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Determinants and modulators of human social decisions

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ABSTRACT

Social decision making is a highly complex process that involves diverse cognitive mechanisms, and it is driven by the precise processing of information from both the environment and from the internal state. On the one hand, successful social decisions require close monitoring of others' behavior, in order to track their intentions; this can guide not only decisions involving other people, but also one's own choices and preferences. On the other hand, internal states such as own reward or changes in hormonal and neurotransmitter states shape social decisions and their underlying neural function. Here, we review the current literature on modulators and determinants of human social decisions.

1. Introduction

Social decisions are at the core of human social behavior, both at individual as well as societal level. Detecting reliable partners is pivotal for successful cooperation, whereas relying on others for help, information, and support is highly advantageous for survival and optimal behavior within highly complex human societies (Heyes, 2016; Kendal et al., 2018).

An agent navigating a complex social environment must sample different types of information in order to cooperate and interact with others (Bang and Frith, 2017). Particularly, and in contrast to nonsocial contexts, the social environment is more dynamic because other agents also exert influence on the environment. This type of information can be defined as "external," since it is provided by another person in the social environment. For example, reward outcomes in social situations are also contingent on the other agent's actions; for example, my delicious meal might be spoiled by my partner's bad mood. On the other hand, social decisions can be influenced by our "internal" states, which can be psychological (such as our emotions), metabolic (such as hormonal states), or neural (or all three combined). Hence, external and internal factors may separately or (most likely) concomitantly alter individual decisions in social contexts.

In this review, we analyze the different factors that affect our social cognition and behaviors. We first focus on how individuals seek and learn in the (external) social environment. Particularly, we discuss how a social behavior like trust can be biased by factors such as other's facial trustworthiness and reputation, and we discuss its underlying neural mechanisms. We will then review (internal), psychological, hormonal and neural factors that impact how individuals evaluate the social information around them. Thereby, we discuss behavioral and neuro-imaging studies showing that evaluations of others are influenced by psychological states (e.g., positive and negative emotions) and neuro-modulators (e.g., oxytocin and dopamine).

Finally, we will address social cognitive and behavioral deficits as important predictors of mental health and quality of life (Fett et al., 2015; Porcelli et al., 2019). From a classical clinical perspective, social behaviors have largely been underappreciated despite the prevalence of specific social dysfunctions in many psychiatric disorders. Their better understanding could contribute to an innovative, transdiagnostic approach to improving our understanding of different mental health conditions, and their detection and prevention (Porcelli et al., 2019). In the following, we review internal and external modulators of social decision making by focusing on a body of studies that are published in last years from the lab. For further insights into related aspects of human

social decision-making in a more broad sense, we refer the interested readers to other recent reviews in the field (Charpentier and O'Doherty, 2021; Engelmann and Rapp, 2018; Lockwood et al., 2020; Marsh et al., 2020).

2. Determinants of social behavior

2.1. Sources of information underlying social decision-making

Pieces of information about others for decisions in social interactions are derived from different sources. The choice of these sources partially hinges on the nature of the interaction with the social partner. When interacting with a previously unknown other, individuals base their behavior on initial impressions (Engell et al., 2007; Sofer et al., 2015; Todorov et al., 2009, 2008). In contrast, when dealing with a known other, two information sources are relevant: 1) direct information acquired via personal experience with the partner, and 2) indirect information via others' experiences and gossip (e.g., indirect reputation) (Bellucci et al., 2017; Bohnet and Huck, 2004; Fouragnan et al., 2013; Heyes, 2016; Kendal et al., 2018; Krueger et al., 2008, 2007). Importantly, these different sources of social information interact dynamically to form, change, revise or update beliefs about others. In the following sections, we will focus on how social information and cognitive biases impact trust decisions and social interactions.

2.2. First impressions as a basis for trust

When no previous knowledge is available about another person, humans rapidly form impressions about that person during an initial encounter, i.e. first impressions (Schiller et al., 2009). It has been shown that specific physical facial features (e.g., the curvature of the mouth, or the distance between the eyes) are central to forming first impressions (e.g., likeability, competence, aggressiveness, attractiveness, trustworthiness, and dominance) (Todorov et al., 2015; Willis and Todorov, 2006), which then guide social behavior (Secord et al., 1954; Todorov et al., 2011). For instance, impressions of competence impact voting behavior (Todorov et al., 2005), while impressions of trustworthiness are associated with approach/avoidance behavior (Fenske et al., 2005) and individual trust behaviors (Bellucci et al., 2020, 2019b; van' t Wout and Sanfey, 2008).

Economic games (e.g., trust game, ultimatum game) have been widely employed to investigate individuals' social behaviors. In particular, the trust game has been employed in different studies to measure trust and reciprocity (Berg et al., 1995; Strang and Park, 2016). During this two player's game an investor gets a monetary endowment and can decide whether to share part of it with the trustee. Here, the shared amount of money is usually tripled and passed on to the trustee who can decide to return money back (or to keep all or any portion of the money). Thus, trust and reciprocity can be measured according to the investor's and trustee's behaviors, respectively (Strang and Park, 2016). Interestingly, it has been shown that individuals whose faces are perceived as trustworthy are trusted more in the trust game (van' t Wout and Sanfey, 2008). However, this impression-based trust might also be due to variables other than trustworthiness, such as facial attractiveness. Indeed, a previous study shows that attractiveness information from faces explains up to 30 % of the variance in trusting behavior (Stirrat and Perrett, 2010). In many experimental designs, trustworthiness correlates with attractiveness, leaving the unique contribution of facial trustworthiness impressions on trust unspecified.

A recent study filled this gap by investigating the specific effects of facial trustworthiness on trust, keeping attractiveness constant (Bellucci et al., 2020). In particular, in this study female participants performed a one-shot trust game in the role of investor where they played with the trustee only once. Importantly, in this situation, the investors' trust decisions relied only on their first impressions of the trustees, whose faces varied maximally along the trustworthiness dimension but

minimally along the attractiveness dimension. Results demonstrate that trust increased as a function of increasing facial trustworthiness, such that trustworthy-looking partners were entrusted with significantly more money in the one-shot trust game. Moreover, the facial trustworthiness, but not attractiveness, of the partner was significantly associated with participants' behavioral trust, providing evidence on the unique impact of subjective trustworthiness impressions on trusting behaviors in single interactions with unknown others (Bellucci et al., 2020).

2.3. Neural predictors of trust

With respect to facial trustworthiness evaluations, neuroimaging studies have provided evidence on the recruitment of brain regions generally associated with social cognition, such as the superior temporal sulcus (STS) (Winston et al., 2002), the amygdala and insula (Santos et al., 2016; Todorov, 2008), as well as the medial prefrontal cortex (mPFC) and precuneus (Harris et al., 2007; Todorov et al., 2008, 2005)

Similar brain regions have also been found for trusting behaviors evoked by trustworthiness evaluations. For example, an early functional magnetic resonance imaging (fMRI) study investigated participants' investment decisions when paired with another human partner or a computer (McCabe et al., 2001). Results showed that a decision to trust a human (but not computer) counterpart recruits the mPFC—a region with a central role in inferences of others' personality traits (see Section 3) (Derks et al., 2015; Fouragnan et al., 2013; Krueger et al., 2007; McCabe et al., 2003; Wunderlich et al., 2009). Similarly, a more recent study found that trust engaged the mPFC and precuneus during both decision and outcome phases, the dorsolateral prefrontal cortex (dlPFC) specifically during the decision phase, and the orbitofrontal cortex (OFC) and temporo-parietal junction (TPJ) specifically during the outcome phase (Lauharatanahirun et al., 2012).

These brain regions have consistently been shown to be part of a brain network, the default-mode network (DMN), that is highly interconnected at rest and is recruited in many social cognitive tasks that involve inferences about others' intentions, belief updating and understanding others' goals and behaviors (Adelstein et al., 2011; Alves et al., 2019). Interestingly, a preliminary electroencephalography (EEG) study found that resting-state functional connectivity (RSFC) could predict propensity to trust and EEG electrodes with the highest contribution to the prediction were located over the TPJ (Hahn et al., 2015).

A recent study investigated the involvement of the DMN in trust by using whole-brain multivariate analyses combined with RSFC-neuroimaging techniques. Results showed that the DMN was the only resting-state brain network predicting individual differences in the propensity to trust in a one-shot trust game. In particular, mPFC, precuneus and TPJ contributed more strongly to predictions of trust decisions. Interestingly, the DMN was seen to play an important role for reciprocity decisions of trustees as well, although reciprocity was predicted by different functional connections than trust, mainly involving the connectivity between the temporal cortex and the anterior and posterior cingulate (Bellucci et al., 2019a).

Neural activity in these brain regions has been observed during trustworthiness learning as well (Bellucci et al., 2019b). In particular, trustworthiness information of partners was represented in the dlPFC, precuneus, and parietal cortex and activity in these regions was stronger for untrustworthy partners. Participants more strongly revised their behavior for untrustworthy than trustworthy partners, suggesting these regions play a role in tracking the partner's behavior for optimal behavior revision. Importantly, neural patterns underlying trustworthiness learning (stronger functional connectivity between the mPFC and TPJ) predicted subsequent trust decisions with the same partners in a later interaction (Bellucci et al., 2019b).

2.4. Factors biasing trust

Since learning another person's character traits, such as trustworthiness, is dependent on social cognition, this process can be influenced by various cognitive biases that affect inferences and decisions (Olsson et al., 2020). Cognitive biases impacting trust processing originate from at least two sources: (i) external (e.g., the reputation of the other person); and (ii) internal (e.g., one's subjective psychological states).

As an external factor, others' reputations can affect an individual's information sampling patterns. For example, a bad reputation, such as being dishonest, can profoundly undermine a person's trust, as it corrupts positive expectations (Haran and Shalvi, 2020; Rousseau et al., 1998). Reputation impacts information processing and updating, impairing the formation of accurate impressions and optimal behavior revision. For example, a bad reputation might impede accurate learning mechanisms in social interactions by inducing an oversampling of negative over positive feedback (Duradoni et al., 2020; Suzuki et al., 2016). More strikingly, in a recent study, Bellucci and Park (2020) investigated how others' reputation can influence individual's trust behavior. The study applied an advice-taking paradigm in which advisees (the participants) had to pick the card with the highest number out of two available cards to win money. Thereby, they relied on the advice of different advisers (pre-programmed opponents) whose trustworthiness in honest advice-giving varied. The advisees were able to learn trial-by-trial the advisers' trustworthiness from feedback about the true state of the world (Bellucci and Park, 2020). Importantly, after an initial period of reputation building, the adviser's trustworthiness reversed, and participants needed to track this change in trustworthiness. At the beginning of the interaction, participants easily learned and revised their behavior according to the advisers' good or bad trustworthiness reputation, more strongly discarding the advice of dishonest advisers than the advice of honest advisers. However, when the behavior of the advisers ceased being consistent with their reputation, a good reputation impaired participants' ability to optimally revise their beliefs about the initially trustworthy advisers. As a result, they were not able to optimally adjust to the new behavior of the advisers (Bellucci and Park, 2020).

Strikingly, a reinforcement learning model further indicated a reputation-dependent asymmetry of positive and negative feedback about honest and dishonest behavior of the advisers. In particular, participants weighted positive and negative information about the advisers' behaviors in a fashion consistent with the adviser's reputation. Further, dishonest behavior of advisers with a bad reputation were valued significantly more than the same dishonest behavior of advisers with a good reputation, which led to less favorable trustworthiness impressions. Notably, participants' trustworthiness impressions of the advisers were consistent with the advisers' reputation even though their reputation did not reflect their actual conduct. These results suggest that a good reputation overshadowed the impact of dishonest behaviors, biasing impression formation and hindering belief updating (Bellucci and Park, 2020).

3. Social modulations of individual valuation

3.1. Learning from others: social feedback influences self-relevant processing

Our evaluations about others and ourselves can be influenced by how people respond to us. To this end, in this section, we will revise and integrate the current knowledge about how social feedback on character traits influences individual self-evaluation.

A large behavioral literature in psychology and cognitive neuroscience has shown that people tend to evaluate themselves as having more positive (or less negative) personality traits than others. This phenomenon is referred to as self-positivity bias and reflects how people tend to put more weight on information on themselves with positive valence rather than information with negative valence (Fields et al., 2019; Leary, 2007; Lin et al., 2003; Sears, 1983; Zhang et al., 2013). Given that recent studies on psychiatric disorders demonstrated reduced self-positive bias among clinical populations compared with healthy individuals (Korn et al., 2016; Lou et al., 2019), investigating self-positive bias is of great importance for both psychiatry and health psychology (Porcelli et al., 2019; Shestyuk and Deldin, 2010).

The evidence that incoming social information is positively biased suggests that a reward component may be involved in social feedback processing (Bhanji and Delgado, 2014; Korn et al., 2012) and that different rewards (e.g., food, money, positive social feedback) may be processed in similar brain areas (Izuma et al., 2008; Sescousse et al., 2013; Sherman et al., 2018; Terenzi et al., 2018; Wake and Izuma, 2017). In addition, when processing self-related social feedback such as character traits, people also compare themselves to others. This comparison component is subserved by the mentalizing network (Frith and Frith, 2006, 2003; Porcelli et al., 2019). However, the specific mechanisms underlying self-related social feedback processing still require further investigation.

An fMRI study by Korn and colleagues (2012) has filled this gap by focusing on both a reward-related-component and a comparison-component of social feedback processing in the human brain. In this study, participants performed a task in which they received feedback on their personality traits from peers after a face-to-face interaction. Results showed that participants changed their evaluation of themselves and another peer more after receiving positive feedback than after receiving negative feedback (that is, they showed a self-positivity bias). fMRI analysis revealed that this biased social feedback processing was related to two components: a reward-related component and a comparison component. Specifically, neural responses in a network of areas including the ventral striatum and the anterior cingulate cortex/medial prefrontal cortex (ACC/mPFC) tracked the reward component, whereas changes in parts of the mentalizing network, including the mPFC, STS and TPJ, tracked the comparison component. Importantly, a cluster within the mPFC correlated with the behavioral self-related updating positive bias (Korn et al., 2012). In line with these findings, in a recent fMRI study by Fields and colleagues (2019) participants were presented with sets of two-sentence social vignettes that could be either self-relevant or non-self-relevant with a positive, negative or neutral valence. More in detail, in all of the social vignettes the first sentence introduced a situation in which another person (other-condition) or the participant (self-condition) was named. The self-conditions were created by changing the named person to "you". The second sentence of the scenario was always the same across valence conditions except for one critical word that could be positive, negative or neutral. Participants were asked to read these scenarios without making any explicit self-evaluation. Results showed an interaction between self-relevance and positive valence within the mPFC, which further confirms the evidence of a self-positivity bias in this area (Fields et al., 2019).

The study by Korn et al. (2012) provides a possible neurocognitive model of self-relevant feedback processing. According to this model, mPFC might play a crucial role in linking evidence on reward processing and mentalizing with studies on the self-positivity bias. Thus, future studies should continue to investigate the neural computations underlying self-positivity bias by integrating theories on reward processing and mentalizing.

3.2. Changing social behavior

3.2.1. Unfairness and negative emotions in economic decision-making

Social decisions can be influenced by temporary conditions such as momentary, emotional states (e.g., happiness or anger) (Zheng et al., 2017). Unfairness is an interesting phenomenon of a violation of human cooperation (Rand and Nowak, 2013; Yang et al., 2019) and its punishment has been considered a tool that maintains cooperative behavior in society (Boyd et al., 2003; Nowak et al., 2000). Specifically, when

someone is treated unfairly, he or she may experience negative emotions such as anger or frustration (Civai, 2013; Zhu et al., 2019). These emotions can, in turn, have consequences in subsequent economic decisions in social contexts. For example, if a person is unfair to another, the recipient may return a similar unfair behavior (Strang and Park, 2016). This phenomenon is known as negative reciprocity (Chernyak et al., 2019; Falk and Fischbacher, 2006; Kaltwasser et al., 2016; Nowak et al., 2000). Moreover, unfair behavior might be passed on to independent (innocent) third persons provoking a chain of unfairness and negative emotions. This phenomenon is referred to as generalized negative reciprocity (Gray et al., 2014; Hu et al., 2018; Pfeiffer et al., 2005).

Notably, this generalized negative reciprocity can be dampened by emotion regulations. In a study conducted by Strang and colleagues (2016), an emotion regulation strategy (e.g., message writing) could indeed interrupt the phenomenon of generalized negative reciprocity. In this study (Strang et al., 2016), participants performed an economic game, the dictator game, in which the dictator gets a monetary endowment and can decide to offer part of this to the receiver. The receiver has to passively take the amount offered by the dictator without any possibility to reject the option, even when the offer is unfair (Forsythe et al., 1994). The dictator game is therefore a task measuring altruism and inequity aversion. The authors showed that writing a message which is forwarded to the dictator who made an unfair offer (compared to control conditions such as writing a message not forwarded, describing a neutral picture and just waiting for three minutes) regulated participants' negative emotions. In addition, individuals who were able to reduce their negative emotions by forwarding the message also gave higher allocations of money to a third person when they played subsequently the dictator game in the role of the dictator (Strang et al., 2016). In line with this study, other studies have employed another economic game, the ultimatum game (Güth et al., 1982), to investigate the link between cooperation, emotions and economic decision-making (Strang and Park, 2016). In an ultimatum game, the receiver can accept or reject the money offered by the proposer. If this offer is accepted, then the receiver gets the amount offered while the proposer gets the endowment minus the amount of money just split. In case the receiver rejects the offer, both players do not get money. The rejection in the task is also referred to as punishment of unfair behavior (Strang and Park, 2016). In a study conducted by Xiao and colleagues (2005), participants responded less sensitively to unfair offers in the ultimatum game, in the case that they could express their emotions to the proposers (lower rejection rate to unfair offers) (Xiao and Houser, 2005). Similarly, in another study (Grecucci et al., 2013), by using an emotion regulation strategy (e.g., reappraisal) participants reduced punishment behavior in the ultimatum game. Furthermore, this study also found that reappraising the proposer's behavior as less negative (downregulation of responder's negative emotions) was related to activity in the middle frontal gyrus (MFG) and the posterior insula. The activity of the posterior insula was lower when negative emotion was downregulated and higher when negative emotions were upregulated (Grecucci et al., 2013). Recent meta-analyses on human cooperation neuroimaging studies have confirmed the association between unfairness and brain regions involved in mediating aversive affective experiences and conflict such as the anterior insula, ACC, inferior parietal lobule (IPL) and midbrain (Bellucci et al., 2018; Yang et al., 2019).

Taken together, these studies have increased awareness of the crucial role of negative emotions in punishment decisions during economic decision-making (Zheng et al., 2017). Particularly, the results of Strang et al. (2016) shed new light on understanding how emotions influence social economic decisions and how emotion-regulation may reduce the generalized negative reciprocity in human's social interactions (Strang et al., 2016). However, further research is needed to comprehensively capture the neural processes underlying these phenomena.

3.2.2. The relationship between prosocial behavior and happiness

In addition to others' behavior, our own social behavior can impact our emotions. It has been proposed that generous behavior may lead to increased happiness (Aknin et al., 2013). Indeed, over the years, different studies have shown that generous people are happier than selfish people (Aknin et al., 2015; Dunn et al., 2008; Ko et al., 2019; Lyubomirsky et al., 2005).

A recent study has shed light on the neural processes linking generosity to happiness (Park et al., 2017). In the study, a public pledge method was applied. Specifically, participants were told that they would receive weekly a monetary endowment. Participants in the experimental group were asked to commit to spending their endowment on others during the next four weeks, while the control group participants were asked to commit to spending endowment on themselves. Then, all participants performed an independent decision-making task measuring generosity while brain activity was measured using fMRI. The study compared the brain activity of participants in the experimental group with that of in the control group. Results showed that, compared to the control group, the experimental group was more generous in the decision-making task and reported enhanced subjective happiness. Importantly, the experimental group showed greater TPJ activation while making generous choices compared to the control group. Moreover, the generous behavior commitment modulated TPJ connectivity with the OFC and the striatum. Further, the striatal region was not only modulated by the TPJ but also predicted increases in self-reported happiness. These results demonstrated the important role of the striatum in linking commitment-induced generosity with happiness (Park et al., 2017). Consistently, other studies have also shown that the activity of reward-related areas such as the striatum and the OFC is associated with positive emotions elicited by prosocial behavior (Strombach et al., 2015; Sul et al., 2015). Moreover, the results of Park and colleagues (2017) confirm the role of TPJ in generous behavior (Park et al., 2017). This area is associated with the capacity to infer another person's 'mind' or internal states, such as intentions and beliefs (Lo Gerfo et al., 2019; Morishima et al., 2012; Saxe and Wexler, 2005; Strombach et al., 2015). In addition, it has been suggested that the TPJ may be involved in overcoming selfish drives during social decisions (Morishima et al., 2012; Park et al., 2017).

3.2.3. The influence of social cues on reward valuation

Humans tend to direct attention to the same object or location as others (Bayliss et al., 2010, 2007; Moore and Dunham, 1997; Ulloa et al., 2015). This "gaze-following" response is the result of an evolutionary adaptation, as it provides information about the surrounding physical and social environment (Tomasello and Carpenter, 2007). Utilizing this information, we can infer the intentions, emotions, and thoughts of others (Adams and Kleck, 2005; Baron-cohen, 1995; Bayliss et al., 2010). More importantly, individuals' subjective value evaluation may be subtly modulated by this "gaze-following" response. Indeed, a vast literature has shown a greater preference for objects that are looked at by others, compared to those that are ignored (Bayliss et al., 2007; Madipakkam et al., 2019; Ulloa et al., 2015), even without conscious awareness of the others' gaze direction (Mitsuda and Masaki, 2018). Recently, an eye-tracking study has tested the influence of gaze direction in print advertisements. Results showed that a model's gaze directed towards the product, rather than straight ahead to the viewers, increased brand evaluation and purchase intention (Adil et al., 2018). Importantly, this liking effect induced by gaze seems to be unique, since this cannot be observed by other social cues such as pointing hands (Ulloa et al., 2015), nor with non-social cues such as arrows (Bayliss and Tipper, 2005). Therefore, eye-gaze is a special social cue modulating humans' choices and preferences (Frischen et al., 2007).

In a recent behavioral and eye-tracking study, the authors tested whether not only evaluations of objects but also evaluations of food items may be affected by gaze-evoked shifts in attention (Madipakkam et al., 2019). In this study, participants were asked to evaluate food

items (e.g., willingness to pay (WTP)) (Plassmann et al., 2007) before and after a gaze-cueing paradigm in which gaze-cue (social cue) would be directed towards the food item (congruent condition), to the opposite direction (incongruent condition) or straight ahead (neutral condition). Results showed that participants increased their WTP for the food items that were looked at by another person, compared to those ignored. Analyses of eye-tracking data showed that these changes in WTP were not dependent on changes in overt attention to the food items (Madipakkam et al., 2019). Taken together, the results of this study showed that food preferences can be implicitly biased through a gaze-evoked shift in attention.

Similarly, in a neuroimaging study, participants increased their preferences for food items after a cue-approach training in which they had to press a button after hearing a tone. The amplified subjective value for food was associated with preference-related activity in the ventromedial prefrontal cortex (Schonberg et al., 2014). Despite this evidence, no studies to date have investigated the neural signatures of gaze-cue induced changes to the subjective value of food. Future studies are therefore warranted in order to investigate this.

4. Neuromodulations of social behaviors

4.1. Neuromodulators and social behavior

The human brain not only interacts with the environment (as external information) but its functioning also relies on the effects of specific neuromodulators (as internal information) that modify neuronal excitability, dynamics, and function, and which therefore change human social behavior (Crockett and Fehr, 2014). Neuromodulators include neurotransmitters (e.g. dopamine, serotonin, and noradrenaline) and hormones (e.g., oxytocin, testosterone, and cortisol). Recent work in both animal and human studies has revealed how different neuromodulators impact social behaviors such as generosity (Oroz Artigas et al., 2019; Strang et al., 2017a), trust (Bellucci et al., 2020; Kosfeld et al., 2005), social evaluation (Bellucci et al., 2019c; Siegel and Crockett, 2013), affiliation and aggression (Insel, 2010; Ma et al., 2016). Without a detailed understanding of the effects of neuromodulators in human social behaviors, it is hard to make good evaluations and predictions of related cognitions and behaviors. In addition, mental disorders are often characterized by dysfunctional social cognition as well as abnormal neuromodulator function (Kishida et al., 2010). Hence, research examining the influence of neuromodulators on healthy social cognition and response may pave the way for the amelioration of social dysfunctions in mental disorders through pharmacological therapies.

In the following sections, we will mainly focus on oxytocin and dopamine, and how these neuromodulators influence social cognition and behavior. Growing research has suggested that oxytocin influences neurons in the brain in a variety of ways (e.g., oxytocin can increase excitability and enables synaptic plasticity in the brain). Besides increasing prosocial behavior and initiating maternal care, oxytocin may act as a modulator of attention, increasing the salience of social information so that different networks can selectively response to social stimuli (Froemke and Young, 2021). The dopaminergic system, including the ventral tegmental area (VTA), nucleus accumbens (NAc) and PFC has been well investigated, and these regions process reward stimuli and guide behavioral responses based on reward memory and expectation (Keiflin and Janak, 2015; Schultz, 2007). Social interactions, like non-social reward stimuli, engage the reward circuitry and rely on dopaminergic signaling (Hung et al., 2017; Kopec et al., 2019; Park et al., 2017).

4.2. Neuromodulation in generosity

It is fundamental that people share resources with both proximate and anonymous others to maintain the common welfare of society. Many studies have focused on individuals' prosocial behavior, such as generosity, as well as the impact of neuromodulators on prosocial behavior (Heinrichs et al., 2009; Skuse et al., 2009). In general, even in contexts where individuals can behave completely selfishly without any repercussions, most people prefer more altruistic behaviors (Camerer, 2003). Despite this preference, people are not equally generous to everyone. Generosity declines as a function of social distance between individuals (Strombach et al., 2015). That is, people tend to be most generous to close others (e.g., parents), less so to distant others (e.g., neighbors), and even less generous to unknown others. To further investigate the specificity of social-distance-dependent generous behavior, social discounting tasks are widely used (Strang et al., 2017a). Previous studies with pharmacological interventions have revealed that the social-distance dependent generosity depends on neuromodulator functioning. In the next three sections, we will discuss how different neuromodulators (oxytocin, dopamine, cortisol, etc.) may affect generosity.

4.2.1. Oxytocin modulates generosity

Oxytocin is a neuropeptide that can act both as a neurotransmitter and as a hormone (Rodrigues et al., 2009). Several studies have found that oxytocin promotes prosocial behaviors such as trust, cooperation and generosity (Marsh et al., 2020, 2015). However, different factors can moderate the effect of oxytocin on such behaviors, including social closeness between individuals. Interestingly, in one study using a social discounting task, intranasally administered oxytocin in male participants selectively increased their generosity towards socially close others (e.g., families, or best friends). However, this effect was dependent on individual differences in trait empathy. Specifically, the oxytocin group (but not the placebo group) showed positive correlations between empathy and generosity at close social distances (parameter V estimated by a hyperbolic discount function). Thus, the higher the empathy level of participants in the oxytocin group, the more they shared money with their close others (Strang et al., 2017a). This is supported by previous literature debating the effects of oxytocin on prosocial behaviors (Nave et al., 2015; Olff et al., 2013), in which not only social context, but also individual traits (e.g., empathy), interact with the effects of oxytocin. The function of oxytocin in individuals' socialization might be subtle and adaptive to biological and social evolution (Steinman et al., 2019). However, another study (Pornpattananangkul et al., 2017) applying the social-discounting paradigm suggests that oxytocin administration selectively enhanced monetary sharing toward total strangers (at social distance 100)—a specific situation that was overlooked in the analysis of Strang and colleagues' (Strang et al., 2017a). Furthermore, the parameters depicting the overall feature of generosity as a function of social distance (parameter V and k, representing the measurement of the reference-point for the money to share and the degree of discounting, respectively) showed no significant treatment effects in these two studies, which may indicate that the estimated parameters in the hyperbolic model are not sensitive enough to the oxytocin effect in the social discounting paradigm (Pornpattananangkul et al., 2017; Strang et al., 2017a). Therefore, studies investigating other models are required to further identify the oxytocin effect in social discounting.

4.2.2. Dopamine modulates generosity

Temporal discounting refers to an individual's tendency to devaluate future rewards by the delay until they can be realized (Green et al., 1997; Myerson et al., 2003; Terenzi et al., 2019). Several studies have shown the crucial role of dopamine (DA) in such reward devaluation. For example, it has been found that reward delay decreases the activity of dopaminergic neurons (Kobayashi and Schultz, 2008; Prevost et al., 2010). Further, DA agonists have been associated with even a higher devaluation of larger/delayed rewards (Aiello et al., 2019; Napier et al., 2020, 2015; Voon et al., 2010).

As mentioned before, social discounting measures how a prosocial behavior such as generosity can decrease depending on the (social) distance between the person and the recipient (Jin et al., 2017).

Recently, the role of DA in modulating social interactions has been suggested (Sáez et al., 2015; Soutschek et al., 2017). Nevertheless, the role of DA on social discounting remains unclear.

To this end, a recent study has investigated the effects of pramipexole, a dopamine D2/D3 receptor agonist, in female participants' generosity towards other people of differing social closeness. Specifically, compared to the placebo session, women in the DA session showed less generosity towards close others. For the degree of discounting as a function of social distances, no significant effect of pramipexole was found (Oroz Artigas et al., 2019). This study revealed a sensitivity to social-context in pramipexole's effect on generous behaviors and highlighted the crucial role of DA in social decisions. Interestingly, another study applied a DA antagonist (amisulpride) in the context of social discounting and investigated possible gender differences. Compared to placebo, amisulpride significantly reduced generosity to socially close others in female participants and significantly increased this in male participants. The authors argued that women may have a higher sensitivity to prosocial rewards than men (Soutschek et al., 2017). Thus, further studies investigating the role of DA in social discounting should take into account gender differences in social preferences (Heilman and Chen, 2005). Taking the two studies together, both the DA agonist and the antagonist in females lead to a reduction in generosity levels to close others, which may be due to interactions between dopaminergic drugs and sex hormones (Jacobs and D'Esposito, 2011). To fully understand the exact role of DA on generosity, future studies are required to reveal the mechanisms of the dopaminergic system in reward-related interpersonal behaviors in different contexts.

Besides pharmacological manipulation, a novel approach has been tested in the nutrient and metabolic framework and its impact on social behaviors (Lihoreau et al., 2015; Pasquaretta et al., 2018), in order to mimic and facilitate current knowledge about social-behavior-modulation driven by pharmacological interventions (Crockett and Fehr, 2014). Particularly, in a study by Strang and colleagues (2017), the researchers manipulated the participants' breakfast macronutrient composition and tested its effect on social decision-making by using an ultimatum game (Strang et al., 2017b). Considering that protein-rich and carbohydrate-rich foods can increase blood tyrosine and tryptophan levels, precursors of the neurotransmitters DA and serotonin, respectively (Fernstrom and Wurtman, 1971; Wurtman et al., 2003), the study found that a breakfast with a high carbohydrate-protein ratio significantly increased participant's sensitivity to unfairness. Particularly, this type of breakfast was associated with higher rejection rates for unfair offers in the ultimatum game compared with that following a low carbohydrate-protein ratio. Furthermore, this macronutrient-driven changes in rejection rates were predicted by changes in blood tyrosine fluctuation. These findings show that tyrosine might alter punishment tendencies to unfair behavior, possibly by influencing DA prediction errors signals generated as a result of unexpected unfair offers in the ultimatum game (Pessiglione et al., 2006; Strang et al., 2017b). Interestingly, one genetic study showed increased altruistic punishment in both a DA and a serotonin gene variation (DRD4 exon III 7-repeat allele, 5-HTTLPR l/l-genotype). Moreover, the 5-HTTLPR l/l-genotype carriers, presumed to have higher serotonin levels in the brain, punished unfair offers more strongly (Enge et al., 2017). Inconsistent with these findings, another study that enhanced dopaminergic tone via inhibiting catechol-O-methyl transferase (COMT, an enzyme responsible for DA catabolism and signal termination), reported increased inequity-averse behavior in humans (Sáez et al., 2015). Given the complexity of dopaminergic and serotonergic systems (e.g., different receptors, transporters) and the different degrees of neurotransmitter manipulations (e.g., depletion, preload, genetic polymorphisms), further studies are required to reveal the specific mechanisms of neurotransmitters' effects on social decisions.

4.2.3. Other neuromodulators in generosity

Some other neuromodulators also showed impact on people's generosity. For example, contrary to oxytocin, testosterone is associated with antisocial and aggressive behaviors. Recent studies investigating the role of testosterone in social distance-dependent generosity have identified that testosterone administration increased social discounting in general, particularly with regard to distant others (Ou et al., 2021; Wu et al., 2019). These results suggest that exogenous testosterone could influence value-based decision-making in human social interactions. In addition, some early research suggests influences of stress exposure not only in reward-processing and decision-making (Porcelli and Delgado, 2017), but also in prosocial decisions by activating the hypothalamic-pituitary-adrenal axis (HPA axis) system (Tomova et al., 2017; Von Dawans et al., 2012). More strikingly, Margittai and colleagues (2015) found that exposure to psychosocial stress in men increased their generosity (20 min after stressor onset) towards close others but not distant others. Importantly, this result was timing-specific, since men who were tested 90 min after stressor onset did not show the same effect (Margittai et al., 2015). Furthermore, this time-dependent effect of stress in modulating an individual's generosity may be related to two neuromodulators, cortisol (CORT) and noradrenaline (NA) (Hermans et al., 2014). Indeed, in another study (Margittai et al., 2018), the authors applied the social discounting task and found that participants' generosity to close others was boosted by hydrocortisone, but that this increase was off ;set by noradrenergic action. This implies different dynamic fluctuations of NA and CORT after stressor onset. To sum up, the studies linking the HPA axis system to generosity highlight the need for future research to consider the effects of multiple neural dynamics on social behaviors.

4.3. Neuromodulation of trust behaviors

4.3.1. Oxytocin modulates trust behaviors

The associations between exogenous administration of oxytocin and trust have mainly been investigated by applying intranasal oxytocin and using different economic paradigms, such as the trust game (Nave et al., 2015; Zhu et al., 2019). Some studies have reported that oxytocin may elicit trust behavior (Mikolajczak et al., 2010; Nave et al., 2015). For example, in a study by Kosfeld and colleagues (2005), participants who received intranasal oxytocin were more willing to give money to strangers in the trust game, compared to control subjects that received placebo (Kosfeld et al., 2005). However, results showing that oxytocin promotes interpersonal trust have not always been replicated (Declerck et al., 2020; Lane et al., 2015; Nave et al., 2015). For example, recent studies could not differentiate between the effects of placebo and oxytocin in trust behaviors (Yan et al., 2018). Further, oxytocin may increase trust only in a context-dependent manner, that is, when the other person is perceived as neutral or trustworthy (but not suspicious) (Mikolajczak et al., 2010).

To sum up, meta-analyses have further indicated the small and unreliable effect size of intranasal oxytocin on trust (Lane et al., 2016; Walum et al., 2016), which suggests a concern about the replicability of oxytocin administration studies on other social behaviors, as well as the effects of other neuromodulators in human trust behaviors.

4.3.2. Dopamine modulates trust behaviors

Evidence from neuroimaging studies suggest that DA may play a role in trust behaviors (Krueger et al., 2007; Phan et al., 2010). However, given that trust may have a rewarding value, the involvement of dopaminergic brain areas in trust behaviors might be related to other factors such as reinforcement learning and reward anticipation (Chang et al., 2010). Further, as facial trustworthiness and facial attractiveness are closely related (see Section 2.2), dopaminergic brain areas that are activated by facial trustworthiness may be related to this confound. Thus, pharmacological studies controlling for facial attractiveness are needed in order to better understand the causal link between trust and the dopaminergic system.

With this aim, in one study, pramipexole (a D2/D3 DA agonist) was

administrated in female participants, who subsequently completed a one-shot trust game with unknown partners varying in facial trustworthiness (Bellucci et al., 2020). This study showed that pramipexole administration significantly decreased impression-based trust across facial trustworthiness dimensions. Notably, pramipexole modulation of trust behavior interacted with participants' hormonal contraceptive use.

By modulating social reward signaling (Enter et al., 2012; Fisher et al., 2005), the administration of pramipexole might alternatively satisfy individuals' need to belong, therefore reducing one's willingness to reciprocate and connect with others (Baumeister and Leary, 1995). Taken together, these findings suggest a reduction effect of DA on human trust behaviors. Further pharmacological studies are needed to understand the role of DA in human trust behavior.

4.4. Neuromodulation in other social behaviors

4.4.1. Dopamine modulates facial evaluation
The dopaminergic system is associated with decision making in both social and non-social contexts (Burke et al., 2018; Sáez et al., 2015), based on increasing evidence linking DA to individuals' social evaluations and decision processes (Rilling and Sanfey, 2011).

As mentioned in previous sections, studies on social evaluations of faces have usually investigated two main trait dimensions: trustworthiness and attractiveness (Mende-siedlecki et al., 2013). Interestingly, in a study applying pramipexole, the authors found increased attractiveness evaluations to unknown facial stimuli after administration of the DA receptor agonist compared to the placebo session (Bellucci et al., 2019c). Furthermore, pramipexole modulated resting-state dynamics in brain regions which predicted increased facial attractiveness evaluations, suggesting the possible involvement of the DA reward system in social approach behaviors. However, no significant modulations of facial trustworthiness evaluations were observed after pramipexole administration (Bellucci et al., 2019c). Consistent with these findings, a study using DA depletion also reported no significant effects on subjects' trustworthiness ratings (Zebrowitz et al., 2018). For the effects of other neuromodulators on trustworthiness, no studies to date have found a modulation effect of oxytocin on facial trustworthiness evaluations (Grainger et al., 2019), but they have revealed a possible modulation of such evaluations by testosterone (Bos et al., 2010). Taken together, these findings suggest that not only DA but also other neuromodulators may influence subjective evaluations of an unknown person's facial trustworthiness.

4.4.2. Oxytocin modulates facial evaluation
There is no doubt that oxytocin is the most well-studied neuromodulator in social evaluation (Ma et al., 2016; Steinman et al., 2019). Beyond the relationship between oxytocin and social evaluations, the underlying behavioral and neural mechanisms have also received more attention recently. For example, one study combined PET with a facial attractiveness evaluation task, in order to establish the effects of oxytocin and their possible reward mechanism underpinnings (Striepens et al., 2014). Oxytocin's effect on DA release was absent, and this implies a non-dopaminergic path which oxytocin may rely on, since oxytocin administration still facilitated attractiveness evaluations and striatal activation (Striepens et al., 2014). Furthermore, as reviewed by Steinman et al. (2019), oxytocin's reinforcement effects on social interaction may contribute to social salience, which is evaluated by the mesolimbic DA system. Therefore, they highlighted the potential role of DA in underlying and mediating the role of oxytocin in social interactions. This review offered a broader view and modelled a systemic consideration of different neuromodulators' roles and their interactions in human social behaviors (Steinman et al., 2019).

4.5. Other neuromodulators in social behaviors

Though we focus mainly on the impact of dopamine and oxytocin on social behaviors in the current review, other neurotransmitters (e.g., serotonin and noradrenaline) and hormones (e.g., cortisol, testosterone, vasopressin, and other peptides) play crucial roles in broad social behaviors. For example, serotonin is involved in modulating fairness and rejection behaviors toward unfair offers (Siegel and Crockett, 2013), in increasing social preferences for positive reciprocity (Siegel and Crockett, 2013), and in inhibiting impulsive social aggression (Montoya et al., 2012). Testosterone is suggested to fluctuate in response to aggression, competitiveness, and mate-seeking behaviors (Geniole and Carré, 2018; Montoya et al., 2012). Vasopressin is important in affiliation, social stress, and social interaction (Heinrichs et al., 2009; Insel, 2010). By investigating how the neuromodulators influence social behaviors and cognition, research may shed light on pharmacological therapies in individuals with social dysfunctions.

5. Conclusions

The current review provides an initial and nuanced understanding of the multifactorial features that determine how individuals make decisions in social contexts. This review identifies both the environmental (external) factors affecting social decisions, and it provides important insights into the role of (internal) psychological determinants and neuromodulators in such decisions.

First, we discussed how social information can impact not only evaluations about our social partners (e.g., their reciprocity) and social learning (Bellucci et al., 2020; Bellucci and Park, 2020), but also preferences related to less social stimuli, such as food items (Madipakkam et al., 2019). In particular, by focusing on trust evaluations and behaviors, studies reviewed in the first section indicate that mentalizing brain regions (e.g., TPJ and mPFC) are involved in learning others' trustworthiness and that the functional connectivity between these brain regions can also predict an individual's trust behavior in future social interactions (Bellucci et al., 2019a, 2019b). More generally, this evidence sheds light on how others' social characters are represented in our brain and influence our decisions in social contexts.

Second, we showed how personality traits, emotions, and neuromodulators impact social decisions. While we demonstrated how DA consistently influenced prosocial evaluations and behaviors, for instance, by improving perceptions of facial attractiveness (Bellucci et al., 2019a), weakening inequity-averse behavior (Strang et al., 2017a), increasing egalitarian tendencies (Sáez et al., 2015), and modulating generous behavior (Artigas et al., 2019; Soutschek et al., 2017) (but see section 4.2. for mixed results on the effect of DA on generosity); the evidence regarding the modulatory effects of oxytocin is inconsistent. On the one hand, the mixed findings may be related to specific social contexts or individual differences (Lane et al., 2016; Nave et al., 2015). For example, in the field of prosocial decisions (generosity), the effects of oxytocin may vary as a function of the features of a social context, since it has been implicated in motivating in-group cooperation, but also out-group defensive aggression (De Dreu, 2012; Marsh et al., 2015). On the other hand, individual differences in the expression of emotions and neural states may also modulate oxytocin's effects on social decisions (Bartz et al., 2011). For instance, studies identified the interaction of oxytocin with empathy and cognitive bias on prosociality (Barraza and Zak, 2011; Strang et al., 2017b). Furthermore, evidence from neuroimaging studies suggests the possible modulatory effect of neural factors in oxytocin. Specifically, oxytocin may promote social interactions through the direct effect of DA neurons (Hung et al., 2017; Striepens et al., 2014; Zak, 2008), emphasizing social salience and reward values that reinforce prosocial behaviors (Steinman et al., 2019). Further, emotions can also modulate the effects of external social information on individuals' social decisions. Indeed, we reported that positive and negative emotions, as well as emotion regulation

strategies, could modulate individuals' social interactions with others (Park et al., 2017; Strang et al., 2016; Strang and Park, 2016).

Our review suggests that the impact of social information on an individual's social responses may depend also on internal factors such as cognitive biases. More strikingly, cognitive bias can also modulate individuals' social decisions in other primate species (Bono et al., 2018). The neural mechanisms underlying the internal factors' influence on social decisions may be related to (at least) two brain networks, the frontoparietal mirror-neuron areas (di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004) and the cortical midline structures (Greicius et al., 2003; Mitchell et al., 2005). By processing and integrating information about physical and mental self and others, these two networks may bridge the gap between self and social factors (Uddin et al., 2007). However, the interaction between external and internal factors and their effect on social decisions has received less attention.

This review offers a broader view in the systematic consideration of how social decisions, such as trust, facial perception, interpersonal reciprocity, and decisions under social context are susceptible to influences from both external and internal modulators. Our review identified not only the unique effects of these possible modulators but also the interaction effects between external and internal factors. These findings may help improve our understanding of social decisions, including their cognitive and neural mechanisms. Thus, future studies on social decisions should consider the potential external and internal factors that impact people's social behaviors. This could eventually lead to more specific and targeted interventions in neurological and psychiatric disorders with impairments in social functioning.

Following this promising avenue of innovative research, in 2016 the European Commission and other funding agencies have launched the PRISM project—a project that attempts to understand the three most common brain disorders in Europe (e.g., Alzheimer's disease, schizophrenia and major depression) by investigating an important social dysfunction shared by these brain disorders, that is, social withdrawal (Kas et al., 2019).

Our review aligns with this current and important avenue of research by providing evidence for the multifactorial features underlying both the optimal and biased functioning of social cognition and behavior.

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Declaration of Competing Interest

The authors report no declarations of interest.

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