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Review article

The role of the anterior insula in social norm compliance and enforcement: Evidence from coordinate-based and functional connectivity meta-analyses

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ABSTRACT

Economic games —trust (TG) and ultimatum game (UG)— combined with fMRI have shown the importance of the anterior insula (AI) in social normative behaviors. However, whether different AI subregions are engaged in different cognitive and affective processes for social norm compliance and norm enforcement during social exchange remains elusive. Here, we investigated the role of the dorsal AI (dAI) and ventral AI (vAI), combining a coordinate-based meta-analysis of fMRI studies using the TG and UG with meta-analytic task-based and task-free connectivity analyses. Our findings showed that the right dAI and vAI were the only common brain regions consistently activated across games. These clusters were part of two functionally distinguishable connectivity networks associated with cognitive (dAI) and emotional (vAI) processes. In conclusion, we propose that dAI mediates cognitive processes that generate expectancy for norm compliance, whereas vAI mediates aversive feelings that generate motivation to norm enforcement. The identified functional differentiation of the right AI in the social domain contributes to a better understanding of its role in basic and clinical neuroscience.

1. Introduction

Human societies need prescriptions and proscriptions for their members to successfully interact with each other. *Social norms* represent a fundamental grammar of social interaction and refer to behaviors collectively approved or disapproved in a group (Bicchieri, 2005). As a "cluster of expectations", they allow individuals to anticipate others' behaviors and to adopt expected behaviors (Bicchieri, 1990, 2014). Social norms (e.g., fairness, reciprocity) promote equal resource distributions and stabilize cooperation with better collective solutions than those attained by the single, self-interested individuals (Buckholtz and Marois, 2012). Group prosperity is enhanced if all members comply with the accepted norms (i.e., social norm compliance). To guarantee this, however, social norms need to be enforced by sanctioning those who violate them (i.e., social norm enforcement). Social norm compliance and enforcement are possible if at least the following conditions are met: the expectancy that others comply with shared norms, the ability to detect behaviors that deviate from those expected norms, and the selection of appropriate actions based on those deviations (Montague and Lohrenz, 2007).

Economic games —played as single or multiple iterations— are a powerful and reliable tool to investigate people's cognitive and affective processes toward social normative behavior. The *trust* (or *investment*) *game* (measuring the reciprocity norm) (TG; Berg et al., 1995; Camerer and Weigelt, 1988) and the *ultimatum game* (measuring the fairness norm) (UG; Güth et al., 1982) elicit in players social norms that trigger norm-compliant and norm-enforcing behaviors. Moreover, although measuring different social norms, both games have the same characteristics regarding the intentions and the outcomes, which play a crucial key role in the case of a social norm violation (Harth and Regner, 2016; McCabe et al., 2003; Xiang et al., 2013). In particular, involved players evaluate the intentions and value the outcomes before or after a social norm violation occurs.

In the TG, two players take the role of a *trustor* or a *trustee*. The

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trustor (i.e., investor) decides to pass any portion of an initial endowment to the trustee (i.e., an index of trusting behavior). This amount is usually tripled by the experimenter and the trustee decides to pass any portion back to the trustor (i.e., an index of reciprocity behavior) (Berg et al., 1995; Camerer, 2003a; Chaudhuri and Gangadharan, 2007; Csukás et al., 2008). During this sequential economic exchange, trustors usually invest more than half of their initial endowment and expect that the trustee will reciprocate their trust (Camerer, 2003b). However, when trustors know that their partners are likely to violate the norm of reciprocity and intend to betray their trust, investments are reduced by about one-third (Aimone and Houser, 2012, 2013; Bohnet and Zeckhauser, 2004). Such expectations imply inferences of the intentions of the partner in the attempt to predict their behavior, and previous work has shown that trustors' decisions are sensitive to other players' intentions (McCabe et al., 2003). For example, trustors send more money when reciprocity depends on a "partner" as opposed to an "opponent", suggesting that trustors only put trust in their partner when expectations of reciprocity are reasonable according to the partner's intentions (Burnham et al., 2000). In addition, previous or iterated experience with the same partner (like in the iterative TG) increases trusting behavior over time, because trust decisions can be based on feedback learning mechanisms about the partner's social behavior (Bellucci et al., 2017; Chang et al., 2010; Krueger et al., 2007). On the contrary, in single interactions (like in the one-shot TG), trustors have to assume that the partner would comply with the accepted social norms without any guarantee that she will, manifesting a strong betrayal aversion (Bohnet et al., 2008; Bohnet and Zeckhauser, 2004).

Similarly, trustees are also sensitive to the norm of reciprocity and return money to restore equality in payoff outcomes (Chang et al., 2011; McCabe et al., 2003). Having more money than their partner after being trusted induces aversive feelings (e.g., guilt), which makes a betrayal less appealing and motivates reciprocating behavior (Chang et al., 2011; Fehr and Schmidt, 1999; Rutledge et al., 2016). This suggests that norm-enforcing behavior during reciprocity builds on emotional processes related to unequal outcomes. Alike, when trustees do not feel compelled to enforce a reciprocity norm (for instance, when trustors threat to sanction defection), reciprocity rate drops notably, suggesting a cognitive shift from norm-sensitive to utility-based behavior (Fehr and Fischbacher, 2003; Johnson and Mislin, 2011; Li et al., 2009).

In the UG, two players are assigned the role of a *proposer* or a *responder*. The proposer provides an offer in the form of a split of an initial endowment to the responder. The responder then can either accept or reject the offer and in the latter case both players receive nothing. Being aware of the fairness norm, proposers usually share about 40% of their endowments and responders expect proposers to behave fairly and not to share less (Oosterbeek et al., 2004; Ruff et al., 2013). Responders reject unfair offers when their expectations of a norm-compliant behavior is intentionally violated (Civai et al., 2010, 2012; Corradi-Dell'Acqua et al., 2013; Güroğlu et al., 2011). This intentional norm violation (due to an unequal resource distribution) triggers aversive feelings (e.g., anger) in responders, which can be measured through ratings or modeled computationally (Camerer, 2003a; Fehr and Schmidt, 1999; Güth et al., 1982; Pillutla and Murnighan, 1996). By rejecting the unfair offer, responders incur personal costs to enforce the fairness norm via a costly punishment decision (Fehr and Gachter, 2002; Pillutla and Murnighan, 1996). Ultimately, as an index of norm-enforcing behavior, costly punishment intends to re-establish equality in resource distributions (Güth et al., 2000, 1982; Nelson, 2002; Zamir, 2001).

Over the last decade, functional magnetic resonance imaging (fMRI) combined with economic games (i.e., TG, UG) has highlighted the role of the anterior insula (AI) in signaling social norm compliance and facilitating enforcement behaviors (Bellucci et al., 2017; Feng et al., 2015; Montague and Lohrenz, 2007; Sanfey et al., 2003). The insular cortex has been implicated in the integration of autonomic and visceral information into emotional, cognitive, and motivational functions (Namkung et al., 2017). The left and right AI process similar aversive feelings (e.g., pain, disgust and unfairness) but in different fashions. The left AI represents general, amodal features of aversive experiences, the right AI manifest segregated activity patterns, which are specific to different modalities of aversive feelings (Corradi-Dell'Acqua et al., 2016). Recent coordinate-based meta-analyses of fMRI studies using the TG and the UG have demonstrated that the right AI is consistently activated during decisions to trust in the one-shot TG and to reciprocate in the iterative TG (see also Methods) (Bellucci et al., 2017) and during decisions to reject offers in the one-shot UG (Feng et al., 2015; Gabay et al., 2014). However, it remains unclear whether different AI subregions represent cognitive processes that generate expectancy for norm compliance and aversive feelings that generate motivation to norm enforcement. Previous parcellation studies indicate that the AI can be subdivided into a dorsal AI (dAI) region associated with a cognitive network and a ventral AI (vAI) region linked to an affective network (Chang et al., 2013; Kelly et al., 2012; Kurth et al., 2010), suggesting that different clusters within the AI may be engaged in different cognitive or emotional functions across economic games.

Here, we performed a coordinate-based meta-analysis —implementing the activation likelihood estimation (ALE) method (Eickhoff et al., 2009)— to investigate the consistent activation patterns of the right AI across two economic games (TG, UG) measuring different social norm behaviors. While single fMRI studies have small sample sizes that undermine the statistical power and reliability of their isolated findings (Feredoes and Postle, 2007; Raemaekers et al., 2007), a coordinate-based meta-analysis increases the population sample for better generalization by integrating data across several studies (Eickhoff et al., 2006; Price et al., 2005; Wager et al., 2007). Further, we employed meta-analytic connectivity mapping (MACM) and resting-state functional connectivity (RSFC) to investigate task-based and task-free functional connectivity of the dAI and vAI. An increasing number of meta-analytic neuroimaging studies have combined task-based (MACM) and task-free (RSFC) connectivity analyses to reveal converging connectivity patterns of a brain region (Eickhoff et al., 2017; Goodkind et al., 2015; Hardwick et al., 2015; Krall et al., 2015; Wang et al., 2015). Importantly, different connectivity patterns as revealed by these analyses indicate the presence of different brain modules underlying distinct functional roles (Eickhoff et al., 2017). Based on this evidence, we hypothesized that the dAI —because of its connectivity with a cognitive network— is consistently activated during social interactions, in which cognitive processes elicited by inferences about the intentions of others lead to an expectancy of social norm compliance. Further, we predicted, that the vAI —because of its connectivity with an affective network— is consistently activated during social interactions, in which aversive feelings elicited by unequal outcome distributions motivate to social norm enforcement.

2. Materials and methods

2.1. Meta-Analysis

Literature search and selection. Independent meta-analyses of neuroimaging studies on trust and reciprocity (using the TG) and on response to unfairness (using the UG) were conducted. We performed a systematic online database search on PubMed, ISI Web of Science, and Google Scholar by entering various combinations of relevant search items (up to November 16, 2016). For the meta-analysis on trust and reciprocity, we used the following keywords: 'trust', 'trust game', 'trust game', 'trustor', 'investor', 'trustee', 'trustworthiness', 'reciprocity', 'fMRI', 'magnetic resonance imaging', and 'neuroimaging'. For the meta-analysis on responses to fairness, we used 'normative decision making', 'fair', 'altruistic punishment', 'ultimatum game', 'fMRI', 'magnetic resonance imaging', and 'neuroimaging'. In addition, we explored several other sources, including (i) the BrainMap database