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How serotonin shapes moral judgment and behavior

Jenifer Z. Siegel[1] and Molly J. Crockett[1,2]

[1]Wellcome Trust Centre for Neuroimaging, University College London, London, United Kingdom. [2]Laboratory for Social and Neural Systems Research, University of Zürich, Zürich, Switzerland

Address for correspondence: Molly J. Crockett, Wellcome Trust Centre for Neuroimaging, University College London, 12 Queen Square, London WC1N 3BG, United Kingdom. mollycrockett@gmail.com

Neuroscientists are now discovering how hormones and brain chemicals shape social behavior, opening potential avenues for pharmacological manipulation of ethical values. Here, we review recent studies showing how altering brain chemistry can alter moral judgment and behavior, focusing in particular on the neuromodulator serotonin and its role in shaping values related to harm and fairness. We synthesize previous findings and consider the potential mechanisms through which serotonin could increase the aversion to harming others. We present a process model whereby serotonin influences social behavior by shifting social preferences in the positive direction, enhancing the value people place on others' outcomes. This model may explain previous findings relating serotonin function to prosocial behavior, and makes new predictions regarding how serotonin may influence the neural computation of value in social contexts.

Keywords: serotonin; moral judgment; harm aversion; fairness

Introduction

How does the brain produce moral behavior? What biological mechanisms determine whether a given individual harms or helps others? And can our neurobiology be manipulated for good? Of late, questions like these have arisen at the interface of neuroscience, ethics, and the law. Here, we examine the contributions of a single brain chemical—serotonin—to moral judgment and behavior.

Serotonin is a monoamine neurotransmitter that is evolutionarily ancient and well preserved across mammals. It is one of the most widely distributed neurochemicals in the mammalian nervous system, making its precise functions difficult to pinpoint; however, serotonin is more concentrated in certain structures than others. Anatomical studies illustrate the highest densities of serotonin concentrations in various limbic structures, such as the cingulate, entorhinal, insular, and temporopolar regions, along with the ventral and pallidal regions of the striatum[1] and the medial orbitofrontal cortex.[2] Notably, this set of regions bears a striking resemblance to the so-called social brain[3]—those regions supporting social cognition and decision making.

Not surprisingly, then, serotonin has long been implicated in social behavior across species.[4,5] For example, polymorphisms in the serotonin transporter gene have been linked to personality traits related to aggression, neuroticism, and impulsivity.[6–11,30] In both primates and humans, serotonin function tends to covary positively with prosocial behaviors such as grooming, cooperation, and affiliation, and tends to covary negatively with antisocial behaviors such as aggression and social isolation.[12–19] Such prosocial and antisocial behaviors are likely precursors to human morality.[20–22]

Despite abundant evidence linking serotonin to morally relevant social behaviors, the neurobiological and psychological mechanisms mediating these relationships remain unclear. A recent meta-analysis encompassing 175 independent samples and over 6,500 total participants found a reliable inverse relationship between serotonin and aggression, but failed to identify the specific factors explaining the heterogeneity in study outcomes.[23] One challenge facing research in this area is the complexity of both moral behavior and the serotonin system itself. Understanding how serotonin modulates moral behavior thus requires precise behavioral tools for

measuring aspects of moral behavior, combined with targeted pharmacological tools for manipulating serotonin in the brain.

Moral codes dictate how people should treat one another, and most of these focus on two facets of social relationships. The first prescribes caring for others and prohibits harm; the second relates to the fair distribution of resources and reciprocity in social interactions.[24,25] Concerns for harm and fairness play a central role in moral codes across cultures,[26] and there is some evidence that these building blocks of morality shape social behavior in primates.[27–29]

In the following, we present evidence that serotonin modulates human concerns for harm and fairness, and we examine the potential mechanisms. We first consider how serotonin influences harm aversion in moral judgment and aversive processing more generally, and then examine how serotonin shapes behavioral responses to fairness and reciprocity. Finally, we synthesize these findings into a theoretical process model whereby serotonin influences social behavior by shifting social preferences in the positive direction, enhancing the value people place on others' outcomes. This is not a comprehensive review; instead, we focus specifically on studies conducted in humans employing controlled, experimental manipulations of the serotonin system in the laboratory. For a recent comprehensive review of serotonin and social behavior, we refer readers to Kiser *et al.*,[5] for a discussion of genetic polymorphisms of the serotonin system and their relation to social cognition, see Skuse.[30]

Harm aversion and morality

Violence toward others is restrained by a seemingly deep-rooted aversion to harmful actions.[31,32] Such *harm aversion* infuses moral judgments;[33] people tend to judge harming an innocent person as forbidden, even when doing so would ultimately achieve a greater good.[34,35] Harm aversion appears to shape judgments in moral dilemmas, in which people must judge whether it is morally permissible to harm one person in order to save many others. One classic set of dilemmas involves a runaway trolley that is heading down the tracks toward five workers, who will die if you do nothing. In one variant of the problem ("switch"), you have access to a switch that will divert the trolley onto a different set of tracks, where there is a single worker. If you flip

the switch, the single worker will die, but the five others will be saved. In another variant ("push"), you and a large man are standing on a footbridge over the tracks. You can push the large man off the footbridge and onto the tracks, where his body will stop the trolley before it hits the five workers. Although the switch and push variants are matched with reference to outcomes, people are much less likely to judge it morally permissible to push the man than to flip the switch.[34–36]

Why do people react so differently to the two scenarios? One influential hypothesis posits that personal cases like push elicit stronger emotional responses than do impersonal cases like switch, and these emotional reactions drive harm-averse judgments in the former to a larger extent than in the latter.[37] Incidental negative emotions like disgust increase the likelihood of harm-averse judgments, even when the emotions are unrelated to the dilemmas under consideration.[38,39] Neuroimaging studies have demonstrated that harm-averse moral judgments engage brain regions previously implicated in emotional processing.[34,40–42] Further evidence for the relationship between emotional responses to harm and moral judgment comes from a recent report that physiological reactivity to witnessing fake violent acts against people (vs. violent acts against objects) predicted moral judgments; those people who showed the strongest physiological reaction to witnessing violent acts were the least likely to endorse harming one to save many others.[32]

Note that most studies of moral judgment ask participants whether it is morally permissible to actively cause harm, for example, "Is it morally permissible to push the man?" In these studies, negative cues associated with the harmful action in question could trigger a withdrawal reflex, making subjects less likely to endorse active responses. We might expect this Pavlovian aversive withdrawal process to be particularly strong in personal scenarios that often involve lurid descriptions of the violent actions. There is some evidence supporting this hypothesis. Increasing the vividness of the descriptions of harm in moral dilemmas reduces endorsement of harmful actions.[43] Ugazio *et al.*[39] found that disgust, a withdrawal-related negative emotion, reduced subjects' endorsement of harmful actions, whereas anger, an approach-related negative emotion, had the opposite effect. Finally, Pastötter *et al.*[44] recently reported that negative emotions reduced the

endorsement of harming one to save many when subjects were asked explicitly whether harming one was morally permissible. However, negative emotions increased the endorsement of harming one to save many when subjects were asked explicitly whether not harming one was morally permissible. In other words, negative emotions increased the likelihood that subjects would say "no, that is not permissible," regardless of the question asked. These findings support the notion that aversive states promote behavioral withdrawal, which can translate into harm-averse moral judgments when those judgments are framed in relation to action permissibility.

Serotonin and harm aversion

It turns out that serotonin has been implicated in precisely this aspect of aversive processing—namely behavioral withdrawal in the presence of aversive cues. Early studies in rats demonstrated that global brain serotonin depletion made them insensitive to punishment.[45] In humans, serotonin levels are positively correlated with harm-avoidant personality traits,[46,47] and psychiatric disorders involving aversive processing, such as anxiety and depression, are associated with serotonergic abnormalities. The precise motivational processes driving these findings have been subject to a long debate that has yet to be fully resolved.[48–54] However, recent attempts have made considerable progress, both by integrating previous theories of serotonin function and by extending the logic from existing computational models of dopamine.[50,53,54]

One current hypothesis is that serotonin plays a key role at the intersection of aversion and inhibition. Under normal conditions, the presence of aversive outcomes leads to behavioral inhibition, which can manifest in a reduced probability of action or in slowed response times. Modest depletion of brain serotonin in humans abolishes this aversively motivated behavioral inhibition,[4,55,56] suggesting that serotonin is important for promoting behavioral suppression or withdrawal in the face of aversive predictions. Note that behavioral inhibition in response to aversive outcomes reflects at least two concurrent processes: instrumental aversive predictions linking actions to outcomes and Pavlovian aversive predictions linking stimuli and contexts to outcomes. Recent data suggest that serotonin mediates reactions to the latter, Pavlovian process; serotonin depletion

abolished inhibition of responses in the presence of aversive stimuli, regardless of whether the responses themselves led to punishment.[56]

Serotonin's involvement in these rather basic aspects of aversive processing suggests that its influence could translate upward into effects on moral judgment. There is some evidence pointing in this direction; neuroimaging studies of moral judgment have shown that imagining harmful acts against others engages brain regions with dense serotonergic projections, including the anterior cingulate cortex, ventromedial prefrontal cortex (vmPFC), amygdala, and striatum.[34,40,42,57] Moreover, patients with damage to the vmPFC show impaired harm aversion in moral judgment, in the sense that they are more likely to endorse harming one person to save many others.[58,59] If serotonin plays a key role in harm aversion, could enhancing serotonin function produce effects on moral judgment opposite to those observed in the vmPFC patients?

Crockett et al.[60] tested this hypothesis by investigating the effects of the selective serotonin reuptake inhibitor (SSRI) citalopram on moral judgments in a set of moral dilemmas. Citalopram enhances serotonin function by blocking its reuptake into the presynaptic terminal following release, thus prolonging its actions in the synapse. The set of dilemmas included personal and impersonal variants similar to the push and switch cases described above. The effects of citalopram were contrasted with those of atomoxetine, a noradrenaline reuptake inhibitor, and placebo in a double-blind within-subjects study. Relative to both atomoxetine and placebo, citalopram made people less likely to endorse harming one to save many others. In other words, citalopram enhanced harm aversion in moral judgment[60] (Fig. 1A).

Crockett et al. further examined whether individual differences in empathy moderated the effects of the drug. On the basis of their scores on the Interpersonal Reactivity Index,[61] subjects were split into high- and low-empathy groups. Subjects with lower empathy scores showed almost no effect of citalopram on moral judgment; the effect of the drug in the group overall was driven almost entirely by subjects with higher empathy scores, who showed a strong effect of citalopram on judgment (Fig. 1B). Subjects high in empathy may possess higher levels of harm aversion at baseline, which were further boosted by citalopram.
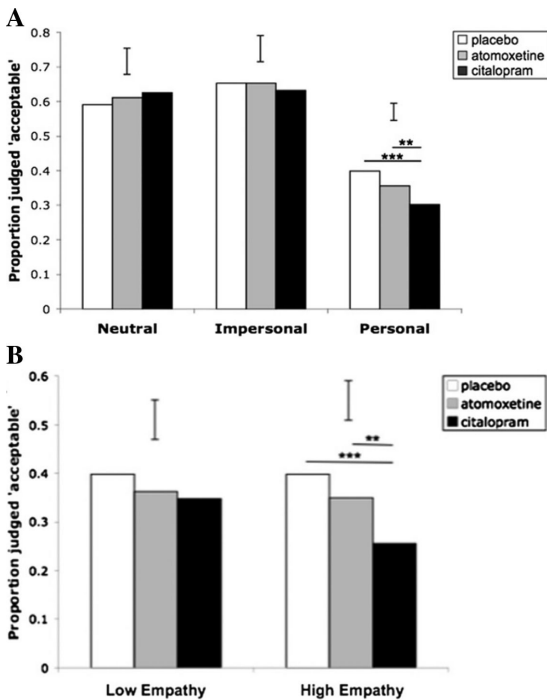
Figure 1. Serotonin shapes moral judgments. (A) Relative to placebo and the noradrenaline reuptake inhibitor atomoxetine, the serotonin reuptake inhibitor citalopram made subjects less likely to endorse harming one person to save many others, specifically when harms were emotionally salient. (B) The effects of citalopram on moral judgment were strongest in subjects high in empathy. Figures adapted from Ref. 60.

Notably, the effects of citalopram on moral judgment were specific to personal dilemmas involving emotionally salient harms. Recall the data suggesting that serotonin is critical for translating aversive Pavlovian cues into behavioral inhibition.[56] If a similar process unfolds as subjects ponder moral dilemmas, then enhancing serotonin function could boost subjects' responsiveness to the aversive Pavlovian cues present in the descriptions of the dilemmas, making them more averse to the suggested harmful action and more likely to disapprove of it. The results described in Crockett et al.[60] are consistent with this proposal.

Blair[31] proposed that human aggression is constrained by a "violence inhibition mechanism" that initiates a withdrawal response when activated by distress cues. We suggest that a similar mechanism operates for imagined harms in the case of moral judgment, which could account for serotonin's parallel effects in inhibiting actual harms (in the case

of aggression) and imagined harms (in the case of moral judgment).

Serotonin, fairness, and reciprocity

Humans are often selfish, but also care about the interests of others—for example, people are sometimes willing to incur costs to achieve fair outcomes, punish unkind behavior, and reward kind behavior.[62] Such social preferences may have played an important role in human evolution, as they could maximize one's fitness in social contexts.[62–65] Preferences for positive reciprocity (repaying kindness with kindness) motivate cooperation in social dilemmas that pit personal profit against social welfare. Preferences for negative reciprocity motivate costly punishment of those who violate social norms. Preferences for fairness motivate actions that seek to establish equitable outcomes. Here, we review evidence that serotonin modulates social preferences across these domains.

Cooperative behaviors in social dilemmas have been linked to serotonin function. One study found that after 2 weeks' treatment with citalopram, participants were significantly less likely to behave in a self-interested manner in a modified version of the prisoner's dilemma that allowed participants to act selfishly, cooperatively, or charitably.[66] Modest depletion of brain serotonin levels produced the opposite effect on cooperation in the prisoner's dilemma.[67] These findings suggest that serotonin function is related to positive social preferences, that is, the positive valuation of others' outcomes. However, one disadvantage of social dilemmas as measures of social preferences is their complexity. Preferences for positive reciprocity undoubtedly motivate cooperation in the prisoner's dilemma, but cooperative behavior is also sensitive to other factors, most notably subjects' beliefs about whether their partner is likely to cooperate—subjects are more likely to cooperate if they believe their partner will also cooperate.[62] These studies thus cannot establish whether serotonin modulates social preferences themselves, or alternatively, the beliefs upon which the preferences are predicated.

Preferences for negative reciprocity and fairness have been extensively studied using the ultimatum game (UG). The UG consists of two players, a proposer and a responder, who must agree on a way to share a sum of money, or neither will receive anything. The proposer must offer a division of the

sum to the responder, who must make a decision to either accept or reject this proposal. If the responder accepts the offer, both players are paid; if he rejects, neither is paid. Perfectly selfish responders will accept any nonzero offer, but responders with preferences for fairness or reciprocity will reject offers perceived to be unfair—typically less than about 30% of the stake.[68] Rejecting an unfair offer satisfies fairness goals because the resulting outcome—zero for both players—is perfectly equitable. Rejecting an unfair offer satisfies preferences for negative reciprocity because it punishes the proposer, depriving him of a larger amount.

Several studies have investigated the relationship between serotonin function and responder behavior in the UG. Emmanuele *et al.*[69] reported that platelet serotonin levels were inversely correlated with responders' rejection rates. However, given that serotonin does not penetrate the blood–brain barrier, plasma levels may not correspond to central serotonin levels. A more recent study found that the density of serotonin transporters in the dorsal raphe nucleus—a proxy measure for serotonin function—was inversely correlated with responders' rejection rates.[70] Although these studies suggest an association between serotonin and preferences for fairness and reciprocity, pharmacological manipulations have furthered these claims with causal evidence.

Crockett *et al.*[71] examined the effects of reducing serotonin availability on responders' behavior in the UG. Responders were more likely to reject unfair offers following depletion of central serotonin, relative to placebo.[71] A subsequent study tested whether enhancing serotonin function with the SSRI citalopram would produce the opposite effect on rejection behavior. Relative to both placebo and the noradrenaline reuptake inhibitor atomoxetine, citalopram reduced responders' rejection rates in the UG.[72] In both studies, the behavioral changes resulting from the serotonin manipulations could not be attributed to changes in mood, the ability to inhibit motor responses, or judgments about the fairness of the offers—suggesting that the manipulations affected behavior by directly altering social preferences.

Rejection of unfair offers in the UG can be explained by either preferences for fairness or preferences for reciprocity. Crockett *et al.*[73] combined pharmacological manipulations with func-
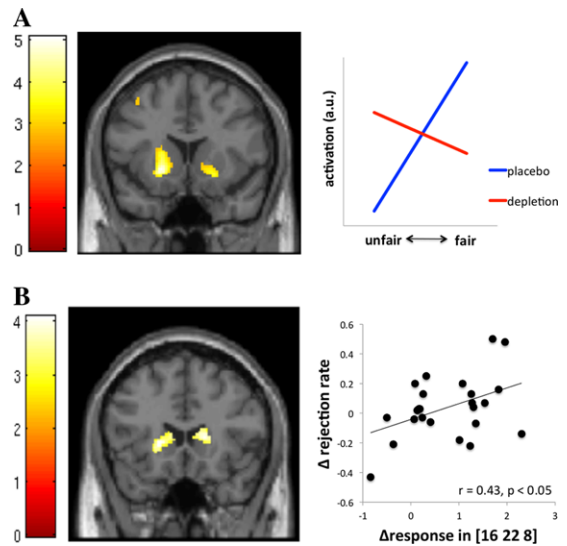

Figure 2. Serotonin shapes social preferences in the striatum. (A) Relative to placebo, serotonin depletion blunted responses in the ventral striatum during the receipt of fair offers in the ultimatum game (UG). (B) Relative to placebo, serotonin depletion enhanced responses in the dorsal striatum during the rejection of unfair offers in the UG. Individual differences in the effects of depletion on dorsal striatal activity were positively correlated with individual differences in the effects of depletion on rejection behavior. Figures adapted from Ref. 73.

tional neuroimaging to investigate how serotonin modulates each of these preferences separately. Previous neuroimaging studies demonstrated that fair social exchanges stimulate activity in the ventral striatum and medial PFC,[74–76] suggesting that activity in these regions reflects preferences for fairness. Crockett *et al.*[73] examined the effects of serotonin depletion on ventral striatal and medial PFC responses to the receipt of fair offers in the UG, and found that serotonin depletion blunted these regions' responses to fairness (Fig. 2A). Serotonin levels, therefore, appear to positively correlate with (neural) preferences for fairness.

Meanwhile, negative reciprocity has been associated with activation in the dorsal striatum. Neuroimaging studies found activation in the dorsal striatum during retaliatory actions following both reception and observations of unfair behaviors.[77,78] This activity was only observed for effective punishment; symbolic reciprocal actions that did not reduce the norm violator's payoff did not stimulate activity in the dorsal striatum.[78] Furthermore, the magnitude of dorsal striatal activity was correlated

with the amount the subject was willing to pay to punish the violator. Collectively, these findings suggest that the dorsal striatum signals the instrumental value of negative reciprocity, consistent with its broader role in goal-directed reward processing.[79] Crockett *et al.*[73] demonstrated that serotonin depletion enhanced responses in the dorsal striatum during rejection of unfair offers in the UG, relative to placebo. This effect was specific to trials in which subjects actively rejected the unfair offers, relative to trials in which subjects simply received unfair offers but did not have the opportunity to reject. Moreover, the effects of the serotonin manipulation on dorsal striatal activity were positively correlated with the effects of the serotonin manipulation on rejection behaviors (Fig. 2B). These results suggest that the dorsal striatum plays a causal role in negative reciprocity, and that serotonin levels are negatively correlated with neural and behavioral preferences for negative reciprocity.

The association between serotonin and social reward processing dovetails with previous reports linking serotonin function to the processing of nonsocial rewards[80,99,100] and recent studies showing that social and monetary rewards engage overlapping regions of the striatum.[81,82] Collectively, these findings indicate that the role of serotonin in value computation goes beyond a simple enhancement or inhibition of reward processing in general; instead, serotonin's effects appear to depend on the social context. We suggest that serotonin amplifies neural representations of positive social preferences, whereas serotonin depletion shifts neural value computations toward selfish or even negative social preferences. This perspective is consistent with earlier behavioral research indicating a positive correlation between serotonin function and prosocial behaviors, but goes a step further by proposing how serotonin affects the preferences that drive those behaviors (Fig. 3).

Synthesis: serotonin and social preferences?

Our synthesis of experimental findings advocates a causal role for serotonin in both harm aversion and social preferences for fairness and reciprocity. Could these two ostensibly distinct facets of morality instead reflect a single underlying dimension? More specifically, can harm aversion be thought of as a type of positive social preference?
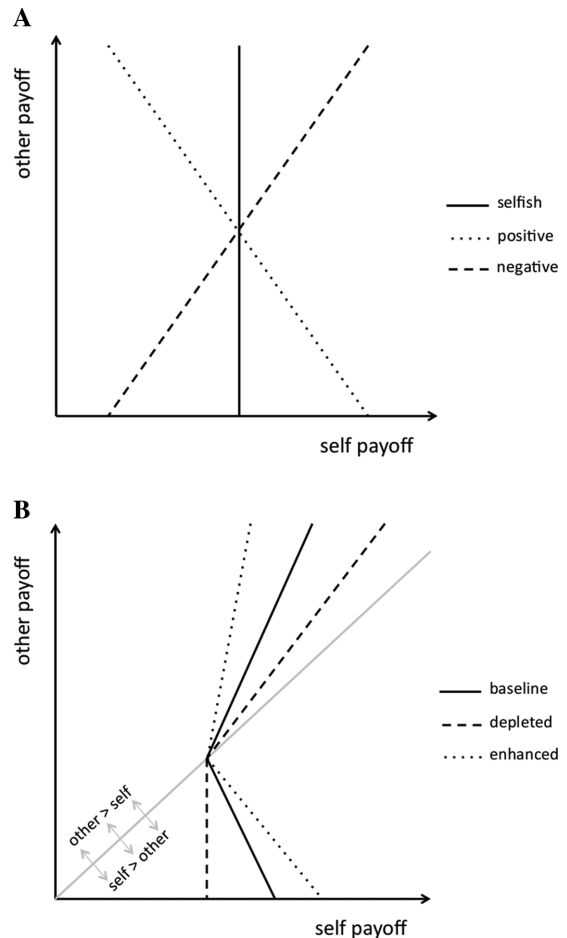

Figure 3. How serotonin shapes social preferences. (A) Theoretical social preference profiles, represented as indifference curves. All points on the curve have equivalent subjective value. Pure selfishness (solid line) is represented by a vertical indifference curve; for a given self-payoff, others' payoffs do not affect utility. Positive social preferences (dotted line) are represented by a downward-sloping indifference curve; altruists are willing to sacrifice some of their own payoff to benefit others. Negative social preferences (dashed line) are represented by an upward-sloping indifference curve; spiteful individuals are willing to sacrifice some of their own payoff to reduce the payoffs of others. (B) Theoretical social preference profiles representing inequality aversion and its hypothesized modulation by serotonin. Inequality-averse individuals display downward-sloping positive social preferences when they are in an advantageous position (to the right of the gray equality line), and upward-sloping negative social preferences when they are in a disadvantageous position (to the left of the gray equality line). We propose that serotonin shifts social preferences in the positive (counterclockwise) direction.

Figure 3A illustrates three theoretical social preference profiles, represented as indifference curves (where all points on the curve have equivalent subjective value). An examination of Figure 3A demonstrates how harm aversion can be thought of as a type of positive social preference. Individuals with positive social preferences show downward sloping indifference curves, which means that harm to others results in utility losses for the self. As the indifference curve rotates in the clockwise direction, preferences move toward pure selfishness. Once the slope of the curve is positive, we can see that the individual in question displays negative social preferences—in which harm to others results in utility gains for the self. Counterclockwise rotations of the indifference curve thus result in increased harm aversion, whereas clockwise rotations of the indifference curve result in decreased harm aversion.

Often the social context determines whether social preferences are positive or negative: one notable example is inequality aversion.[83] Inequality-averse individuals (Fig. 3B) show positive social preferences when they are in an advantageous position (to the right of the gray line denoting equal payoffs), and negative social preferences when they are in a disadvantageous position (to the left of the gray line denoting equal payoffs). The indifference curves in Figure 3B capture most people's behavior in the UG.[68]

We suggest that serotonin shifts the slope of the indifference curve in the direction of positive social preferences. Crockett et al.[71,73] demonstrated that serotonin depletion amplifies negative social preferences under conditions of disadvantageous inequality (Fig. 3B, dashed line), whereas serotonin enhancement diminishes negative social preferences in this setting (Fig. 3B, dotted line). Our model can also account for previous studies of serotonin's influence on cooperation. Assuming that people are predisposed to cooperate in social dilemmas[65] (i.e., that their indifference curves are downward-sloping, absent concerns about inequality), serotonin augmentation should shift preferences further counterclockwise, making people more cooperative,[84] whereas serotonin depletion should shift preferences clockwise, making people less cooperative.[67] Finally, previous studies have shown that serotonin manipulations influence aggressive behavior, particularly in people predisposed to aggression. Assuming that aggressive individuals have upward-sloping indifference curves (i.e., they are motivated to harm others) serotonin augmentation again should shift preferences counterclockwise, reducing aggression,[85] whereas serotonin depletion should shift preferences further clockwise, increasing aggression.[86–91]

Our model is primarily descriptive at the behavioral level, but makes predictions that can be tested at the neural level. For example, value-processing regions such as the ventral striatum and the medial PFC show a pattern of activation consistent with inequality aversion;[76] we predict that serotonin manipulations would alter responses in these regions as illustrated in Figure 3B (for preliminary evidence, see Ref. 73).

Finally, it is worth mentioning that social cognitive and emotional processes concerning the representation of others' mental states and emotions (i.e., mentalizing and empathy) clearly play a role in shaping concerns for harm and fairness.[92,93] Recent studies have shown that the structure and function of brain regions involved in mentalizing, such as the temporoparietal junction (TPJ) and the superior temporal sulcus, can predict positive social preferences and subsequent generosity.[94,95] Similarly, regions associated with empathy, such as the anterior insula and anterior cingulate cortex, are sensitive to the moral status of others[96] and are correlated with altruistic helping.[97,98] A still-open question, therefore, is whether serotonin modulates moral behavior indirectly by affecting empathic representations in the TPJ, insula, and anterior cingulate cortex, or directly by altering the neural computations of social preferences in the striatum and the medial PFC. Although initial evidence supports the latter view,[73] further work is needed in this area to understand how individual differences in empathy moderate the effects of serotonin on moral judgment and behavior.[72]

Concluding remarks

Research into the neural basis of moral judgment and behavior has exploded over the past decade. The vast majority of this work has involved neuroimaging; these studies have provided valuable insights into the neural correlates of moral decisions, but are correlational in nature. More recent studies employing intervention methods, such as pharmacological manipulations and brain stimulation, have provided additional information about the

brain systems that are causally involved in moral decisions. Future work employing these techniques will benefit from specified theoretical frameworks that generate novel predictions about how targeted interventions will modify moral judgment and behavior.

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Conflicts of interest

The authors declare no conflicts of interest.

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