

13 Neuromodulators and the (In)stability of Moral Cognition

Molly J. Crockett and Regina A. Rini

Ancient moral codes may be written in stone, but human moral cognition is malleable. Moral judgments and decisions are susceptible to influence from a variety of factors, many of which are nonnormative in the sense that they are not relevant to the moral dilemma under consideration. For example, people make harsher moral judgments in the presence of disgusting smells (Schnall, Haidt, Clore, & Jordan, 2008) and are more likely to cheat when the lights are low (Zhong, Bohns, & Gino, 2010). Many of these incidental influences on morality have been reviewed elsewhere (Greene, 2011, 2014; Huebner, Dwyer, & Hauser, 2009). This chapter explores how and why physiological changes in the brain and body can influence human moral cognition.

One especially striking example of nonnormative influences on moral judgments comes from a study conducted with Israeli judges. Danziger and colleagues (2011) were interested in testing empirically the common trope that “justice is what the judge ate for breakfast” (Kozinski, 1992). To investigate this question the researchers examined over a thousand sequential parole decisions made by experienced judges and tested whether the judges’ two daily food breaks influenced their decisions. Strikingly, they found that judges were substantially more likely to grant parole when the decision took place directly following a food break compared with when the decision took place long after a food break. The effect of food breaks remained significant even when controlling for legally relevant factors such as the prisoner’s history of repeat offenses and whether he was enrolled in a rehabilitation program (Danziger, Levav, & Avnaim-Pesso, 2011).

The fact that something as trivial as a snack break can influence hugely consequential judicial decisions is deeply problematic if we intend for our legal systems to operate on the basis of normative principles. It is therefore

essential that we investigate how such extraneous factors influence moral judgment and decision making. Studying the brain can advance this agenda by illuminating the mechanisms through which the environment can affect moral cognition.

One potential mechanism through which extraneous factors influence moral cognition is the context-sensitive modulation of neuronal activity by *neuromodulator* systems. Neuromodulators are chemicals that modify neuronal dynamics, excitability, and synaptic function. These include neurotransmitters (e.g., serotonin, norepinephrine, acetylcholine, and dopamine) as well as hormones (e.g., testosterone, oxytocin, vasopressin). These chemical systems may serve the function of preparing organisms to interact optimally with the environment, adaptively shaping behavior to fit the current context. Activation of one or more neuromodulator systems is an efficient way to globally alter the computational properties of neural networks (Robbins & Arnsten, 2009). Recent work in neuroscience has demonstrated that manipulating the function of neuromodulators in the laboratory can influence moral cognition in humans (Crockett & Fehr, 2013, 2014). Here, we review this evidence and explore its normative implications.

How Neuromodulators Shape Moral Cognition

Moral Judgment

How do people *judge* whether an action is morally permissible, and how is moral judgment shaped by neuromodulators? Perhaps the most widely used tool for probing human moral judgment is the (in)famous *trolley problem*. In one variant (“push”), a trolley is heading down a track toward five workers, who will be killed if no action is taken. An unwitting protagonist (call him Joe) is standing on a footbridge overlooking the tracks, along with another person wearing a large, heavy backpack. If Joe pushes the backpacker off the footbridge and onto the tracks, the backpacker’s body will stop the trolley before it hits the five workers, killing him but saving the five workers. Participants reading the scenario are asked to judge whether it is morally acceptable for Joe to push the backpacker off the footbridge.

Moral dilemmas like these generate conflicting responses from two major traditions in normative ethics. *Consequentialism* judges the moral acceptability of actions based on their outcomes, so according to this tradition, it is morally acceptable, indeed even required, for Joe to kill one

person in order to save five others. *Deontology*, on the other hand, judges the acceptability of actions based on factors other than outcomes, such as whether the action involves treating a person as a means to an end. Certain actions, such as killing an innocent bystander as a means of saving others, are strictly prohibited, no matter the potential benefits; according to this tradition, it is unacceptable for Joe to kill one to save five in this way.

Much ink has been spilled in the quest to understand when, why, and how people adopt consequentialist versus deontological perspectives in moral judgment (Crockett, 2013; Cushman, 2013; Greene, 2014; Mikhail, 2007). More recently, researchers have begun to investigate how manipulating neuromodulator systems influences judgment in moral dilemmas (see table 13.1). In a typical design participants are randomly assigned to receive a drug or a placebo, and subsequently make a series of moral judgments in a set of moral dilemmas like the trolley problem. In some studies these dilemmas are divided into “personal” dilemmas that involve emotionally salient harms (such as the “push” scenario above) and “impersonal” dilemmas

Table 13.1

Neuromodulation of moral judgment

Treatment	Effect on neuromodulator	Personal dilemmas	Impersonal dilemmas	References
Citalopram, 30 mg (SSRI)	↑ serotonin	↑ deontological	—	Crockett et al., 2010
Propranolol, 40 mg (β-blocker)	↓ norepinephrine ↑ norepinephrine	↑ deontological —	— —	Terbeck et al., 2013 Crockett et al., 2010
Atomoxetine, 60 mg (SNRI)				
Trier Social Stress Task	↑ stress	↑ deontological	—	Youssef et al., 2012
Public speech anticipation	↑ stress	↑ deontological	↑ deontological	Starcke et al., 2012
Intranasal oxytocin, 24 IU	↑ oxytocin	n/t	↑ deontological (ingroup only)	De Dreu et al., 2011
Sublingual testosterone, 0.5 mg	↑ testosterone	↓ deontological (inevitable harms, covariate 2D:4D)	—	Montoya et al., 2013

Abbreviations: SSRI, selective serotonin reuptake inhibitor; SNRI, selective norepinephrine reuptake inhibitor; IU, intranasal units; 2D:4D, second- to fourth-digit ratio, a measure of prenatal testosterone exposure; —, no effect; n/t, not tested.

where harms are less salient (e.g., the “switch” scenario, in which Joe has the option to flip a switch to divert the trolley onto a different set of tracks where there is one worker instead of five).

In the first of such studies Crockett, Clark, Hauser, and Robbins (2010) investigated how the neuromodulator serotonin influences moral judgment. Serotonin has long been implicated in social behavior (Insel & Winslow, 1998); in general, impaired serotonin function has been associated with aggression and antisocial behavior, whereas intact or enhanced serotonin function has been associated with prosocial behavior. To test how serotonin influences moral judgment, Crockett and colleagues examined the effects of citalopram (a selective serotonin reuptake inhibitor, which enhances serotonin function by prolonging its actions in the synapse) on judgments in personal and impersonal scenarios. Citalopram promoted deontological responding, thereby reducing subjects’ willingness to endorse harming one to save many others (Crockett et al., 2010). This effect was selective to emotionally salient personal scenarios and was stronger in individuals who scored higher on an independent measure of empathy. These results are consistent with other work suggesting that serotonin facilitates aversive processing (Crockett, Clark, & Robbins, 2009; Dayan & Huys, 2009), which could result in a serotonergic enhancement of harm aversion in social settings (Siegel & Crockett, 2013).

Other studies have examined the role of norepinephrine in moral judgment. Norepinephrine is a neuromodulator thought to play a role in sharpening attention in response to arousal and stress (Robbins & Arnsten, 2009). Terbeck et al. (2013) tested the effects of blocking the α -adrenergic receptor on judgments in personal and impersonal dilemmas. Noradrenergic blockade increased deontological responding in personal but not impersonal scenarios, suggesting that norepinephrine may normally facilitate consequentialist responding (Terbeck et al., 2013). However, enhancing noradrenergic function with the norepinephrine reuptake inhibitor atomoxetine had no effect on moral judgment (Crockett et al., 2010).

Both serotonergic and noradrenergic neurons are stimulated by acute stress (Robbins & Arnsten, 2009). A few recent studies have examined how stress influences moral judgments. Youssef and colleagues (2011) showed that acute stress induced via the Trier Social Stress Test increased deontological responding in personal, but not impersonal, dilemmas. Starcke and colleagues (2012), using a different method of acute stress induction

(anticipated public speech), also found that stress increased deontological responding, but this effect was present in both personal and impersonal dilemmas (Starcke, Ludwig, & Brand, 2012).

Another neuromodulator that is released in response to stress is the hormone oxytocin. Commonly referred to by catchy monikers such as the “love hormone” or “moral molecule,” oxytocin plays many important roles in social behavior, although its function is far more complex than popular accounts imply (Bartz, Zaki, Bolger, & Ochsner, 2011). One account, proposed by Taylor (2006), is that during stress, oxytocin promotes a “tend and befriend” social affiliation response. Consistent with this account De Dreu and colleagues report that oxytocin administration increases deontological responding in moral dilemmas—reducing subjects’ approval of harming one to save many—but only when the target of harm is an ingroup member (De Dreu, Greer, Kleef, Shalvi, & Handgraaf, 2011).

Testosterone is a hormone thought to be involved in the pursuit of social dominance (Eisenegger, Haushofer, & Fehr, 2011). The effects of testosterone on moral judgment appear to run in the opposite direction of oxytocin; high baseline testosterone levels are associated with decreased deontological responding in moral dilemmas (Carney & Mason, 2010), and testosterone administration decreased deontological responding, although the effects were specific to individuals who likely experienced higher prenatal testosterone exposure, as indicated by the second- to fourth-digit ratio (Montoya et al., 2013).

Considering these findings together, a few broad conclusions emerge. First, the majority of studies have reported neuromodulatory effects on moral judgment that are selective to personal dilemmas. This suggests that neuromodulators influence moral judgment through emotional channels. Second, the bulk of the evidence is consistent with the idea that stress shifts moral judgment toward a deontological style by stimulating the release of monoamines and hormones that may have synergistic effects. Finally, it is worth noting that these results should be interpreted with caution. Most of these studies have been carried out in relatively small samples; the reported effect sizes are small; few effects have been replicated; and most have used the same small set of moral dilemmas, which themselves have important limitations (Christensen & Gomila, 2012). Further work is needed to replicate these basic findings and extend them to a broader range of moral dilemmas.

Moral Decision Making

How do neuromodulators shape moral *decisions* about whether to behave ethically? Although it is challenging to capture ethical decision-making processes in the laboratory, behavioral paradigms have been used to measure ethically relevant behaviors such as aggression, generosity, and cooperation (table 13.2). Early work in this area investigated the effects of neuromodulators on laboratory measures of aggression. These tasks measure subjects' responses to provocation by an opponent, typically in the form of imposed monetary losses, electric shocks, or loud noises. Aggression is operationalized as the level of stimulus intensity or monetary loss delivered in return

Table 13.2
Neuromodulation of moral decision making

Treatment	Effect on neuromodulator	Aggression	Generosity	Cooperation	References	
ATD	↓ serotonin	↑			Bjork et al., 1999	
		↑			Bjork et al., 2000	
		↑			Dougherty et al., 1999	
		↑			Marsh et al., 2002	
		↑			Moeller et al., 1996	
					↓	Wood et al., 2006
		↑				Crockett et al., 2008
		↑			Crockett et al., 2013	
Paroxetine, 40mg (SSRI)	↑ serotonin	↓			Berman et al., 2009	
Citalopram, 10 mg (SSRI)				↑	Tse & Bond, 2002	
Citalopram, 30 mg (SSRI)		↓			Crockett et al., 2010	
MDMA, 125 mg			↑		Hysek et al., 2013	

I-DOPA, 300 mg	↑ dopamine	↓		Pedroni et al., 2014
Trier Social Stress Test	↑ stress	↑		von Dawans et al., 2012
		↓		Vinkers et al., 2013
Intranasal oxytocin, 24 IU (40 IU)	↑ oxytocin		↑ (avoidant attachment)	De Dreu, 2012
			↑	Rilling et al., 2012
			↑ (familiar)	Declerck et al., 2010
			↑ (ingroup)	De Dreu et al., 2010
			↑	Israel et al., 2012
		↑		Chang et al., 2012
		↑		Barraza et al., 2011
Sublingual testosterone, 0.5mg	↑ testosterone	↑		Eisenegger et al., 2010
			↑ (2D:4D)	van Honk et al., 2012

Abbreviations: ATD, acute tryptophan depletion; SSRI, selective serotonin reuptake inhibitor; I-DOPA, levodopa; IU, intranasal units; 2D:4D, second- to fourth-digit ratio, an index of prenatal testosterone exposure.

to the opponent. Several studies have shown that manipulating serotonin influences behavior in these paradigms. Depleting the chemical precursor of serotonin, tryptophan, increases aggression (Bjork, Dougherty, Moeller, & Swann, 2000; Cleare & Bond, 1995; Crockett et al., 2013; Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008; Dougherty, Bjork, Marsh, & Moeller, 1999; Marsh, Dougherty, Moeller, Swann, & Spiga, 2002; Moeller et al., 1996; Pihl et al., 1995). Aggressive responding decreases following fenfluramine (Cherek & Lane, 1999), tryptophan augmentation (Marsh et al., 2002), and SSRI administration (Berman, McCloskey, Fanning, Schumacher, & Coccaro, 2009; Crockett et al., 2010), all of which enhance serotonin function.

Generosity is typically measured with the dictator game, in which subjects are given a sum of money and have the opportunity to donate any

amount to another person or a charity. Generosity is enhanced by the serotonin-releasing agent MDMA (Hysek et al., 2013). Testosterone administration increases generosity only when the recipient has the option to punish, suggesting that testosterone influences strategic social concerns (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010). Meanwhile, enhancing dopaminergic neurotransmission with L-DOPA decreases generosity (Pedroni, Eisenegger, Hartmann, Fischbacher, & Knoch, 2014). Oxytocin has more complex effects on generosity. Barraza and colleagues report no effect of oxytocin on decisions to donate to charity; however, among subjects who chose to donate, those who received oxytocin donated more money than those who received placebo (Barraza, McCullough, Ahmadi, & Zak, 2011). A study in rhesus monkeys found that oxytocin increased generous choices to reward another when the alternative was to reward no one, but oxytocin also increased selfish choices to reward oneself when the alternative was to reward another monkey (Chang, Barter, Ebitz, Watson, & Platt, 2012). Evidence for acute stress effects on generosity is also mixed; one study reported increased generosity following acute stress (von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012), whereas another reported reduced generosity following stress (Vinkers et al., 2013). One possible explanation for these conflicting findings is that von Dawans et al. studied generosity toward other participants in the lab (who could have been construed as ingroup members), whereas Vinkers et al. studied donations to UNICEF (which could have been construed as providing for outgroup members). If stress promotes generosity toward ingroup members but reduces generosity toward outgroup members, this could account for the observed pattern of results (Vinkers et al., 2013).

Preferences for social cooperation have been studied using the prisoner's dilemma and the public goods game. In these games subjects have the option to cooperate, which results in higher average payoffs for the group as a whole, or to defect, which results in higher average payoffs for oneself. Enhancing serotonin function with the SSRI citalopram increases cooperation (Tse & Bond, 2002), whereas depleting the serotonin precursor tryptophan decreases cooperation (Wood, Rilling, Sanfey, Bhagwagar, & Rogers, 2006). Testosterone administration increases cooperation—but only among individuals with lower prenatal testosterone exposure (van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). Meanwhile, oxytocin generally increases cooperation (Rilling et al., 2012), but in some studies

the effects of oxytocin interact with individual difference variables such as attachment avoidance (De Dreu, 2012). In addition, oxytocin appears to selectively enhance cooperation with familiar others or ingroup members (Declerck, Boone, & Emonds, 2013; De Dreu et al., 2010; but see also Israel, Weisel, Ebstein, & Bornstein, 2012).

From these findings it becomes apparent that serotonin and oxytocin both generally promote prosocial decision making; these two systems may even have synergistic effects in light of evidence that they interact in the brain (Dölen, Darvishzadeh, Huang, & Malenka, 2013). However, there are not yet enough data on the effects of testosterone, stress, and dopamine manipulations to draw any firm conclusions. Moreover, it is clear that the effects of neuromodulators on moral decision making are highly sensitive to changes in context and individual personality traits. Further work is required to flesh out the nature of these interactions.

Discussion: Normative Implications

Neuromodulators have been shown to affect moral judgment and decision making in a number of different ways. Some scholars have recently proposed that we could use this knowledge to improve ourselves and our societies (Douglas, 2008; Persson & Savulescu, 2012). Aside from the fact that we are not even close to understanding the precise ways in which neuromodulators shape moral cognition, applying this knowledge is far from straightforward. Think again about Danziger and colleagues' (2011) study of judges. We can all agree that one's chance at parole should not come down to a judge's snack schedule. Suppose we came to understand the neuromodulators involved in this effect, and we could prescribe "stabilizer" drugs for judges that ensured they would make the same judgments no matter when they had last eaten. This could seem like an improvement in justice. But notice that to do this we would have to decide which type of judge is the *better* one. Do we want judges who judge as if they were hungry and so are tougher on potential parolees? Or do we want judges who judge as if they were satiated and so are less tough? We can all agree that judges should judge consistently—but consistently in which direction? And how would we decide?

These are normative questions about what *should* be done. If neuromodulators are ever going to be of any practical use, we shall have to address

these normative questions. We do not claim to be able to resolve any of these questions here. Instead, we can only try to make clear two important sets of considerations for future work on the normative implications of neuromodulation.

First: *who decides* which neuromodulators to use? It might seem obvious that individuals should be allowed to choose for themselves which substances they ingest, but this point runs into problems with moral neuromodulation. Suppose that you are convinced that deontological moral judgments are gravely morally wrong. Would you agree that individuals should be able to choose for themselves to take substances that shift them toward *more* deontological judgments? In fact, you might think that individuals should be *compelled* to take neuromodulators promoting consequentialist judgments.

Obviously such ideas trigger important worries about liberty and authenticity (Harris, 2011); we have strong background assumptions that people should be in control of their minds and their own decision making. But moral neuromodulation is not like, say, drinking lattes to get a caffeine buzz. Because moral neuromodulation is specifically about *morality*, it is directly concerned with *interpersonal* decisions with great significance to people beyond the individual. We already recognize limitations on individual discretion when it comes to ingesting certain substances with morally problematic consequences (such as alcohol before driving, or strong hallucinogens at any time). If moral neuromodulators cut directly to affecting moral decisions, is it so obvious that their use should be wholly up to individual choice?

A second question is: what are the implications of neuromodulation for our understanding of *morality itself*? The evidence reviewed here shows that our moral judgments and decisions are malleable and contingent. That is, if you had different levels of serotonin, oxytocin, or testosterone, then you might disapprove of some things that now seem right to you and accept some of what now seems wrong. Because neurochemical levels fluctuate naturally, in response to everyday events such as changes in diet or stress, even without artificially manipulating your brain chemistry, your judgments might shift. Most of us want to believe that our moral judgments and decisions are far less contingent than this. Some may feel strongly that what we consider *right* and *wrong* should not depend on the happenstance of neurochemistry. The very concept of moral neuromodulation may

therefore bring with it an unnerving sense of uncertainty in some of our most important choices.

A natural suggestion, then, is that we should seek to think about morality from some morally “neutral” neurochemical state. But what would that mean? All of our thinking—every brain event—is facilitated by some combination of neurochemicals. How do we decide which state is the “neutral” one? This is the problem of the snacking judges again, applied more generally: we know that we do not want our moral commitments to fluctuate arbitrarily, but do we want to be like the sated judges or like the hungry judges? Even if it seems to you that, say, being a tough judge is a good thing, *this* opinion is the result of some combination of neurochemicals. How do you know *that* combination is the right one?

All of this means that we will have difficulty answering questions about *how* to decide which (if any) neuromodulators to use. Absurdly, one can imagine rival moral philosophers prescribing rival drugs to one another: “if only you’d take this drug, then you’d agree with me about consequentialism (and that you ought to take this drug!).” But this problem seems inescapable—moral neuromodulation is centrally about altering our tendencies toward certain types of judgments and decisions, and we have no basis for choosing such alterations other than those very same judgments and decisions. This is obviously a knotty problem, which in some ways will seem familiar to moral philosophers. If moral neuromodulation becomes a practical possibility, it is a problem that will have to be addressed by everyone: scientists, policy makers, and all morally conscientious people.

References

- Barraza, J. A., McCullough, M. E., Ahmadi, S., & Zak, P. J. (2011). Oxytocin infusion increases charitable donations regardless of monetary resources. *Hormones and Behavior*, *60*(2), 148–151.
- Bartz, J. A., Zaki, J., Bolger, N., & Ochsner, K. N. (2011). Social effects of oxytocin in humans: Context and person matter. *Trends in Cognitive Sciences*, *15*(7), 301–309.
- Berman, M. E., McCloskey, M. S., Fanning, J. R., Schumacher, J. A., & Coccaro, E. F. (2009). Serotonin augmentation reduces response to attack in aggressive individuals. *Psychological Science*, *20*(6), 714–720.
- Bjork, J. M., Dougherty, D. M., Moeller, F. G., Cherek, D. R., & Swann, A. C. (1999). The effects of tryptophan depletion and loading on laboratory aggression in men: time course and a food-restricted control. *Psychopharmacology*, *142*(1), 24–30.

Bjork, J. M., Dougherty, D. M., Moeller, F. G., & Swann, A. C. (2000). Differential behavioral effects of plasma tryptophan depletion and loading in aggressive and nonaggressive men. *Neuropsychopharmacology*, *22*(4), 357–369.

Carney, D. R., & Mason, M. F. (2010). Decision making and testosterone: When the ends justify the means. *Journal of Experimental Social Psychology*, *46*(4), 668–671.

Chang, S. W. C., Barter, J. W., Ebitz, R. B., Watson, K. K., & Platt, M. L. (2012). Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (*Macaca mulatta*). *Proceedings of the National Academy of Sciences USA*, *109*(3), 959–964.

Cherek, D. R., & Lane, S. D. (1999). Effects of *d,l*-fenfluramine on aggressive and impulsive responding in adult males with a history of conduct disorder. *Psychopharmacology*, *146*(4), 473–481.

Christensen, J. F., & Gomila, A. (2012). Moral dilemmas in cognitive neuroscience of moral decision-making: A principled review. *Neuroscience and Biobehavioral Reviews*, *36*(4), 1249–1264.

Cleare, A. J., & Bond, A. J. (1995). The effect of tryptophan depletion and enhancement on subjective and behavioural aggression in normal male subjects. *Psychopharmacology*, *118*(1), 72–81.

Crockett, M. J. (2013). Models of morality. *Trends in Cognitive Sciences*, *17*(8), 363–366.

Crockett, M. J., Apergis-Schoute, A., Herrmann, B., Lieberman, M. D., Muller, U., Robbins, T. W., et al. (2013). Serotonin modulates striatal responses to fairness and retaliation in humans. *Journal of Neuroscience*, *33*(8), 3505–3513.

Crockett, M. J., Clark, L., Hauser, M. D., & Robbins, T. W. (2010). From the cover: Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *Proceedings of the National Academy of Sciences USA*, *107*(40), 17433–17438.

Crockett, M. J., Clark, L., & Robbins, T. W. (2009). Reconciling the role of serotonin in behavioral inhibition and aversion: Acute tryptophan depletion abolishes punishment-induced inhibition in humans. *Journal of Neuroscience*, *29*(38), 11993–11999.

Crockett, M. J., Clark, L., Tabibnia, G., Lieberman, M. D., & Robbins, T. W. (2008). Serotonin modulates behavioral reactions to unfairness. *Science*, *320*(5884), 1739.

Crockett, M. J., & Fehr, E. (2013). Pharmacology of economic and social decision making. In P. Glimcher & E. Fehr (Eds.), *Neuroeconomics: Decision making and the brain* (pp. 255–275). New York: Academic Press.

Crockett, M. J., & Fehr, E. (2014). Social brains on drugs: Tools for neuromodulation in social neuroscience. *Social Cognitive and Affective Neuroscience*, *9*(2), 250–254.

- Cushman, F. (2013). Action, outcome, and value: A dual-system framework for morality. *Personality and Social Psychology Review*, *17*(3), 273–292.
- Danziger, S., Levav, J., & Avnaim-Pesso, L. (2011). Extraneous factors in judicial decisions. *Proceedings of the National Academy of Sciences USA*, *108*(17), 6889–6892.
- Dayan, P., & Huys, Q. J. M. (2009). Serotonin in affective control. *Annual Review of Neuroscience*, *32*(1), 95–126.
- Declerck, C. H., Boone, C., & Emonds, G. (2013). When do people cooperate? The neuroeconomics of prosocial decision making. *Brain and Cognition*, *81*(1), 95–117.
- De Dreu, C. K. W. (2012). Oxytocin modulates the link between adult attachment and cooperation through reduced betrayal aversion. *Psychoneuroendocrinology*, *37*(7), 871–880.
- De Dreu, C. K. W. D., Greer, L. L., Handgraaf, M. J. J., Shalvi, S., Kleef, G. A. V., Baas, M., et al. (2010). The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science*, *328*(5984), 1408–1411.
- De Dreu, C. K. W. D., Greer, L. L., Kleef, G. A. V., Shalvi, S., & Handgraaf, M. J. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences USA*, *108*(4), 1262–1266.
- Dölen, G., Darvishzadeh, A., Huang, K. W., & Malenka, R. C. (2013). Social reward requires coordinated activity of nucleus accumbens oxytocin and serotonin. *Nature*, *501*(7466), 179–184.
- Dougherty, D. M., Bjork, J. M., Marsh, D. M., & Moeller, F. G. (1999). Influence of trait hostility on tryptophan depletion-induced laboratory aggression. *Psychiatry Research*, *88*(3), 227–232.
- Douglas, T. (2008). Moral enhancement. *Journal of Applied Philosophy*, *25*(3), 228–245.
- Eisenegger, C., Haushofer, J., & Fehr, E. (2011). The role of testosterone in social interaction. *Trends in Cognitive Sciences*, *15*(6), 263–271.
- Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, *463*(7279), 356–359.
- Greene, J. D. (2011). Emotion and morality: A tasting menu. *Emotion Review*, *3*(3), 227–229.
- Greene, J. (2014). *Moral tribes: Emotion, reason and the gap between us and them*. London: Atlantic Books.
- Harris, J. (2011). Moral enhancement and freedom. *Bioethics*, *25*(2), 102–111.

- Huebner, B., Dwyer, S., & Hauser, M. (2009). The role of emotion in moral psychology. *Trends in Cognitive Sciences*, *13*(1), 1–6.
- Hysek, C. M., Schmid, Y., Simmler, L. D., Domes, G., Heinrichs, M., Eisenegger, C., et al. (2013). MDMA enhances emotional empathy and prosocial behavior. *Social Cognitive and Affective Neuroscience*, nst161. doi:10.1093/scan/nst161.
- Insel, T. R., & Winslow, J. T. (1998). Serotonin and neuropeptides in affiliative behaviors. *Biological Psychiatry*, *44*(3), 207–219.
- Israel, S., Weisel, O., Ebstein, R. P., & Bornstein, G. (2012). Oxytocin, but not vasopressin, increases both parochial and universal altruism. *Psychoneuroendocrinology*, *37*(8), 1341–1344.
- Kozinski, A. (1992). What I ate for breakfast and other mysteries of judicial decision making. *Loyola of Los Angeles Law Review*, *26*, 993.
- Marsh, D. M., Dougherty, D. M., Moeller, F. G., Swann, A. C., & Spiga, R. (2002). Laboratory-measured aggressive behavior of women: Acute tryptophan depletion and augmentation. *Neuropsychopharmacology*, *26*(5), 660–671.
- Mikhail, J. (2007). Universal moral grammar: Theory, evidence and the future. *Trends in Cognitive Sciences*, *11*(4), 143–152.
- Moeller, F. G., Dougherty, D. M., Swann, A. C., Collins, D., Davis, C. M., & Cherek, D. R. (1996). Tryptophan depletion and aggressive responding in healthy males. *Psychopharmacology*, *126*(2), 97–103.
- Montoya, E. R., Terburg, D., Bos, P. A., Will, G.-J., Buskens, V., Raub, W., et al. (2013). Testosterone administration modulates moral judgments depending on second-to-fourth digit ratio. *Psychoneuroendocrinology*, *38*(8), 1362–1369.
- Pedroni, A., Eisenegger, C., Hartmann, M. N., Fischbacher, U., & Knoch, D. (2014). Dopaminergic stimulation increases selfish behavior in the absence of punishment threat. *Psychopharmacology*, *231*(1), 135–141.
- Persson, I., & Savulescu, J. (2012). *Unfit for the future: The need for moral enhancement*. Oxford: Oxford University Press.
- Pihl, R. O., Young, S. N., Harden, P., Plotnick, S., Chamberlain, B., & Ervin, F. R. (1995). Acute effect of altered tryptophan levels and alcohol on aggression in normal human males. *Psychopharmacology*, *119*(4), 353–360.
- Rilling, J. K., DeMarco, A. C., Hackett, P. D., Thompson, R., Ditzen, B., Patel, R., et al. (2012). Effects of intranasal oxytocin and vasopressin on cooperative behavior and associated brain activity in men. *Psychoneuroendocrinology*, *37*(4), 447–461.
- Robbins, T. W., & Arnsten, A. F. T. (2009). The neuropsychopharmacology of fronto-executive function: Monoaminergic modulation. *Annual Review of Neuroscience*, *32*(1), 267–287.

- Schnall, S., Haidt, J., Clore, G. L., & Jordan, A. H. (2008). Disgust as embodied moral judgment. *Personality and Social Psychology Bulletin*, *34*(8), 1096–1109.
- Siegel, J. Z., & Crockett, M. J. (2013). How serotonin shapes moral judgment and behavior. *Annals of the New York Academy of Sciences*, *1299*(1), 42–51.
- Starcke, K., Ludwig, A.-C., & Brand, M. (2012). Anticipatory stress interferes with utilitarian moral judgment. *Judgment and Decision Making*, *7*(1). Retrieved from <http://journal.sjdm.org/11/11729/jdm11729.html>.
- Taylor, S. E. (2006). Tend and befriend biobehavioral bases of affiliation under stress. *Current Directions in Psychological Science*, *15*(6), 273–277.
- Terbeck, S., Kahane, G., McTavish, S., Savulescu, J., Levy, N., Hewstone, M., et al. (2013). Beta adrenergic blockade reduces utilitarian judgement. *Biological Psychology*, *92*(2), 323–328.
- Tse, W., & Bond, A. (2002). Serotonergic intervention affects both social dominance and affiliative behaviour. *Psychopharmacology*, *161*(3), 324–330.
- Van Honk, J., Montoya, E. R., Bos, P. A., van Vugt, M., & Terburg, D. (2012). New evidence on testosterone and cooperation. *Nature*, *485*(7399), E4–E5.
- Vinkers, C. H., Zorn, J. V., Cornelisse, S., Koot, S., Houtepen, L. C., Olivier, B., et al. (2013). Time-dependent changes in altruistic punishment following stress. *Psychoneuroendocrinology*, *38*(9), 1467–1475.
- Von Dawans, B., Fischbacher, U., Kirschbaum, C., Fehr, E., & Heinrichs, M. (2012). The social dimension of stress reactivity: Acute stress increases prosocial behavior in humans. *Psychological Science*, *23*(6), 651–660.
- Wood, R. M., Rilling, J. K., Sanfey, A. G., Bhagwagar, Z., & Rogers, R. D. (2006). Effects of tryptophan depletion on the performance of an iterated Prisoner's Dilemma game in healthy adults. *Neuropsychopharmacology*, *31*(5), 1075–1084.
- Youssef, F. F., Dookeeram, K., Basdeo, V., Francis, E., Doman, M., Mamed, D., et al. (2012). Stress alters personal moral decision making. *Psychoneuroendocrinology*, *37*(4), 491–498.
- Zhong, C.-B., Bohns, V. K., & Gino, F. (2010). Good lamps are the best police. Darkness increases dishonesty and self-interested behavior. *Psychological Science*, *21*(3), 311–314.

