

Chapter 8

The “(a)moral brain”: When things go wrong

ANA SEARA-CARDOSO*

Psychology Research Centre, School of Psychology, University of Minho, Braga, Portugal

Abstract

In the past decades, a growing interest of neuroscience on moral judgment and decision-making has shed new light on the neurobiological correlates of human morality. It is now understood that moral cognition relies on a complex integration of cognitive and affective information processes that implicate a widely distributed brain network. Moral cognition relies on the coordination of several domain-general processes, subserved by domain-general neural networks, rather than a specific moral cognition system subserved by a specific neural network. In this chapter, we will first briefly review what is currently known about the “moral brain,” i.e., the network of brain regions consistently implicated in studies of moral cognition, which include decision-making, affective processing, mentalizing, and perspective-taking processing regions. We will then review the evidence of the impairments found in this network in individuals with psychopathy, a condition whose characteristics indicate profound disturbances in appropriate moral processing. We will present data from neuroimaging studies with forensic/clinical, general population, as well as child and adolescent samples, which seem to converge to support the notion that the moral dysfunction observed in individuals with psychopathy may stem from a disruption of affective components of moral processing rather than from an inability to compute moral judgments per se.

INTRODUCTION

In the past decades, a growing interest of neuroscience on moral judgment and decision-making has shed new light on the neurobiological correlates of human morality. This research has advanced our understanding of the processes involved in moral cognition, and motivated a paradigm shift where human morality is no longer conceptualized as a product of pure reasoning skills but rather as emerging from an interaction of reasoning, emotion and motivation. It is now understood that moral cognition relies on a complex integration of cognitive and affective information processes that implicate a brain network housed all over the brain (Young and Dungan, 2012; Buon et al., 2016; Garrigan et al., 2016; Eres et al., 2018; Fede and Kiehl, 2020). This prompted the notion that moral cognition relies on the coordination of several domain-general processes which are subserved

by domain-general neural networks, rather than a specific moral cognition system subserved by a specific neural network (Cushman et al., 2010; Young and Dungan, 2012; Yoder and Decety, 2018).

In this chapter, we will first briefly review what is currently known about the “moral brain,” i.e., the network of brain regions consistently implicated in studies of moral cognition, which include decision-making, affective processing, mentalizing and perspective-taking processing regions (Fumagalli and Priori, 2012; Young and Dungan, 2012; Garrigan et al., 2016; Boccia et al., 2017; Eres et al., 2018; Fede and Kiehl, 2020). We will then review the evidence of the impairments found in this network in individuals with psychopathy. Psychopathy is a term that is used to describe a constellation of cognitive, emotional, and behavioral characteristics that indicate profound disturbances in appropriate moral processing. Individuals with psychopathy show blunted affect, lack

*Correspondence to: Ana Seara-Cardoso, School of Psychology, University of Minho, Campus de Gualtar, 4710-057 Braga, Portugal. Tel: +351-253601397, E-mail: ana.searacardoso@psi.uminho.pt

of guilt, marked irresponsible lifestyle and frequent engagement in antisocial behavior (Hare and Neumann, 2008). Although the prevalence of psychopathy is relatively low—approximately 1% of the population (Hare and Neumann, 2008; Coid et al., 2009a,b)—psychopaths account for a high proportion of violent crime and cause substantial emotional distress to their victims (Kiehl and Buckholtz, 2010). We will present behavioral and neuroimaging data from forensic/clinical samples, general population as well as child and adolescent samples and will advance the proposal that the moral dysfunction in individuals with psychopathy may stem from a disruption of affective components of moral processing rather than from an inability to compute moral judgments per se.

THE “MORAL BRAIN”

The early days of the neuroscience of morality

Early studies of the neural basis of moral cognition relied mostly on brain lesion studies, particularly on the consequences of ventromedial prefrontal cortex (vmPFC) lesions to moral cognition and behavior. Lesions to the vmPFC have long been associated with the onset of disinhibited and antisocial behavior. One of the first descriptions of this type of lesion was the famous case report of Phineas Gage provided by Harlow in the 19th century (Damasio et al., 1994). Phineas Gage was a railroad worker who suffered severe frontal injury after an explosion during railroad works. An iron bar penetrated his skull, injuring most of his frontal lobe. Although he survived with most of his cognitive abilities intact, his social behavior was severely impaired. When Gage died, no autopsy was performed. But his skull was preserved and, in 1994, Damasio and colleagues re-examined it using modern neuroimaging techniques to determine the probable location of the lesion (Damasio et al., 1994). Damasio and colleagues found that the damage involved the ventromedial prefrontal portion of both left and right cortices. The location of the lesion in Gage’s skull was consistent with the location of brain lesions in contemporary brain lesion patients who presented a similar pattern of behavioral changes. Around the same time, other studies also suggested that acquired damage to the prefrontal cortex results in impaired moral behavior. For example, war veterans with vmPFC lesions present increased levels of aggressive behavior (Grafman et al., 1996), neurological patients show reduced autonomic reactivity to social stimuli and psychopathic-like behavior (e.g., Damasio et al., 1990; Saver and Damasio, 1991; Damasio, 1996, 2000; Anderson et al., 1999; Bechara et al., 2000a), and congenital malformations of the vmPFC or lesions acquired during development are associated

with particularly severe antisocial behavior and impaired moral judgment later in adolescence and adulthood (Boes et al., 2011; Taber-Thomas et al., 2014).

However, extant research has also shown that vmPFC patients’ deficits do not seem to be circumscribed to moral judgment or moral behavior. Patients with lesions in this region present impairments in making personal and social decisions in general, in spite of spared cognitive ability (Bechara et al., 1996, 2000a,b). They present diminished emotional responses when making a wide range of decisions, have difficulties in choosing between options with uncertain outcomes, have difficulties in learning from their one mistake and seem to be insensitive to the future consequences of their actions (Bechara et al., 1996, 2000a,b). In the influential “Somatic marker hypothesis,” Damasio (1994, 1996) suggested that these impairments in decision making are due to an underlying somatic marker deficit. This hypothesis proposed that appropriate decision making depends on the appropriate integration of somatic markers—i.e., emotional states evoked by the experience of reward or punishment which signal the potential occurrence of an outcome—and that the vmPFC serves a critical role in the generation and integration of these somatic markers. These emotional associations, or “gut feelings,” would guide our everyday decisions about how to behave.

Damasio’s seminal work, alongside Haidt’s influential paper on the role of quick intuitions vs. deliberate reasoning in moral reasoning (Haidt, 2001), and the spread of neuroimaging techniques, prompted a new wave of research interest on which specific psychological and neurocognitive mechanisms are involved in human morality (e.g., Greene et al., 2001, 2004; Moll et al., 2002b; Berthoz et al., 2006; Moll and de Oliveira-Souza, 2007). In 2001, Greene and colleagues published one of the most influential studies on moral neuroscience (Greene et al., 2001). In this study, participants responded to a set of classic philosophical moral dilemmas, “Trolley Dilemmas.” In these dilemmas, the agent has to decide whether it is appropriate or not to sacrifice the life of one person to save the life of many. The agent stands between two conflicting moral obligations: a *deontological* obligation to do no harm (e.g., do not kill); and a *utilitarian* obligation to maximize overall welfare (e.g. maximize the number of lives saved). Interestingly, most people consider it to be morally appropriate to sacrifice the life of one person to save the life of many when this is done in an *impersonal* manner (for example, by pressing a switch to divert a runaway trolley from a track with five workers to a track with just one worker), thus endorsing an utilitarian response. However, when this implies a more *personal*, direct action (such as pushing a person from a bridge to stop the runaway trolley to hit five workers on the tracks), most

people consider it be morally unacceptable, thus reflecting a deontological response. Greene and colleagues (2001, 2004) observed a differential pattern of brain responses when participants responded to personal and impersonal types of dilemmas. Whilst impersonal dilemmas elicited greater responses in areas typically associated with deliberative reasoning, such as the dorsolateral prefrontal cortex (dlPFC) and inferior parietal lobe, personal dilemmas yielded responses in regions typically associated with emotional and social processing—such as the vmPFC, amygdala and posterior superior temporal sulcus (pSTS). According to Greene and colleagues, moral judgments rely on both automatic emotional responses and controlled cognitive processes (Greene et al., 2004, 2008, 2009). Responses to personal dilemmas would mainly be driven by automatic emotional responses, while impersonal dilemmas would mainly be driven by controlled cognitive processes (Greene et al., 2008).

Following Greene's seminal work, in the past two decades, an increasing number of studies have used functional magnetic resonance imaging (fMRI) to attempt to identify the neural correlates of moral cognition, adding to our understanding of the cognitive and affective processes it involves. These studies have focused on a wide range of different processes (e.g., moral judgments, i.e., “Is it wrong to do X?”; moral decisions, i.e., “Would you do X?”; moral emotions, i.e., “How would you feel if you did X?”) with a variety of different tasks (e.g., morally-laden visual stimuli, hypothetical moral dilemmas, situational vignettes, economic games). Interestingly, rather than finding specific systems dedicated to moral cognition, the bulk of studies have identified an extensive network of brain regions which include decision-making, affective processing, mentalizing, and perspective-taking processing regions (Fumagalli and Priori, 2012; Young and Dungan, 2012; Garrigan et al., 2016; Boccia et al., 2017; Eres et al., 2018; Fede and Kiehl, 2020). This prompted the notion that moral cognition relies on the coordination of several domain-general processes, subserved by domain-general neural networks, rather than a specific moral cognition system subserved by a specific neural network (Cushman et al., 2010; Young and Dungan, 2012; Yoder and Decety, 2018).

Neural correlates of morality

As previously suggested by brain lesion studies, the vmPFC seems to be one of the brain region most consistently implicated in fMRI studies of moral cognition (Garrigan et al., 2016; Eres et al., 2018; Fede and Kiehl, 2020). The vmPFC is activated when participants make explicit moral decisions (e.g., Greene et al., 2004), passively observe morally charged visual (e.g., Moll

et al., 2002a), or reflect on moral emotions (e.g., Moll et al., 2002b, 2008). This region is also consistently recruited both during economic decision-making, including the valuation of both appetitive and aversive goals (Plassmann et al., 2010; Litt et al., 2011), as well as during more complex social and moral decisions, such as deciding when to donate money to charities (Hare et al., 2010) or when to sacrifice the life of one person to save the life of many (Shenhav and Greene, 2014). As such, it has been hypothesized that the role of the vmPFC is to integrate positive and negative reward signals into a representation of the overall expected value or utility of a decision (Wallis, 2007; Hare et al., 2010; Hutcherson et al., 2015). Thus, although it now seems unlikely that the vmPFC is a source of gut feelings as proposed by Damasio (1994, 1996), this region does seem to function as a hub wherein such feelings are incorporated with or weighed against other considerations before making a decision (Shenhav and Greene, 2014; Hutcherson et al., 2015).

Along with the vmPFC, extant studies have also implicated affective processing regions in moral cognition, including the amygdala and the anterior insula. The amygdala is known to respond to emotional stimuli and is thought to play a crucial role in detecting emotional saliency in moral situations (Adolphs, 2010; Adolphs et al., 2013), while the anterior insula is thought to support interoception of subjective emotional states (Critchley et al., 2004; Craig, 2009; Critchley and Harrison, 2013). Response in the anterior insula seems to vary with the strength of overall emotional appraisals of moral situations (Shenhav and Greene, 2014; Hutcherson et al., 2015). The anterior insula has been consistently identified in work examining the neural correlates of moral emotions, such as in imaging studies where participants read guilt-eliciting sentences or stories, recalled past guilt-eliciting situations or were given guilt-eliciting feedback (Berthoz et al., 2006; Wagner et al., 2011; Michl et al., 2014; Fourie et al., 2014; Yu et al., 2014). Response in the anterior insula has also been found to vary as a function of reported anticipated guilt to everyday moral transgressions (Seara-Cardoso et al., 2016a). Thus, the anterior insula is thought to play an important role in encoding aversive responses to moral transgressions and processing feelings of guilt that result from moral wrongdoings.

The extensive network identified in studies of moral cognition also largely overlaps the so-called “social brain,” a network of brain regions involved in social interaction and communication which includes regions such as the temporoparietal junction/posterior superior temporal sulcus (TPJ/pSTS), angular gyrus, supramarginal gyrus (SMG), and temporal pole (Frith and Frith, 2010). Meta-analyses (Bzdok et al., 2012; Sevinc and

Spreng, 2014) have found consistent activation of the TPJ/pSTS, angular gyrus and temporal pole during moral judgment tasks, particularly when participants were required to make active judgments of other people's actions. These regions play a central role in mentalizing—i.e., inferring and representing another people's beliefs and mental states, including the detection and analysis of their goals and intentions (Schultz et al., 2005; Young et al., 2007). The activation of these mentalizing regions is unsurprising; moral evaluations are thought to require thinking about not only others' actions but also about their intentions (Buon et al., 2016). The TPJ/pSTS, in particular, is linked to the attribution of intent in moral judgment. For example, activity in this region increases during the evaluation of attempted harms (Young et al., 2007; Young and Saxe, 2008) and with the intensity of wrongness judgments of moral transgressions (Seara-Cardoso et al., 2016a), and predicts individual variability in judgments of accidental and intentional harms (Koster-Hale et al., 2013). Plus, disruption of the TPJ with transcranial magnetic stimulation seems to make participants judge attempted harms more leniently (Young et al., 2010).

To date, few studies have inspected the neural mechanisms underlying moral cognition during development. Results from these studies point to developmental changes in the neural substrates of moral judgment and in the integration of affective and cognitive processes in moral judgment. For example, relative to adults, adolescents present weaker neural responses in temporal and prefrontal regions when making moral judgments (Harenski et al., 2012) and when observing scenarios depicting harm to others (Decety and Michalska, 2010). At the same time, they present stronger emotional responses and amygdala reactivity and weaker connectivity between amygdala and prefrontal regions (Decety and Michalska, 2010). That is, while response to harmful actions in affective processing regions seems to decrease with age, the connectivity between these affect processing regions and prefrontal regions seems to increase throughout development. Although sparse and preliminary, these studies point to an increasing integration of cognitive and affective information processes in moral cognition throughout development.

WHEN THINGS GO WRONG

Psychopathy

Delineating the neural basis of moral cognition is critical for understanding individual differences in moral behavior. Why, for example, a minority of individuals routinely engages in irresponsible and immoral behavior? Psychopathy is a personality disorder characterized by lack of guilt and empathy, manipulativeness, impulsiveness,

and repeated antisocial behavior (Blair, 1995; Viding et al., 2014). Despite the relatively low prevalence (Hare and Neumann, 2008; Coid et al., 2009a,b), psychopaths create considerable costs for society (Kiehl and Buckholtz, 2010).

Individuals with psychopathy seem to show a distinctive pattern of antisocial behavior, with a putative distinct underlying etiology, than those with antisocial personality disorder but without psychopathy. While the latter seems to repeatedly engage in emotionally charged and reactive aggression, individuals with psychopathy seem to be emotionally flat and engage in instrumental (i.e., goal-oriented) aggression (Hodgins et al., 2009). Individuals with psychopathy seem to be emotionally flat, show distinct emotional deficits and are characterized by traits of fearlessness, low anxiety and average verbal skills (Hare, 1996; Viding et al., 2014).

Several decades of experimental research have probed the deficits of individuals with psychopathy (see Chapter 7). Extant evidence converges in finding that individuals with psychopathy present reduced autonomic responses to the distress of others and reduced recognition of others' sad and fearful (and possibly other) expressions (Dolan & Fullam, 2010; Blair, 2013). Given the extent of emotional dysfunction exhibited by these individuals, early fMRI studies on psychopathy focused on whether these individuals presented differential brain activity when processing affective content (Kiehl et al., 2001; Müller et al., 2003) and emotional learning (Birbaumer et al., 2005). Unsurprisingly, these studies found atypical brain responses to emotional and salient stimuli in affective processing brain regions, in particular in the amygdala and the vmPFC (Kiehl et al., 2001; Müller et al., 2003; Birbaumer et al., 2005).

Callous unempathic behavior is one of the central hallmarks of individuals with psychopathic characteristics. Indeed, behavioral and neuroimaging data are consistent with the notion that these individuals do not find other people's distress as salient as their peers do (Blair, 2013; Viding et al., 2014). Across a wide range of tasks—from the simple observation of emotional facial expressions and of others' experiences of pain, to more complex paradigms where participants are asked to infer others' affective states—individuals with psychopathy consistently show atypical engagement of the amygdala, anterior insula, anterior cingulate cortex and TPJ, brain areas typically associated with emotional salience, emotional resonance and emotional understanding (see for comprehensive reviews Seara-Cardoso and Viding, 2015; Seara-Cardoso et al., 2022). Interestingly, evidence from these studies also suggests that individuals with psychopathy do not necessarily display difficulties in inferring others internal states when these do not include affective content. Individuals with psychopathy do not

appear to have impairments in ToM and inhibitory control tasks, as long as these tasks do not require processing of affective content (Blair et al., 2006; Shamay-Tsoory et al., 2010).

It has been proposed that this absence of a robust response to other people's distress helps to explain why these individuals have a propensity to harm others (Blair et al., 2005; Blair, 2013). Over time, failure to respond to others' suffering may lead to impaired moral development, making individuals high in psychopathic traits more prone to engage in antisocial behavior (Blair et al., 2005; Blair, 2013). To date, a number of studies have directly inspected neural correlates of moral judgment in individuals with psychopathy. These studies focused on judgment of different moral stimuli, such as moral dilemmas, morally-laden scenarios or morally-laden visual stimuli (Glenn et al., 2009a,b; Harenski et al., 2010; Pujol et al., 2012; Decety et al., 2015). Interestingly, when compared with controls, individuals with psychopathy did not present behavioral differences in terms of their behavioral responses in the tasks. However, they did present reduced neural response in the amygdala and vmPFC (Glenn et al., 2009a; Harenski et al., 2010; Pujol et al., 2012; Decety et al., 2015), regions thought to be involved in evaluative and affective processing of moral content. At the same time, some of these studies found increased response in regions typically associated with cognitive control, such as the DLPFC, during moral judgment of extreme moral dilemmas (Glenn et al., 2009b; Pujol et al., 2012). The evidence of these studies converges to support the notion that individuals with psychopathy may present spared moral judgment ability but they may use different strategies, and engage different brain regions, to compute their judgments.

As with many forms of mental disorder, evidence indicates that the structure of psychopathic personality is dimensional rather than categorical; psychopathic traits appear to be continuously distributed in the general population, and individuals with a diagnosis of psychopathy represent an extreme end of that distribution (Hare and Neumann, 2008; Neumann et al., 2015). This dimensional perspective of psychopathy has led to a growing interest in the correlates of psychopathic traits in the general population (Lilienfeld and Fowler, 2006; Carré et al., 2013). Not surprisingly, extant findings from behavioral studies with community samples mostly mirror those from forensic samples, pointing to the existence of continuities in the mechanisms underlying psychopathic traits in community and forensic samples (Seara-Cardoso & Viding, 2015; Seara-Cardoso et al., 2022). Individual differences in psychopathic traits in the general population can be mapped onto dysfunctional behavioral and neural processes systematically reported

in individuals with a diagnosis of psychopathy. For example, akin to forensic samples, higher levels of psychopathic traits in the general population have been found to be associated with reduced startle potentiation (Benning et al., 2005; Justus and Finn, 2007) and autonomic responses to aversive images (Benning et al., 2005; Osumi et al., 2007), blunted affective responses to others' emotions (Ali et al., 2009; Seara-Cardoso et al., 2012, 2013), reduced empathic concern for others (Seara-Cardoso et al., 2012, 2013), poor decision-making during gambling tasks (Mahmut et al., 2008) and atypical responses to moral content (Cima et al., 2010; Seara-Cardoso et al., 2012, 2013).

At the neural level, fMRI research with samples from the general population also mostly mirror those observed in forensic/clinical samples. The bulk of fMRI research on the neural correlates of psychopathic traits in the general population suggest an overall negative association between variance in these traits and brain response in regions typically involved in affective processing, such as the amygdala and anterior insula. From research on the neural correlates of basic emotional recognition (Gordon et al., 2004; Carré et al., 2013; Hyde et al., 2014); Sethi et al., 2018 to research on more complex forms of social cognition (Harenski et al., 2009; Seara-Cardoso et al., 2015, 2016a,b; Vieira et al., 2017), the evidence converges on increasingly poorer responses in these regions to affective content as psychopathic traits increase.

Importantly, evidence from studies with samples from the general population suggest that psychopathic traits are associated with atypical neural responses to the emotional content of moral transgressions rather than with atypical neural responses in the computation of moral judgments per se (Seara-Cardoso et al., 2016a,b). For example, Seara-Cardoso et al. (2016a,b) used a moral transgressions paradigm where participants were asked to rate how guilty they would feel in scenarios depicting everyday moral transgressions. These scenarios involved transgressions where the protagonist inflicted harm to others to achieve a personal goal, compared with morally neutral scenarios where the protagonist inflicted harm to himself to achieve the same personal goal. Of note, in this paradigm, the emotional content of experimental and control scenarios was well equated. When instructed to imagine themselves as the protagonist of the moral transgression scenario and rate how guilty they would feel, participants recruited the set of brain regions typically associated with moral processing—including the vmPFC, TPJ, and anterior insula. As expected, given its role in interoception, response in anterior insula varied as a function of anticipated guilt. However, this modulation of guilt in the anterior insula also varied as a function of psychopathic traits. In a follow-up experiment, the

authors used the same stimuli and asked participants to judge the wrongness of the scenarios. Although participants recruited the same network of regions as before, no interaction, nor any other associations with psychopathic traits were found. This study provides further evidence that (a)moral behavior linked to psychopathic traits may be driven by dysfunctional affective/motivational processes rather than by difficulties in judging the correctness of a situation.

Callous-unemotional traits

Further evidence that the moral dysfunction in individuals with psychopathy may stem from a disruption of affective components of moral processing rather than from an inability to compute moral judgments comes from developmental studies. The presence of callous-unemotional (CU) traits during development are thought to be a precursor of psychopathy in adulthood. Callous-unemotional (CU) refers to a constellation of personality traits that include blunted affect, lack of empathy and remorse, uncaring behavior and disregard for others' feelings and well-being (Essau et al., 2006; Viding and Kimonis, 2018; Frick and Marsee, 2019).

Akin to psychopathic traits in adults, the presence of high levels of CU traits seems to distinguish a cohort of youth who exhibit instrumental and planned violence, and who display a subtype of conduct disorder that is more severe, more stable and more resistant to treatment (e.g., Frick et al., 2003; Kruh et al., 2005; Viding and Kimonis, 2018). High levels of CU traits are thought to contribute to the development of a more persistent and aggressive type of antisocial behavior in youth, found across forensic (e.g., Vincent et al., 2003; Kruh et al., 2005), community (e.g., Frick et al., 2003; Essau et al., 2006) and mental health samples (e.g., Christian et al., 1997). Even in the absence of conduct disorder, high levels of CU traits have been associated with higher risk for disruptive behavior (Frick et al., 2003; Meier et al., 2008; Rowe et al., 2010). Longitudinal data indicate that CU traits add to the prediction of serious and persistent criminal behavior in boys, over and above the presence of conduct disorder symptoms and oppositional defiant problems (Pardini and Fite, 2010).

Also akin to adults with high levels of psychopathy, children and adolescents with high levels of CU traits seem to present a dissociation between affective and cognitive aspects of empathy (Dadds et al., 2009; Jones et al., 2010; Sebastian et al., 2012; Seara-Cardoso et al., 2012; Lockwood et al., 2013; Winter et al., 2017; Kajonius and Björkman, 2020). Youth with high levels of CU traits seem to present impairments in affective empathy, i.e., they fail to resonate with others' feelings, while showing somewhat preserved cognitive empathy skills, i.e., they seem to be able to infer and describe what others feel (Dadds et al., 2009; Jones et al., 2010).

Although only a few studies to date have inspected behavioral and neural correlates of moral cognition in children with high levels of CU traits, extant evidence seems to suggest that a similar dissociation between emotional and cognitive components of moral cognition is already at play during development. For example, like adults with high psychopathic traits (Blair, 1995; Blair and Cipolotti, 2000), youth with high CU traits show difficulties in distinguishing between conventional and moral transgressions (Blair, 1997; Dolan and Fullam, 2010). Moral transgressions are defined by their consequences to the welfare of others (e.g., hitting a peer), while conventional transgressions are defined by their consequences for the social order and the understanding of appropriate social behavior (e.g., talking in class). This failure to distinguish between the two—children with high CU traits consider equally acceptable to break both types of rules if given permission by a figure of authority such as a teacher—is thought to reflect diminished emotional resonance to the harm caused to the victim.

Higher CU traits have also been associated with lower feelings of guilt (Fragkaki et al., 2016; Vasconcelos et al., 2021), and to moderate the association between feelings of guilt and wrongness judgments of moral transgressions. That is, while for youth with low levels of these traits anticipated feelings of guilt for moral transgressions seem to be a strong predictor of wrongness judgments of such transgressions, this does not seem to be the case for those with higher levels of these traits (Vasconcelos et al., 2021). For adolescents with higher levels of CU traits, affective responses to moral transgressions do not seem to play such an important role on moral appraisals. This is interesting, because it suggests that the dissociation between moral emotions and moral judgment linked to psychopathic traits may already be present during adolescence and may evolve through adulthood. Findings from neuroimaging research, albeit sparse, seem to be in-line with this idea. For example, adolescents with higher CU traits show a negative association between ratings of moral violations severity and amygdala response (Harenski et al., 2014) and show reduced amygdala response during implicit moral judgment (Marsh et al., 2011). Additionally, they show a reduced connectivity between amygdala and vmPFC during both explicit and implicit moral judgment (Marsh et al., 2011; Harenski et al., 2014).

CONCLUSION

In sum, in the past decades findings from experimental psychology and cognitive neuroscience have shed new light on our understanding of the psychological and biological bases of human morality. Interestingly, rather than finding specific systems dedicated to moral cognition, extant studies have identified an extensive network

of brain regions which include decision-making and affective processing regions that also largely overlaps the so-called “social brain,” a network of brain regions involved in social interaction and communication. This prompted the notion that we rely on the coordination of several domain-general processes for moral cognition rather than a specific moral cognition system. This notion is backed-up by recent computational neuroscience studies which suggest that we rely on the same algorithms and neural mechanisms to make moral judgments and decisions and to make everyday decisions (e.g., Shenhav and Greene, 2014; Hutcherson et al., 2015; Crockett et al., 2017). Moral cognition appears to rely on a complex interaction of cognitive and affective information processes that implicate a widely distributed brain network.

Moral dysfunction in adults with high levels of psychopathic traits seem to stem from a disruption of the affective and motivational components of moral processing rather than from an inability to tell right from wrong. At the behavioral level, high levels of psychopathic traits seem to be associated with reduced propensity to feel moral emotions (i.e., guilt) and reduced difficulty in judging actions in moral dilemmas, but not with endorsement of such actions per se. At the neural level, they are associated with reduced responses in affective brain regions during moral processing, despite apparent intact moral judgment ability. Developmental studies suggest that youths with high CU present a remarkably similar pattern of behavioral and neural correlates.

It has been suggested that, in the absence of an emotional response to moral transgressions, individuals with high levels of psychopathic traits use alternative cognitive strategies to process moral judgments (Buon et al., 2016). Individuals with high levels of psychopathy seem to know (and apply) the rules that are relevant to make moral judgments but do seem to do so without using “standard” affective routes that are taken by those with low levels of these traits (Glenn et al., 2009a,b; Cima et al., 2010). Another possibility, if not mutually exclusive, is that adults with high levels of psychopathic traits display typical moral judgment due to an intact ability to understand the thoughts of others (Dolan & Fullam, 2010; Lockwood et al., 2013), as well as others’ expectations (Gong et al., 2019), although they may lack the motivation to do so (Roberts et al., 2020). This would enable adults with high levels of psychopathic traits to respond to moral tasks and questionnaires in the same way they think other people would, thus engaging in, at least apparently, intact moral judgment.

Despite recent research advances in the understanding of how moral impairments are linked to psychopathy, there is still substantial work to be done to gain a fine-grained picture of the precise neurocognitive processing deficits that affect individuals with high levels of these

traits. In particular, there is substantial work to be done to disentangle precisely which distinct dimensions of moral cognition (e.g., moral judgment, moral decision-making, moral emotions) are impaired in these individuals. Given the extreme behavior exhibited by these individuals, characterizing the cognitive and neural processes and mechanisms associated with their antisocial conduct has important theoretical and societal implications as it enables the development of more individualized prevention and treatment approaches for this heterogeneous population and thus has the potential to help reduce the financial and human costs of offending behavior.

Furthermore, despite the importance of inspecting the etiology of moral dysfunction associated with psychopathy in a developmental manner, only a few studies have inspected neurocognitive correlates of moral cognition in youth—either in typically developing (Decety and Michalska, 2010; Harenski et al., 2012) or forensic samples (Marsh et al., 2011; Harenski et al., 2014)—and these have these focused almost exclusively on moral judgment tasks. Future work is needed to further characterize the cognitive-affective processing deficits that underlie moral dysfunction in youth with antisocial behavior, particularly in those with high levels of CU and who are at heightened risk for psychopathy in adulthood. Understanding the specific psychological and neural processes that are compromised during development has important potential treatment and public policy implications. In particular, identifying the specific deficits that underpin persistent and severe patterns of violence can provide valuable information for the development of targets for rehabilitation and early prevention programs.

ACKNOWLEDGMENTS

ASC was supported by a Portuguese Foundation for Science and Technology (FCT) research grant (PTDC/MHC-PCN/2296/2014), cofinanced by FEDER through COMPETE2020 under the PT2020 Partnership Agreement (POCI-01-0145-FEDER-016747), at the Psychology Research Centre (PSI/01662) supported by FCT through the Portuguese State Budget (UIDB/PSI/01662/2020), at the time of writing.

REFERENCES

- Adolphs R (2010). What does the amygdala contribute to social cognition? *Ann N Y Acad Sci* 1191: 42–61. <https://doi.org/10.1111/j.1749-6632.2010.05445.x>. PMID: 20392275. PMCID: PMC2871162.
- Adolphs R, Tranal D, Damasio AR (2013). The human amygdala in social judgment. In: *The science of mental health vol. 2: autism*.

- Ali F, Amorim IS, Chamorro-Premuzic T (2009). Empathy deficits and trait emotional intelligence in psychopathy and Machiavellianism. *Personal Individ Differ* 47: 758–762.
- Anderson SW, Bechara A, Damasio H et al. (1999). Impairment of social and moral behavior related to early damage in human prefrontal cortex. *Nat Neurosci* 2: 1032–1037.
- Bechara A, Tranel D, Damasio H et al. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cereb Cortex* 6: 215–225.
- Bechara A, Damasio H, Damasio AR (2000a). Emotion, decision making and the orbitofrontal cortex. *Cereb Cortex* 10: 295–307.
- Bechara A, Tranel D, Damasio H (2000b). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain* 123: 2189–2202.
- Benning SD, Patrick CJ, Iacono WG (2005). Psychopathy, startle blink modulation, and electrodermal reactivity in twin men. *Psychophysiology* 42: 753–762.
- Berthoz S, Grèzes J, Armony JL et al. (2006). Affective response to one's own moral violations. *NeuroImage* 31: 945–950.
- Birbaumer N, Veit R, Lotze M et al. (2005). Deficient fear conditioning in psychopathy: a functional magnetic resonance imaging study. *Arch Gen Psychiatry* 62: 799–805.
- Blair RJR (1995). A cognitive developmental approach to morality: investigating the psychopath. *Cognition* 57: 1–29.
- Blair RJR (1997). Moral reasoning and the child with psychopathic tendencies. *Personal Individ Differ* 22: 731–739.
- Blair RJR (2013). The neurobiology of psychopathic traits in youths. *Nat Rev Neurosci* 14: 786–799.
- Blair RJR, Cipolotti L (2000). Impaired social response reversal. A case of 'acquired sociopathy'. *Brain* 123: 1122–1141.
- Blair J, Mitchell D, Blair K (2005). The psychopath: emotion and the brain, Blackwell Publishing.
- Blair J, Marsh AA, Finger E et al. (2006). Neuro-cognitive systems involved in morality. *Philos Explor* 9: 13–27.
- Boccia M, Dacquino C, Piccardi L et al. (2017). Neural foundation of human moral reasoning: an ALE meta-analysis about the role of personal perspective. *Brain Imaging Behav* 11: 278–292.
- Boes AD, Grafft AH, Joshi C et al. (2011). Behavioral effects of congenital ventromedial prefrontal cortex malformation. *BMC Neurol* 11.
- Buon M, Seara-Cardoso A, Viding E (2016). Why (and how) should we study the interplay between emotional arousal, theory of mind, and inhibitory control to understand moral cognition? *Psychon Bull Rev* 23: 1660–1680.
- Bzdok D, Schilbach L, Vogeley K et al. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Struct Funct* 217: 783–796.
- Carré JM, Hyde LW, Neumann CS et al. (2013). The neural signatures of distinct psychopathic traits. *Soc Neurosci* 8: 122–135.
- Christian RE, Frick PJ, Hill NL et al. (1997). Psychopathy and conduct problems in children: II. Implications for subtyping children with conduct problems. *J Am Acad Child Adolesc Psychiatry* 36: 233–241.
- Cima M, Tonnaer F, Hauser MD (2010). Psychopaths know right from wrong but don't care. *Soc Cogn Affect Neurosci* 5: 59–67.
- Coid J, Yang M, Ullrich S et al. (2009a). Prevalence and correlates of psychopathic traits in the household population of Great Britain. *Int J Law Psychiatry* 32: 65–73.
- Coid J, Yang M, Ullrich S et al. (2009b). Psychopathy among prisoners in England and Wales. *Int J Law Psychiatry* 32: 134–141.
- Craig AD (2009). How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci* 10: 59–70.
- Crutchley H, Harrison N (2013). Visceral influences on brain and behavior. *Neuron* 77: 624–638.
- Crutchley HD, Wiens S, Rotstein P et al. (2004). Neural systems supporting interoceptive awareness. *Nat Neurosci* 7: 189–195.
- Crockett MJ, Siegel JZ, Kurth-Nelson Z et al. (2017). Moral transgressions corrupt neural representations of value. *Nat Neurosci* 20: 879–885.
- Cushman F, Young L, Greene JD (2010). Our multi-system moral psychology: towards a consensus view. In: *The Oxford handbook of moral psychology*, Oxford University Press, Oxford, pp. 47–71.
- Dadds MR, Hawes DJ, Frost ADJ et al. (2009). Learning to 'talk the talk': the relationship of psychopathic traits to deficits in empathy across childhood. *J Child Psychol Psychiatry Allied Discip* 50: 599–606.
- Damasio AR (1994). *Descartes' error: emotion, reason, and the human brain*, G.P. Putnam, New York.
- Damasio AR (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philos Trans Roy Soc B Biol Sci* 351: 1413–1420.
- Damasio AR (2000). A neural basis for sociopathy. *Arch Gen Psychiatry* 57: 128–129.
- Damasio AR, Tranel D, Damasio H (1990). Individuals with sociopathic behavior caused by frontal damage fail to respond autonomically to social stimuli. *Behav Brain Res* 41: 81–94.
- Damasio H, Grabowski T, Frank R et al. (1994). The return of Phineas Gage: clues about the brain from the skull of a famous patient. *Science* 264: 1102–1105.
- Decety J, Michalska KJ (2010). Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Dev Sci* 13: 886–899.
- Decety J, Chen C, Harenski CL et al. (2015). Socioemotional processing of morally-laden behavior and their consequences on others in forensic psychopaths. *Hum Brain Mapp* 36: 2015–2026.
- Dolan MC, Fullam RS (2010). Moral/conventional transgression distinction and psychopathy in conduct disordered adolescent offenders. *Personal Individ Differ* 49: 995–1000.
- Eres R, Louis WR, Molenberghs P (2018). Common and distinct neural networks involved in fMRI studies

- investigating morality: an ALE meta-analysis. *Soc Neurosci* 13: 384–398.
- Essau CA, Sasagawa S, Frick PJ (2006). Callous-unemotional traits in a community sample of adolescents. *Assessment* 13: 454–469.
- Fede SJ, Kiehl KA (2020). Meta-analysis of the moral brain: patterns of neural engagement assessed using multilevel kernel density analysis. *Brain Imaging Behav* 14: 534–547.
- Fourie MM, Thomas KGF, Amadio DM et al. (2014). Neural correlates of experienced moral emotion: an fMRI investigation of emotion in response to prejudice feedback. *Soc Neurosci* 9: 203–218.
- Fragkaki I, Cima M, Meesters C (2016). The association between callous-unemotional traits, externalizing problems, and gender in predicting cognitive and affective morality judgments in adolescence. *J Youth Adolesc* 45: 1917–1930.
- Frick PJ, Marsee MA (2019). Psychopathy developmental pathways to antisocial behavior in youth. In: CJ Patrick (Ed.), *Handbook of psychopathy*. 456–476.
- Frick PJ, Cornell AH, Barry CT et al. (2003). Callous-unemotional traits and conduct problems in the prediction of conduct problem severity, aggression, and self-report of delinquency. *J Abnorm Child Psychol* 31: 457–470.
- Frith U, Frith C (2010). The social brain: allowing humans to boldly go where no other species has been. *Philos Trans Roy Soc B Biol Sci* 365: 165–175.
- Fumagalli M, Priori A (2012). Functional and clinical neuroanatomy of morality. *Brain* 135: 2006–2021.
- Garrigan B, Adlam ALR, Langdon PE (2016). The neural correlates of moral decision-making: a systematic review and meta-analysis of moral evaluations and response decision judgements. *Brain Cogn* 108: 88–97.
- Glenn AL, Raine A, Schug RA (2009a). The neural correlates of moral decision-making in psychopathy. *Mol Psychiatry* 14: 5–6.
- Glenn AL, Raine A, Schug RA et al. (2009b). Increased DLPFC activity during moral decision-making in psychopathy. *Mol Psychiatry* 14: 909–911.
- Gong X, Brazil IA, Chang LJ et al. (2019). Psychopathic traits are related to diminished guilt aversion and reduced trustworthiness during social decision-making. *Sci Rep* 9.
- Gordon HL, Baird AA, End A (2004). Functional differences among those high and low on a trait measure of psychopathy. *Biol Psychiatry* 56: 516–521.
- Grafman J, Schwab K, Warden D et al. (1996). Frontal lobe injuries, violence, and aggression: a report of the Vietnam head injury study. *Neurology* 46: 1231–1238.
- Greene JD, Sommerville RB, Nystrom LE et al. (2001). An fMRI investigation of emotional engagement in moral judgment. *Science* 293: 2105–2108.
- Greene JD, Nystrom LE, Engell AD et al. (2004). The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44: 389–400.
- Greene JD, Morelli SA, Lowenberg K et al. (2008). Cognitive load selectively interferes with utilitarian moral judgment. *Cognition* 107: 1144–1154. <https://doi.org/10.1016/j.cognition.2007.11.004>. Epub 2007 Dec 26. PMID: 18158145; PMCID: PMC2429958.
- Greene JD, Cushman FA, Stewart LE et al. (2009). Pushing moral buttons: the interaction between personal force and intention in moral judgment. *Cognition* 111: 364–371. <https://doi.org/10.1016/j.cognition.2009.02.001>. Epub 2009 Apr 16. PMID: 19375075.
- Haidt J (2001). The emotional dog and its rational tail: a social intuitionist approach to moral judgment. *Psychol Rev* 108: 814–834.
- Hare RD (1996). Psychopathy: a clinical construct whose time has come. *Crim Justice Behav* 23: 25–54.
- Hare RD, Neumann CS (2008). Psychopathy as a clinical and empirical construct. *Annu Rev Clin Psychol*.
- Hare TA, Camerer CF, Knoepfle DT et al. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *J Neurosci* 30: 583–590.
- Harenski CL, Sang HK, Hamann S (2009). Neuroticism and psychopathy predict brain activation during moral and nonmoral emotion regulation. *Cogn Affect Behav Neurosci* 9: 1–15.
- Harenski CL, Harenski KA, Shane MS et al. (2010). Aberrant neural processing of moral violations in criminal psychopaths. *J Abnorm Psychol* 119: 863–874.
- Harenski CL, Harenski KA, Shane MS et al. (2012). Neural development of mentalizing in moral judgment from adolescence to adulthood. *Dev Cogn Neurosci* 2: 162–173.
- Harenski CL, Harenski KA, Kiehl KA (2014). Neural processing of moral violations among incarcerated adolescents with psychopathic traits. *Dev Cogn Neurosci* 10: 181–189.
- Hodgins S, de Brito S, Simonoff E et al. (2009). Getting the phenotypes right: an essential ingredient for understanding aetiological mechanisms underlying persistent violence and developing effective treatments. *Front Behav Neurosci* 3: 44. <https://doi.org/10.3389/neuro.08.044.2009>.
- Hutcherson CA, Montaser-Kouhsari L, Woodward J et al. (2015). Emotional and utilitarian appraisals of moral dilemmas are encoded in separate areas and integrated in ventromedial prefrontal cortex. *J Neurosci* 35: 12593–12605.
- Hyde LW, Byrd AL, Votruba-Drzal E et al. (2014). Amygdala reactivity and negative emotionality: divergent correlates of antisocial personality and psychopathy traits in a community sample. *J Abnorm Psychol* 123: 214–224.
- Jones AP, Happé FG, Gilbert F et al. (2010). Feeling, caring, knowing: different types of empathy deficit in boys with psychopathic tendencies and autism spectrum disorder. *J Child Psychol Psychiatry* 51: 1188–1197.
- Justus AN, Finn PR (2007). Startle modulation in non-incarcerated men and women with psychopathic traits. *Personal Individ Differ* 43: 2057–2071.
- Kajonius PJ, Björkman T (2020). Individuals with dark traits have the ability but not the disposition to empathize. *Personal Individ Differ* 155.
- Kiehl KA, Buckholtz JW (2010). Inside the mind of a psychopath. *Sci Am Mind* 21: 22–29.

- Kiehl KA, Smith AM, Hare RD et al. (2001). Limbic abnormalities in affective processing by criminal psychopaths as revealed by functional magnetic resonance imaging. *Biol Psychiatry* 50: 677–684.
- Koster-Hale J, Saxe R, Dungan J et al. (2013). Decoding moral judgments from neural representations of intentions. *Proc Natl Acad Sci U S A* 110: 5648–5653.
- Kruh IP, Frick PJ, Clements CB (2005). Historical and personality correlates to the violence patterns of juveniles tried as adults. *Crim Justice Behav* 32: 69–96.
- Lilienfeld SO, Fowler KA (2006). The self-report assessment of psychopathy: problems, pitfalls, and promises. In: *Handbook of psychopathy*, The Guilford Press, pp. 107–132.
- Litt A, Plassmann H, Shiv B et al. (2011). Dissociating valuation and saliency signals during decision-making. *Cereb Cortex* 21: 95–102.
- Lockwood PL, Bird G, Bridge M et al. (2013). Dissecting empathy: high levels of psychopathic and autistic traits are characterized by difficulties in different social information processing domains. *Front Hum Neurosci*.
- Mahmut MK, Homewood J, Stevenson RJ (2008). The characteristics of non-criminals with high psychopathy traits: are they similar to criminal psychopaths? *J Res Pers* 42: 679–692.
- Marsh AA, Finger EC, Fowler KA et al. (2011). Reduced amygdala-orbitofrontal connectivity during moral judgments in youths with disruptive behavior disorders and psychopathic traits. *Psychiatry Res Neuroimaging* 194: 279–286.
- Meier MH, Slutske WS, Arndt S et al. (2008). Impulsive and callous traits are more strongly associated with delinquent behavior in higher risk neighborhoods among boys and girls. *J Abnorm Psychol* 117: 377–385.
- Michl P, Meindl T, Meister F et al. (2014). Neurobiological underpinnings of shame and guilt: a pilot fMRI study. *Soc Cogn Affect Neurosci* 9: 150–157.
- Moll J, de Oliveira-Souza R (2007). Moral judgments, emotions and the utilitarian brain. *Trends Cogn Sci* 11: 319–321.
- Moll J, De Oliveira-Souza R, Bramati IE et al. (2002a). Functional networks in emotional moral and nonmoral social judgments. *NeuroImage* 16: 696–703.
- Moll J, De Oliveira-Souza R, Eslinger PJ et al. (2002b). The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. *J Neurosci* 22: 2730–2736.
- Moll J, De Oliveira-Souza R, Zahn R (2008). The neural basis of moral cognition: sentiments, concepts, and values. *Ann N Y Acad Sci* 1124: 161–180. <https://doi.org/10.1196/annals.1440.005>. PMID: 18400930.
- Müller JL, Sommer M, Wagner V et al. (2003). Abnormalities in emotion processing within cortical and subcortical regions in criminal psychopaths: evidence from a functional magnetic resonance imaging study using pictures with emotional content. *Biol Psychiatry* 54: 152–162.
- Neumann CS, Hare RD, Pardini DA (2015). Antisociality and the construct of psychopathy: data from across the globe. *J Pers* 83: 678–692.
- Osumi T, Shimazaki H, Imai A et al. (2007). Psychopathic traits and cardiovascular responses to emotional stimuli. *Personal Individ Differ* 42: 1391–1402.
- Pardini DA, Fite PJ (2010). Symptoms of conduct disorder, oppositional defiant disorder, attention-deficit/hyperactivity disorder, and callous-unemotional traits as unique predictors of psychosocial maladjustment in boys: advancing an evidence base for DSM-V. *J Am Acad Child Adolesc Psychiatry* 49: 1134–1144.
- Plassmann H, O'Doherty JP, Rangel A (2010). Appetitive and aversive goal values are encoded in the medial orbitofrontal cortex at the time of decision making. *J Neurosci* 30: 10799–10808.
- Pujol J, Batalla I, Contreras-Rodríguez O et al. (2012). Breakdown in the brain network subserving moral judgment in criminal psychopathy. *Soc Cogn Affect Neurosci* 7: 917–923.
- Roberts R, McCrory E, Bird G et al. (2020). Thinking about others' minds: mental state inference in boys with conduct problems and callous-unemotional traits. *J Abnorm Child Psychol*.
- Rowe R, Maughan B, Moran P et al. (2010). The role of callous and unemotional traits in the diagnosis of conduct disorder. *J Child Psychol Psychiatry Allied Discip* 51: 688–695.
- Saver JL, Damasio AR (1991). Preserved access and processing of social knowledge in a patient with acquired sociopathy due to ventromedial frontal damage. *Neuropsychologia* 29: 1241–1249.
- Schultz J, Friston KJ, O'Doherty J et al. (2005). Activation in posterior superior temporal sulcus parallels parameter inducing the percept of animacy. *Neuron* 45: 625–635.
- Seara-Cardoso A, Viding E (2015). Functional neuroscience of psychopathic personality in adults. *J Pers* 83: 723–737.
- Seara-Cardoso A, Neumann C, Roiser J et al. (2012). Investigating associations between empathy, morality and psychopathic personality traits in the general population. *Personal Individ Differ* 52: 67–71.
- Seara-Cardoso A, Dolberg H, Neumann C et al. (2013). Empathy, morality and psychopathic traits in women. *Personal Individ Differ* 55: 328–333.
- Seara-Cardoso A, Viding E, Lickley RA et al. (2015). Neural responses to others' pain vary with psychopathic traits in healthy adult males. *Cogn Affect Behav Neurosci* 15: 578–588.
- Seara-Cardoso A, Sebastian CL, McCrory E et al. (2016a). Anticipation of guilt for everyday moral transgressions: the role of the anterior insula and the influence of interpersonal psychopathic traits. *Sci Rep* 6.
- Seara-Cardoso A, Sebastian CL, Viding E et al. (2016b). Affective resonance in response to others' emotional faces varies with affective ratings and psychopathic traits in amygdala and anterior insula. *Soc Neurosci* 11: 140–152.
- Seara-Cardoso A, Vasconcelos M, Sampaio A et al. (2022). 3—Neural correlates of psychopathy: a comprehensive review. In: PB Marques, M Paulino, L Alho (Eds.), *Psychopathy and criminal behavior*. Academic Press.
- Sebastian CL, McCrory EJP, Cecil CAM et al. (2012). Neural responses to affective and cognitive theory of mind in

- children with conduct problems and varying levels of callous-unemotional traits. *Arch Gen Psychiatry* 69: 814–822.
- Sethi A, McCrory E, Puetz V et al. (2018). Primary and secondary variants of psychopathy in a volunteer sample are associated with different neurocognitive mechanisms. *Biol Psychiat Cogn Neurosci Neuroimag* 3: 1013–1021.
- Sevinc G, Spreng RN (2014). Contextual and perceptual brain processes underlying moral cognition: a quantitative meta-analysis of moral reasoning and moral emotions. *PLoS ONE* 9: e87427.
- Shamay-Tsoory SG, Harari H, Aharon-Peretz J et al. (2010). The role of the orbitofrontal cortex in affective theory of mind deficits in criminal offenders with psychopathic tendencies. *Cortex* 46: 668–677.
- Shenhav A, Greene JD (2014). Integrative moral judgment: dissociating the roles of the amygdala and ventromedial prefrontal cortex. *J Neurosci* 34: 4741–4749.
- Taber-Thomas BC, Asp EW, Koenigs M et al. (2014). Arrested development: early prefrontal lesions impair the maturation of moral judgement. *Brain* 137: 1254–1261.
- Vasconcelos M, Viding E, Sebastian CL et al. (2021). Callous-unemotional traits moderate anticipated guilt and wrongness judgments to everyday moral transgressions in adolescents. *Front Psychiatry* 12.
- Viding E, Kimonis ER (2018). Callous-unemotional traits. In: *Handbook of psychopathy*, The Guilford Press, pp. 144–164.
- Viding E, McCrory E, Seara-Cardoso A (2014). Psychopathy. *Curr Biol* 24: R871–R874.
- Vieira JB, Tavares TP, Marsh AA et al. (2017). Emotion and personal space: neural correlates of approach-avoidance tendencies to different facial expressions as a function of coldhearted psychopathic traits. *Hum Brain Mapp* 38: 1492–1506.
- Vincent GM, Vitacco MJ, Grisso T et al. (2003). Subtypes of adolescent offenders: affective traits and antisocial behavior patterns. *Behav Sci Law* 21: 695–712.
- Wagner U, N'Diaye K, Ethofer T et al. (2011). Guilt-specific processing in the prefrontal cortex. *Cereb Cortex* 21: 2461–2470.
- Wallis JD (2007). Orbitofrontal cortex and its contribution to decision-making. *Annu Rev Neurosci*.
- Winter K, Spengler S, Bermpohl F et al. (2017). Social cognition in aggressive offenders: impaired empathy, but intact theory of mind. *Sci Rep* 7.
- Yoder KJ, Decety J (2018). The neuroscience of morality and social decision-making. *Psychol Crime Law* 24: 279–295.
- Young L, Dungan J (2012). Where in the brain is morality? Everywhere and maybe nowhere. *Soc Neurosci* 7: 1–10.
- Young L, Saxe R (2008). The neural basis of belief encoding and integration in moral judgment. *NeuroImage* 40: 1912–1920.
- Young L, Cushman F, Hauser M et al. (2007). The neural basis of the interaction between theory of mind and moral judgment. *Proc Natl Acad Sci U S A* 104: 8235–8240.
- Young L, Campodon JA, Hauser M et al. (2010). Disruption of the right temporoparietal junction with transcranial magnetic stimulation reduces the role of beliefs in moral judgments. *Proc Natl Acad Sci U S A* 107: 6753–6758.
- Yu H, Hu J, Hu L et al. (2014). The voice of conscience: neural bases of interpersonal guilt and compensation. *Soc Cogn Affect Neurosci* 9: 1150–1158.