett test of homogeneity of variances (Bartlett's K-squared(1)=0.002, p=0.961).

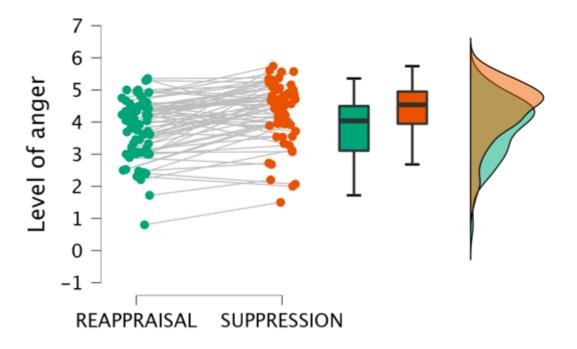


Figure 5.2 The level of anger when using reappraisal vs. suppression. Graphical representation of the mean level of anger when choosing reappraisal vs. suppression as regulatory strategies, plotted for each subjects (on the left), as boxplots (in the middle) or as density plots (on the right).

A Wilcoxon signed-rank test was conducted to compare the mean level of anger for each participant when reappraisal vs. suppression was chosen in the previous trial. Indeed, while the assumption of homogeneity of variance was satisfied with Bartlett test (Bartlett's K-squared(1)=0.154, p=0.695), the assumption of normality of the means' difference was not satisfied with the Shapiro test of the means' difference (W=0.95, p<0.05).

There was a significant difference in anger scores when reappraisal (M=4.09, SD=0.99) or suppression (M=4.31, SD=0.94) was chosen to regulate the emotion in the previous trial. V = 631.5, p=0.004.

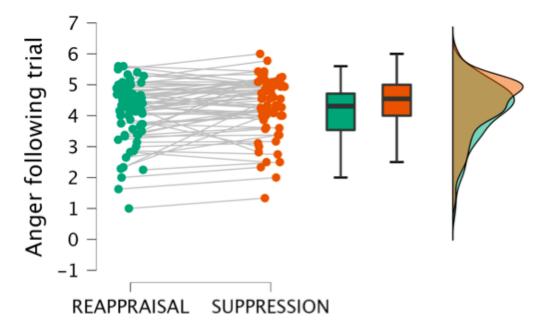


Figure 5.3 The level of anger after using reappraisal vs. suppression. Graphical representation of the mean level of anger when reappraisal vs. suppression were chosen in the previous trial as regulatory strategies, plotted for each subject (on the left), as boxplots (in the middle) or as density plots (on the right).

Results of the generalized linear model indicated that there was a collective significant effect between the level of anger in a specific trial and the level of anger and the chosen strategy in the previous trial (p<0.001). The individual predictors were further examined and indicated that both the level of anger in the previous trial (t = 2.49, p = 0.013) and the chosen strategy in the previous trial (t=-2.36, p=0.019) were significant predictors of the level of anger in the current trial. This means that anger accumulates over time, but the regulatory strategy used to cope with this emotion can reduce or enhance this effect of accumulation. However, their interaction was not significant (t = 1.03, p = 0.305). Therefore, even if there is an effect of accumulation (the level of anger elicited in the previous trial influences the following one) and an effect of the previous strategy (the strategy used in the previous trial influences the rating in the following one), their influences on the level of anger in the following trial are independent. This means that, as the level of anger increases in the previous trial, it also increases in the following trial independently from the strategy used; or, when reappraisal is used in the previous

trial, it reduces the level of anger induced in the following trial independently from the specific level of anger elicited in the previous trial.

Discussion

The main purpose of this study was to examine the effect of anger intensity on the choice of the regulatory strategy that is preferred to cope with provocative interpersonal situations. In particular, the usage of reappraisal, based on a change in the interpretation of the situation, will be compared to suppression, based on the expressive suppression of the behavioral and emotional outcomes of the situation.

Consistently with predictions, reappraisal was preferred when the mean anger intensity was lower, while suppression was preferred when the mean anger intensity was higher (see Figure 5.2). This result is coherent with the concept of flexibility in emotion regulation, according to which people can change their regulatory processes according to the context of the situation and, in this particular case, to the intensity of the emotional experience (Sheppes et al., 2011). Even if a few previous studies relied on the Emotion-Regulation Choice Task when considering anger (Robbig et al., 2021) or the comparison between reappraisal and suppression (Szczygiel and Baryla, 2019), this is the first evidence considering the role of these two emotion regulation strategies in anger management. Furthermore, differently from previous studies based on autobiographical memories (as in Robbig et al., 2021) or images (as in Szczygiel and Baryla, 2019), this study relies on different standardized stimuli that describe provocative situations that can elicit different levels of anger. Indeed, on one side autobiographical memories cannot be standardized since they are different for each participant, and on the other hand images can represent stimuli suitable to provoke a threatening response, but this is not always true when considering the elicitation of anger (Mattevi, 2018; Gilam and Hendler, 2015). Therefore, this new paradigm finally allowed the evaluation of the relation between anger intensity and the regulatory strategies chosen to cope with this emotion.

Results are in line with previous evidence suggesting that the usage of reappraisal requires higher levels of cognitive resources in particular when the emotional intensity is higher (Ortner et al., 2016). Indeed, high intensity stimuli reduce the available cognitive resources (Derakshan & Eysenck, 2009; Eysenck & Calvo, 1992; Mather & Sutherland, 2011), therefore reducing the possibility to efficiently

use reappraisal as a regulatory strategy given its need of cognitive effort (Szczygiel and Baryla, 2019). Therefore, when people are too much involved in interpersonal situations that evoke anger, the tendency is to prefer suppression of the behavioral outcome since it requires less cognitive resources when compared to reappraisal.

However, the suppression and inhibition of behavioral or emotional outcomes can lead to negative consequences. For example, when compared to reappraisal, suppression leads to poorer memory performance (Szczygiel and Baryla, 2019), and it is associated with higher self-reported stress-related, PTSD, anxiety and depressive symptoms (Moore et al., 2008). Also clinical evidence showed that reappraisal seems to be a more effective strategy when compared to suppression. For example, when these two strategies were compared, the higher usage of suppression predicted worse outcomes of psychotherapy (Scherer et al., 2015), while cognitive-behavioral therapy increased the effectiveness of reappraisal in association with a reduction in depressive symptoms (Forkmann et al., 2014).

Given the negative consequences and outcomes linked to suppression, the second aim of this study is to clarify the effects of the usage of reappraisal or suppression on the level of anger in the following trial. In particular, the hypothesis is that after reappraisal, the mean level of anger in the following trial would be reduced when compared to the mean level of anger after the usage of suppression. However, given that the usage of one specific strategy is linked to the level of anger (since the first hypothesis is confirmed), both variables (the level of anger and the chosen strategy) were taken into account when considering the effects on the level of anger in the following trial.

Accordingly, the results show that there is a significant influence of the anger intensity in a specific trial on the level of anger in the following trial, supporting the hypothesis that anger accumulates over time (see Figure 5.3). Importantly, to our knowledge this is the first evidence scientifically supporting this accumulatory effect of anger in time. Furthermore, as predicted, there was also a significant effect of the chosen strategy on the level of anger in the following trial. This means that the accumulation effect of anger can be more effectively regulated through a specific strategy, that is reappraisal.

Conclusions

Future studies are needed to better understand and deepen this evidence. However, the accumulation of anger over time and the possibility to modulate this effect on the basis of specific emotion regulation strategies is of fundamental importance especially in clinical contexts in which anger can be problematic. For example, the accumulation of anger over time seems to be a factor associated with the Korean "anger illness" (Kim and Kim, 2017) and anger can be problematic in different disorders such as Borderline Personality Disorder (De Panfilis et al., 2019; Dadomo et al., 2016; 2018; Kernberg, 2012), Antisocial Personality Disorder (Kolla et al., 2016), and the intermittent explosive disorder (Coccaro et al., 2014).

From this evidence it is of fundamental importance to try to understand which methods can be used in order to improve the regulation of anger and, in particular, to improve the usage of reappraisal versus suppression, given its advantages and potential in the regulation of anger.

Therefore, in the following study the effects of mindfulness training will be evaluated considering the level of anger experienced by each participant and the preferred regulatory strategy before and after a training of 6 weeks.

Chapter 6

Study 5: How can we regulate anger with mindfulness?¹⁴

This chapter will focus on the last empirical study. The first chapters focused on the neural correlates of different aspects of anger, while the previous chapter focused on the mechanisms of the regulation of anger in simulated social situations of everyday life. Finally, in this chapter the potential of mindfulness training in the regulation of anger will be evaluated. In particular, both the bottom-up and top-down mechanisms of mindfulness will be considered: the former is more related with the automatic affective reaction while the latter is more related with a cognitive evaluation of the situation. The literature suggests that mindfulness could play an important role especially, but not only, in the bottom-up mechanisms of emotion regulation. However, while the effects of mindfulness training on other emotions such as anxiety have been widely investigated, there is still poor empirical evidence on the regulation of anger. Therefore, this chapter aims to better deepen the relation between mindfulness, emotion regulation and anger.

Introduction

One of life's major challenges is to successfully regulate emotions (Gross et al., 2002). Indeed, our emotions imply a coordinated set of behavioral, experiential and physiological responses that influence how we respond to perceived events in our life. However, sometimes these emotional responses can be mismatched to different situations in life, affecting the following behavior of each individual. This may happen when emotion regulation (the ability to influence which emotions we have, when we have them and how we experience and express them) fails, leading to emotional dysregulation (an impaired ability to regulate unwanted emotional states) (Gross et al., 1998; 2002).

¹⁴ This chapter is in preparation for publication as "Sorella et al., *The effects of mindfulness training on the regulation of anger".*

Scientific evidence supports the idea that emotional dysregulation underlies several psychological disorders, such as personality disorders, bipolar disorder, interpersonal trauma, anxiety disorders and mood disorders (Dadomo et al., 2016). According to this view, conditions of emotional dysregulation or psychological inflexibility can lead to different psychopathologies, characterized by the inability to flexibly enhance or suppress emotional expression in accordance with situational demands (Dadomo et al., 2016; Bonanno et al., 2004).

Notably, psychological flexibility and emotion regulation seems to be improved throughout mindfulness experience or abilities, since they reduce cognitive vulnerability to stress and emotional distress (Farb et al., 2014). Indeed, mindfulness-based programs in clinical conditions widespread in the last years, since they can reduce the psychological distress and promote adaptive emotion regulation, self-regulated behavior and positive emotional states also in different clinical and affective disorders (Hofmann et al., 2010; Piet et al., 2011; Brown et al., 2007; Baer, 2003; Bohlmeijer et al., 2010; Crescentini and Capurso, 2015).

Mindfulness is defined as a nonjudgmental awareness to the present moment, implying two main mechanisms: a self-regulation of attention, that is maintained on immediate experience with an emphasis on body sensations rather than cognitive deliberation, and a particular orientation of curiosity, openness and acceptance (Bishop et al., 2004). This second feature related to the attitude is known as "non judgment", which means the suspension of judging experience as good or bad in favor of a more general attitude of acceptance. These two principles, attention and attitude, mutually support the gradual process of reconfiguring attention and cognition, extinguishing maladaptive patterns of reactivity, and introducing cognitive flexibility in response to stress (Bishop et al., 2004; Farb et al., 2014). It has been hypothesized in literature how this process could evolve; at first the cultivation of momentary awareness leads participants to explore their reactions to life events "in real time" rather than conceptually interpreting or predicting responses to events. In this way one can gain insight into one's own emotional appraisals, noticing the kind of situations that trigger automatic reactions. Then, this process is complemented with an intention to refrain from judgment and cognitive reactivity, which involves the acceptance of experience and the decentering from the attribution of self-relevance to experience. In this way, self-appraisal is viewed on par with physical sensation, a momentary experience that does not imply the existence of a temporally extended, enduring self. Indeed, mindfulness practice increases the ability to create a detached perspective from

mental events. Further, the ability to experience one's thoughts and emotional reactions from a more objective point of view has been shown to be a determining factor in whether reflection on emotion can be constructive or degenerate into maladaptive rumination (Bishop et al., 2004; Farb et al., 2014; Kross et al., 2012).

However, even if many studies have shown the beneficial effects of mindfulness training on different psychological abilities, such as a greater facility in letting go negative thoughts and lower levels of avoidance and rumination (Frewen et al., 2007; Kumar et al., 2008) and reduced physiological response to stress (Crescentini et al., 2016), the mechanisms by which mindfulness training can improve mood, emotion regulation and related behavior have yet to be fully elucidated, as discussed in the next section.

Emotion Regulation and Mindfulness

In the context of the Process Model of emotion regulation (Gross, 1998), mindfulness can be considered as a regulatory strategy that has a fundamental role in the third stage of the model, when attention deployment is involved. However, additional effects can also follow this stage (Farb et al., 2014).

Indeed, on one hand, the mindful process of orienting attention toward what is happening in the present moment is related to the attention deployment step of the Process Model. On the other hand, if mindfulness involved only attentional deployment, there would be little difference with other regulation strategies such as distraction. Nevertheless, even if distraction is also an emotion regulation strategy that involves attention deployment, it is characterized by an avoidance motivation: attention is oriented toward different sources that do not involve pain or suffering, such as the negative emotion. In fact, mindfulness involves the intention to direct attention *toward* what is happening in the present moment, even when it is characterized by pain or suffering. It means that it is the opposite of avoidance. However, directing the attention toward negative experiences is not easy, and this is the reason why mindfulness not only involves attention, but also intention and attitude. In other words, it involves not only the orienting of attention, but also the *way* in which we pay attention to the present moment. This attitude involves an open and exploratory attention even toward unpleasant objects (Farb et al., 2014). This is a fundamental feature especially when facing negative

emotions that one needs to regulate, because it can weaken the natural avoidance we naturally have toward negative events.

Accordingly, dispositional or treatment-related enhancement of mindfulness has been associated with lower levels of avoidance and rumination (Kumar et al., 2008; Farb et al., 2014).

Another related feature involved in the mindfulness process, that seems to be particularly related to the attitude, is reappraisal. Indeed, through mindfulness the habitual and automatic process of appraisals (such as those that characterize rumination) and responses that usually follow a negative emotion is temporarily suspended; this, in turn, can gradually lead to novel appraisals, responses and more adaptive and appropriate outcomes.

As explained by Grecucci and colleagues (2015a), different models on mindfulness imply, more or less explicitly, that the effects of mindfulness can also be related to reappraisal abilities. For example, according to the model of Shapiro and colleagues (2006) three main components of mindfulness training, i.e. the intention to self-regulate, the attention to the present moment and the attitude of openness and compassion, lead to the reappraisal of people's relationship with their emotional experience and habitual responses. Therefore, this and other models show that there could be two different components related to the training of mindfulness: a bottom-up experiential process that involves moment-to-moment awareness and a top-down cognitive process that involves selfregulation and reappraisal. The former, defined as an "intimately detached or decentered accepting point of view", seems to be more characteristic of the mindfulness ability to regulate our emotions. Indeed the top-down processes involved in reappraisal are not specific to mindfulness training (Grecucci et al., 2015a). For example, it has been demonstrated that while practiced meditators, when compared to beginner ones, were more able to use an "intimate detachment" to cope with social unfairness situations, the two groups were comparable when using a cognitive reappraisal strategy. This suggests that mindfulness does not necessarily improve the ability to regulate emotions relying on reappraisal strategies (Grecucci et al., 2015b).

However, while the above study compared the effectiveness of reappraisal in meditators, no study investigated the specific effect of mindfulness on the frequency of reappraisal use. In line with this hypothesis, a study suggests that mindfulness training can lead to a more flexible usage of emotion regulation strategies. In particular, participants of a mindfulness course used reappraisal more often

when the stimulus intensity was lower and distraction when it was higher (Alkoby et al., 2019). Similar evidence on the emotion regulation flexibility was found in a study investigating autobiographical memories that elicit anger. The authors found that only older adults relied on a flexible regulation choice according to which reappraisal was chosen in low-intensity situations while distraction was used in high-intensity situations (Röbbig et al., 2021).

However, the role of mindfulness in anger regulation is still unclear. Only a few studies took into account the effects of mindfulness on anger, usually relying on self-report questionnaires (Borders et al., 2010; Peters et al., 2015) or on single-case observations (Clark, 2020), finding a positive effect of mindfulness that seems to reduce rumination and, secondarily, anger and aggression. Nevertheless, further studies are needed to better understand the relationship between mindfulness and anger regulation, especially when comparing strategies as reappraisal and suppression. Indeed, as explained in the previous chapter, suppression can lead to more negative consequences when compared to reappraisal, which seems to be more effective. Therefore, this study aims to understand whether mindfulness training can increase the frequency of use of reappraisal when compared to a less efficient strategy, that is suppression. To this aim, I used the same paradigm of Chapter 5 to measure the emotional experience and the preferred emotion regulation strategy before and after a mindfulness course.

According to the literature, which shows that mindfulness emotion regulation is linked to both topdown and bottom-up strategies, this study aims to test the effect of mindfulness training on these two aspects of emotion regulation. In particular, in line with the cognitive-based top-down processes linked to mindfulness, I expect that mindfulness can increase the usage of reappraisal when compared to suppression. In line with the affect-based bottom-up processes linked to mindfulness, I expect that, after the mindfulness training, the mean level of anger experienced in the same situations (simulated by the paradigm used in this study) would decrease. Finally, an additional aim consists in testing whether there is a relationship between bottom-up and top-down effects of mindfulness, i.e. between the reduction of anger intensity experienced and the greater use of reappraisal after the mindfulness training.

Methods

This study involved 38 participants (27F, mean age = $22,34\pm2,62$), who performed a new study developed to investigate the experience of anger and its regulation (Mattevi et al., 2019). The task is based on the emotion regulation choice paradigm of Sheppes and colleagues (2011) in which participants are presented with stimuli and then they choose a regulatory strategy that they would apply to regulate the elicited emotion.

The task consisted in 90 trials and each of them included the fixation point (1000ms), the presentation of a stimulus (5000ms), the evaluation of the level of anger experienced (7 point Likert Scale) and the choice of a regulatory strategy (Reappraisal, Suppression or nothing).

The stimuli were created in a previous phase (see the previous chapter), and 45 provocative target stimuli and 45 neutral stimuli were selected for the present research. Each of them included a verbal stimulus describing a situation and a neutral face used to simulate the agent of the interpersonal event. Images were taken from the Chicago Face Database (CFD; Ma et al., 2015).

Mindfulness Training

The mindfulness course was proposed to bachelor students of the Department of Psychology and Cognitive Science of the University of Trento as a free choice course. It lasts 6 weeks (4 hours each week) with mandatory frequency. Participants were tested at the beginning and at the end of the course. In addition, some of the participants also agreed to participate in a pre-test phase 6 weeks before the beginning of the course in order to control for the test-retest reliability of the paradigm.

Even if the course lasted 6 weeks, it mainly consisted in the activities and meditations of the Mindfulness-based Cognitive Therapy program (Segal et al., 2013). The following table includes the main topic of each session and the meditations that the students practiced at home (see Table 6.1).

Table 6.1 Mindfulness Training. In the first column there is the session (1 through 6), in the second column there is the main topic of each session, and in the last column there are the meditations that participants were invited to practice at home.

| Session | Theme of the Session | Meditation at home |
|---------|---|---|
| 1 | Introduction to Mindfulness; Models on Mindfulness; First session of the program MBCT (awareness and the automatic pilot). | 10 minutes of body scan and 10 minutes of mindful breathing |
| 2 | Second (how the mind works) and third sessions (coming back to the present moment) of the program MBCT. Introduction to the programs of mindful eating and mindfulness for addictive behaviors. | 10 minutes mindful breathing and 10 minutes of body scan or mindful stretching |
| 3 | Fourth session of the program MBCT (recognize aversion). Introduction to the program MBSR ¹⁵ (particular attention to attachment and aversion). | 30 minutes sitting meditation or walking meditation; 3 minutes of mindful breathing whenever possible during the day. |
| 4 | Fifth (acceptance) and sixth sessions (thoughts are not facts) of the program MBCT. | 30 minutes sitting meditation and 3 minutes of mindful breathing whenever possible |
| 5 | Mindfulness and Compassion. Applications of the MBCT to depression and OCD. | Participants were allowed to choose one or more meditations, trying to set up a mindful routine. |
| 6 | Seventh (take care of yourself) and eighth sessions (plan a new way to live) of the program MBCT. | / |

¹⁵ Mindfulness-based Stress Reduction (Kabat-Zinn, 2003).

Analysis - main

A paired t-test was conducted to compare the mean level of anger for each participant before and after the mindfulness course. The same method was also applied to compare the percentage of usage of reappraisal vs. suppression (Strategy Index) for each participant before and after the mindfulness course (calculated as the number of trials in which reappraisal was chosen, divided by the sum of trials in which suppression or reappraisal were used).

Finally, in case of significant results in both the previous analyses, a correlation test would be applied to determine whether the difference in the Strategy Index between t1 and t2 could be explained by the difference in mean anger level between t1 and t2 for each participant.

Analysis - Control condition

In order to control for test and retest effects of the paradigm used, 6 weeks before the beginning of the mindfulness course participants were asked to perform the same task. 12 participants agreed and performed the task 6 weeks before the course, at the beginning of the course and at the end of the course. In order to control the previous results on the level of anger and the frequency of use of reappraisal, a Friedman test and an ANOVA were conducted.

Results

A Wilcoxon signed-rank test was conducted to compare the mean level of anger for each participant before and after the mindfulness course. Indeed, while the assumption of homogeneity of variance was satisfied with Bartlett test (Bartlett's K-squared (1)=2.25, p=0.134), the assumption of normality of the means' difference was not satisfied with the Shapiro test of the means' difference (W=0.80, p<0.05).

Results show that there was a significant difference in anger scores before (M=5.01, SD=0.86) and after (M=4.46, SD=1.10) the mindfulness course. V = 655.5, p<0.001.

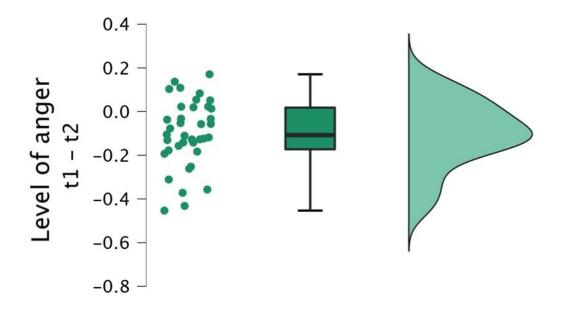


Figure 6.1 The difference in the mean level of anger before and after the mindfulness training. Graphical representation of the difference between the mean level of anger before and after the mindfulness training, plotted for each subject (on the left), as boxplots (in the middle) or as density plots (on the right).

A paired-samples t-test was conducted to compare the proportion of reappraisal's choice vs. suppression of each participant before and after the mindfulness course. There was a significant difference in reappraisal usage before (M=0.47, SD=0.20) and after (M=0.57, SD=0.16) the mindfulness course. t(37) = -4.06, p=0.0003.

The assumptions were successfully controlled with the Shapiro test of the means' difference (W=0.97, p=0.326) and the Bartlett test of homogeneity of variances (Bartlett's K-squared (1)=2.55, p=0.111).

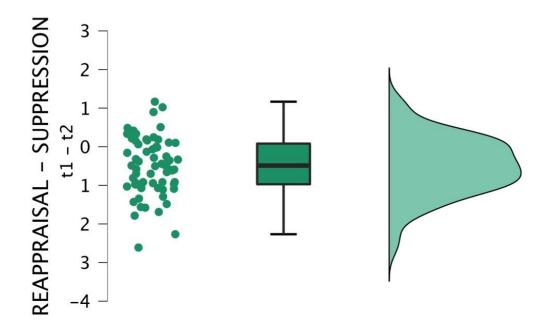


Figure 6.2 The difference in the mean level of suppression vs. reappraisal before and after the mindfulness training. Graphical representation of the difference between the proportion of reappraisal (<0) vs. suppression (>0) before and after the mindfulness training, plotted for each subject (on the left), as boxplots (in the middle) or as density plots (on the right).

Results of the correlation test indicated that there was a significant relation between the Strategy Index and the mean level of anger for each participant (R=-0.35, p=0.032). The relation was negative, meaning that as the mean level of anger decreased, the percentage of use of reappraisal increased.

Control condition

A Friedman test was conducted to compare the mean level of anger for each participant 6 weeks before, at the beginning and at the end of the mindfulness course. Indeed, while the assumption of sphericity was satisfied with Mauchly's sphericity test (Mauchly's W=0.597, p=0.076), the assumption of normality was not satisfied for all three conditions (t0, t1, t2) with the Shapiro test (W(t0)=0.83, p=0.02; W(t1)=0.89, p=0.12; W(t3)=0.91, p=0.21); therefore one-way repeated measures ANOVA was not applicable. The Friedman test evidenced a significant difference in the mean level of anger between groups ($\chi^2(2)$ = 11.17, p= 0.004). The post hoc test with Holm correction for multiple comparisons showed no significant difference in anger when comparing scores of 6 weeks before

(M=4.91, SD=1.03) and at the beginning (M=4.79, SD=0.94) of the mindfulness course (t = 0.48, p=0.639). On the other hand, a significant difference was observed both when comparing scores of 6 weeks before (M=4.91, SD=1.03) and at the end (M=4.21, SD=1.34) of the course (t = 2.93, p=0.023), and when comparing scores at the beginning (M=4.79, SD=0.94) and at the end (M=4.21, SD=1.34) of the mindfulness course (t = 2.46, p=0.045).

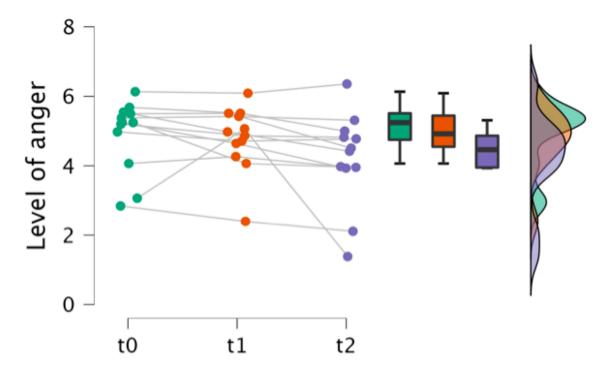


Figure 6.3 The mean level of anger 6 weeks before, at the beginning and at the end of the mindfulness training. Graphical representation of the mean level of anger 6 weeks before, at the beginning and the end of the mindfulness training, plotted for each subject (on the left), as boxplots (in the middle) or as density plots (on the right).

A one-way repeated measures ANOVA was conducted to compare the proportion of reappraisal vs. suppression for each participant 6 weeks before, at the beginning and at the end of the mindfulness course. Indeed, the assumption of sphericity was satisfied with Mauchly's sphericity test (Mauchly's W=0.587, p=0.069), and the assumption of normality was satisfied for all three conditions (t0, t1, t2) with the Shapiro test (W(t0)=0.96, p=0.80; W(t1)=0.95, p=0.61; W(t3)=0.94, p=0.46). The test evidenced a significant difference in the proportion of reappraisal between groups (F(2, 22)= 6.94, p= 0.005). The post hoc test with Holm correction for multiple comparisons showed no significant difference in the proportion of reappraisal vs. suppression when comparing scores of 6 weeks before (M=0.48, SD=0.09) and at the beginning (M=0.51, SD=0.13) of the mindfulness course. t = -0.76, p=0.456. On the other hand, a significant difference was observed both when comparing scores of 6

weeks before (M=0.48, SD=0.09) and at the end (M=0.63, SD=0.19) of the course (t = -3.54, p=0.006) and when comparing scores at the beginning (M=0.51, SD=0.13) and at the end (M=0.63, SD=0.19) of the mindfulness course (t = -2.78, p=0.022).

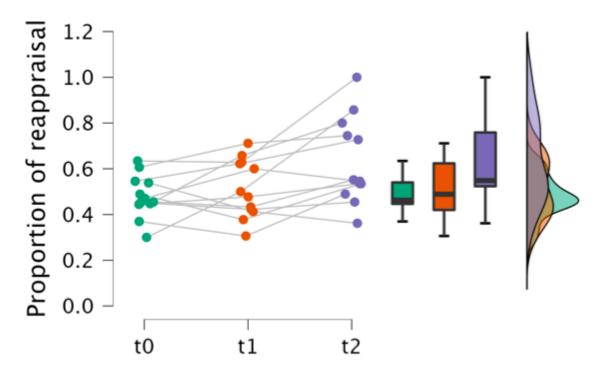


Figure 6.4 The proportion of reappraisal use 6 weeks before, at the beginning and at the end of the mindfulness training. Graphical representation of the proportion of reappraisal (vs. suppression) 6 weeks before, at the beginning and the end of the mindfulness training, plotted for each subject (on the left), as boxplots (in the middle) or as density plots (on the right).

Discussion

Mindfulness is defined as a nonjudgmental awareness to the present moment, implying a selfregulation of attention and a particular orientation of curiosity, openness and acceptance (Bishop et al., 2004). In recent decades, mindfulness training has become widely popular as evidence on the positive effects of mindfulness has been demonstrated.

In this study, new evidence on the effects of mindfulness on the regulation of anger has been demonstrated. Participants of a mindfulness training performed a new experiment aimed to elicit anger in different social situations (simulated with the computer), and then they were asked to evaluate the level of anger experienced followed by the regulatory strategy they would use to regulate their emotion. It has been found that after the mindfulness training the mean level of anger decreased.

Furthermore, participants after the training were more likely to choose reappraisal as a regulatory strategy when compared to suppression.

The effectiveness of mindfulness training on both different negative states (such as anxiety, threat, stress) and clinical disorders (such as depression or anxiety disorders) has already been established in the last decades (Didonna, 2008).

However, the effects of mindfulness on anger, and in particular on the regulation of anger, are still unclear. In fact, fewer studies have taken into account this emotion. Nevertheless, it has been hypothesized that mindfulness can also improve different conditions linked with anger problems (Wright et al., 2009). In particular, the authors argued that in order to regulate anger, it is fundamental to recognize as soon as possible the automatic cognitive, arousal or behavioral signs of this emotion. Therefore, through mindfulness the individual gradually learns to suspend the consequences of these initial automatic reactions. In a second moment, he/she would learn to automatize new "non-anger responses".

However, there is still poor empirical evidence on the effects of mindfulness on the regulation of anger, if we do not consider self-report questionnaires (Borders et al., 2010; Peters et al., 2015) or single-case observations (Clark, 2020); moreover, it is not yet known what mechanisms are involved. Anyway, if we do not consider only anger, scientists tried to better understand whether mindfulness-based emotion regulation is more linked with top-down and cognitive processes, or bottom-up and experiential processes (Grecucci et al., 2015a;b).

Regarding top-down processes, cognitive reappraisal has been taken into account as a possible target of mindfulness training. Indeed, it has been hypothesized that mindfulness can regulate negative emotions through a positive reappraisal (Hölzel et al., 2011), since an increase in positive reappraisal seems to mediate the relationship between mindfulness and stress levels (Garland et al., 2011) and neuroscientific evidence on meditators suggest an enhancement of brain activity in brain regions involved in cognitive change strategies such as reappraisal (Hölzel et al., 2011).

For example, higher activations of the medial prefrontal cortex have been associated with a downregulation of the emotional reactivity of the amygdala, especially in novel meditators (Taylor et al., 2011) and in people with high dispositional mindfulness (Modinos et al., 2010). However, since in the former study the same prefrontal activity was not found in expert meditators, it has been proposed

that cognitive change and control is mainly involved in novel meditators, since top-down regulation is more required; on the other hand, expert meditators would rely more on experiential bottom-up processes of emotion regulation (Grecucci et al., 2015a). Indeed, Grecucci and colleagues (2015b) found that while experienced meditators were more able to regulate their emotions and social behaviors relying on an experiential "intimate detachment" strategy, the ability to rely on reappraisal strategy was the same when they were compared to beginner meditators. Therefore, the authors concluded that bottom-up strategies, such as detachment, are more characteristic of the capacity of mindfulness to improve emotion regulation. This is in line with the results of the current study on the effect of mindfulness training in diminishing the intensity of anger experienced during provocative social interactions.

However, the above studies investigated the effectiveness of a regulatory strategy asking participants to apply it. A still unclear point, however, concerns the possibility that mindfulness may increase the tendency to use reappraisal rather than the ability to implement it, thus also acting on top-down mechanisms.

Indeed, the results of the current study show that after mindfulness training participants increased their tendency to choose reappraisal to regulate anger, while their tendency to choose suppression diminished. Even if future studies should consider a comparison between experienced and novice meditators, these results demonstrate that mindfulness not only influences bottom-up mechanisms of emotion regulation, but also top-down mechanisms. In particular, the results suggest that mindfulness can change the preferred regulatory strategy that people can use to cope with negative emotions, increasing the probability to choose a more optimal strategy (see Chapter 5 for a discussion on reappraisal and suppression).

Therefore, this chapter supports an integrated view according to which "mindful emotion regulation" involves both top-down cognitive-based and bottom-up affective-based processes. In particular, taking into account the model of Gross (1998), it has been proposed that mindfulness can influence any of the five stages of emotion regulation of the Process Model (Gross, 1998; for more details see Chapter 5), including both top-down and bottom-up regulatory strategies (Guendelman et al., 2017). However, on one hand it has to be recognized that while top-down processes are a common feature of Western psychotherapeutic approaches, bottom-up processes of emotion regulation focused on the sensory and interoceptive components of emotions represent a more distinctive feature of mindfulness

training. On the other hand, mindfulness also involves a strong emphasis on the attitude (Shapiro et al., 2006), such that the attention to the present moment is supported by an attitude of openness, acceptance, kindness and non-judgment. I suggest that this attitude is the key feature that, after the attentional deployment, can also influence the top-down mechanisms of mindful emotion regulation. Indeed, during mindfulness training there is a shift from a self-narrative perspective that can be characterized by rumination, avoidance and suppression (i.e. maladaptive strategies of emotion regulation), to a self-experiential present-centered perspective (Guendelman et al., 2017). In this way, there is a sort of gradually automatic shift in the cognitive evaluation of negative emotions. This is also in line with the proposal of Farb and colleagues (2014) according to which mindfulness is characterized by the acceptance of aversive emotional events, rather than distraction, withdrawal or suppression of them. Therefore, this suspension of action characterized by a non-judgmental attention to moment-to-moment experience gradually leads to the extinction of habitual secondary appraisals and reactions. This, in turn, allows mindfulness practitioners to consider new aspects of the situation, i.e. new appraisals that are more flexible and effective than the usual ones (Farb et al., 2014). In particular, this process is characterized by three steps: attentional deployment toward habitual reactions, which allows one to be aware of habitual reactions and regulatory responses that are not as effective, such as expressive suppression, rumination, or distraction; the ability to disrupt these patterns, especially when considering rumination; and, a gradual self-change. Therefore, the authors hypothesized the possibility that this process can improve the selection of regulatory strategies that are more effective in the regulation of negative emotions. The data previously reported in this chapter confirm this model, showing that mindfulness training leads to an increased probability of choosing reappraisal to regulate anger rather than suppression.

To my view, previous evidence reported in this chapter shows that mindfulness could be more specifically linked to bottom-up processes; however, these bottom-up processes can also be influenced and can influence top-down processes. In particular, referring to the model of Farb and colleagues (2014) there seems to be three mechanisms involved in the mindful emotion regulation process, and these mechanisms seem to involve both top-down and bottom-up processes. In particular, at the beginning of mindfulness training, there is a bottom-up process of attentional deployment in order to bring moment-to-moment awareness toward habitual emotional reactions; this

is complemented with a top-down process of cognitive control, especially in novel meditators, which is fundamental in order to suspend and disrupt habitual emotional reactions. However, the authors proposed that there is also a third mechanism of gradual self-change. I propose that this self-change in particular could underlie the top-down cognitive change responsible for the greater frequency of reappraisal, as opposed to suppression, used to regulate anger.

Furthermore, these three mechanisms can support each other. In particular, the greater use of reappraisal could be sustained by the higher availability of cognitive resources derived from the lower intensity of anger experienced in the same situation. Indeed, it has been found that working memory abilities influence not only the capacity to avoid the expression of negative emotions, but also the ability to use reappraisal (Schmeichel et al., 2008). And, in the previous chapter it was demonstrated that when anger intensity increases, the usage of reappraisal diminishes. Therefore, my hypothesis is that in mindfulness training bottom-up and top-down mechanisms interact and support each other. In particular, considering mindful emotion regulation, there could be a relationship between the reduction of emotional intensity experienced and the ability to rely more on reappraisal, as opposed to suppression.

To test this hypothesis an additional correlation test was performed. It was found that the higher proportion of preferred reappraisal correlates with the lower intensity that participants show after the mindfulness training. This means that the bottom-up processes are strictly linked with the top-down processes of "mindful emotion regulation", and suggests that these mechanisms interact and strengthen each other. To better understand how these processes act and how they interact, future studies should consider the possibility of distinguishing between these components, maybe organizing two different training respectively focused on the attentional deployment versus the attitude characteristic of mindfulness training. This could help the development of more personalized mindfulness-based treatments, considering in particular the specific difficulties of the patients in the regulation of emotions.

To note, this study comes with some limitations in particular regarding the control conditions. Indeed, the only control condition consisted in a pre-test 6 weeks before the start of the course, and only 12 participants agreed to participate to this phase. In addition, what is missing is a control group that would carry out the experiment two or three times, at the same time intervals as the participants in the mindfulness course. Only in this way it could be verified with certainty that the obtained effects are

exclusively due to the training and not to a possible test-retest effect. Future data collections will attempt to overcome these limitations.

Chapter 7

Conclusions - The psychological and neural mechanisms of anger and its regulation

Summary of the results

The present project aimed to investigate the psychological and neural bases of different mechanisms involved in the elicitation and regulation of anger.

Anger can be defined as an intense emotional state involving a strong uncomfortable and hostile response to a perceived provocation, hurt or threat (Videbeck, 2006).

In the first study, the evidence in literature on the neural bases of anger was analyzed relying on a meta-analytic approach, in order to summarize and clarify what is known so far about the brain mechanisms of this emotion. In particular, the neural bases of anger perception and anger experience, the two main kinds of mechanisms of anger investigated in literature, were not only distinguished, but also combined in order to find a common brain area responsible for both processes. The results showed that anger perception involved mainly posterior perceptual areas such as the amygdala, the rhinal cortex, the superior temporal gyrus and the right IFG (see Figure 7.1, green areas); on the other hand, the experience of anger involved the bilateral ventrolateral PFC and insula (see Figure 7.1, red areas); finally, the right IFG was identified as a common brain area responsible for both processes, and it was suggested that it could be particularly involved in the conceptualization of anger.

The second study further deepened the neural mechanisms of anger, in particular investigating the neural networks associated with individual differences in trait anger and anger control. Being a stable affective trait of personality, trait anger was significantly associated with a structural network involving Fusiform gyrus, different parts of the Cerebellum, the Temporal pole, the Lingual gyrus, the Visual

Association Area, the Posterior Cingulate cortex and the Inferior Parietal lobule (see Figure 7.1, yellow areas); on the other hand, anger control was associated with a functional network, i.e. the default mode network (see Figure 7.1, blue areas).

The third chapter also considered individual differences related to anger, but in this section other two aspects of this emotion were taken into account: the tendency to externalize and internalize anger, after its elicitation. In particular, for the first time the prefrontal asymmetry hypothesis mainly based on EEG and tDCS studies was confirmed throughout functional connectivity evidence. In particular, it was found that the externalization of anger is associated with left frontal connectivity, while the internalization of anger is associated with right frontal connectivity (see Figure 7.1).

Finally, the following two studies focused on the regulation of anger, in particular considering two different strategies, reappraisal versus suppression, and the related effect of a mindfulness course on the regulation of anger. Confirming the existing evidence on other negative emotions, such as anxiety and threatening stimuli, our results showed that anger is also flexibly regulated. Indeed, for low intensity situations people increase the frequency of reappraisal use, while for high intensity situations people increase the frequency of reappraisal use, while for high intensity situations people increase the frequency of suppression. However, this also shows that a more efficient strategy, i.e. reappraisal, can be used only when sufficient cognitive resources are available, and so when the intensity of the stimuli and of the emotion is lower, while in more difficult situations the preferred strategy is suppression. Therefore, in the final chapter it was investigated how we can improve the regulation of anger. Specifically, it was discussed how mindfulness training can improve anger regulation by relying on both bottom-up and top-down mechanisms, respectively decreasing the intensity of experienced anger and increasing the frequency of use of reappraisal versus suppression.

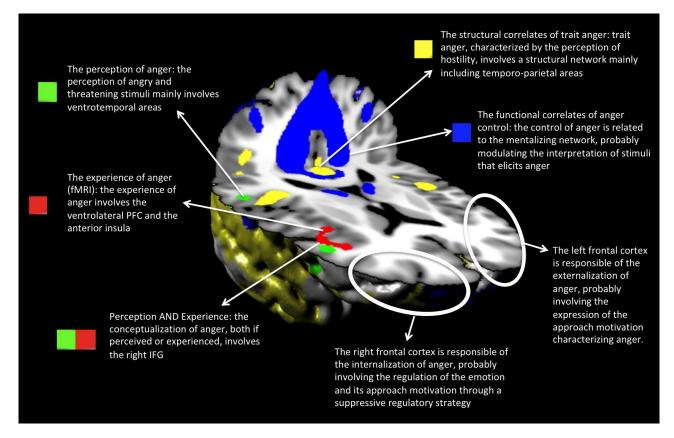


Figure 7.1 The neural correlates of anger. The figure summarizes the results of the studies showed in the previous chapters. Green: anger perception (chapter 2); red: anger experience (chapter 2); yellow: structural features of trait anger (chapter 3); blue: functional features of anger control (chapter 3); white circles: frontal asymmetry associated with anger internalization and externalization (chapter 4).

A comprehensive model on anger

In this section, I will try to organize the previous results.

The first aim of this thesis was to understand and organize the literature on anger from a neural point of view. Indeed different studies relied on different techniques to investigate the neural bases of anger. However, since anger is not so deeply understood as other emotions, such as anxiety or fear, the evidence in literature did not always lead to clear and established results. Indeed, while some studies tried to elicit this emotion with different paradigms, others investigated the neural bases of anger throughout the presentation of angry faces. Therefore, the two main mechanisms that have been previously involved in the study of anger were distinguished: the neural bases of its experience and its perception. For the first time, relying on a meta-analytic approach, a brain area involved in both the experience and the perception of the same emotion was identified. Indeed, the right IFG emerged from the conjunction analysis, probably linked to a conceptualization of the emotion that can be responsible for processes such as categorization, appraisal but also reappraisal in the context of emotion regulation (see Chapter 2 for more details). Instead, the experience of anger mainly relies on the ventrolateral prefrontal cortex and the insula, bilaterally. Indeed, the insula is known to be involved in the interoceptive mechanisms linked to emotions and emotion regulation, while the ventrolateral PFC seems to be involved in the affective evaluation of the situation and of its possible outcomes. On the other hand, anger perception relies on the activation of perceptual brain areas: the bilateral amygdala, the left rhinal cortex, the right superior temporal gyrus and also the right ventrolateral PFC. While temporal areas have been linked to emotion detection, the amygdala is known to be involved in emotional affect and arousal.

Anger perception in this case involves a perceived angry face or voice; however, these stimuli can be considered anger-related triggering stimuli that can elicit aggressive impulses in some individuals; for example, the STG has been found to mediate the relation between amygdala reactivity in response to angry faces, and the consequent aggressive behavior in the same task (Buades-Rotger et al., 2016). This is probably due to the interpretation of angry faces as hostile stimuli.

Interestingly, also trait anger was found to be associated with a structural network involving perceptual brain areas such as the Fusiform Gyrus, the Cerebellum and ventromedial temporal areas (see Chapter 3). Indeed, the hostile interpretation of a perceived stimulus, as an angry face, increases in people with high trait anger (Veenstra et al., 2018). Therefore, this structural network associated with trait anger could explain why high trait anger individuals are characterized by a higher hostility in the perception of external stimuli. However, in addition to perceptual areas involved in different perceptual processes (e.g. the perception of angry stimuli but also the perception of hostile stimuli linked to trait anger), the structural trait anger network also involved parietal areas, in particular the posterior cingulate. Indeed, the posterior cingulate is associated with certainty (Luttrell et al., 2016) that is one of the main features characterizing high levels of anger (Lerner and Keltner, 2000). Therefore, this structural network could be related to the high certainty and hostility associated with the perception of external stimuli, characteristic of high trait anger individuals.

Interestingly, it seems that these perceptual features could be modulated by mentalizing processes, for example when we try to understand the hidden reasons after exposure to a provocative situation. Indeed, it was found that the DMN is associated with the control of anger. Accordingly, frontal brain regions have been proposed to effortfully control anger, probably top-down regulating subcortical

brain regions (Wilkowski and Robinson, 2007). Furthermore, an additional analysis revealed that the DMN is inversely related to both trait anger and its associated structural network. These results suggest that the mentalization process associated with the DMN could play a key role in the regulation of anger. In particular, the DMN could play a role of control through a mentalization based on the possible consequences of anger expression, especially when considering social contexts.

It has to be noted that the right IFG, a brain area included in the DMN, emerged in both the categorization and experience of anger (see Chapter 2 for more details), and therefore could be particularly involved in a process of conceptualization of anger. In particular, when anger is experienced, my hypothesis is that the right IFG could be responsible for its recognition, and then other areas of the DMN could determine which process would follow: the meaning of the situation (appraisal), the consequences (externalization or internalization of anger), its regulation (for example with strategies such as reappraisal or suppression) or dysfunctional mechanisms such as rumination, in particular when the DMN activity is altered (see for example, Sambataro et al., 2013, and Garland, 2021, for alterations of the DMN in depression and addiction).

On the other hand, this process of control linked to the DMN could also be improved by mindfulness training. Accordingly, in the previous chapter it was shown that mindfulness training can enhance the regulation of anger. I hypothesize that this process could be linked with a modulation of the DMN. Indeed, the DMN of meditators, when compared to controls, is characterized by greater functional connectivity (Jang et al., 2011).

In addition, the DMN is also associated with emotion regulation strategies. For example, it is involved in social emotion regulation and reappraisal (Xie et al., 2016; Suhn et al., 2018) but also in expressive suppression strategies (Pan et al., 2018; Burr et al., 2020).

Since in Chapter 6 it was shown that mindfulness training enhances the usage of reappraisal when compared to suppression, future studies are needed to understand whether the DMN could mediate this shift, playing a possible role in the determination of a specific way, more or less effective, to regulate emotions. Indeed, alterations of the DMN have been also linked with mental disorders characterized by emotional dysregulation, such as depression (Sambataro et al., 2013; 2014) and addiction (Garland, 2021). Interestingly, it has been proposed that mindfulness can influence the DMN; in particular, mindfulness could "reset the aberrant default mode network dysfunction, reducing

excessive self-referential processing and thereby transforming the maladaptive cognitive-affective habits" (Garland, 2021).

The effect of mindfulness in enhancing reappraisal when compared to suppression is also supported by evidence linked with the frontal asymmetry (for more details about this theory see Chapter 4). Indeed, it has been shown that mindfulness enhances left frontal activity while diminishing right frontal activity, and this shift is related to different aspects of well being (Davidson et al., 2003; 2004). In line with this evidence and the results of Chapter 6, it seems that while reappraisal is associated with higher left frontal activity (Choi et al., 2016; Li et al., 2021), suppression is associated with higher right frontal activity (Kim et al., 2012; Hasani et al., 2009).

In addition, it has to be noticed that anger requires special attention when considering the frontal asymmetry and its role in the emotional experience. As deeply explained in Chapter 4, initially the frontal asymmetry hypothesis associated higher left activity with positive emotions and higher right activity with negative emotion. However, anger seems to be more associated with higher levels of left prefrontal activity (see Harmon-Jones et al., 2004); interestingly, anger is the only negative emotion characterized by an approach motivation rather than a withdrawal one, and this led scientists to build a new model where positive and negative emotions were replaced by approach and withdrawal motivation and behavior. Nevertheless, relying on frontal connectivity analyses, we demonstrated that the asymmetry seems to be explained by affective reactions (i.e. the externalization and internalization of anger), rather than by motivations, behaviors or basic emotions. Furthermore, this hypothesis is also supported by the significant correlation between self-reported levels of anger-in (the internalization and suppression of anger) and the Beck Depression Inventory shown in chapter 4. Indeed, many studies found associations between depressive symptoms, including ruminative processes and suppression of emotions and motivations, with higher right prefrontal activity (Henriques and Davidson, 1991; Pizzagalli et al., 2002; Lacey et al., 2020). However, right frontal activity has been also associated with anger rumination (Fabiansson et al., 2012; Kelley et al., 2013). These data and the correlation between the BDI and the internalization of anger suggest that the higher levels of right frontal activity characterizing these patients could be associated in particular with ruminative processes, and suppression and internalization of emotions, also when considering the emotion of anger.

Therefore, both the DMN and the frontal asymmetry are involved in affective and emotional processes; in particular, the DMN is associated with the control of anger, but its activity alterations characterize different disorders such as depression. In addition, the suppression of emotions, ruminative processes, and the internalization of anger are associated with right frontal connectivity. On the other hand, the externalization of anger is associated with left frontal connectivity.

Interestingly, mindfulness training seems to influence both kinds of neural mechanisms; indeed it has been found that it could "reset" the DMN, especially when altered in different disorders, and it can increase the left vs. right frontal activity index associated with higher wellbeing and mental health.

Nevertheless, the association between anger and the externalization of anger with left frontal activity should be further investigated in future studies. Indeed, one possible explanation of the previous evidence is that a good strategy to cope with anger is to externalize it in a balanced way. Indeed, on the other hand the suppression of anger is associated with rumination and depression, and could be linked to reduced wellbeing. Future studies should investigate if excessive outbursts of anger are also associated with left frontal activity, and whether their regulation throughout a mindfulness training change the relationship between left and right frontal activity, in order to further improve our knowledge on mindfulness, emotion regulation, anger and the frontal asymmetry hypothesis.

The aim of my doctoral program consisted in trying to bridge the gaps between the research and clinical fields, at least with regard to some aspects of anger and its regulation. In fact, my two major interests, in research and in the clinic, are still characterized by independent and too little integrated fields, despite the great progress achieved in the last decades.

The hope is that in the coming years this integration will be increasingly strong, so that we can develop not only scientifically validated treatments, but also modulated and continuously improved based on specific psychological and neuroscientific evidence.

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Appendix

The following table contains the set of stimuli used in chapter 5 and chapter 6, with the mean level of anger elicited in the pilot study aimed to verify that the target stimuli significantly elicited anger when compared to the neutral ones.

Then, the following analysis shows the mean difference in the level of anger between target vs neutral. To note, during the task the agent (name and gender) was randomized.

TARGET STIMULI:

| Stimulus | Level of anger |
|--|----------------|
| Per colpa di Angela il tuo progetto è fallito | 4,53 |
| Eleonora ti fa arrivare in ritardo al lavoro | 3,93 |
| Per colpa di Chiara non puoi andare al concerto della tua band preferita | 3,3 |
| Silvia parla al telefono in aula studio mentre tu cerchi di studiare | 3,7 |
| Matilde non ti permette di andare a dare l'esame | 4,8 |
| Per colpa di Giuseppe non potrai laurearti | 5,33 |
| Ivan ha deciso che stasera tu non andrai al cinema | 3,8 |
| Daniel è in ritardo, e se non si sbriga ti farà perdere il treno | 3,5 |
| Non hai ottenuto i documenti per colpa dell'incompetenza di Giada | 4,27 |
| Dario ti obbliga a rinunciare al viaggio che tanto sognavi | 4,93 |
| Grazie all'intromissione di Angelica la tua idea è fallita | 4,17 |
| La tua possibilità di carriera è fallita per colpa di Letizia | 5,1 |
| L'incompetenza di Riccardo ti impedisce di consegnare il lavoro in tempo | 4,2 |
| L'errore di Asia ti è costato la promozione che speravi | 4,67 |
| Marco ha fatto in modo che tu non raggiungessi i tuoi obiettivi | 5,17 |
| Davide incolpa te di un errore che in realtà ha commesso lui | 4,97 |
| Christian ti costringe a lavorare anche di domenica | 3,87 |
| Il tuo capo, Alberto, ti paga molto meno di quanto dovrebbe | 4,37 |
| Jessica ti fa pagare di più il biglietto dell'autobus | 3,83 |
| Sara prende il voto più alto anche se ha dato il contributo minore al progetto | 4,4 |
| Luigi ha vinto il concorso imbrogliando | 4,27 |
| Il capo incolpa te del danno commesso da Francesco | 4,8 |
| Per colpa di Giovanni dovrai pagare una grossa multa | 4,7 |
| Roberto ti ha mentito per ottenere un favore da te | 4,1 |
| Il bonus viene assegnato a Michela, nonostante tu lo meritassi di più | 3,73 |
| Elisa viene premiata per il lavoro che hai svolto tu | 4,97 |
| Devi svolgere tutte le mansioni che Emma non ha voglia di fare | 4,67 |
| Filippo ti costringe a fare anche la sua parte di lavoro | 4,67 |
| Paolo viene assunto al tuo posto, nonostante sia meno qualificato di te | 4,13 |
| Simona sceglie te come capro espiatorio per qualsiasi cosa | 4,7 |
| Federica ti mette in ridicolo di fronte ai tuoi colleghi | 4,33 |
| Margherita mette in giro voci sul tuo conto | 4,23 |
| Antonio si diverte a sottolineare i tuoi fallimenti | 4,63 |
| Daniele ti ha messo ripetutamente e di proposito in imbarazzo in pubblico | 4,8 |
| Alice continua a suonare il clacson gridandoti "Dove hai imparato a guidare?" | 4,63 |
| Jacopo sparla di te quando non sei presente | 4,2 |
| Erika non perde occasione per prenderti a male parole | 4,73 |
| Elena critica aspramente il tuo lavoro per farsi notare dal capo | 5 |
| Serena ti prende in giro ogni volta che ti incontra | 4,27 |
| Angelo ti segue passo a passo nel lavoro perché ti ritiene incompetente | 4,1 |
| Valerio ti insulta davanti a tutta la tua famiglia | 4,8 |
| Lorenzo ti mette in ridicolo durante un pranzo di lavoro | 4,3 |
| Greta elenca i tuoi difetti con tono compiaciuto | 4 |
| Valentina gode nel metterti in ridicolo | 4,8 |
| Mentre parli con i tuoi amici Federico ti grida che sei una nullità | 4,1 |

NEUTRAL STIMULI:

| Stimulus | Level of anger |
|--|----------------|
| Stai facendo un progetto insieme ad Alessio | 0,27 |
| Laura ritiene di condurre una vita serena | 0,3 |
| Beatrice prende tutte le mattine il treno per andare al lavoro | 0,33 |
| A Giulio piace molto andare ai concerti e spettacoli teatrali | 0 |
| Salvatore si chiude in biblioteca per riuscire a studiare al meglio | 0,13 |
| L'esame che Fabio ha fatto martedì era scritto | 0,2 |
| Lo scorso ottobre Emanuele si è laureato in matematica | 0,07 |
| Lunedì Sofia ha visto un film al cinema | 0 |
| Veronica sta organizzando la sua festa di compleanno | 0,13 |
| Carlotta deve andare in comune a ritirare alcuni documenti | 0,07 |
| Arianna da piccola ha vinto una gara di sci | 0,03 |
| Alessandra lavora in un negozio di abbigliamento | 0 |
| Pietro sta pensando di trasferirsi in Belgio per cercare lavoro | 0,13 |
| Il capo di Vittoria è fissato con l'ordine e la puntualità | 0,23 |
| Gabriele ha appena consegnato la bozza per un nuovo progetto | 0,23 |
| Sabrina non è stata promossa, e perciò dovrà ripetere l'esame | 0,53 |
| Ilaria ha comprato un nuovo obiettivo per la sua macchina fotografica | 0 |
| Giorgia sa sempre cosa ordinare al ristorante | 0,03 |
| Domenica scorsa Ludovica ha lavorato tutto il giorno | 0,57 |
| Aurora si occupa della contabilità del suo ufficio | 0,2 |
| Simone deve prendere due autobus per raggiungere il centro | 0,43 |
| Noemi era entusiasta all'idea di contribuire alla scelta del regalo per la mamma | 0,3 |
| Mattia si è iscritto ad un concorso | 0,07 |
| Matteo si sente in colpa per non aver salutato il suo supervisore | 0,4 |
| Giacomo ha dovuto richiedere alla banca un nuovo libretto di assegni | 0,07 |
| Alex ha vinto il secondo premio alla lotteria di paese | 0,23 |
| Pasquale non ha voglia di andare a cena fuori stasera | 0,53 |
| Roberta lavora nell'azienda di famiglia | 0,33 |
| Prima di essere assunto Giorgio ha dovuto sostenere un colloquio con il capo | 0 |
| Vincenzo compra qualsiasi cosa trovi in saldo | 0,47 |
| Gaia spiega ai suoi colleghi come funziona la nuova fotocopiatrice | 0,07 |
| Sabato Tommaso ha fatto un giro in montagna | 0,03 |
| Edoardo ha fatto alcuni ottimi affari ad aste fallimentari | 0,33 |
| Viola non ha mai avuto problemi a parlare in pubblico | 0,47 |
| Domenico fa il commesso in un supermercato in centro | 0 |
| Claudia è stata la prima della sua classe a prendere la patente | 0,07 |
| Miriam ha le spalle larghe dopo molti anni di nuoto | 0,37 |
| Nicola ha una passione per i rebus e i giochi di parole | 0,07 |
| Michele ha una collezione di figurine d'epoca | 0 |
| Giulia ha incontrato sua zia mentre faceva la spesa | 0,03 |
| Thomas segue con interesse il lavoro di un gruppo di ricerca svedese | 0,2 |
| Francesca andrà in vacanza con tutta la sua famiglia | 0,37 |
| Enrico controlla che il nuovo prototipo sia privo di difetti | 0,1 |
| Manuel si sta mettendo in forma per partecipare ad una gara | 0,03 |
| Anna dice che è inutile lavorare se poi non ci si gode le ferie | 0,4 |

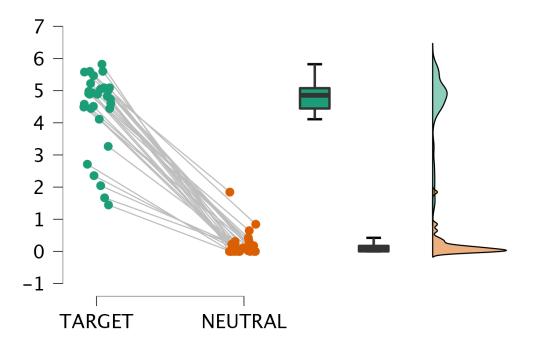


Figure A1 The plot shows the significant difference in the mean level of anger elicited by target stimuli (mean = 4.41, sd=1.20) and the neutral stimuli (mean = 0.20; sd=0.37). W=465; p<0.001. The post hoc calculation of the power is 1 and the effect size 9,00.

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