Neuroscience of Moral Decision Making

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Introduction

As moral agents, we human beings are equipped with the capability to make judgments about the moral appropriateness of the other's behaviors (i.e., moral judgment) (Baron, 2014; Malle et al., 2014; Wojciszke et al., 2015) and henceforth to form the beliefs about the moral character of the other (i.e., moral inference) (Everett et al., 2016; Kleiman-Weiner et al., 2017; Knobe, 2010). Moreover, we are able to handle situations in which we need to trade off our own profits against the other's welfare (i.e., moral decision making) (Andreoni, 1990; Batson et al., 1981; Charness and Rabin, 2002; Fehr and Schmidt, 1999; Gneezy, 2005; Rand et al., 2012; Shalvi et al., 2015).

Given the complexity and multifaceted nature of morality, questions such as "what is morality" and "how the moral domain is defined" are very often raised by philosophers, social scientists (especially psychologists) and the general public. Rather than coming up with a comprehensive and commonly agreed definition of morality (or moral domain), researchers often define morality from different angles (Bartels et al., 2014; Crockett, 2013; Haidt, 2007). Two of those are commonly adopted. The first approach highlights the compliance with norms, which describes expectancies, beliefs, and rules of how people should (not) act in all or certain cases (e.g., fairness, honesty, justice) (Graham et al., 2011, 2013). The other addresses the concern for the other's welfare, typically accompanied by the cost of personal interests (e.g., relieving the other's suffering) (Cushman, 2015). Accordingly, immorality refers to the behaviors violating norms and causing harm to others' welfare (typically accompanied by the increase of personal profits), which intrinsically deserve blame and punishment and can elicit outrage as well as other negative affect (Schein and Gray, 2018). Notably, these two definitions are not mutually exclusive and can be seen as different sides of the same coin, because most moral rules concern others' interests (despite some exceptions that do not explicitly involve others' welfare, such as purity).

How does our brain enable (im)morality? This is one of the most crucial research questions at the intersection of several fields, such as ethics, social psychology, and cognitive neuroscience. With the rapid development of non-invasive brain imaging techniques (e.g., functional magnetic resonance imaging, fMRI) in the past two decades, there has been a large body of literature investigating the neurobiological basis of human morality (Dolan, 1999; Eres et al., 2017; Fede and Kiehl, 2019; Garrigan et al., 2016; Moll et al., 2005). In brief, most of these studies have focused on uncovering the neural underpinnings of moral judgment (Greene, 2015; Killen and Smetana, 2008; Liao, 2016). While these studies have made indelible contributions to our knowledge of the moral brain, the design properties and analytical approaches of these studies potentially preclude us from a deeper understanding of how real-life moral decisions are made at the neurobiological level. One of the properties is that stimuli commonly adopted in these studies consist of vignettes inspired by moral philosophy describing certain hypothetical moral-laden scenarios. Decisions made in these studies do not lead to any real consequences. However, recent evidence has clearly shown that people's (im)moral behaviors (

2012) and the underlying neural activation patterns (FeldmanHall et al., 2012; Gospic et al., 2013) are different in hypothetical versus real contexts. Moreover, most of these previous studies were not designed to provide a mechanistic account for the moral behaviors, namely the computation our brains perform to transform the input information (e.g., components of moral dilemmas) into behavioral outputs (e.g., moral judgments and decisions; but see Crockett, 2016; Yu et al., 2019).

In this article, we provide an overview of the latest progress in the field of moral neuroscience, with a specific highlight on human fMRI studies investigating the neural substrates of moral decision-making. To distinguish the current article from previous review articles (Forbes and Grafman, 2010; Garrigan et al., 2016; Greene, 2015; Moll et al., 2008; Moll et al., 2005) and meta-analyses. (Eres et al., 2017; Fede and Kiehl, 2019) that are mainly based on traditional moral neuroscience studies, we will mainly consider studies adopting interactive games which are usually based on incentivized economic paradigms. In these tasks, individuals are required to trade off their own profits against others' welfares (or certain moral principles) or to interact with real persons, and their decisions will bring real consequences. Notably, a fair amount of them carries out the approach of computational modeling, which can specify the latent variables involved in the neurocomputational process during the decision period in certain morally relevant contexts (Charpentier and O'Doherty, 2018; Crockett, 2016; Cushman and Gershman, 2019; Hackel and Amodio, 2018; Konovalov et al., 2018) under the general framework of value-based decision making.

Moral Decision-Making in the Brain: A Multi-Stage Framework

We make moral decisions in everyday life. For example, how would you decide when facing the conflict between receiving illicit money and sticking to the bottom line of being an honest person? To uphold the inner conscience by forgoing personal gains, or to succumb to material interests at the cost of moral value? A recent theory in neuroeconomics has offered a computational account of how people make such moral decisions. Essentially, it assumes that these decisions are made by computing a subjective value for all the potential actions (or options) available on a commeasurable scale and then executing the one with the highest value (Levy and Glimcher, 2012; Padoa-Schioppa, 2011). Such computational process can be decomposed into three stages which recruit several neural networks (Platt and Plassmann, 2014; Rangel et al., 2008; Ruff and Fehr, 2014) (see Fig. 1). Stage 1 focuses on the

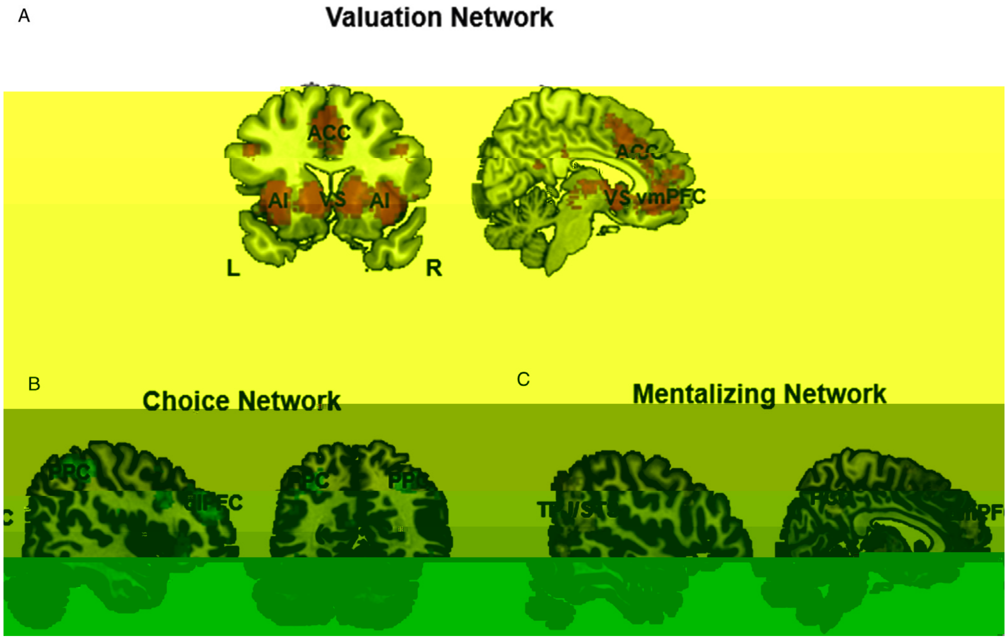

Fig. 1 Neural Networks Engaged in Value-Based Decision-Making. (A) The valuation network. This network includes regions encoding positive and negative value of stimuli (i.e., VS and AI), and regions involved in value integration and comparison (i.e., vmPFC and ACC). These regions mainly function in Stage 1 (value-based choice); some of the regions are also involved in Stage 2 (outcome evaluation; e.g., VS and AI) and Stage 3 (calculation of prediction error for optimization of later choices; e.g., VS). (B) The choice network. This network includes regions that transform decision values to choice behaviors (i.e., dlPFC, PPC), which mainly function in Stage 1. (C) The mentalizing network. This network mainly contains regions involved in inferring the other's intention (e.g., dmPFC, TP, TPJ/STS, PCC), which informs the evaluation of contexts before making choices (Stage 1). Notably, these networks are also found to be critically involved in moral decision-making. Abbreviations: L = left, R = right; ACC = anterior cingulate cortex, AI = anterior insula, dlPFC = dorsolateral prefrontal cortex, dmPFC = dorsomedial prefrontal cortex, PCC = posterior cingulate cortex, PPC = posterior parietal cortex, STS = superior temporal sulcus, TP = temporal pole, TPJ = temporo-parietal junction, vmPFC = ventromedial prefrontal cortex, VS = ventral striatum. All brain maps are rendered based on the uniformity test meta-analytical maps generated from the Neurosynth database (https://neurosynth.org/analyses/terms/), using "value", "choice", and "mentalizing" as the key terms respectively.

process of value-based choice. Specifically, the decision-maker is supposed to represent multiple attributes with regard to each option (stimulus); this representation is often supported by the reward circuitry (e.g., ventral striatum [VS], including Nucleus Accumbens [NAcc]) (Fareri and Delgado, 2014; Haber and Knutson, 2009) and the network encoding negative information (e.g., anterior insula [AI]) (Namkung et al., 2017). In some complex scenarios, the decision-maker also needs to evaluate the other's intention via recruitment of the mentalizing network (e.g., temporoparietal junction [TPJ] and dorsomedial prefrontal cortex [dmPFC]) (Schaafsma et al., 2015; Schurz et al., 2014). Then the integrated subjective value (SV) of each option is computed and compared against each other on a common scale, potentially via the ventral medial prefrontal cortex (vmPFC) and the anterior cingulate cortex (ACC) (Bartra et al., 2013; Kolling et al., 2016; Levy and Glimcher, 2012). This is followed by a stimulus-action value transformation enabling choice selection (Rangel and Hare, 2010). At the neural level, the frontoparietal network, typically consisting of the dorsolateral prefrontal cortex (dlPFC) and the posterior parietal cortex (PPC) (Domenech et al., 2017), converts such value signal into a choice and finally a motor command, which recruits the motor areas to implement the action (Hare et al., 2011; Rangel and Hare, 2010). Stage 2 mainly involves the evaluation of the outcome brought by certain acts (e.g., a reward/punishment feedback) via the value encoding system (e.g., VS, amygdala, AI). In a dynamic environment, the decision-maker is required to compute the disparity between the expected and the actual outcomes, forming the so-called "prediction error (PE)", which is typically reflected in (but not limited to) the VS (Schultz and Wolfram, 2015). In Stage 3, the decision-maker is assumed to use such PE signals to optimize future decisions (Sutton and Barto, 2018). Notably, Stages 2 and 3 take place in more complex decision contexts, such as learning (e.g., inferring other's moral characters based on the observation of their behaviors).

In the remaining part of this section, we will introduce recent advancements in the neuroscience of moral decision-making within this framework. Because most of the studies mentioned below adopted a task that requires the tradeoff between personal profits and various moral costs, the current article focuses on the neurocomputational mechanisms underlying value-based choice in moral contexts (Stage 1), mainly covering the topics such as *harm* (e.g., harming others for personal gains), *help* (e.g., helping others in need or donating to a charity at the cost of personal gains), *(un)fairness* (e.g., preferring selfish or generous resource distribution), *(dis)honesty* (e.g., lying for personal gains), and *betrayal* (e.g., breaking a promise for personal gains). After that, we introduce the existing neural evidence about how decision-makers respond to given the outcome of the other's behavior (Stage 2). We will also briefly discuss the emerging evidence regarding the morality-relevant learning process (Stage 3).

Value-Based Choice

Harm

Harm is considered as one of the core components (or even the only core component) of morality (Graham et al., 2013; Haidt, 2008; Schein and Gray, 2018). Supporting this claim, previous studies have shown that people take advantage of the cue of the other's suffering to distinguish immorality from unconventional behaviors (Hauser et al., 2010; Turiel et al., 1987) and they universally regard harm avoidance as a critical moral principle (Gert, 2004). Even some non-human primates have been shown to exhibit an aversion to profiting themselves at the cost of harming conspecific partners (Masserman et al., 1964).

To investigate harm-based moral decision-making in laboratory settings, researchers have designed behavioral assays in which participants trade off personal monetary profits against physically harming others (Crockett et al., 2014; FeldmanHall et al., 2012). Leveraging such a behavioral paradigm, Crockett and colleagues examined the computational mechanisms and individual differences underlying harm-based moral decision-making (Crockett et al., 2014, 2015). Participants in these studies were requested to voluntarily decide between two options consisting of different amounts of monetary reward and different numbers of painful electric shocks. Critically, the investigators manipulated the recipient of these painful shocks (self vs. other) while always keeping the participants as the beneficiary. Combining computational modeling with choice behaviors, they were able to quantify the latent parameter, namely the harm aversion (defined as the reluctance to cause harm for personal gains), which determines the computational process underlying such decision-making. Model-based analyses across several studies surprisingly revealed that participants displayed a higher level of harm aversion for others than for themselves. A follow-up fMRI study further uncovered the neural mechanisms underlying such "hyperaltruistic" behaviors (Crockett et al., 2017). Specifically, reduced money-sensitive signals of profiting from harming others (vs. oneself) in the lateral prefrontal cortex (lPFC) and dorsal striatum was positively correlated with the individual differences in hyperaltruism (i.e., the differential harm aversion for others than for oneself), indicating that morality originates from a devaluation of ill-gotten profits.

Another line of research stems from studies on proactive aggression, i.e., behaviors deliberately aiming to achieve personal gains (or goals) by planned attacks that cause physical or psychological harm on others (Anderson and Bushman, 2002; Wrangham, 2018). To our knowledge, three studies have so far explored the neural basis of proactive aggression through non-invasive brain stimulation techniques, with a focus on the role of dlPFC, but with mixed results. In an earlier transcranial magnetic stimulation (TMS) study (Perach-Barzilay et al., 2013), participants first received an inhibitory continuous theta-burst magnetic stimulation (cTBS) on dlPFC of either hemisphere. They then participated in a point subtraction task where the aggressive behaviors could be specifically measured by times of button press to cause monetary loss of a fictitious gender-matched partner. Importantly, proactive aggression was defined as aggressive behaviors only when these behaviors were not preceded by the partner's provocative act in previous trials. Results showed that compared with the ones after inhibition of the right dlPFC through cTBS, proactive aggressive responses increased after inhibition of the left dlPFC, suggesting a hemispheric asymmetry in dlPFC modulating proactive aggression. A later study (Dambacher et al., 2015) revealed that after the right dlPFC activity was enhanced by anodal transcranial direct current stimulation (tDCS), male participants displayed less proactive aggression (i.e., the intensity of noise administered to punish the partner), which was measured by the no-provocation trials in the Taylor reaction-time aggression paradigm (Taylor, 1967). However, a recent tDCS study showed that enhancing the right dlPFC activity merely reduced the intention to commit aggressive behaviors in hypothetical scenarios rather than influencing the real proactive aggressive behaviors (Choy et al., 2018). Given the mixed results, more studies are needed to clarify the specific role of dlPFC in regulating proactive aggression.

Help

Helping behaviors reflect the care for the other's welfare at the cost of the helper's own interest, touching upon the key value of morality. One of the most representative helping behaviors is charity donation, which has been extensively investigated in the arena of moral neuroscience. In a pioneering fMRI study, participants decided whether to accept or oppose a proposal of donating to real charitable organizations with or without a personal cost. Results showed that the subgenual part of the ACC was more active when participants accepted the donation proposal than when they received a monetary reward for themselves. Moreover, the donation-related activity in the VS was positively correlated with inter-individual differences in the frequency of accepting the costly donations (Moll et al., 2006). Using a similar design, investigators also revealed a crucial role of reward-related circuitry (especially the VS) in charitable donations. For instance, an increased reward-related signal in the VS persisted even when such donations were mandatory (Harbaugh et al., 2007). A later study further revealed that such VS signal during the charitable decision period could be specifically enhanced by the presence of observers, accompanied by an increase in donation rates (Izuma et al., 2010).

To increase the external validity of the paradigm, Hare et al. (2010) modified the task such that the participants were required to indicate the exact amount of money they would like to donate to a charity, rather than making a binary choice. They found that the monetary amount of voluntary donation was encoded in the vmPFC. Interestingly, the functional connectivity between the vmPFC and the social brain network, including the right TPJ extending to pSTS and bilateral AI, was stronger when participants made donation choices than when they made purchasing decisions, suggesting a specific neural network underpinning the valuation of donation. The contribution of these regions to charitable decisions was also confirmed in a recent study using multivariate decoding techniques (Tusche et al., 2016).

Given these findings, researchers further explored whether and how neurocomputational mechanisms underlying charitable decisions differ from those of immoral choices, namely profiting oneself at the cost of moral values. To answer this question, Qu et al. (2019) established a novel task in which participants decided whether to accept or reject an offer involving either a monetary cost to oneself and an amount of money donating to a charity (a positive moral value) or a personal gain and an amount of money sending to a morally-negative social cause (a negative moral value). Surprisingly, they observed two separate valuation networks functioning for each decision context, with the bilateral caudate engaged in value computation for the charitable decisions and the AI along with the (left) dlPFC for the immoral choices. A separate TMS study uncovered the causal role of the right TPJ in resolving such context-dependent tradeoff between personal profits and moral values (Obeso et al., 2018). Combining multivariate analyses with clinical populations, a recent fMRI showed that the representation of moral contexts (i.e., weighing personal gains/losses against positive/negative moral values) in the right TPJ was selectively impaired in individuals with autism spectrum disorders, further identifying a specific role of the right TPJ in representing moral contexts (Hu et al., 2021).

Another task widely used for measuring altruism, a generalized form of helping, is the dictator game (DG) (Kahneman et al., 1986a,b). In this task, participants are endowed with an amount of money and could voluntarily decide how much to distribute it between themselves and a matched partner (this task is also adopted to investigate fairness, see the next section). One recent fMRI study adopted the modified version that the participants needed to decide between two pre-determined monetary distributions between themselves and another person in which the gains for each party vary independently (Hutcherson et al., 2015). They found that the VS encoded the personal profits, while the right TPJ encoded the other's gains. In addition, the vmPFC was involved in representing gains for both parties but was more sensitive to personal profits. In another study, the right TPJ was found to encode the egoism bias, measured by the difference between one's own reward and the social-distance-dependent other-regarding utilities, especially during generous choices (Strombach et al., 2015). This area's connectivity with the vmPFC was also enhanced when participants made generous choices.

Apart from charity donation and resource distribution, reducing the other's suffering at a cost to oneself also denotes the nature of helping behavior and is commonly seen in our daily life. To explore the neural substrates of such decisions, Feldmanhall et al. (2012) established a paradigm where participants in the MRI scanner decided how much money they would forgo to reduce the intensity of painful electrical shocks inflicted on an anonymous stranger. They found that the socio-affective neurocircuitry, consisting of bilateral TPJ, ACC, and amygdala, was strongly activated during the decision period, especially when the participants' decisions brought real consequences. In a follow-up fMRI study adopting the same behavioral paradigm, the authors provided direct neural evidence supporting the empathy-altruism hypothesis, stating that the trait empathic concern motivated costly helping behaviors by modulating the decision-relevant activity in the neural network crucial for social attachment and caregiving, including the ventral tegmental area and the subgenual part of ACC (FeldmanHall et al., 2015). A recent fMRI study extended these findings by using computational modeling. Model-based analyses suggest that individuals were likely to integrate their own monetary costs with non-linearly transformed recipients' benefits. At the neural level, it identified a functional dissociation of adjacent but different sub-regions within the AI for different processes underlying altruistic behaviors. While the dorsal AI was involved in the valuation of benefactors' costs, the ventral/middle AI, as empathy-related regions, reflected individual variations in valuating recipients' benefits (Hu et al., 2021). Another study investigated the costly helping behaviors in a virtual reality environment where participants decided whether to risk their own lives to save someone trapped in a building on fire in the virtual scenario, revealing an association between the anatomical structure of right AI and the decision to help (Patil et al., 2018).

Notably, all studies mentioned above assumed that helping behaviors would surely reduce the other's suffering, which was not always true in real life. To address this issue, a study combining both fMRI and tDCS techniques developed a new paradigm in which participants were asked to consider the probability of being punished (i.e., receiving a 1s noise administration) for both themselves (self-risk) and a partner in need (other-need) while deciding whether to help. At the neural level, the right dlPFC was shown to causally influence both the effect of self-risk and that of other-need on helping behaviors, whereas the right inferior parietal lobule (IPL) selectively modulated the other-need effect (Hu et al., 2018).

(Un)Fairness

When distributing resources between oneself and the other, individuals commonly prefer fairness as they dislike the difference between themselves and the other (Fehr and Schmidt, 1999). This inequity aversion can emerge not only when individuals receive less (i.e., disadvantageous inequity) than others, but also when individuals receive more (i.e., advantageous inequity) than others (Fehr and Schmidt, 1999). The distinction between these two types of inequity aversion has been demonstrated in different disciplines, providing clues for potentially differential neurocognitive mechanisms underpinning these two types of inequity aversion. For example, behavioral studies showed that individual's responses to advantageous inequity are usually not as strong as the ones to disadvantageous inequity (Bechtel et al., 2018; Fehr and Schmidt, 1999; Loewenstein et al., 1989). While disadvantageous inequity aversion emerges at early stages of evolution and human development, advantageous inequity aversion has only been observed in chimpanzees (Brosnan and de Waal, 2014) and humans over eight years old, who are equipped with relatively mature social and cognitive control abilities (McAuliffe et al., 2017).

In a seminal study (Tricomi et al., 2010), participants evaluated monetary transfers from the experimenter to him/herself or to another person. The researchers found that the process of inequity aversion was associated with activity in the reward system that computes abstract subjective value (Bartra et al., 2013), including the ventral striatum and ventromedial prefrontal cortex. The activity of these areas was more responsive to transfers to others than to oneself in the "high-pay" participants, whereas the activity of such areas in the "low-pay" right lPFC function had opposite effects on voluntary norm compliance and norm compliance under sanction threat (see also Strang et al., 2014). However, studies using the trust game (TG) showed opposite results as the trustee returns less money to the investor when the investor imposes a punishment threat on the trustee, and decreased activations were observed in the lOFC and vmPFC when punishment threat was present (Li et al., 2009). A further study (Zhang et al., 2016) indicated that the discrepancy in previous evidence might arise from the intention behind the threat. In this study, participants divided an amount of money between themselves and a co-player. The co-player (intentionally) or a computer program (unintentionally) decided to retain or waive the right to punish the participant upon selfish distribution. As compared to the unintentional condition, participants allocated more when the co-player intentionally waived the power of punishment, but less when the co-player retained such power. The right lOFC showed greater activation when the co-player waived than when the computer waived or when the co-player retained the power. The functional connectivity between the right lOFC and the brain network associated with intention/mentalizing processing (e.g., dmPFC and TPJ) was associated with the allocation difference induced by intention. The role of lOFC in intention-based fairness norm compliance was further confirmed by the brain stimulation evidence, showing inhibition or activation of the right lOFC decreased or increased, respectively, the participant's reliance on the co-player's intention during monetary allocation (Yin et al., 2017; Zhang et al., 2016).

(Dis)Honesty

Honesty serves as the cornerstone of morality (Graham et al., 2011, 2013 turn may facilitate the patient's recovery. Does such other-serving dishonesty share the same neural representation as self-serving dishonesty? If not, how do the neural mechanisms differ between the two forms of dishonesty? To our knowledge, Abe et al. (2014) first addressed these questions in a fMRI study in which participants were asked to decide whether they would lie in hypothetical life scenarios associated with either harmful or helpful outcomes. They found a stronger activity in the mentalizing network, especially the dorsomedial prefrontal cortex (dmPFC) and the right TPJ, when participants made harmful dishonest (vs. honest) decisions, whereas no such effect was detected in the helpful decisions. In a later study with a modified message game (Yin et al., 2017), researchers showed that compared with the self-serving dishonesty, the other-serving dishonesty (here refers to the lie benefiting a charity) showed reduced activity in the right AI. Moreover, the activity in AI specific to the other-serving dishonesty also positively correlated with the relevant behavioral index that measures the relative financial costs due to the other-serving honesty. However, similar results were not observed in another study adopting the coin task (Pornpattananangkul et al., 2018). Instead, the vmPFC along with its functional network with the dlPFC was commonly activated in both forms of dishonesty, whereas the striatum-middle MPFC coupling sensitive to individual differences distinguished the two forms of dishonesty. From a different angle, Garrett et al. (2016) revealed that only the intensity of self-serving dishonesty increased with time (i.e., escalation), accompanied by a time-dependent reduced amygdala activity. More intriguingly, such escalation of self-serving dishonesty could be explained by the adapted amygdala activity, indicating a critical role of the amygdala in supporting the gradual enhancement of the self-serving dishonesty.

Betrayal

Betrayal is widely seen in every aspect of our real life, ranging from the unfaithfulness in a marriage (e.g., as a husband), the disloyalty to a sports team (e.g., as a soccer fan), to the infidelity to a country (e.g., as an official). These behaviors of betrayal are commonly regarded as moral violations and pervasively unacceptable (Feldman et al., 2000), as they ubiquitously disobey the moral principles of maintaining an interpersonal relationship (Turiel, 1998) and cause intentional harm to other's well-being, particularly those that one has a trusting bond with (Rachman, 2010).

In the social/moral neuroscience literature, betrayal is usually operationalized as the return behavior in the trust game (Berg et al., 1995). The standard version of this game includes two roles, i.e., an investor and a trustee. The investor is initially endowed with a certain amount of money and then decides whether (and how much) to invest an anonymous trustee. The investment amount would be multiplied by some factor (often 3 or 4) and be sent to the trustee, who decides whether to return a certain proportion (e.g., 50%) of the received investment to the investor or to keep it to him/herself. Combining this paradigm with hyper-scanning fMRI, King-Casas et al. (2005) in a pioneering study investigated the neural processing of the investor-trustee dyad during the dynamic interaction. They showed that the signals in the caudate of the trustee could track the return behavior (i.e., the amount transferring back to the investor) depending on the intention of the investor (i.e., the amount giving to the trustee). More complex analyses further revealed that the peak activity in caudate shifted its temporal occurrence as the trustee formed the impression of the investor's reputation in time, indicating the involvement of the reinforcement learning in the social context. A more direct test of the betray-brain causal relationship came from a lesion study, which showed a decreased repayment when patients with a lesion in the vmPFC acted as trustees, relative to the lesion and healthy control groups (Moretto et al., 2013).

Later studies examined additional factors that potentially influence the neural activation related to the trustee's return behaviors, with a focus on the role of guilt, a negative emotional state elicited by the violation of social norms or personal standards (Haidt, 2003). For example, Chang et al. (2011) showed increased activity in the left NAcc when the trustee returned less than what the investor had expected. Interestingly, such betrayal-like NAcc signal was modulated by the trustee's degree of guilt sensitivity. Using both fMRI and tDCS in combination with computational models, investigators also revealed the crucial role of the right dlPFC in gating the trustees' level of guilt aversion (Nihonsugi et al., 2015). Taking a novel approach of inter-subject representational similarity analysis, a model-based fMRI study published recently further differentiated trustees employing different moral strategies according to the association between model-based parameters and decision-related neural patterns involving the contributions of dlPFC, vmPFC, ACC, and AI (van Baar et al., 2019). Other factors were also demonstrated to affect the betrayal of trustees as well as decision-related neural signals, including the threat of investors (Li et al., 2009), the benefit of betrayal (van Den Bos et al., 2009), and the developmental characteristics of the trustee (van den Bos et al., 2011).

Under some circumstances, betrayal involves breaking an explicit promise, which is often considered as a stronger violation of moral values given the key role of promise in facilitating cooperation (Ellingsen and Johannesson, 2004; Kerr and Kaufman-Gilliland, 1994) and enhancing trustworthiness (Blue et al., 2020; Charness and Dufwenberg, 2006; Ismayilov and Potters, 2015). Baumgartner et al. (2009) explored the neural foundation of promise-based betrayal by using a modified trust game in a fMRI study. Here, participants in the role of trustee, in half of the trials, were additionally asked to make a promise at the beginning whether they plan to send back half of the money to the paired investor for the next three trials. Categorizing participants into two groups based on the average return rates, this study found that the amygdala signal in the untrustworthy participants was stronger during the decision period in the promise (vs. no promise) condition than that in the trustworthy group. Moreover, the promise-specific neural activity in the frontoinsular cortex during the promise and anticipation period was negatively correlated with the return rate regardless of groups. A follow-up study further revealed that the resting-state activity of the left AI reflected by the electroencephalography (EEG) signals positively predicted inter-individual difference in the degree of betrayal (measured by the difference between the average rate of promise and the rate of returns) (Baumgartner et al., 2013).

In everyday life, individuals evaluate the outcomes of the other's moral decision and make corresponding behavioral responses, such as acting kindly to the other's helpful behavior and unkindly to the other's harmful behavior. This kind of reciprocal behaviors happens not only when interactions involve the individuals directly (direct reciprocity), but also when these acts have been directed not to us but to others (indirect reciprocity). Both direct and indirect reciprocity are vital for human cooperation, adaption, and survival (Nowak and Sigmund, 2005).

Direct Reciprocity

Positive Reciprocity

Previous neuroimaging studies have mainly focused on reciprocal behaviors in the contexts of trust (see the section Betrayal above) and favor-receiving. When receiving favors, individuals commonly feel grateful and are motivated to reciprocate the benefactor. Such motivation in gratitude has been emphasized as a core feature of this emotion (McCullough et al., 2001). Two studies have investigated the neural bases underlying gratitude-induced reciprocity in the favor-receiving context. In one study (Yu et al., 2017), participants played a multi-round interactive game where they received pain stimulation. In each round, the participant interacted with an anonymous co-player who either intentionally or unintentionally (i.e., determined by a computer program) bore part of the participant's pain; the participant could transfer monetary points to the co-player with the knowledge that the co-player was unaware of this transfer. Relative to unintentional help, intentional help led to higher reciprocity (money allocation) and higher activation in value-related structures such as the vmPFC. Moreover, the vmPFC activation was predictive of the individual differences in gratitude ratings and subsequent reciprocal behaviors. A follow-up study (Yu et al., 2018) further demonstrated that neural signals representing cognitive antecedents of gratitude (e.g., benefactor-cost and self-benefit) were passed to the vmPFC via effective connectivity, suggesting an integrative role of the vmPFC in generating gratitude. Moreover, participants who were most willing to translate their grateful feelings into actual reciprocation showed stronger responses in the gyral part of ACC to the benefactor's help.

Negative Reciprocity

A widely used behavioral task in the research of negative reciprocity is the ultimatum game (UG). In a typical UG, participants act as a responder and decide whether to accept a fair or unfair division of money suggested by a proposer (Sanfey et al., 2003). If the division is accepted, the money would be split as proposed; but if the division is rejected, neither one would receive anything. Participants commonly accepted offers when the divisions comply with the fairness norm (fair offers). Although participants could have obtained a certain amount of money by accepting the unfair offers, they rejected more offers (i.e., receiving nothing) as the extent of the proposer's norm violation increase (i.e., the offers become less fair), indicating the negative reciprocity and negative cost implying that higher demands in moral mentalizing are required in social decision-making when the decision to reject could not be readily justified (Güroglu et al., 2010 revealing that the resting-state brain activity in the left ventral AI (as well as other regions) was correlated with the PIF response (Wu et al., 2015). Together, these findings suggest that the AI is not only engaged in signaling social norm violation during UG but also recruited in guiding subsequent adaptive behaviors (e.g., PIF response).

Learning

In real life, we not only make moral choices in one shot, but often need to form and update our beliefs about the moral trait of others, thereby guiding how we should get along with them in the future (Siegel et al., 2018). Although a substantial amount of

The third issue is related to methodological approaches that should be taken to provide additional information from different viewpoints, thereby characterizing a panoramic view of the moral brain. Obviously, the current literature predominantly considers which parts of the brain (and the inter-regional connections) are associated with a specific form of moral decision using fMRI, supplemented by the causality methods such as brain lesion and non-invasive brain stimulation (e.g., TMS, tDCS). There have been several studies adopting the EEG technique (e.g., event-related potential, ERP) to explore the temporal features of moral decision making at the neural level, especially those related to (un)fairness (Alexopoulos et al., 2012; Boksem and De Cremer, 2010; Cui et al., 2019; Ma et al., 2015; Mothes et al., 2016; Qu et al., 2013; Sun et al., 2015; Wu et al., 2011; Wu et al., 2011; Yu et al., 2015). However, most of these studies concern with the evaluation of the resource distribution, rather than the decision per se. Future studies could incorporate more advanced EEG analyses and other techniques with a high temporal resolution (e.g., magnetoencephalography, MEG) and/or a high spatial resolution (e.g., intracranial EEG) to uncover the temporal-frequency characteristics underlying the process of moral decision making.

From a more realistic perspective, how neuroscience could inform our real-life moral behaviors is another promising but challenging direction guiding the future development of moral neuroscience. For instance, many real-life choices cannot be made individually but rather collectively (Black, 1948; Hwang and Lin, 2012), with no exception to the moral domain (e.g., a decision made by members of the board regarding whether to misreport the sewage discharge to profit the enterprise). Recently, there is a growing trend interrogating the neural mechanisms of such group-based decisions with multi-brain measures, especially via hyper-scanning functional near-infrared spectroscopy (fNIRS) (Ferrari and Quaresima, 2012; Quaresima and Ferrari, 2019). This technique, in combination with more ecologically valid paradigms, enables future investigation on how neural information would flow between and be coordinated among several persons while they are making a collective decision in the moral context.

In sum, this article provides an overview of the recent advances in neuroscientific studies of moral decision making, highlighting human fMRI research which adopted economically incentivized paradigms with real consequences. Although these findings have extended and deepened our knowledge about the neural mechanisms of moral decision making, our current understanding of the moral brain is still far from complete, thereby urgently requiring insights from future investigations addressing the issues above and other related issues with novel methodological approaches.

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