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Neural bases of prosocial decision making

Por

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Neural bases of prosocial decision making

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Neural bases of prosocial decision making

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Dedicatoria

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I. Summary

In the present document, an empirical approach for the study of human decision making will be presented. Firstly, a theoretical and empirical contextualization of the subject will be provided; secondly, it will be presented a research article approaching a specific research question; and, finally, a broad discussion of the research results and their contribution will be proposed. The empirical work consisted in the use of a slightly modified version of the dictator game for testing the hypothesis that the inclusion of another person into a decision-making setting increases prosocial decisions in young adults, and that this increase is higher when the other person is associated with others in need. At the brain level, the hypothesis tested was that the increase in prosocial decisions correlates with frontal theta activity and that this activity can be taken as a marker of empathy saliency. Results showed that the inclusion of another person into the decision setting increased prosocial behavior only when this presence was associated with someone in need, and that this was associated with an increase in fronto-central theta-oscillatory activity. These results suggest that the presence of someone in need enhances both empathy concern and norm compliance, raising the participant's prosocial decision making.

II. Theoretical and empirical review of the study of prosocial decision making

In general terms, decision making can be understood as a process that involves the weighing of previous knowledge and present evidence in order to extract the value (utility) from given options associated to a given goal (Gold & Shadlen, 2007). A common prediction derived from this general view is that a decision maker will choose options with higher utilities to him/herself. The concept of utility summarizes the decision maker's preferences in a given set of options. Prosocial behavior refers to any action that is addressed to benefit another

individual (Balconi & Canavesio, 2013). Altruism, defined as a costly act that confers benefits to others, has been of particular interest since it is commonly observed even between unknowns (Fehr & Fischbacher, 2003). Based on the traditional assumptions about value and utility, classic game theory models usually predicted that humans were motivated primarily by the maximization of their immediate utilities and that any social or emotional factor influencing the decision-making process was a fertile field for irrationality (Hewig et al., 2011). Empirical data, however, suggest a much more complex scenario in which social and strategic motives altogether with concerns about the own and others' wellbeing explain people's preferences. Profuse and consist evidence has shown that prosocial behavior can be associated to the concerns of other’s wellbeing, along to long-term benefits to the own benefactor, and that both variables are commonly involved in the decision making process. While empathy-based prosociality is related to the influence that interacting with others under physical suffering or distress has in helping behavior, strategic-based prosociality, in turn, is related to the short and long-terms benefits that prosocial behavior has in terms of reciprocity and reputation. This review aims to present the behavioral and neural evidence regarding the influence of both empathy and strategic concerns in the decision-making process, and to propose a model of the brain activity associated to these variables in order to advance in the understanding of prosociality.

Empathy is defined as the sharing and comprehension of others' feelings and thoughts (de Waal, 2008). This involves an emotional resonance between an observed and the empathizer, and a cognitive component related to the ability of taking the perspective of others' feelings (de Waal, 2008). There is profuse evidence showing a relation between these variables and prosociality. For instance, there is evidence showing a relation between prosocial behavior and emotional resonance (Williams, O'Driscoll, Moore, 2014), cooperation

rates and levels of empathetic perspective-taking in woman have been correlated (Batson & Moran, 1999) and the perception-action model has proposed empathy as the key motivator for altruistic behavior (Decety & Grèzes, 2006). Brain evidence has shown an overlapping of structures related to empathy feelings while observing others in pain and areas traditionally associated to decision making such as the ventromedial prefrontal cortex (VMPFC), the anterior cingulate cortex (ACC) and the anterior insula (AI). This evidence has related activity of the AI to being more prosocial towards people perceived as victims of pain (Masten, Morelli, Eisenberger, 2011), AI and ACC activity related to helping behavior (Rameson, Morelli, Lierberman, 2012), and VMPFC activation to other's suffering and involved in charity donations (Hare, Camerer, Knoepfle, O'Doherty, Rangel, 2013). These data suggest that the mechanism by which empathy can promote prosociality is by including the representation of affective and mental states of others into the evaluation of options. In other words, by considering others' wellbeing via emotional resonance or cognitive perspective-taking, people would be prone to sacrifice their immediate benefits for helping others.

Another approach for explaining prosocial behavior between unknowns is through strategic long-term considerations. People can help others because this increases the chance of getting help by others when needed in the future. Reciprocity refers to the tendency of people to help those who help them (known as direct reciprocity or DR) (Trivers, 1971), and to help those who help others (known as indirect reciprocity or IR) (Alexander, 1987; Roberts, 2008). This latter form of reciprocity (IR) is the mechanism by which it would pay to develop a reputation for being prosocial with unknowns. There is evidence showing positive correlations between activity in the DLPFC and orbitofrontal cortex (OFC) and being more prosocial within strategic contexts (Steinbeis, Bernhardt, Singer, 2012). Also, impairment of the right dorsolateral prefrontal cortex (DLPFC) by transcranial magnetic stimulation (TMS) has been

related to an impairment in strategic abilities when receiving unfair offers in economic interactions (Baumgartner, Knoch, Hotz, Eisenegger, Fehr, 2011; Knoch, Pascual-Leone, Meyer, Treyer, Fehr, 2006). This data suggests that right DLPFC might inhibit selfish impulses leaving people prone to show prosocial behavior when pertinent. Thus, given that there is IR, profrontal structures would control the influence of immediate selfish-related payoffs in order to develop a long-term beneficial prosociality. This approach is known as the reflective prosocial model (Yamagishi et al., 2016). Although there seems to be a general agreement about the relevance of IR, there are still some important controversies. Recently authors have come up with an opposite interpretation of profrontal control known as the intuitive prosociality model (Yamagishi et al., 2016). This interpretation based on gray-matter thickness and TMS studies (Christov-Moore, Sugiyama, Grigaityte, Iacoboni, 2016; Yamagishi et al, 2016), points out that prefrontal control inhibits the intuitive prosocial tendency of people, and then the activity of the right DLPFC is related to control prosociality when there is not a strategic value on it (Christov-Moore et al., 2016; Yamagishi et al, 2016). Thus, it is still unclear whether the strategic process of prosocial decision making relates to the hypothesized reputational value of such decisions, and which intuitive tendency prefrontal structures are in fact inhibiting.

In this theoretical and empirical review, we will present a summary of the behavioral and brain evidence regarding prosocial decision in order to contextualize the empirical work reported conducted and reported in the article.

Prosocial behavior

Classical decision-making perspective, which emerged from the economic theory

during the 19th century, considered people as rational agents whose decisions were made after an evaluation of costs and benefits (Heilbroner, 1969). Experiments based upon bounded-rationality models during the 70s (Kahneman, 2003; Tversky & Kahneman, 1974), and later used in behavioral economics (Ariely, Gneezy, Loewenstein, Mazar, 2009; Gigerenzer, Todd, 1999; Goldstein & Gigerenzer, 2002) and neurosciences (Fehr & Camerer, 2007; Hewig et al., 2011; Sanfey, 2007) have shown that human decision-making process is more complex than that. Experiments using economic interactions based upon game theory models (Camerer, 2003) have shown that people do not guide their decisions just by the immediate payoffs offered by the options (even in one-shot interactions). For example, in the Ultimatum Game (UG) a proposer player (the "proposer") has to divide a sum of money with a responder player (the "recipient"), who can accept or reject the offer. If the offer is accepted, both players receive the amounts proposed by the proposer, but if the recipient rejects the offer then neither player receive anything. According to the classical decision-making perspective, a self-motivated responder should accept any non-zero offer given by the proposer in one-shot interactions. Therefore, the proposer should offer the minimum non-zero amount to the responder. However, behavioral evidence contradicts this prediction in that an approximate 50/50 split is usually observed (Boksem & De Cremer, 2010; Nowak, Page, & Sigmund, 2000), and that offers that go below the 20% of the total amount tend to be rejected (Sanfey, Rilling, Aronson, Nystrom, Cohen, 2003). This experimental evidence suggests that proposers' offers are guided by the strategic anticipation of recipient responses. In this kind of interactions, subjects acting as proposers have to think about the strategy that recipients might follow in order to avoid the punishment of a rejection. Since low offers elicit recipients' negative emotions, accurate proposer's anticipation responses are related to give higher offer. This behavior is related to perspective-taking abilities (Yamagishi et al., 2016). Recipients' responses suggest that the value of their earnings is dependent of proposers'

payoffs and recipients are willing to earn nothing if proposers do not follow a fair norm (Yamagishi et al., 2016). Thus, for extracting better payoffs from the interaction participants have to consider both their own benefits and also others' earnings.

Since in the UG the prosociality of the fair offer has short-term benefits to proposers (by avoiding rejections), his strategic value is straightforward. This can be an example of direct reciprocity. However, there are scenarios in which without immediate benefits people still show prosocial behavior. In the Dictator Game (DG), one player (the "dictator") receives an amount of money and donates a desired part of it to the recipient. This decision ends the game and the recipient has no chances of punishing the dictator if the amount was not “acceptable” to him. Thus, there are not direct incentives for the *dictator* to share any portion of the received money, and, then, donations are by definition an act of altruism (Lee, 2008; Rilling & Sanfey, 2011). Behavioral evidence shows that even when participants play this game with unknowns, proposers tend to donate around 25% of their money to the recipient (Camerer, 2003). Although the average amount given in the DG is lower than that observed in the UG (Fehr & Fischbacher, 2003; Forsythe, Horowitz, Savin & Sefton, 1994), donations around 25% are high considering the costs and the lack of direct immediate benefits for the dictator. Computational models have shown that reputation-based altruism is expected when building a reputation is as probable outcome of de decision (Roberts, 2008). There is evidence showing precisely that people use reputational information when available to choose their strategies, and this has an impact on how people trust in others (Wedekind & Milinski, 2000). There have been recent efforts for including social knowledge about the recipient in the DG in order to increase the ecological validity of the interaction (Harbaugh, Mayr, Busghart, 2007; Moll et al., 2006). This has shown, for example, higher trends of donation when people are inform that the recipient is someone in needs (as people from a

real charity organization) or when the recipient is described as prosocial (Moore, 2009; Prencipe & Zelazo, 2005). Such experimental settings have shown that the knowledge about who the recipient is and how the game is explicitly described to the players are factors that influence prosociality (Camerer 2003; Eckel & Grossman 1996). This evidence, moreover, shows that along with the structure of economic incentives in short and long-terms, there are social and emotional factors that influence the way in which subjects weigh such incentives.

The perception-action model, for instance, proposes empathy as a key motivator and the proximate mechanism of prosocial behavior (Decety & Grèzes, 2006). It is argued that when an individual perceives and shares the distress of another person then he/she will act in order to reduce that suffering, showing helping and prosocial behavior (Preston & de Waal, 2002). In this line several experiments have shown that perceiving others in needs or suffering increases prosocial, fair and altruistic tendencies (Batson & Moran, 1999; Hein et al., 2016; Rosen, Brand, Kalbe, 2016; Williams, O'Driscoll, Moore, 2014). The interpretation of such observed behavior is that empathy may have an evolutionary origin as a mechanism selected to promote social bonding between members within social groups (de Waal, 2008). Prosociality, in this sense, can be taken as an expression of this social bonding, which also benefits the collective as a whole.

There is evidence showing also an indirect sense of strategy involved in the interactions that adds even more complexity to the motives behind prosocial behavior. For instance, when dictators make their offers facing eyespots in the screen as an indicator of observability they increase their offers over the expected 25% (Haley & Fessler, 2005). This involves that when participants interact in such economic contexts they might be responding not just in terms of the economic payoffs or the empathy concerns about the recipient, but

also in terms of the social value that prosocial behavior supposes. The idea of indirect reciprocity refers precisely to this idea (Roberts, 2008). While direct reciprocity makes sense in restrictive conditions (small groups for instance), IR is essential to understand why it might pay to develop reputation for being cooperative interacting with unknowns with low (or at least uncertain) chance of future interactions (Roberts, 2008). The idea behind this is that prosocial behavior can be driven, besides empathetic concerns, by reputational motives as a long-term strategy. Computational models have shown that reputation-based altruism is expected when reputation is as reliable as direct experience in deciding whether to be prosocial or not (Roberts, 2008). There is evidence showing precisely that people use reputational information when available to choose their strategies, and this has an impact on how people trust in others (Wedekind & Milinski, 2000). Thus, prosocial behavior, even in one-shot interactions, can have a strategic component of reputation.

Brain evidence for empathy and strategic-based prosocial decision-making

As the behavioral evidence suggests, long-term rationality and empathy concerns appears as two related variables that modulate prosocial behavior. However, the conclusions are highly speculative and dependent on experimental designs, or even; participants' self-reports. In order to enrich the discussion several experiments have registered brain activity of subjects engaged in decision making tasks. This evidence, although not conclusive, allows hypothesizing about the actual impact of empathy concerns and long-term benefits in the brain network of the decision making process, and their role in prosociality. This evidence will be presented and discussed in order to contribute to the understating of prosocial decision

making.

Empathy-based prosocial decision making

Empathy is related to sharing feelings and thoughts of others. There is brain evidence suggesting that pain-related empathetic responses might by the brain substrate of empathy-based prosocial behavior. In other words, observing others under physical suffering or victims of unfair behavior activates the pain-related networks (specifically the AI and ACC) which leave people prone to show helping behavior. There is evidence also suggesting a cognitive component of empathy related to the understanding of other feelings and thoughts. This is related to prefrontal and temporo-parietal activity which also has influence in prosocial behavior. Both sources of evidence are, as mentioned, strongly based just upon pain-related empathetic responses.

Neuroimaging studies have shown that when people see or imagine the pain of another person, they map their pain onto the network activated during firsthand experience (Lamm, Decety, Singer, 2010). ACC and AI are part of the pain matrix, involved in the affective-motivational dimension of nociception. AI and ACC have strong connections between each other, the limbic system and prefrontal cortex, suggesting a key position in empathic processing (Craig, 2002). The AI has strong connections with the ventromedial nucleus of the thalamus that convey emotional and homeostatic information, and connects reciprocally with sensory cortex, playing a key role in integrating and representing emotional states (Craig, 2002). AI then is thought to have two crucial functions: 1) generating subjective awareness of own affective states and predict at the same time emotional consequences of different stimuli in our bodies, as well as 2) having a prospective representation of how other people feel in similar circumstances. On the other hand, ACC is the motivational-action

counterpart of insular cortex functions. ACC has been proposed as a part of neural hub of diverse socially driven cognitive-affective processes (Lavin et al., 2015), based on three of its key recognized roles: motor control mechanism, cognitive monitoring (in which its connections with prefrontal cortex provides access to higher executive functions) and emotional-arousal regulation. These functions are related to the ACC connectivity to midline thalamus and the brainstem as well as with limbic structures such as amygdala (Paus, 2001). This pain-related empathy network associated to AI and ACC has been associated to prosocial behavior. Higher insular empathetic responses to social pain predicts prosocial behavior toward victims (Masten et al., 2011), and activation in AI together with ACC has been associated with prosocial behavior towards a perceived victim of pain (Hein et al., 2016) and daily helping behavior to friends (Rameson et al., 2012). This suggests that empathic affective representation in AI may motivate prosocial behavior. This is consistent with studies in non-human primates in which stimulation of the insula inhibited aggression in monkeys (Caruana, Jezzini, Sbriscia-Fioretti, Rizzolatti, Gallese, 2011), and with studies showing association between insular activation and sense of fairness and justice distribution (Dawes et al., 2012; Hsu, Anen, Quartz 2008). Likewise, psychopaths show significantly less empathic activation of AI and ACC to others' emotions compared with controls (Meffert, Blanken, Blair, White, Blair, 2013), establishing an indirect link between affective and sensoriomotor representation in empathy and prosocial behavior. This relation is indirect since psychopathy is well-characterized by strong antisocial behavior (Decety, Skelly, Kiehl, 2013). Accordingly, contextual factors that modulate pain-related empathetic responses can affect prosocial motivation. For instance, there is greater costly helping behavior to in-group members in pain compared to prosociality towards out-group subjects in physical suffering (Hein, Silani, Preuschoff, Batson, Singer, 2010). This suggests that modulation of affective sharing system by social context can influence prosocial actions toward others.

Brain imaging studies have provided evidence also regarding activity related to selfish behavior. This evidence show AI and ACC activation in response to unfair offers compared with fair splits which relates to rejections (Corradi-Dell'Acqua, Civai, Rumiati, Fink 2013; Dulebohn, Conlon, Sarinopoulos, Davison, McNamara, 2009; Guo et al., 2013; Sanfey et al., 2003; Tabibnia Satpute, Lieberman, 2008;; Dulebohn et al 2009). The role of the ACC-AI complex when observing unfair behavior seems to be a negative affective response to a general social norm violation and social defection (King-Casas et al., 2008; van Den Bos, van Dijk, Westenberg, Rombouts, Crone, 2009). Importantly, personal traits can modulate this activation. For instance, when prosocial individuals do not reciprocate cooperation, they show increased activity in ACC and AI. Strikingly, selfish individuals show the opposite pattern, showing stronger activity of these areas after they reciprocate cooperation (van den Bos, 2009). This interesting result suggests that people personal features could determine actions and pattern of activation of the complex ACC-AI. This indicates that this complex is more active when participants behave in a way that is inconsistent with their personal trait or past history.

There is also a prefrontal network underlying cognitive-related empathic responses to others' suffering. This cognitive neural system refers to the ability of taking the perspective of others' feelings and thoughts involving mental state attribution and the sense of agency, associated to cognitive self-other distinction (Decety et al., 2013). As empathy is a more complex process than emotional contagion, it is crucial for the empathizer distinguishing whose feelings belong to whom, in order to avoid merely personal distress in response to others' pain (Decety & Jackson, 2004). This role is accomplished particularly by the temporo-parietal junction (TPJ) and VMPFC, which decouple computational mechanism between first-

person information and second-person information, giving sense of agency in empathy (Decety and Jackson, 2004). TPJ plays a critical role in the distinction between self-produced actions and actions generated by others (Samson, Apperly, Chiavarino, Humphreys, 2004; Saxe and Kanwisher, 2003; Morishima, Schunk, Bruhin, Ruff, Fehr, 2012; Decety & Jackson, 2004). Likewise, VMPFC is involved in self-other distinction in empathy (Zaki & Mitchell, 2013) and asses similarities and differences between own and others' mental states (Mitchel, 2009). Both areas have strong connections with sensory cortex, limbic system, and other prefrontal areas, involving multisensory body-related information processing, and integrating cognitive aspects and self-awereness (Blanke and Arzy, 2005). Thus, TPJ and VMPFC network arise as key neural locus for self and other processing in empathy.

Importantly, this cortical component of empathy is also relevant to prosocial behavior. Mathur et al. (2011) showed that greater responses in prefrontal cortex to in-group compared to out-group members in pain predicted altruistic behavior to in-groups. This is consistent with findings revealing that dorsomedial prefrontal cortex (DMPFC) responses to others' suffering predicts helping behavior to the victim and general altruistic behavior (Masten et al., 2010; Rameson et al., 2013). In the same line psychopaths show less empathic VMPFC activation to others' suffering compared to controls (Decety et al., 2013), consistent with evidence revealing that VMPFC is involved in socially-driven behavior towards others and to charity donations (Hare et al., 2013; Janowski, Camerer, Rangel, 2013). Finally, instructions to explicitly empathize with negative situations are related with prosocial interventions and tendency to benefit others (Van Lange, 2008; Balconi & Canavesio, 2013); suggesting that effort for understanding what the others are feelings generating more altruistic behaviors. Thus, these data suggest that affective bottom-up resonance cannot explain completely the link between empathy and social decision making. Rather, cognitive representation of

affective and mental states of others is important in order to elicit prosocial behavior.

Taken together, these data suggest empathetic responses toward others can modulate prosociality. Much of the evidence shows overlapping of brain areas and evidence of the empathetic responses toward prosocial behavior. However, the precise connectivity and influence of such empathetic responses in the decision making process remains unclear. Most of the studies operationalize empathy as a brain response towards others' pain, leaving the ecological broader component of empathy observed in social relations understudied.

Strategic-based prosocial decision making

Along with empathy, strategic concerns related to reciprocity and reputation, have been proposed as an explanation for prosociality. Strategic-based prosocial behavior is based upon the idea that people is prosocial when it pays better. The main hypothesis in this regard is that prefrontal areas exert control over people's decisions letting prosocial behavior to appear when it reports either short or long-term benefits to subjects. This idea is in line with the relation of midfrontal theta activity and “self-control” behavior, related to the norm-informed activity in order to pursue long-term benefits (Billeke et al., 2014; Cavanagh & Frank, 2014). As the ACC-AI complex might participate in the affective response that facilitates prosocial actions within economic settings, the prefrontal regions would play a strategic role. There are controversies, nevertheless, regarding the target of this prefrontal control and whether long-term benefits relate to a reputational value.

There is evidence of prefrontal activity involvement in prosociality that reflects a basic short-term strategic component within economic interactions. This activity is thought to mediate the strategic considerations towards others, influencing more generous offers and

consequently reducing rejections rates in the UG. In an experiment performed by Spitzer et al. (2007), participants performed a DG and an UG. Results showed that subjects proposed significantly fairer offers in the UG than in the DG condition. These fairer offers within a UG setting were accompanied by higher activation in right DLPFC and VMPFC. The involvement of these areas suggests predictions about possible rejection by recipient (Kringelbach, 2005; O'Doherty, Kringelbach, Rolls, Hornak, Andrews, 2001), and the inhibition of immediate self-oriented responses in order to higher final payoffs (Aron, Robbins, Poldrack, 2004; Miller and Cohen, 2001; Sanfey et al., 2003). This can be interpreted as the action of a high control mechanism acting in proposers when recipients can punish unfair splits. This suggests that prosociality has a strategic component related to the inclusion of others' considerations as a function of increasing proposers' own payoffs. Supporting this view there is evidence relating prefrontal activity to cognitive control over general impulsiveness (Blain, Hollard, Pessiglione, 2016).

Within social-economic interactions evidence has shown an even more complex form of strategic concerns. Rejections of unfair offers does not provide direct benefits to recipients in the UG, but rather it has been interpreted as an action with long-term reputational value when there are chances of future interactions (Baumgartner et al., 2011; Knoch et al., 2006). Disrupting the function of the right DLPFC by means of low-frequency rTMS (Baumgartner et al., 2011; Knoch et al., 2006; van't Wout, Kahn, Sanfey, Aleman, 2005) and cathodal transcranial direct-current stimulation (Knoch et al., 2008) have shown to decrease rejection rates to unfair offers which has been interpreted as a dysfunction of strategic considerations. In other words, the role of the right DLPFC would be linked also to a more long-term form of strategic decision-making related to the reputational value of decisions. This evidence has been interpreted as that people are intuitively guided by immediate self-oriented impulses, but that right DLPFC exerts control over such impulses when there are alternative long-term

benefits.

This view, however, has been recently challenged by an alternative interpretation of the role of prefrontal control areas. This alternative view, known as the intuitive prosociality model, suggest that prefrontal control areas strategically control the prosocial impulses of people when there is not a strategic value in being prosocial (Christov-Moore et al., 2016; Yamagishi et al, 2016). One argument for this view is that cortical thickness of the DLPFC is not related to the amounts giving in the UG, but is negative correlated to giving in the DG (Yamagishi et al., 2016). Since the DG does not have the chance of punishing non-prosocial behavior, as it is possible in the UG, giving in the DG would not provide of strategic value to the donor. Thus, the authors suggest that lower strategic abilities, operationalized as less cortical thickness in the DLPFC, would leave people incapable of controlling their intuitive prosocial impulses (Yamagishi et al., 2016). In the same line, there is evidence showing that disruption of the right DLPFC increased prosociality in the DG (Christov-Moore et al., 2016). This suggests that decreasing activity in this control area leave people prone to follow their prosocial, but not self-oriented, impulses in the absence of strategic values.

Besides the controversies, there seems to be agreement about the relevance of the prefrontal areas in decision settings that involve conflicts between self and others' welfare. Brain models of social cognition have shown different networks related to activity in the TPJ and DMPFC related to inferring others’ mental states; ventral premotor cortex (PMv) related to action observation; and amygdala and VMPFC related to the affective value of social behavior (Apps, 2016; Apps and Tsakiris, 2013; Frith and Frith, 2006; Hampton et al., 2008; Lee, 2008; Lee and Seo, 2016; Billeke, Soto-Icaza, Aspé-Sánchez, Villarroel Rodríguez-Sickert, 2017). Recent evidence has shown the relevance of the anterior cingulate cortex

gyrus (ACCg) in social cognition, particularly given his connectivity to the listed regions and his modulation to other-oriented information. Macaque studies have shown that lesion to the ACCg decreased the value that those animals give to social stimuli, and more specifically this area responds to rewarding outcomes delivered to another (Chang, 2013; Apps, 2016). Human studies have shown that ACCg seems to process cues that are informative to know what events will impact another person, providing the interpretation that this area is, at least in general terms, relevant to the monitoring of others' behavior (Apps, 2016). Taken together this evidence suggests a relation between prosocial behavior and brain areas related to control and self-inhibition, which is modulated in turn by relevant social information. Additionally, there is consistent evidence showing frontal theta activity related to fair, and even altruistic, behavior in social games (Edele et al., 2013; Billeke et al., 2014) which has been interpreted as result of ACC activation. There is evidence that relates midfrontal theta activity to the ACC, particularly showing synchronized activity of a subset of cells in the ACC as predictive of theta-activity in tasks associated with sensory-motor control in macaques (Womelsdorf et al, 2010). Thus, it can be hypothesized that ACC, and particularly ACCg, is a sub-region that do not merely reflects general cognitive control processes, but it is specialized in encoding others' regarding information when outcomes are relevant to them (Apps, 2016).

Based upon the previous empirical and theoretical discussion, the empirical work developed will be presented. Firstly, the objectives and hypothesis of the research will be proposed, and then the research article containing a brief theoretical introduction, methods, results and discussion. The article is currently under review in the *Scientific Report* journal. Finally, a broad discussion of results and its implications will be presented.

III. Objectives

General Objective

To identify the influence of the inclusion of another person into the decision setting in human prosocial decision making and its brain correlate.

Specific objectives

1. To observe the influence of the inclusion of another person with different levels of empathy saliency into the decision setting in people's prosocial behavior.
2. To identify whether different degrees of emotional involvement related to others impact differently in the levels of prosocial decision making.
3. To test whether prefrontal oscillations participate in the mechanism by which other-related concerns are integrate into prosocial decision making.

IV. Hypotheses

General hypothesis

1. The inclusion of another person into the decision setting increases prosocial behavior by recruiting prefrontal oscillatory activity.

Specific Hypotheses

1. The inclusion of another person into the decision setting increases prosocial decisions in young adults
2. The increase of prosocial decisions is higher when the other person is associated with others in need.
3. The increase in prosocial decisions correlates with prefrontal theta activity as a marker of empathy saliency.

Research Article

Empathy concerns enhance prosociality and modulate frontal theta oscillatory activity in young adults

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ABSTRACT

Decision making is a process that can be strongly affected by social factors. Profuse evidence has shown how people deviate from traditional rational-choice predictions under different levels of social interactions. The emergence of prosocial decision making, defined as any action that is addressed to benefit another individual even at the expense of personal benefits, has been reported as an important example of such social influence. Furthermore, brain evidence has shown the involvement of structures such the prefrontal cortex, the anterior insula and the midcingulate cortex during the decision settings in which a decision maker interacts with others under physical pain or distress, or while being observed by others. Using a slightly modified version of the dictator game, we tested the hypothesis that the inclusion of another person into the decision setting increases prosocial decisions in young adults, and that this increase is higher when the other person is associated with others in need. At the brain level we hypothesized that the increase in prosocial decisions correlates with frontal theta activity as a marker of empathy saliency. Results showed that the inclusion of another person into the decision setting increased prosocial behavior only when this presence was associated with someone in need, and that this was associated with an increase in fronto-central theta-oscillatory activity. These results suggest that the presence of someone in need enhances both empathy concern and norm compliance, raising the participant's prosocial decision making.

Key words: Decision-making ; prosociality ; empathy

INTRODUCTION

In everyday life there are several examples of decisions that could have direct consequences on others, such as deciding how much money to donate to charity, how much food to buy when there are supply problems or whether to give back a wallet full of cash that has just fallen down from someone's pocket. In all these cases, people may take into account, to different extents, the consequences that their own behavior has on the wellbeing of both others and themselves. This processing is crucially affected by the circumstances in which the decision has to be made. For example, to be observed by others or to observe someone who is under physical pain or distress changes our tendency to take into account other's well-being in our decisions. Even though the influence of others seems clear, the psychological and neurobiological mechanisms underlying this process remain unclear.

Prosocial behavior refers to any action that is addressed to benefit another individual (Balconi & Canavesio, 2013), and in its extreme form of altruism, it implies a costly act that confers benefits to others (Fehr & Fischbacher, 2003). Although traditional approaches assumed a primarily selfish impulse of the maximization of immediate utilities in every human decision (Hewig et al., 2011), several empirical data has shown a much more complex scenario in which social and emotional factors, altogether with concerns about their own and others' wellbeing, explain people's social preferences (Balconi & Canavesio, 2013; Fehr & Fischbacher, 2003). Indeed, consistent evidence has shown that prosocial behavior can be associated not only with direct and indirect benefits to the decision-maker, but also with his/her concerns about other's well-being. In this line, empathy, which has been defined as the sharing and comprehension of others' feelings and thoughts (Waal, 2008), is an important modulator of prosociality by enhancing the presence of the other within the decision setting (Waal, 2008).

There is evidence showing the impact that the presence of others has in subjects' decisions. The way that other persons appear varies depending on the experimental settings and goes from eye-spots on the wall observing people's decisions, to helping others under "real" physical pain. Evidence comparing public and anonymous decisions has described that individuals behave in a more prosocial way, and adjust their behavior to a norm while they are being observed (Baumgartner et al., 2011; Campanha et al., 2011; Hare et al., 2010; Knoch et al., 2006; Masten et al., 2011; Morelli et al., 2014; Rameson et al., 2012; Steinbeis et al., 2012; Trivers, 1971; Williams et al., 2014). This evidence has suggested that, through emotional resonance and perspective-taking, the representation of another person can influence both decisions and brain activity associated with that process. Accordingly, different experimental manipulations have modulated the presence of another person in the decision-making setting, through variations in both the level of emphatic-related responses and the reputational value of the decisions.

The relationship between empathy and prosociality has been well-established by behavioral and brain studies. There is evidence that relates prosocial behavior and emotional resonance in children (Edele et al., 2013; Rodrigues et al., 2014; Williams et al., 2014), as well as cooperation rates and empathetic perspective-taking in women (Batson & Ahmad, 2001; Graaff et al., 2017). Moreover, the perception-action model proposed empathy as an important factor for explaining altruistic behavior (Decety & Grèzes, 2006). Neuroimaging evidence shows that, in experimental tasks that involve observing others in pain, there is brain activity that overlaps to areas which are traditionally related to decision-making tasks. These structures include brain areas such as the ventromedial prefrontal cortex (vmPFC), the anterior insula (AI) and the midcingulate cortex (MCC, commonly referred to as dorsal anterior cingulate cortex, see (Vogt, 2016)). Specifically, AI activity has been related to being

more prosocial towards people perceived as victims of pain (Masten et al., 2011), AI and MCC activity has been related to helping behavior (Rameson et al., 2012), and vmPFC activation to other's suffering and involved in charity donations (Hare et al., 2010). There is also electroencephalographic (EEG) evidence showing oscillatory activity related to the presence of others with different degrees of empathy involvement. For instance, increased frontal theta activity has been related to observing others in pain (compared to neutral stimuli) as well as to own unpleasant feelings (Han, 2018; Mu et al., 2008). Frontal theta activity has also been related to self-reflexive thinking within social interactions (Mu & Han, 2010) and the prediction of other’s decisions (Billeke et al., 2013; Rodrigues et al., 2014). Taken together, this data supports the relevance of the presence of others on people’s decision making, and that there are different ways in which a given other sneaks into the variables that a decision-maker takes into account while deciding.

Prosocial decisions can also have indirect benefits for the decision-makers in the form of reputation. In this respect, there is evidence showing the tendency of people to cooperate (or defeat) with those who cooperated (or defeat) with them in the past (known as direct reciprocity or DR) (Trivers, 1971), and to help those who help others (known as indirect reciprocity or IR) (Alexander, 1987; Roberts, 2008). This latter form of reciprocity (IR) is proposed as the reason why it would pay to develop a reputation of being prosocial. Thus, the presence of an observer might influence prosociality related to the potential benefits that this behavior provides in the form of reputation and eventual reciprocity. For instance, when dictators make their offers facing eyespots on the screen as an indicator of observability, they increase their offers over the expected (Haley & Fessler, 2005). Moreover, in an experiment performed by (Spitzer et al., 2007), participants who performed the Dictator Game (DG) and the Ultimatum Game (UG) proposed significantly fairer offers in the UG than in the DG

condition. These fairer offers within the UG setting were accompanied by higher activation in the right dorsolateral prefrontal cortex (dlPFC) and the vmPFC. The involvement of these areas suggests predictions about possible rejection by recipient (Kringelbach, 2005; O'Doherty et al., 2001), and the inhibition of immediate self-oriented responses in order to obtain higher final payoffs (Aron et al., 2004; Miller & Cohen, 2001; Sanfey et al., 2003). Brain models of social cognition have shown different networks related to activity in the TPJ and dmPFC related to inferring another's' mental states; and the amygdala and vmPFC related to the affective value of social behavior (Apps et al., 2016; Apps & Tsakiris, 2013; Billeke et al., 2017; Frith & Frith, 2006; Hampton et al., 2008; B.-T. Lee et al., 2007; D. Lee & Seo, 2016; Soto-Icaza et al., 2015; Soto-Icaza & Billeke, 2017). Recent evidence has shown the relevance of the MCC in social cognition, particularly given its connectivity to the listed regions and its modulation to other-oriented information (Apps et al., 2016; Chang et al., 2012).

In this context, the present study aims to assess, through a slightly modified version of the DG, the impact that the presence of another person has in the decision process of a person that has to choose distributions of money for him/herself and for another player. We studied the behavior and brain activity of adult individuals while choosing within three different scenarios: when the decisions were anonymous (control condition, CC), when participants were observed by another person (observer condition, OC), and when the decisions were in the context of another person who is in need (empathy condition, EC). These contextual manipulations aimed to modulate the intensity of the empathy concerns triggered by the presence of another person within the decision setting, or, in other words the "empathy saliency" of someone in need. We hypothesized that the presence of another person would increase prosocial decisions, and that this increase would be higher when the other person is

associated with others in need (EC). At the brain level we hypothesized that the increase in prosocial decisions would correlate with frontal theta activity as a marker of empathy saliency. Results showed that the EC, but not OC, increased prosocial behavior compared to the CC. Brain activity showed an increase in fronto-central theta-oscillatory activity when participants faced unequal advantageous distributions to the other player within the EC. This brain activity can be interpreted as the marker of the social encoding related to the presence and attention given to the other person within the decision process.

MATERIAL AND METHODS

Participants

Thirty-two healthy participants (13 women) with normal or corrected to normal vision, without history of neurological or psychiatric diagnosis, performed the experimental task. Their age range was between 19 and 23 years old (M = 21.4, SD = 1.3). Participants were randomly assigned to one of the two experimental conditions (see experimental task below). The experimental procedures were performed in accordance with institutional guidelines and were approved by the Ethical Committee of the Pontificia Universidad Católica de Chile. All participants gave their written informed consent. All the experiments were carried out at the Laboratorio de Neurociencia Social y Neuromodulación, of the Centro de Investigación en Complejidad Social (neuroCICS), Universidad del Desarrollo, Santiago, Chile.

Power and sample size

To calculate the minimum sample size and the power of the current study, we used the behavioral effect as the primary outcome. A similar study related to the effect of the presence

of others during a social economic decision making (Haley & Fessler, 2005) shows an effect size of η^2=0.149, which is a large effect (Cohen, 1988). Taking into account the publication bias, we set an intermediated effect size of η^2=0.1. Thus, for the between-within factor interaction in a 2x2 mixed anova with a power of (1-β)=0.95 and a significant level of α=0.05, the minimum sample size to find the expected effect was n=32.

Experimental task

The experimental task consisted in a modified version of the DG, in which participants had to choose between two possible allocations of money for themselves and for another player (hereinafter the other). Within the two possible choices, there was always one that gave participants the option of being prosocial. In the case of this task, a prosocial decision is defined as choosing the option that provides higher incomes to the other player regardless of the consequences for the own participant. All participants were informed that they will receive an amount of money at the end of the experiment, which will correspond to the sum of two factors. One composed by one of their own decisions (one trial selected at random), and the other corresponds to the decision made by a previous player, also selected at random. In the latter case, the amount corresponds to the money that a previous participant paid to the other player during his/her performance of the task. This design has the aim of highlighting that decisions have real consequences for both the participants themselves and another person.

The sample was randomly assigned to one of the two groups: Empathy group and Observer group. For both groups, participants first performed a round of the task as a control condition, in which their decisions were told to be anonymous. After this first round, participants assigned to the Empathy group performed a second round of the task under EC. The EC is the same task as in the CC, but at this time, participants were told that this part of the

experiment was part of a bigger study that involves donation of money to a real charity institution, but that these donations did not depend on the specific decision of the participants. They were informed that, under this condition, the decisions were anonymous. It is important to note that, at this point, all the participants received the explicit clarification that the amount of money that they allocated was not a direct donation to the charity institution. No further information was given about the charity institution, and a blurred picture of a child, who would benefit from this donation, was shown to the participants during the rest of the experimental task. Participants assigned to the Observer group, after playing the CC, played a round of the task under the OC. The OC is the same task as in the CC, but at this time, participants were observed by another researcher who is part of the research team, while they were playing, so their decisions were not anonymous anymore. They were informed that the observer was a sociologist who conducted the observation as part of another research. A blurred picture of the observer was shown to the participants for the rest of the experimental task (as in the EC). Moreover, a confederate playing the role of a sociologist entered into the experimental room several times during the experiment, taking notes and observing the participants while playing.

The decision task consisted in the selection of one within two distributions of money that were presented in the higher and lower part of the screen respectively. These distributions or allocations were presented separately 1500 ms each as it is shown in Figure 1. Both allocations involved money for the participant and for another player. The other player was identified as a future participant of the experiment. The amounts for participants were presented on the left side of the screen in yellow, and the amounts to the other player were presented on the right side of the screen in blue (see figure 1). The amounts were presented for 1500ms and a visual cue (green fixation cross) indicated to the participants that the

decision could be delivered. During all conditions, participants faced three types of choices or cases that were randomly presented: other's advantageous inequity (OAI), other's disadvantageous inequity (ODI) and altruistic (ALT) (see Figure 2). In the ALT choices, the prosocial option involves a personal cost to the participant. In the OAI cases there is not such conflict as in the ALT case, given that the prosocial option involves higher earnings for the other participant, but no personal costs to the own players. In the ODI cases, the prosocial option prevents the other participant from getting lower earnings with no personal costs to the player. Finally, participants were told that sometimes the game will choose the opposite option to the one chosen by them (e.g. if the participant chose the prosocial option, then the non-prosocial option will be displayed as the chosen one). If they want to return to their original option they will be punished in that trial by losing a fixed amount of USD$5, but if they want to keep the "error", then that choice (the opposite of the one they wanted) was going to be considered. This was used as a way to confirm the strength of participants' decisions. At the end of the experimental task all participants received a payment from one of the played trials (selected at random) plus what a previous participant left to them.

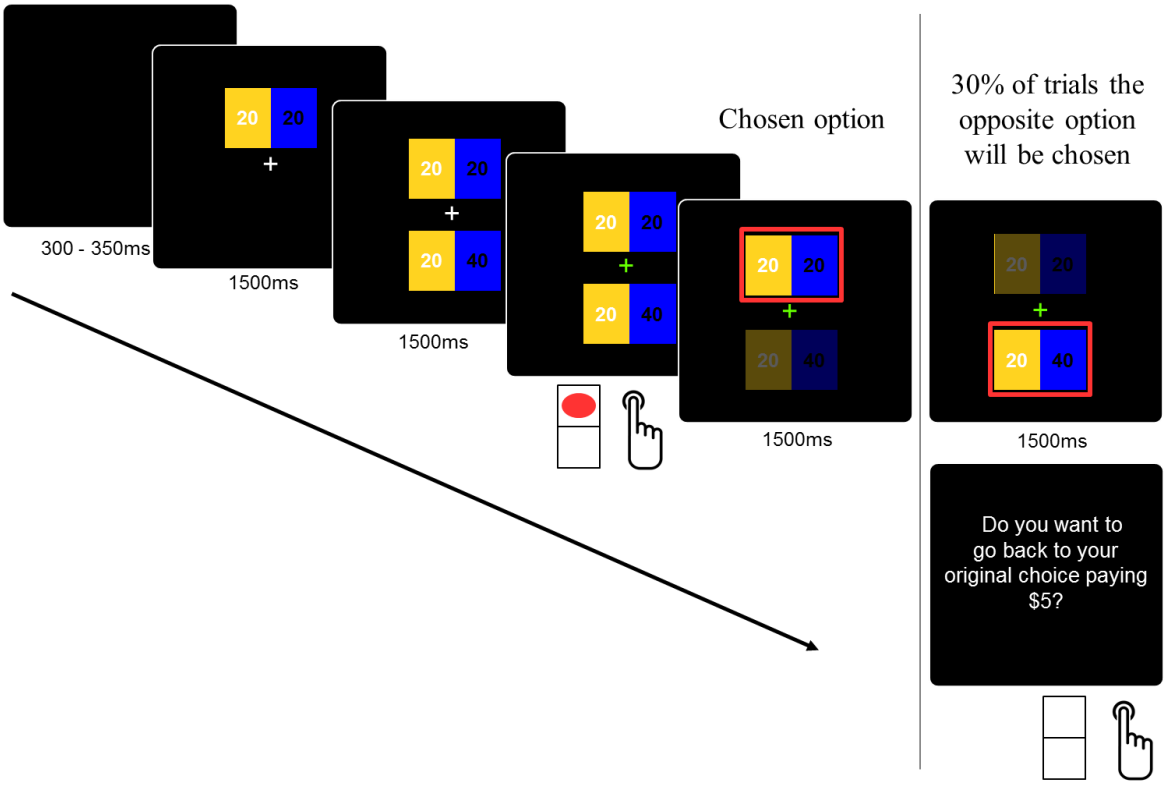

Figure 1. Experimental task, control condition. The decision task consisted in the selection of one within two distributions of money that were presented in the higher and lower part of the screen respectively. Both allocations involved money for the participant and for another player. The other player was identified as a future participant of the experiment. Participants had to press the up or down bottom according to their choice on a normal computer keyboard.

EEG

Brain activity was recorded from 64 scalp electrodes using a Brain Vision amplifier system (BrainProducts, Germany). BrainVision Recorder was used to record brain activity (electrode impedance <5 kΩ, 0.15–500 Hz, 1000 samples/s). All recorded EEG-epochs were individually checked for artifacts by visual inspection. Artifacts were first automatically detected using a threshold of 150 uV and a power spectrum greater than 2 std. dev. for more than 10% of the frequency spectrum (1 to 30 Hz). Blinking was extracted from the signal by means of ICA.

Trials that included artifacts detected automatically and confirmed by visual inspection of the signal were eliminated. The artifact-free EEG material was recomputed to average reference and digitally band-passed filtered to 0.1–45 Hz. Whole power distribution was computed using Wavelet transform, with a 5-cycle Morlet wavelet, in a −1.5 to 1.5 s window around the onset of the second offer. For all analyses, we used the dB of power related to the baseline (15 seconds acquired at the beginning of each block).

	Option 1		Option 2	
	Self	Other	Self	Other
Other's advantageous inequity (OAI)	Low-pay	Low-pay	Low-pay	High-pay
Other's disadvantageous inequity (ODI)	High-pay	High-pay	High-pay	Low-pay
Altruistic (ALT)	Low-pay	High-pay	High-pay	Low-pay

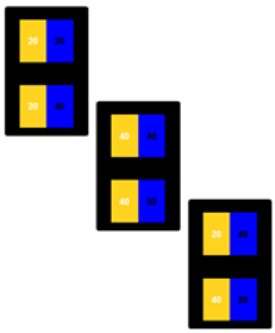

Figure 2. Structure of distributions presented to participants during the experimental task

Statistical Analysis

We used the Kolmogorov-Smirnoff to test for normality. When the data did not meet the normal assumption, we used non-parametric tests. For the EEG statistical analysis, we first fitted a General Linear Model (GLM) of the power of the oscillatory activity per trial in each participant (first level analysis, see (Billeke et al., 2015; Figueroa-Vargas et al., 2020; Larrain-Valenzuela et al., 2017; Soto-Icaza et al., 2019)), using the following equation:

$$\text{Power}(t,f) = \beta_1 + \beta_2 \Delta A1 + \beta_3 \Delta A2 + \beta_4 \Delta A1 * \Delta A2 + \beta_5 T + \beta_6 \Delta A1 * T + \beta_7 \Delta A2 * T + \beta_8$$

$$\Delta A1*\Delta A2*T \qquad (1)$$

where β_1 is the intercept, β_2 is the slope (coefficient) of the variable ΔA1 (differences between the allocation for the player and the other in the first presented distribution), β_3 is the slope of the difference between the allocations for the player and the other in the second presented distribution (ΔA2), and β_4 is the slope of the differences between the allocation for the player and the other in both offers (note that this regressor takes values other than zero only in the ALT case). Additionally, we added a regressor for the experimental condition (T, that takes the value 1 when the decision is during the experimental manipulation, observer or empathy conditions, and 0 in the control condition) with its respective slope (β_5), together with the interactions between the experimental condition and the other regressors (ΔA1*T , ΔA2*T and ΔA1*ΔA2*T). Then, we obtained a 3D matrix of the normalized β-values estimated (electrode, time, frequency, β-value / standard error) for each regressor and participant . We then explored for differences between groups (observer and empathy) and conditions (control and experimental) using the Wilcoxon test (second level analysis). To correct for multiple comparisons in the time-frequency domain, we used the Cluster-based Permutation (CBP) test (Maris & Oostenveld, 2007). Briefly, in this method, the clusters of significant areas were defined by pooling neighboring sites (in the time-frequency chart and adjacent electrodes) that showed the same statistical effect (Cluster threshold detection, CTD, uncorrected $p < .05$). The cluster-level statistics were computed as the sum of the statistics of all sites within the corresponding cluster (e.g., Z value for Wilcoxon test). We evaluated the cluster-level significance under the permutation distribution of the cluster that had the largest cluster-level statistics. The permutation distribution was obtained by randomly permuting the original data (i.e., permuting specific regresor per trial for within-subject analyses or group labels for between-subject analyses). After each permutation, the original statistics test was computed

(i.e., Wilcoxon test), and the cluster-level statistics of the largest resulting cluster were used for the permutation distribution. After 5000 permutations, the cluster-level significance for each observed cluster was estimated as the proportion of elements of the permutation distribution larger than the cluster-level statistics of the corresponding cluster.

RESULTS

Behavioral results

In order to assess participant' decisions, a mixed ANOVA was conducted using case (type of offers, i.e., ALT, OAI or ODI) and condition (control or empathy/observer) as independent variables, and prosocial responses as the dependent variable. The variable group (i.e. observer or empathy) was used as a between subjects factor.

	Sum of Squares	df	Mean Squares	**F**	**p**	η^2
Condition	0.900	1	0.900	17.857	<.001	0.31
Residual	1.966	39	0.050			
Case	23.473	2	11.736	87.905	<.001	0.693
Residual	10.414	78	0.134			
Condition * Case	0.224	2	0.112	3.950	0.023	0.092
Residual	2.216	78	0.028			
Condition * Case * Group (between subjects)	0.302	2	0.151	6.004	0.004	0.06
Residual	1.913	76	0.027			

Table 1. Mixed ANOVA with case, condition and group as independent variables, and responses as the dependent variable.

Significant main effects of case and condition (see Table 1) together with the interaction between condition and case were found. This suggests that participants tended to cooperate differently depending on the case. A between subjects' interaction with condition and case was also found.

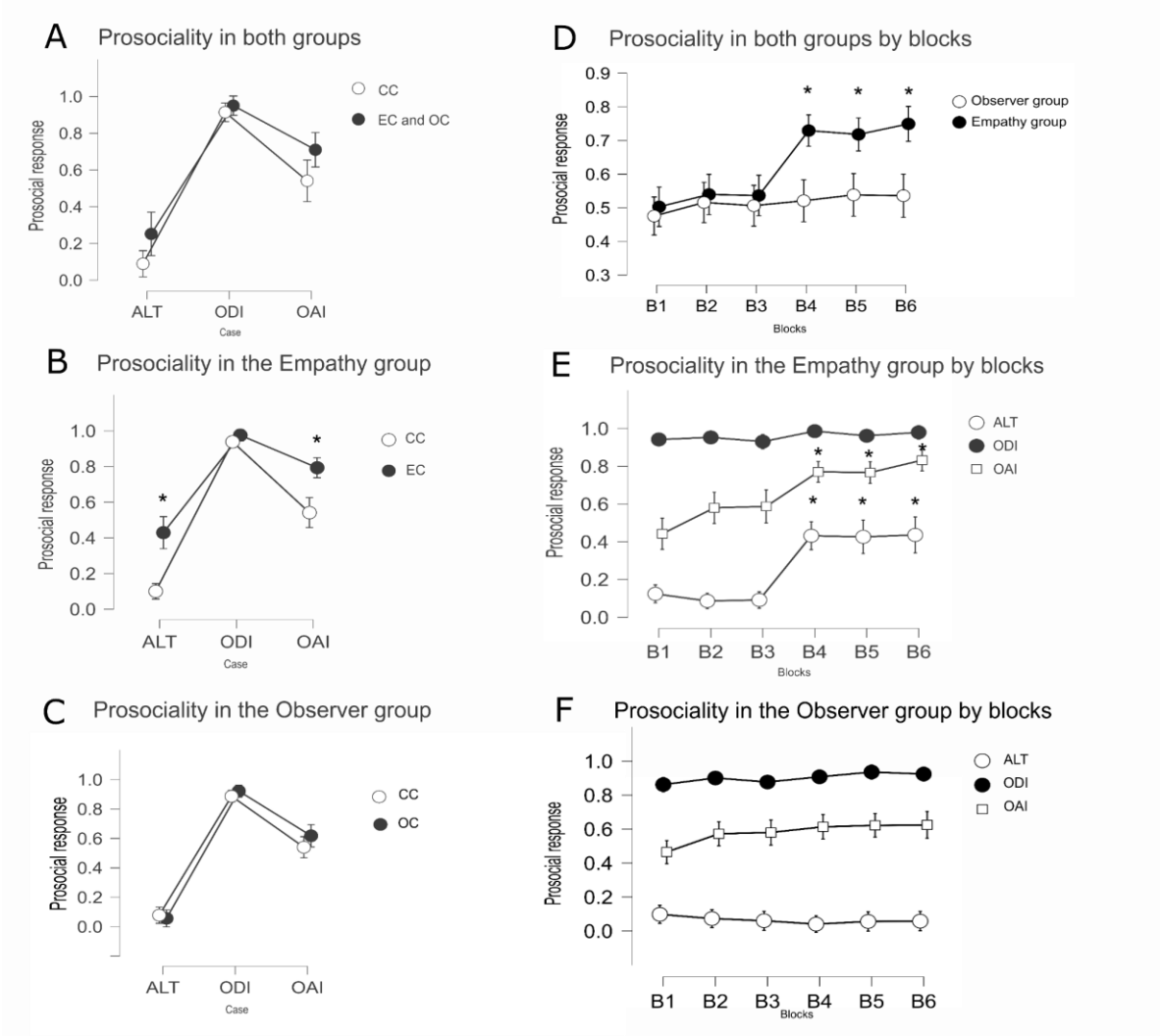

Figure 3. Behavioral results (A) Means and standard deviation of the cooperation rates across each 3 cases by both groups collapsed. (B) Means and standard deviation of the cooperation rates across the 3 cases in the Observer group. (C) Means and standard deviation of the cooperation rates across the 3 cases in the Empathy group. (D) Means and

standard deviation of the prosocial choices across 6 blocks of trials during the experiment. Block 4 is the first block of the experimental condition across both interventions. (E) Means and standard deviation of the cooperation rates by cases across 6 blocks of trials in the Empathy group. (F) Means and standard deviation of the prosociality rates by cases across 6 blocks of trials in the Observer group.

Participants across both groups tended to be less prosocial in ALT cases than in the other two cases (post-hoc ALT-OAI: p(bonf)<0.001, t=-7.891, Cohen's d= -2.087) . This means that when the prosocial options involved personal costs, participants decided to choose it less than when there were no costs associated with this choice. Interestingly, participants decide to be less prosocial in OAI cases than in ODI cases (post-hoc ODI-OAI: p(bonf)<0.001, t= 3.230, Cohen's d= 0.839), even though in both cases there were no personal costs involved in their decisions. This means that participants decide to be more prosocial when this prevents other individuals from earning less than them, but were less prosocial when the other participants could earn more than them in the trial (see figure 3A).

The separate analysis of both groups shows an effect of the EC, but not of the OC (see figure 3). Within the Observer group (figure 3C) there was no effect of the experimental intervention in the prosociality rates (post-hoc control(c) ALT - experimental(e) ALT: p(bonf)=1, t= 0.384; post-hoc cODI-eODI: p(bonf)=1, t=-6.22,; post-hoc cOAI-eOAI: p(bonf)=0.9, t=-1.38). Within the Empathy group (figura 3B) there was an effect of the experimental intervention in both ALT and OAI cases where the prosociality rates increased relative to the control condition (post-hoc cALT-eALT: p(bonf)<0.001, t=-6.153, cOAI-eOAI: p(bonf)<0.001, t=-4.713). There were no differences between the ODI cases (cODI-eODI: p(bonf)=1, t=-6.95). The prosociality rates in the ODI case were high in the control condition across both experimental

interventions. The between subject effects show no differences in the cooperation rates between the two control conditions in all cases (p(bonf)=1 for the three cases).

To closely observe the effect of the experimental intervention, particularly in the Empathy group, a temporal analysis of the prosocial choices was conducted (see figure 3D). The control and experimental conditions were divided into 3 blocks of trials each in order to observe in more detail the changes of the prosocial choices across the experimental task. The variables blocks and cases were used as independent variables, and prosocial responses as dependent. Within the Empathy group (figure 3E) results confirm the effect of the experimental intervention (post-hoc block3-block4: p(bonf)<0.001 t=-6.008), but not in the Observer group (figure 3F) (p(bonf)=1). Prosocial choices within the empathy group remained stable across the 3 last blocks of the EC (post-hoc block4-block5: p(bonf)=1; block5-block6: p(bonf)=1).

As mentioned previously, during the experiment 30% of trials involved that the game chose the opposite option than the one chosen by participants, who had the option to return to their original choice at a monetary cost. We analyzed whether there were differences between the control and experimental conditions in the proportion in which participants maintained or changed their options given their initial choice. The dependent variable for the analysis was the proportion in which subjects maintained a prosocial choice (this means, if they choose the prosocial choice, the game inverted their decisions and then participants return to their original prosocial election) and the proportion in which participants change their original non-prosocial choice to the prosocial selected by the game.

A repeated-measures Anova was conducted using group, experimental conditions and offers as independent variables and the proportion of confirmatory prosocial choices as the dependent variable. Results (see figure 4) show an effect in prosociality ($p<0.001$, $F= 19.572$, $\eta^2=0.177$) in the interaction between group and prosociality ($p=0.046$, $F=4.263$, $\eta^2=0.038$) and in the interaction between condition, group and prosociality ($p=0.003$, $F=10.098$, $\eta^2=0.028$).

Post-hoc analyses show that participants within the Observer group tend to confirm their non-prosocial choice more than their prosocial choice in both control and experimental conditions (post-hoc pro-nonpro p(bonf)<0.001, t= 4.527,). This means that when participants chose the non-prosocial option but the opposite was presented to them, they went back to their original choice in higher proportion than when they chose in the first place the prosocial option. In the Empathy group there were no differences in the proportion of choices between control and experimental condition. The between subject effect shows that there were no differences between both groups in both conditions.

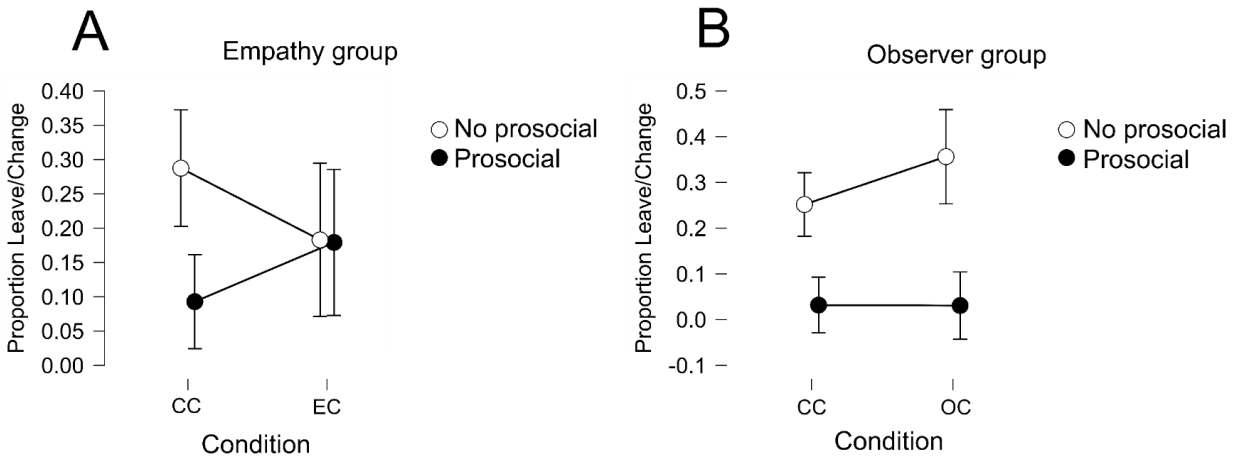

Figure 4. Behavioral results (A) Proportion in which participants of the Empathy group confirm or leave the opposite choice. (B) Proportion in which participants of the Observer group confirm or leave the opposite choice

Brain results

A time frequency analysis was conducted in order to observe the effect of the differences in the spectral activity, particularly in the theta-band oscillatory activity, relative to the unequal monetary distributions during the ODI and OAI cases. As mentioned above, there is consistent evidence showing that theta oscillatory activity is related to the self-inhibitory activity and the encoding of social cues during decision processes. This analysis was conducted given the behavioral differences found between the ODI and OAI cases within the Empathy group. These differences show that while participants decided to be similarly prosocial in the ODI cases in both control and experimental conditions, there were higher rates of prosociality in the OAI experimental treatment. This is interesting given that, in both cases, the players choose between options with same earnings for themselves, but while in the ODI case the prosocial choice prevents the other player to receive less than them, in the OAI case the prosocial choice involves that the other player receives more than them. Thus, we first fitted a GLM of the power of the oscillatory activity per trial during the presentation of the second offer. As a regressor we used the differences on the earnings for participants themselves and for the other player in the first and the second offers separately, and the interaction between them. Note that the interaction captures the variance of the signal given by ALT cases (see method), thus the other regressors capture the variance given by the other cases (ODI and OAI). Specifically, these regressors capture the difference between ODI and OAI when no equal offers are presented in the first distribution (ΔA1) or in the second distribution (ΔA2). We mainly focused on exploring the different modulations in these regressor for experimental conditions (using the interaccion: ΔA1*T and ΔA2*T, see methods). For the contrast of the second levels analysis, we pooled both regressors (ΔA1*T and ΔA2*T) in order to capture the variance related to the decision processing when facing

these cases in experimental condition. Thus, we explored for differences between groups and conditions using the Wilcoxon and CBP tests (see Methods for more details).

Based on prior research (Billeke et al., 2014), we first explored modulation in frontal electrodes (Cz, FCz,C1, C2, FC1, FC2, depicted in the white rectangle in Figure 5E). For the Empathy group, we found a negative modulation of theta/alpha activity around 300 ms after the second offer (Figure 5A). In other words, there is an increase in theta/alpha activity when participants face OAI cases (in comparison with ODI cases) in the experimental (empathy) condition. For the Observer group, we did not find any significant modulation (Figure 5B). These results lead to a significant difference in the fronto-central theta oscillatory activity modulation between Empathy and Observer groups during the experimental intervention (Figure 5C and E). These results indicate that the EC, but not the OC, led to an increase of the fronto-central theta oscillatory activity when participants were exposed to cases in which the other player could earn more than themselves.

These results were corroborated using a whole scalp analysis without a priori assumptions about the localization of the brain modulation between groups (Figure 5D). This analysis shows the emergence of a consistent cluster that overlaps with the activity found in the preceding analysis. Interestingly, the analysis also showed another modulation in theta/alpha oscillatory activity when participants watched the cue that indicated that the decision had to be delivered. Source analysis indicated that theta modulations after the second offer are located in the MCC and right superior frontal gyrus (r-SFG), while the modulations after the response cue are located in the left middle frontal gyrus (l-MFG, or dlPFC).

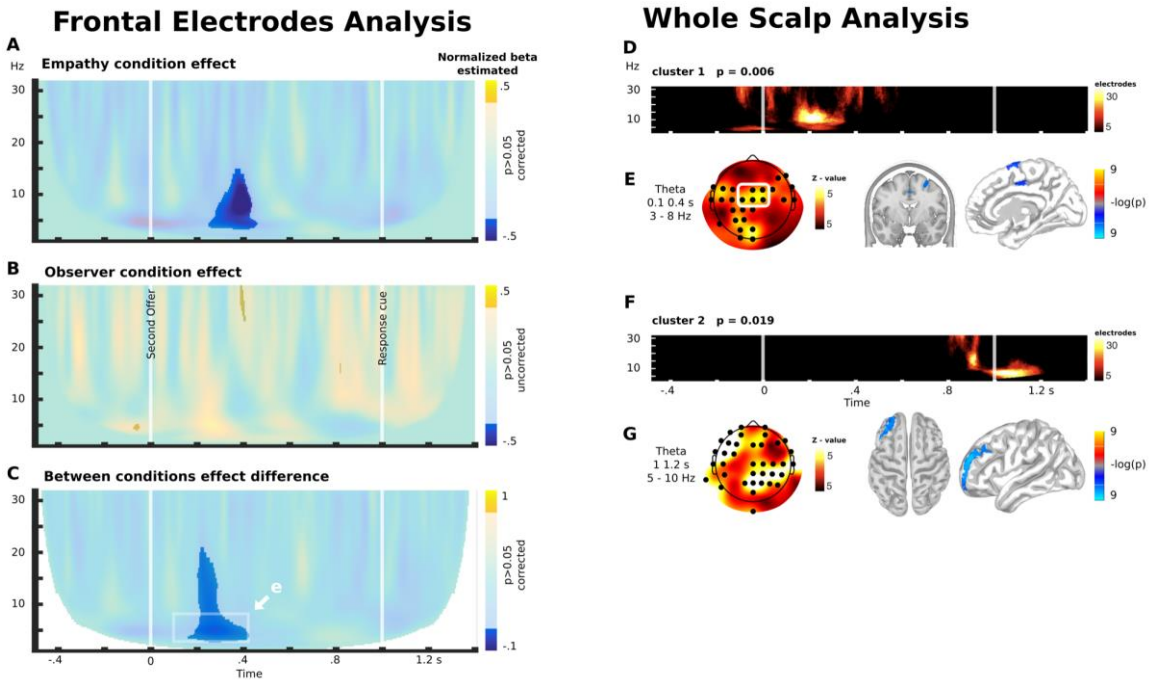

Figure 5. Brain results (A) Difference between control and empathy condition in the correlation between the oscillatory brain activity in the fronto-central electrode (white rectangle in E) and the unequal distribution to the other player during the decision time. (B) Difference between control and observer condition in the correlation between the oscillatory brain activity in the fronto-central electrode (white rectangle in E) and the unequal distribution to the other player during the decision time. (C) Between-groups comparison of the difference between control and experimental condition in the correlation between the oscillatory brain activity in the fronto-central electrode (white rectangle in E) and the unequal distribution to the other player during the decision time. (D) Significant cluster emerging by means of a without a priori whole scalp analysis for the contrast showing in C. (E) Scalp distribution of the theta modulation in the time-frequency windows highlighted in C and its source estimation. (F) Anothers significant cluster emerging by means of a without a priori whole scalp analysis for the contrast shown in C. (G) Scalp distribution of the theta modulation of the cluster showing in F and its source estimation.

Finally, we explored whether the theta/alpha activity after both the second offer and the response cue were related to the rate of prosocial choices. For this we correlated the normalized b-value per subject in both r-SFG after the second offer and in the l-MFG after the response cue with the rate of prosocial decision in OAI cases during the experimental condition. Interestingly, the Spearman partial correlation showed that prosocial decisions in OAI case during treatment correlated with theta activity in r-SFG ($r=-0.57$, $p=0.02$, $n=16$) and not with theta activity in l-MFG ($r=0.3$, $p=0.2$, $n=16$), but only for the Observer group (Empathy group: $abs(r)<0.04$, $p>0.8$). To explore this with more detail we carried out a robust linear regression for the rate of prosocial decision in the OAI case for experimental conditions. In accordance with the preceding result, the relation between theta activity in r-SFG and prosocial decision differed between Observer and Empathy groups theta activity (see Table 2).

	beta	S.E	t-Value	p-Value
Int	0.39	0.08	4.4	0.0001
Theta (l-MFG)	0.03	0.03	1.05	0.3
Theta(r-SFG)	**-0.13**	**0.05**	**-2.3**	**0.027**
Observer Condition (OC)	0.14	0.1	1.4	0.17
Theta (r-SFG)*OC	**0.21**	**0.09**	**2.2**	**0.035**
Theta (l-MFG)*OC	-0.02	0.07	-0.36	0.7
OAI control condition	0.64	0.12	5.2	<0.0001

Table 2: Robust Linear regression of the prosocial decision in OAI case during experimental conditions for both groups.

Taken together, these results show that the empathy intervention increases prosocial decision modulating frontal theta activity when evaluating the different options and when making the decision. The observer intervention did not modulate the prosocial decision on the whole group of subjects, but those subjects that increased their prosocial decision demonstrated a theta modulation that was similar to the one that the subjects in the empathy group showed.

Discussion

Based upon previous experimental results, we hypothesized that the presence of another person would increase prosocial decisions, and that this increase would be higher when the

other person is associated with others in need (EC). At the brain level we hypothesized that the increase in prosocial decisions correlates with frontal theta activity as a marker of empathy saliency. Results showed a differential effect between the two experimental conditions (OC and EC) in both behavior and brain activity. While the Empathy group showed an increase in the prosocial decisions during the experimental condition associated with a modulation of frontal theta activity, there were no effects in the Observer group. The brain activity and behavioral change found in the EC can be interpreted as an enhancement of the saliency of someone in need and / or an increase in the social norm compliance.

Brain results show that the inclusion of someone in need had an effect in the way in which participants faced the decision with favorable inequity to the other player (OAI cases). Oscillatory activity shows that this experimental intervention increased frontal theta activity relative to the unequal favorable distribution to the other player. The source of this activity is compatible with the posterior part of the MCC and superior frontal gyrus. The MCC has been traditionally associated with several processes related to decision making, particularly error detection, self-monitoring, socially-driven interactions and empathy-related responses (Billeke et al., 2015, 2020; Figueroa-Vargas et al., 2020; Lavin et al., 2013; Zamorano et al., 2020). There are reports of a general role of the MCC in the processing of multimodal context-dependent events (Downar et al., 2001, 2002), which has been specifically observed in pain-related experiments that modulate empathy responses (Decety & Jackson, 2006; Jackson et al., 2005, 2006; Lamm et al., 2011; Singer et al., 2004, 2006). Macaque studies, moreover, have shown that lesions to the anterior cingulate gyrus decreased the value that those animals give to social stimuli (Apps et al., 2016), and that activity in this area is related to the observation of rewarding outcomes delivered to another animal (Chang et al., 2012). Human studies have shown that the MCC processes cues that inform about the motivational state of

another person, providing the interpretation that this area participates in the monitoring of others' behavior for learning about and from others (Apps et al., 2016). Taking our results in context to the presented evidence, we can suggest that the frontal theta activity introduced by the empathy condition reflects the participants' detection of relevant social information given by the other person in need. Although the person in need in the EC does not receive a direct benefit from the participants' decision, the recruitment of the preceding brain mechanism can increment the participants' prosocial decisions. It is important to notice that this effect was not present during the OC in spite of the fact that there is also another person present in the decision setting. Interestingly, participants that increased their prosocial choices in the OC showed a theta modulation similar to the EC. The stronger effect observed during the EC can be due to an emotion-related processing elicited by the inclusion of the other in need into the decision setting. Indeed, in accordance with our source analysis, the posterior part of the MCC has been extensively associated with empathic/emotional resonance (Singer et al., 2004; Vogt, 2016; Watson & Greenberg, 2009).

Another possible interpretation for the findings is that the inclusion of another person in need modulated a more general compliance-to-the-norm response. Subjects across both groups tended to be less prosocial when there were personal costs associated with the prosocial choice. This is in line with profuse evidence showing lower rates of prosocial decisions in the dictator game (DG) compared to the ultimatum game (UG) (Christov-Moore et al., 2016; Santamaría-García et al., 2021; Yamagishi et al., 2016). While in the former game there are no monetary incentives for prosociality, in the latter game subjects need to consider others' earnings in order to obtain higher outcomes. Our results show that participants tended to be more prosocial when this prevented other participants from earning less than them but were less prosocial when this led the other with higher earnings. Our brain results show an

increase in frontal theta activity relative to the unequal favorable distribution to the other player. This kind of activity has been previously associated with fair behavior in the DG, and has been interpreted as cognitive control and self-inhibition (Billeke et al., 2014; Zamorano et al., 2020). There is evidence showing medial-prefrontal activity related to rejection of unfair offers in the UG (Corradi-Dell'Acqua et al., 2013), and also specific insular activity related to unfair rejections to third parties. This frontal activity associated with cognitive control and inhibition is in line with evidence that shows the role of the dlPFC (sometimes with specific lateralization to the right hemisphere) related to the compliance of social norms, self-inhibition and cognitive control (Peterburs et al., 2017). Following the preceding interpretation of frontal activity, theta activity in the EC might reflect a general response to adapt the behavior to a norm, in this case related to suppressing inequity-aversion responses when inequity was advantageous to the other player. There is evidence that social norms are reinforced by the presence of a third-party observer (Peterburs et al., 2017). Previous evidence using social observation has shown effects in the way the brain encodes fairness, particularly in the context of social anxiety relative to the observation (Peterburs et al., 2017). Notably, we found behavioral and brain effects only in the Empathy and not in the Observer group. This suggests that the observer-experimental manipulation has to be conducted more strongly in order to produce a more general brain and behavioral changes in the decision process. It can be suggested as future experimental design to include the measurement of personality traits in order to evaluate whether there are different sensibilities related to the influence of making decisions under observation, since we found a correlation between behavior and theta activity within the Observer group.

We have discussed two possible interpretations of our brain and behavioral results, one related to the effect of empathy-related responses associated with a person in need, and

another related to a more general compliance-to-the-norm response. These two interpretations can be considered complementarity. Recently, fairness-related normative decision making in the context of social interaction has been analyzed from the perspective of two complementary processes: an intuitive component and a deliberative one (Feng et al., 2014). The intuitive component is related to the responses towards conflicts between self-interests and a given social context, it is usually related to emotional factors and is reported as being the responsible component for altruistic punishment and general prosocial responses (Haidt, 2001; Roch et al., 2000; Sanfey & Chang, 2008; Santamaría-García et al., 2021; Scheele et al., 2012; Zaki & Mitchell, 2011, 2013). The deliberative component has been related to a reappraisal process of conflict evaluation between, for instance, unfairness-evoked aversive responses (norm enforcement) and self-interest concerns (Feng et al., 2014). The brain areas related to this component are MCC, dlPFC, vlPFC and dmPFC, and are thought to contribute to the development of flexible strategies within decision making settings. Though the source analyses must be interpreted with caution, we can at least point out that the brain activity associated to the EC is in line with the idea of an early component associated to the inclusion of the “other” via the emotionally related component, and that this response may have been reinforced by a norm-compliance adjudgment.

Taken together these results show that the inclusion of a person in need into the decision setting enhances prosocial behavior given by the inhibition of another-advantageous inequity aversion strategy. The modulation of the theta brain activity indicated that these effects can be due to the enhancement of either empathy concerns or norm compliance. Due to the correlative nature of our experiment, it is necessary to inquire about the causal role of these possible brain and cognitive mechanisms testing other experimental approaches, for example, using non-invasive brain stimulation.

Competing interests

The authors report no biomedical financial interest or potential conflicts of interest.

Author contributions

C.L., V.L., P.B. designed the experiment; C.L. , P.B. programmed the experiment; C.L., P.B., conducted the experiments; C.L., P.B., analyzed the data; C.L., P.S-I., V.L., P.B., interpreted and discussed the results; C.L., P.S-I., V.L., P.B., wrote the manuscript.

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Final discussion

In this work we tested the hypothesis that the inclusion of explicit social information into a decision setting influences people's choices. Based upon previous experimental evidence, we hypothesized that the presence of another person would increase prosocial decisions, and that this increase would be higher when the other person is associated with others in need. At the brain level we hypothesized that the increase in prosocial decisions correlates with frontal theta activity as a marker of empathy saliency, activity that would be facilitated by the presence of the other person under necessity. Results showed that, while the Empathy group showed an increase in the prosocial decisions during the experimental condition associated with a modulation of frontal theta activity, there were no effects in the Observer group. The brain activity and behavioral change found in the empathy condition can be interpreted as an enhancement of the saliency of someone in need and / or an increase in the social norm compliance.

These results can be taken as another empirical demonstration of the influence that social variables can have in the decision process. As mentioned at the begging of the theoretical and empirical review, the classic approach of human decision making suggested that people will normally choose options that provide them with the higher possible utilities from a give set of options (Hewig et al., 2011). However, by observing the behavioral results within the Empathy group, we can see that participants tended to increase their prosocial choices even within the altruistic cases in which being prosocial involved monetary costs to themselves. Moreover, when participants have the option of benefiting the other player with no consequences for themselves, they tended to choose the better option to the other player. A superficial interpretation of such effect can be related to the irrationality that emotional

responses can induce in people's behavior, however, a closer look into the previous evidence of the influence that empathy has in decision-making can show that there might be a strategic value under that "irrationality". There is profuse evidence showing that empathy concerns can promote prosocial behavior by including the representation of affective and mental states of others into the evaluation of economic options (Hare, Camerer, Knoepfle, O'Doherty, Rangel, 2013; Masten, Morelli, Eisenberger, 2011; Rameson, Morelli, Lierberman, 2012). Even though empathy and prosocial behavior are not the same, the induction of empathy by salient physical and psychological distress of another person appears as a common modulator of prosocial behavior. The value of including the welfare of others into decisions that involve direct benefits (and costs) can be related to the reciprocal nature of social decision making, in which the building of a reputation can present long-term benefits even though the process is not necessarily conscious (Decety & Grèzes, 2006). The fact that this effect was not found in the Observer group can suggest that the saliency that the other player has for being taken into consideration in the decision process must be strong, and that the mere presence of other person into the decision setting is not necessarily enough to induce such effect. Several experiments have shown that the perception of others in needs (whether under physical suffering or psychological distress) increase prosocial and altruistic behavior, particularly in quick responses, which may suggest an impulsive tendency of helping behavior within such social interactions altogether with top-down strategic considerations. Thus, it is not necessary to suppose a consciences or deliberative component of prosocial behavior, but a bottom-up inclusion of the other by important social cues such as economical necessities of physical pain (Decety & Grèzes, 2006).

The absence of an effect in prosocial behavior by the inclusion of an external observer contradicts evidence that has shown effect in prosociality by even more subtle manipulations.

There is behavioral evidence showing how an external observer influences decisions even by just including eyespots in the decision screen suggesting the observation of others while playing an economic game (Haley & Fessler, 2005). More recently, evidence has shown a completion-to-the-norm effects in people playing as the receipt in the UG, suggesting the influence of external observers in the way participants' decisions (Wei, Zheng, Che, Cheng, Li, Guo, 2018). Using fMRI these authors showed that when participants receive offers being accompanied by three unknown observers who showed social support, participants reported higher unfairness feelings and rejection rates compared to the control condition (without observers). At the neural level, the perception of social support induced (compared to the control condition) higher activation of the anterior cingulate gyrus and right anterior insula when receiving unfair offers. The specific limitations of our experimental manipulation are described below, but it can be stated that the behavioral differences found between the two experimental manipulations can be related to the transversal power that the presence of the other in need had in participants within the Empathy group, which was not found withing the Observer group, in which the observed kept a neutral role and did not participate in any form into the decision process. Results showed that there were some participants within the Observed group that did increase their prosocial rates within the experimental condition and that those subjects demonstrated a theta oscillatory modulation that had a very similar shape as the one that the Empathy group showed, but this effect was not transversal to the whole group of subjects. This suggest that there might be individual differences that can explain a different level of social sensitivity to being observed while deciding, and that a more active role of the observer can enhance the relevance that participant assign to him/her during the decision process.

Brain oscillatory activity showed that the experimental intervention within the Empathy group increased frontal theta activity relative to the unequal favorable distribution to the other player (this is, when the other player could earn more than the participant). The source analysis of this activity suggested that the brain areas involved were with the posterior part of the MCC and superior frontal gyrus. Even though we hypothesized a more prefrontal localization of the activity, the found a frontocentral activity compatible to the MCC, that has been traditionally associated with several processes related to decision making, particularly error detection, self-monitoring, socially-driven interactions and empathy-related responses (Billeke et al., 2015, 2020; Figueroa-Vargas et al., 2020; Lavin et al., 2013; Zamorano et al., 2020). The prefrontal hypothesis emerged from evidence suggesting self-inhibiting processes related to the DLPFC (Billeke & Aboitiz, 2013). There is TMS evidence suggesting that impairment of the right DLPFC affects strategic abilities that inhibit immediate selfish impulses, leaving people prone to inhibit prosocial behavior (Baumgartner, Knoch, Hotz, Eisenegger, Fehr, 2011; Knoch, Pascual-Leone, Meyer, Treyer, Fehr, 2006). Our results suggest a more frontocentral location of the oscillatory activity not necessarily related to cognitive control of impulsive behavior, but consistent to a general role of the MCC processing multimodal context-dependent events (Downar et al., 2001, 2002), which has been specifically observed in pain-related experiments that modulate empathy responses (Decety & Jackson, 2006; Jackson et al., 2005, 2006; Lamm et al., 2011; Singer et al., 2004, 2006). Moreover, the anterior cingulate gyrus area has been related to the observation of rewarding outcomes delivered to others in animal models (Chang et al., 2012), and to the inclusion of active observers during the UG decisions (Wei, Zheng, Che, Cheng, Li, Guo, 2018). Human studies have shown that the MCC processes cues that inform about the motivational state of another person, providing the interpretation that this area participates in the monitoring of others' behavior for learning about and from others (Apps et al., 2016). Taking our results in context

to the presented evidence, we can suggest that the frontal theta activity introduced by the empathy condition reflects the participants' detection of salient social information given by the other person in need. This salient social information was not induced by the presence of another individual into the decision setting, which can explain the absence of a strong effect in the observer condition. Although the person in need in the EC does not receive a direct benefit from the participants' decision, the recruitment of the previously mentioned brain structures might have incremented the participants' prosocial decisions.

Summarizing the findings in light to the proposed hypotheses, we can say that the general hypothesis "The inclusion of another person into the decision setting increases prosocial behavior by recruiting prefrontal oscillatory activity" was partially confirmed. The inclusion of another person by itself was not enough to induce a change in the prosocial rates, but the presence of another person under perceived necessity induced a change in the prosocial rates. These behavioral results are consistent to the specific hypothesis 2 "The increase of prosocial decisions is higher when the other person is associated with others in need". Referring to the neural activity, we found oscillatory activity consistent to previous evidence related to the presence of relevant social information into the decision setting that involved a frontal activity particularly located in the MCC and the anterior cingulate gyrus.

Some limitations can be discussed from the experimental design used to test our hypotheses. Firstly, the observed condition was conducted in a form in which usually actors or actresses are used by researcher in order to simulate a real social situation. In our experimental design we used a college from the laboratory in which the experiment was conducted for this task, and no specific-acting script was elaborated for this intervention. Even though we planned carefully the way in which the observer was going to be presented to the participants and the

story behind her intervention, we think that a professional intervention in terms of acting, and a more carefully planning of the interaction between the observer and the participants would have had a more powerful and controlled effect over participants. Moreover, in light to previous results, we think that a more active role of the observer would have enhanced the relevance of the observer to participants. Secondly, we think that a complementary measurement of personality traits of participants would have been useful to include, in order to observe, for instance, the differential influence of the social components explored in the experimental design and could have helped to explain the lack of a transversal effect found in the observed condition. Finally, the experimental design was conducted with a sample of university student from a similar cultural and socio-economic background. This is sample strategy is very usual in this kind of experiment and in the general experimental approach used within cognitive neuroscience, but it might reduce the external validity of the results and provides a partial view over the cognitive processes studied.

Given the results obtained in this work, there is complementary research that can be conducted in order to deepen the understanding of the brain mechanisms behind the social aspects of decision making. The brain results show an increase in frontal theta activity associated to the increase of prosocial decisions, effect that can be explore in a more direct and causal approach using brain-modulation techniques such as transcranial magnetic stimulation. By artificially inducing or reducing such activity in the brain it can be explore whether there is a direct relation between such brain activity and the enhancement of the saliency that other person can induce in a decision maker, and also explore whether this brain activity is associated to an emotional component of the social interactions or a general social component of norm compliance.

In summary, we can state the present research can be taken as a contribution to the understanding of the neural bases of social decision making. Considering the general objective of the research as “To identify the influence of the inclusion of another person into the decision setting in human prosocial decision making and its brain correlate”, we can state that it was complied since the research provides a view of the way in which the inclusion of salient social information change the way in which people make decisions that have consequences to themselves and to other people. We could observe the induction of specific brain activity consistent to previous evidence, showing that salient social information can induce frontal activity that suggest the integration of such social information into the decision process with the observed behavioral consequences. Results suggest also that the different degrees of emotional-related responses via empathy concerns induce different influence on people’s prosocial decision making.

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