Social Neuroscience

ISSN: 1747-0919 (Print) 1747-0927 (Online) Journal homepage: http://www.tandfonline.com/loi/psns20

Common and distinct neural networks involved in fMRI studies investigating morality: An ALE meta-analysis

Robert Eres , Winnifred R. Louis & Pascal Molenberghs

To cite this article: Robert Eres , Winnifred R. Louis & Pascal Molenberghs (2017): Common and distinct neural networks involved in fMRI studies investigating morality: An ALE meta-analysis, Social Neuroscience, DOI: 10.1080/17470919.2017.1357657

To link to this article: http://dx.doi.org/10.1080/17470919.2017.1357657

Accepted author version posted online: 20 Jul 2017.

Common and distinct neural networks involved in fMRI studies investigating morality: An ALE meta-analysis

Robert Eres[1], Winnifred R. Louis[2], Pascal Molenberghs[1*]

[1] School of Psychological Sciences and Monash Institute of Cognitive and Clinical Neurosciences, Monash University, Australia

[2] School of Psychology, The University of Queensland, Australia

*Correspondence should be addressed to pascalmolenberghs@gmail.com

Tel: +61 3 9905 3901
Fax: +61 3 9905 3948
Pascal Molenberghs
School of Psychological Sciences and Monash Institute of Cognitive and Clinical Neurosciences
Monash University
Clayton, VIC 3800
Australia

Number of Figures: 4

Number of Tables: 1

Running head: Common and Distinct Morality Networks

Keywords: activation likelihood estimation (ALE); meta-analysis; morality; moral emotions; moral judgment and decision making

Abstract

Morality is an important social construct necessary for understanding what is right and wrong. Neuroimaging studies investigating morality have used a wide variety of paradigms and implicated many different brain areas. Yet, it remains unclear whether differences amongst morality tasks are the cause for such heterogeneous findings. Therefore, in the present study, a series of activation likelihood estimation (ALE) meta-analyses were conducted on 123 datasets (inclusive of 1963 participants) to address this question. The ALE meta-analyses revealed a series of common brain areas associated with all moral tasks, including medial prefrontal cortex, lateral orbitofrontal cortex, amygdala, temporoparietal junction, and precuneus. However, individual and contrast analyses also revealed unique networks associated with each moral modality, suggesting that different moral tasks recruit specialised brain regions.

Introduction

One of the most common moral tasks, the trolley dilemma, asks people if it is permissible to pull a lever to redirect a trolley that is about to kill five people, even if that action will kill one person laying on the other track. In this situation, participants typically (i.e., 89% of the time) say it is permissible to pull the lever (Hauser et al., 2007) because saving five lives by sacrificing one is the most rational, utilitarian option. However, in an alternative version of the dilemma, the footbridge dilemma, people are asked if it is permissible to push a person off a footbridge to have the same outcome (i.e., stop the trolley to save five people laying on the track but sacrificing one). In this situation, people only rarely (i.e., 11% of the time) think the action is permissible (Hauser et al., 2007). The opposite outcomes of two different versions of the same dilemma (i.e., sacrificing one life to save the life of several others) provide important insights into the complex nature of morality. Morality is not purely rationalising about the best outcome of a situation, rather moral decisions are influenced by a wide variety of factors such as emotions, instructions, role of the perpetrator and victim, and proximity to the target. This suggests that a wide variety of brain regions are involved in moral decision making.

The neuroscience of morality

Indeed, a wide range of brain regions have been associated with morality, which has led some to conclude that morality is everywhere and maybe nowhere in the brain (Young & Dungan, 2012). Here we will provide a brief overview of the brain regions most commonly associated with morality including the ventromedial prefrontal cortex (vmPFC), dorsomedial prefrontal cortex (dmPFC), dorsolateral prefrontal cortex (dlPFC), lateral orbitofrontal cortex (lOFC), amygdala, anterior cingulate cortex (ACC), temporoparietal junction (TPJ) and precuneus. The vmPFC has previously been implicated in moderating emotions during moral decision making (Young & Dungan, 2012), obeying social norms and values (Moll et al., 2002a, 2002b) and integrating intentions of others with the outcomes of moral decisions (Cooper et al., 2010).

The dmPFC, is consistently activated across higher-order social tasks including empathy, theory of mind, and morality (Bzdok et al., 2012*)*. Young and Saxe (2008) have shown that negative beliefs recruit the dmPFC more so than neutral beliefs of an agent, which suggests the dmPFC is involved in decoding belief valence surrounding moral judgments. There is also evidence that the dmPFC is preferentially recruited by those who score higher on other-related moral emotion measures, when performing actions deemed as bad (Yoder & Decety, 2014). The dlPFC plays a role in morality by overriding moral decisions through reasoning (see review by Mendez, 2009), whereas the OFC has been associated with guilt (Molenberghs et al., 2014a, 2015), moral sensitivity (Molenberghs et al. 2014b) and processing emotionally salient information related to moral value (Moll et al., 2002a).

The amygdala has been implicated with intentionally making a moral violation (Berthoz, Grèzes, Armony, Passingham, & Dolan, 2006), viewing images of interpersonal harm (Luo et al., 2006) and sensitivity to basic emotions such as fear and disgust (Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005a). The ACC on the other hand, has been associated with implicit moral attitudes (Luo et al., 2006), utilitarian approaches (Shackman et al., 2011) and is often involved in self-referential tasks (Moll et al., 2005a) and moral conflict monitoring (Greene et al., 2004). Finally, Young and Saxe (2008) have shown that the temporoparietal junction (TPJ) and precuneus respond to the encoding of an agent's mental state which suggests that this encoded information can be used to inform moral judgments regarding the agent (Young and Koenings, 2007). The TPJ has also been associated with retrospectively justifying moral decision making (Kliemann, Young, Scholz,

& Saxe, 2008; Liane Young, Nichols, & Saxe, 2010; Young, Scholz, & Saxe, 2011) and the precuneus with personal moral judgments and difficult moral dilemmas (Greene et al., 2004).

As is clear from this overview, a wide variety of brain regions have been associated with different aspects of morality but there does not seem to be a consensus. A common criticism of individual fMRI studies is that they can produce unreliable findings because of the limited sample size used (e.g., Yarkoni, 2009). Neuroimaging meta-analyses provide a quantitative method to pool individual datasets together to identify consistent and reliable brain activations associated with morality tasks across studies. Thus, the goal of this meta-analysis is to see which brain areas are consistently associated with particular aspects of morality so that we get a better understanding of how each area contributes to morality.

Potential moderating factors

Investigating the variation in brain regions involved in morality is an important step for understanding how morality is interpreted and represented in the brain. Evidence from meta-analyses investigating other higher-order socio-cognitive processes, for example Theory of Mind (ToM), have shown that specific brain regions and networks are associated with specific ToM tasks (Molenberghs, Johnson, Henry, & Mattingley, 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). This suggests that by dividing complex social functions, such as morality, into more specific processes we can get a better understanding of how specific brain regions and networks contribute to what we call morality. For example, Young and Dungan (2012) in their comprehensive review already showed that moral tasks recruit different areas depending on what they labelled, social (here referred to as cognitive mentalising) and emotional (referred to here as affective mentalising) brains. They suggest the former relies more on understanding the intent and beliefs of the agent in any given scenario, and the latter is more concerned with the emotional aspects of moral scenarios. Here we distinguish between four moderating factors: *mentalising method*, *instructional cues*, *role* and *proximity*.

Mentalising method can be subdivided into affective (sharing the emotional experience of the victim or perpetrator) or cognitive (understanding the intent behind a person's actions). Affective mentalising tasks involve, for example, being presented with images of people suffering (e.g., Mercadillo et al., 2011), whereas with the cognitive mentalising method, there may be additional information that highlights the underlying intention (e.g., Young & Saxe, 2009). For example, to save the lives of his family the man shot another man to death.

Instructional cues can be dichotomised into explicit (instructed to focus on the morally salient information of the stimuli) or implicit (instructed to focus on non-morally salient information, e.g. age or gender). For example, when reading statements of morally wrong behaviour, an explicit instructional cue would enquire about the moral nature of the event ("Was this morally wrong?"; see Schaich Borg et al., 2011). An implicit instructional cue would, for example, ask participants to identify the colour of a dot cue superimposed on a moral transgression video ("What was the colour of the dot?"; see Sinke et al., 2010).

Role encompasses both agency and victim, and can also be dichotomised into two levels: the person eliciting the harm or experiencing the harm could be the participant themselves (self), or the agent and potential victim is another person (other). For example, when reading statements where bodily harm is described, "self" conditions would emphasise the participant eliciting or experiencing the harm (e.g., Molenberghs et al., 2014a), whereas "other" conditions would emphasise a third party experiencing or eliciting the harm (e.g., Young & Saxe, 2009).

Proximity refers to the psychological or imagined physical distance between perpetrator and victim. This can be either proximal (the participant is close to the victim, e.g., Molenberghs et al., 2015) or distal (the participant is far removed from the victim, e.g., Parkinson et al., 2015). An example of a proximal scenario would be the footbridge dilemma, where participants have to imagine pushing a large man off the bridge. Conversely, a distal dilemma would be illustrated by the traditional trolley dilemma, where a lever needs to be pulled.

The current study

Previous meta-analyses on morality have focused on whether moral cognition overlaps with other complex social cognition processes (i.e., theory of mind and empathy; Bzdok et al., 2012) and single modality comparisons, (e.g., contextual and perceptual factors; Sevinc et al., 2014; Bryant et al., 2016; Garrigan et al., 2016, as well as first and third person perspectives; Boccia et al., 2016). However, in order to have a more comprehensive understanding of distinct and shared neural circuitry for morality, it is necessary to include several influencing factors. Specifically, the current ALE meta-analysis seeks to further differentiate task types based on the aforementioned categories: instructional cues, mentalising method, role and proximity. To accomplish this, activation likelihood estimation (ALE; Eickhoff et al., 2009) meta-analyses are performed to assess the shared and unique areas associated with different morality tasks. First, brain areas which are consistently engaged in moral tasks were identified by running a meta-analysis across all relevant studies. Subsequently, independent ALE analyses as well as contrast and conjunction analyses are performed to identify distinct and shared networks between the different parameters.

Method

Literature selection and exclusion criteria

Studies included in this meta-analysis were those which investigated moral judgment and decision making processes and/or moral emotions. Studies that did not have a specific morality component were not included. The search terms ‘morality’, ‘harm’, ‘guilt’ ‘moral emotion’ ‘fMRI’, ‘moral decision making’, and their alternative constituents (for example, moral rather than morality) were entered into the Web of Science and Pub Med databases yielding over 900 studies. In addition to this we used previous reviews and meta-analyses on morality to identify further studies. Inclusion criteria for the current investigation included the following:

1. To infer consistency across studies, only functional MRI studies were included
2. Considering the assumptions of ALE meta-analyses, studies were only included if they reported whole brain activation coordinates. This was to ensure that the likelihood of activation under the null hypothesis is equal across the brain (Eickhoff et al., 2009).
3. Studies were only included if coordinates were represented in standardised space, either Montreal Neurological Institute (MNI) coordinates or talairach (TAL) coordinates. If coordinates were localised in TAL, they were converted to MNI space using GingerALE software (Eickhoff et al., 2009).
4. Coordinates were only included if they were the result of a contrast analysis that directly tested morality, either as a whole or the individual constituents identified below.
5. Finally, only studies that used healthy participants were included in the study to help eliminate individual differences in brain activation across clinical populations.

After the exclusion criteria had been applied, a total of 84 separate studies were found to meet criteria (as of January 2016). This corresponded to a total of 123 experiments with

1963 participants and 989 foci (a subset of studies can be seen in Table 1, the full list of studies and MNI coordinates can be seen in supplementary materials). Separate meta-analyses were conducted based on aforementioned moderating factors. *Mentalising method*: the affective component of mentalising method included 473 foci from 48 experiments with 1084 participants, whereas the cognitive component included 433 foci from 35 experiments with 856 participants. *Instructional cues*: explicit instructional cues included 540 foci from 48 experiments with 1256 participants, and implicit instructional cues resulted in 366 foci from 36 experiments with 691 participants. *Role*: when related to the self, 455 foci from 42 experiments with 1007 participants were found, and when related to others, 451 foci from 40 experiments with 920 participants were found. *Proximity*: Proximal tasks yielded 443 foci from 45 experiments with 1086 participants, and distal tasks 463 foci from 38 experiments with 899 participants.

[INSERT TABLE 1 HERE]

Meta-analytic method: activation likelihood estimation (ALE) meta-analysis

To identify the consistent brain regions involved in morality, a series of meta-analyses were conducted using GingerALE 2.3.6 software (Eickhoff et al., 2009). To identify the consistent brain regions involved across all morality tasks, the first analysis involved running an ALE meta-analysis on all activation foci. Following this analysis, individual analyses were conducted on each of the eight individual sets of data associated with the different moderating factors. In these analyses, activation foci are represented as the centre point of a three-dimensional Gaussian probability distribution which encompasses the spatial variation surrounding each coordinate. Where coordinates were reported in Talairach space (TAL), TAL-MNI conversion software, embedded within GingerALE, was used to transform the coordinates to Montreal Neurological Institute (MNI) space. This was completed before the analysis using the Lancaster method as prescribed by Laird and colleagues (2010). Modelled activation (MA) maps were then created by collating the three-dimensional probability distributions for each voxel (Eickhoff et al., 2009) where each of the MA maps includes ALE scores which describe the level of convergence of activations within each of the voxels (Turkeltaub et al., 2012). Following this, the ALE scores are converted to z scores for ease of interpretation and compared against a null distribution. In line with Eickhoff and colleagues (2009) conventions, the global and individual meta-analysis was given a cluster-level inference threshold of $p < .05$ with a cluster-forming method of $p < .001$ to identify an above chance effect of finding convergence with a minimum cluster size automatically determined by the GingerALE software.

Following the individual meta-analyses, conjunction and contrast analyses were conducted to identify the areas consistent within each of the superordinate moderating factors, as well as, the areas unique to each individual component. The conjunction analyses were conducted on mentalising method (affective + cognitive), instructional cues (explicit + implicit), role (self + other) and proximity (proximal + distal). Next, using the conventions dictated by Eickhoff and colleagues (2009), the voxel-wise minimum value for each of the individual MA maps from each dyad were used to create a conjunction image highlighting the shared activation between the two datasets. Simultaneously, contrast images were created by subtracting each of the converged activations from one component away from the other within the same superordinate factor (i.e., affective – cognitive, explicit – implicit, proximal – distal, and self – other). Clusters in the contrast analyses were thresholded at uncorrected $p < 0.05$ with 5000 permutations and a minimum cluster size of $50mm^3$.

Results

Global Meta-Analysis

An ALE meta-analysis of all the foci revealed a series of 6 brain areas consistently associated with morality tasks (see Figure 1 and Supplementary Table 2). Clusters were located in the mPFC (encompassing both vmPFC and dmPFC), left and right TPJ, left amygdala, precuneus, and left lOFC extending into neighbouring anterior insula.

[INSERT FIGURE 1 HERE]

Independent meta-analyses for each component

The meta-analysis conducted on the individual datasets associated with the eight different modalities are presented in Figure 2 and Supplementary Tables 3 to 10.

Mentalising method: 4 clusters were consistently associated with affective mentalising including the vmPFC, dmPFC, left TPJ, and precuneus. Cognitive mentalising was associated with 5 clusters including vmPFC, dmPFC, left and right TPJ and precuneus.

Instructional cues: Explicit instructions were associated with 5 clusters including dmPFC extending into the vmPFC, left and right TPJ, precuneus and left lOFC extending into neighbouring anterior insula. Implicit instructions were associated with 3 clusters including dmPFC, left TPJ and precuneus.

Role: Self was associated with 5 clusters including 2 areas in dmPFC, left TPJ, precuneus and left lOFC extending into neighbouring anterior insula. Other was associated with 4 clusters including dmPFC extending into vmPFC, left and right TPJ and precuneus.

Proximity: Proximal distance was associated with 4 clusters including dmPFC, left TPJ, precuneus, and left lOFC extending into neighbouring anterior insula. Distal distance was also associated with 4 clusters including dmPFC extending into vmPFC, left and right TPJ, and precuneus.

[INSERT FIGURE 2 HERE]

Conjunction and contrast analyses

A series of conjunction (Figure 3, Supplementary Tables 11 - 14) and contrast (Figure 4, Supplementary Tables 15 - 18) analyses were conducted for each dyad pairing: mentalising method, instructional cues, role and proximity.

Mentalising method

The conjunction analysis between affective and cognitive mentalising method revealed consistent activations in 4 clusters including vmPFC, dmPFC, left TPJ and precunues. The affective minus cognitive contrast analysis revealed one cluster in the left TPJ. The reverse contrast revealed 6 clusters including vmPFC, dmPFC, left and right TPJ, precuneus and left lOFC extending into neighbouring anterior insula.

Instructional cues

The conjunction analysis between explicit and implicit revealed consistent activations in 3 clusters including dmPFC, left TPJ and precuneus. The explicit minus implicit contrast revealed 9 clusters including vmPFC, 2 clusters in dmPFC, left and right TPJ, 2 clusters in the precuneus and 2 clusters in left lOFC. The reverse contrast revealed one cluster in anterior dmPFC.

Role

The conjunction analysis between Self and Other revealed consistent activations in 4 clusters including two clusters in dmPFC, left TPJ and precuneus. The Self minus Other contrast revealed 2 clusters including left TPJ and left lOFC extending into anterior insula.

The reverse contrast revealed 6 clusters including vmPFC, dmPFC, left and right TPJ, precuneus and left lOFC.

Proximity

The conjunction analysis between Proximal and Distal revealed consistent activations in 3 clusters including the dmPFC, left TPJ and precuneus. The Proximal minus Distal contrast revealed one cluster in left lOFC. The reverse contrast revealed 4 clusters including vmPFC, 2 clusters in dmPFC and left TPJ.

[INSERT FIGURE 3 HERE]
[INSERT FIGURE 4 HERE]

Discussion

Previous meta-analyses in social cognition have focused primarily on theory of mind (Schurz, et al., 2014; Molenberghs et al., 2016), empathy (Fan et al., 2011), or on social cognition more broadly (van Overwalle et al, 2009; Bzdok et al., 2012). Recently, several meta-analysis on moral cognition have been conducted using single modality comparisons (Sevinc et al., 2014; Boccia et al., 2016; Bryant et al., 2016; Garrigan et al., 2016). In our investigation, we sought to delve deeper into moral cognition and compare different task modalities that may influence how moral decisions are made. As such the current investigation is both relevant and novel for three reasons. First, we included more studies than previous meta-analyses (84 compared to 67, the next highest). Second, for the first time, we analysed data by several task modalities (i.e., mentalising method: affective vs cognitive, instructional cue: explicit vs implicit, role: self vs other, and proximity: proximal vs distal) which provided novel insights into the neuroscience of moral cognition. Finally, for the first time, we conducted contrast analyses between each of these modalities within the same study to illustrate distinct neural networks associated with specific processes involved in morality.

Global Morality Network

Our first aim was to identify the most consistent brain regions involved in morality by conducting an ALE meta-analysis across all studies. Similar to Bzdok et al. (2012) we showed consistent activation in a range of brain regions often implicated in higher order cognitive processing. Specifically, we found consistent activation in the vmPFC, dmPFC, TPJ, precuneus, and left amygdala. Unlike Bzdok and colleagues, we did not find activation in temporal regions, we did, however, find activation in the left lOFC.

Previous research has shown that the mPFC plays a pivotal role in social cognition (ToM; Amodio & Frith, 2006). However, the role of mPFC activity varies according to its anatomical location. For example, the dorsal components have been implicated in inferring the mental states of others (van Overwalle, 2009; Denny et al., 2012), whereas the ventral components are more involved in emotional processing (Saxe, 2006). The role of mPFC in moral neuroscience is to form enduring social and interpersonal scripts that involve the capacity to recollect (in)appropriate behaviours across contexts, to identify the goal of these behaviours, and to link these behaviours with the agents completed or proposed actions (van Overwalle, 2009). In relation to morality, the vmPFC is often involved when moral decisions need to be moderated by emotions (Young and Dungan, 2012).

The lOFC is consistently associated with processing displeasure (Berridge & Kringelbach, 2013), which may lead to a change in ongoing behaviour (Kringelbach and Rolls, 2004). Precuneus activity on the other hand, often coincides with introspection, and is thought to play an important role in successful autobiographical memory retrieval in relation to one's current emotional state (Cavanna & Trimble, 2006; Maddock, Garrett, & Buonocore, 2001). Quantitative reviews of connectivity studies have shown that the precuneus has increased connections with other default network regions (including mPFC and TPJ) during higher-order social cognition tasks including emotion perception, empathy, and ToM (Li et al., 2014). Therefore, the role of the precuneus in morality may be to integrate memories of previous experiences with one's current emotional state to determine the best decision making process.

Activation of the TPJ has been linked with orienting attention to salient information, encoding agency, and applying temporary states onto others (van Overwalle et al., 2009). Additionally, the TPJ has also been linked with higher-order functions including ToM and empathy (Decety & Lamm, 2007; Decety, 2011). TPJ activity occurs consistently when reasoning about the thoughts, intentions, and beliefs of others as well as when differentiating the self from others. This suggests that the role of the TPJ in moral judgment and decision making is to discern whether a behavioural outcome is appropriate based on the agent's mental state. This view is supported by previous research linking TPJ activity with retrospective justifications of behaviours and mentalising capabilities (Kliemann, et al., 2008; Young et al, 2010; Young et al., 2011).

The last structure implicated in the global analysis was the amygdala. Previous research on amygdala function has extensively shown links with emotion processing, emotional learning, emotional memory formation and retrieval, and a moderating role in attention and perception (Phelps, 2006; Sergerie et al., 2008). The role of the amygdala in moral judgment and decision making may be to act as a functional hub for disseminating bottom-up emotional information to top-down processes. This view is supported by connectivity studies showing strong functional and structural connections between the amygdala and mPFC (Kim et al., 2011).

Individual meta-analyses

The dmPFC, left TPJ, and precuneus were consistently activated across all of the individual meta-analyses, suggesting that to some extent each of the modalities relied on similar functions. Furthermore, activation of the vmPFC was specifically implicated in tasks involving affective and cognitive mentalising, explicit instructions, other as agent and distal proximity, whereas lOFC activation was shown specifically for explicit instructions, self as agent, and proximal distance. Right TPJ activation was specifically shown for cognitive mentalising, explicit instructions, other as agent, and distal proximity.

Mentalising Method

The combination of affective and cognitive mentalising revealed consistent activation in vmPFC, dmPFC, left TPJ and precuneus. However, there were also distinct networks associated with each mentalising method. Affective mentalising was more associated with activation in left TPJ. Here the left TPJ activation overlaps with the angular gyrus. In a recent meta-analysis, Kohn and colleagues (2014) showed that the angular gyrus is involved in executing emotion regulation processes and that it maintains functional connectivity with executive areas in the frontal cortex. Therefore, the role of the left TPJ in affective morality may be to regulate emotional responses to ensure appropriate moral judgment and decision making.

The vmPFC, dmPFC, left and right TPJ, precuneus and lOFC were more consistently associated with cognitive mentalising. The mPFC, left and right TPJ and precuneus are often involved during behaviours that enable inferences to be made about the goals, beliefs, or moral issues presented in abstract terms (Van Overwalle & Baetens, 2009). This suggests that the mentalising network underlying ToM may also underlie the cognitive mentalising modality in morality tasks, particularly when trying to reason about how the internal states of self and others lead to moral or immoral behaviours. Whereas TPJ activity for affective morality overlapped with subdivisions of the angular gyrus, in cognitive morality tasks TPJ activity overlapped with the supramarginal gyrus. Carter and Huettel (2013) suggest that the supramarginal gyrus is involved in shifting attention across salient information. As such, the activation of TPJ in cognitive tasks may be to shift attention between salient dilemmas and mental state reasoning as a way of externally extracting oneself from internally driven processes. Finally, the lateral OFC is often involved when context has to be taken into account when evaluating moral situations (Zahn et al., 2011). For example, lOFC is not activated by watching accidental harm but rather becomes active when watching intentional harm inflicted onto others (Decety & Cacioppo, 2012; Decety et al., 2012). Therefore, it is unsurprising that this region was more active during cognitive tasks.

Instructional Cues

Convergent evidence for explicit and implicit instructional cues was found in dmPFC, left TPJ and precuneus. There was also evidence for distinct regions associated with each of the instructional cue modalities. Explicit (compared with implicit) task instructions consistently employed vmPFC, dmPFC, bilateral TPJ, left lOFC and the precuneus. The engagement of this mentalising network is expected given that explicit moral tasks require an active evaluation of a moral transgression. This process relies heavily on our ability to reason about the motives, beliefs and desires of ourselves and others. Moreover, the lOFC has previously been associated with moral sensitivity (Molenberghs et al., 2014b). Since, the nature of explicit moral tasks is to identify and make decisions about a salient moral dilemma, it is unsurprising that left lOFC was observed for explicit moral tasks.

Tasks that required implicitly focusing on stimulus qualities unrelated to the moral content recruited the anterior dmPFC. The anterior dmPFC is often involved when performing a main goal while at the same time the participant is focused on other goals

(Koechlin et al., 1999; Koechlin & Hyafil, 2007). Often in morally salient situations, when an action is made, regardless of attention being oriented to this directly, we make backward inferences to identify the intention of the agent (Kliemann, Young, Scholz, & Saxe, 2008; Leslie, Knobe, & Kohen, 2006; Knobe, 2005). Implicit moral tasks frequently involve unknowingly processing information about a person's mental state in absence of any explicit mental state information. The activation of the anterior dmPFC in the implicit moral conditions may therefore represent a spontaneous moral inference, while at the same time the participant is focussed on the main non-moral task. This has been shown previously by Young and Saxe (2009) who reported similar findings when studying implicit morality tasks.

Proximity

The dmPFC, left TPJ and precuneus were consistently activated across both proximal and distal modalities. More consistent activation of the lOFC was found for proximal compared to distal moral tasks. The lOFC, has previously been implicated in processing moral sensitivity (Molenberghs et al., 2014b), guilt (Molenberghs et al., 2014a; Molenberghs et al., 2015; Eres et al., 2016) and displeasure in general (Berridge & Kringelbach, 2013; Dominguez et al., 2016). Activation in this area often leads to a change in ongoing behaviour (Kringelbach and Rolls, 2004). In tasks where participants play a more direct role in eliciting harm (e.g., footbridge dilemma), the activation in this region may be due to increased moral sensitivity and guilt. When located proximally to a moral dilemma we may prioritise activation in areas of the brain associated with displeasure to ensure that we do not repeat these behaviours in the future.

More consistent activation of the vmPFC, dmPFC and left TPJ were shown to be associated with tasks that employed a greater psychological and/or physical distance between the agent and harm doing (e.g., trolley task). It may be the case that when presented with a moral dilemma that we have some psychological distance from, we inherently rely on this mentalising network to overcome the distance between ourselves and others. This is supported by Tamir and Mitchell (2011) who implicate the dmPFC when completing a distal task relating to social interactions.

Role

Common activation in dmPFC, left TPJ and precuneus was found for self and other moral judgments. Contrast analyses revealed more consistent activation in left lOFC for moral tasks that involved the self. Whether we elicit harm ourselves, or when we ourselves are being harmed, directly involves a violation of wellbeing. As mentioned previously, the lOFC has been implicated in processing guilt, moral sensitivity and displeasure in general. Therefore, similar to proximal tasks, the increased role of lOFC in self related moral tasks may be to increase feelings of guilt when responsible ourselves for harming others or increased displeasure or moral sensitivity when we ourselves are the victim of an immoral act.

Tasks that involved others uniquely activated mPFC, bilateral TPJ and precuneus. Previous work in social cognition has consistently shown that these regions are involved in attributing mental states onto others (Harada et al., 2009; Molenberghs et al., 2016; Moor et al., 2012; Schurz et al, 2014; Young et al., 2010; Young & Dungan, 2012; Young & Saxe, 2009). Thus, it is unsurprising that when deliberating on moral judgments and decisions concerning others, regions underlying self-other distinctions are employed.

Limitations

Though there are clear benefits of using a pooled data approach, there are also limitations that need to be addressed. Probably the most evident criticism of the pooled approach is the potential for increased variability introduced through different conceptualisations of the same task. We have expressed throughout this paper that there are different tasks used to measure morality, however, within each of these tasks comes a different definition and explanation of this complex social construct. This variance in methodologies could potentially make it difficult to identify a clear set of neural regions involved in morality. Indeed, pooling across tasks can be problematic in identifying nuances between the different breakdowns of task types. Theoretically, though, it is possible for these differences to be abolished when collapsing across the different tasks, allowing for a series of consistent regions to be identified. Considering this variability and previous meta-analyses on complex social processes (see for example Molenberghs et al., 2016), we identified discrete moral tasks and analysed these separately. This allows us to identify any nuances that may have been obscured by the potential method variance problem but does so at the cost of reduced statistical power; a direct result of reducing the number of studies being examined. Perhaps, then, it is this loss of statistical power that may explain why certain regions (for example the amygdala) were consistent in the global analysis but was not consistently shown across all individual meta-analyses.

A second criticism surrounds how we categorised each task. In the current investigation, affective tasks were associated with emotionally salient information (the expression of guilt, shame, anger, etc.) whereas cognitive tasks required the addition of a reasoning component of the task (e.g., reasoning whether an action was appropriate or inappropriate). Thus, to be categorised as an affective task it needed to be isolated from any form of reasoning. Conversely, the cognitive tasks did not need to be isolated from the affective counterpart. To some degree, then, each moral task has an affective component. As such, the lack of engagement from the expected emotion regions (e.g., insula, amygdala, vmPFC) in the affective tasks may represent comparatively less engagement of these areas rather than the absence of these areas completely. This is evidenced by the individual meta-analysis of affective modality which showed activation patterns in vmPFC and insula.

Finally, in the social neuroscience literature, agency refers to a person, either the self or another person, who elicits harm towards an external agent. We included an additional component in the categorisation of *role* by including studies where the person being harmed was identified as either the self or other. Thus, the findings may reflect more of a self-other distinction rather than an effect of agency. Though these factors are important distinctions to make, we decided to collapse across these categories to ensure that there was enough studies included for this analysis. Eickhoff and colleagues (2016) suggest that to have sufficient power to make inferential claims, each condition should include at least 30 experiments. Including the typical definition of agency would not result in sufficient studies to make this threshold.

Conclusions

The current ALE meta-analysis highlights a distributed network of brain regions associated with the complex social construct of morality. Young and Dungan (2012) reviewed an array of moral neuroscience studies and concluded that morality is a widespread construct that relies on several neural networks. The findings from our study support their claims that morality is implicated in a diverse range of brain areas, including the mPFC (including sections of the vmPFC and dmPFC), left and right TPJ, precuneus, amygdala and lOFC extending into the anterior insula. Extending on previous literature, the current ALE meta-analysis revealed shared and distinct neural networks between modality dyads. These unique contributions to the moral network suggest that the heterogeneous findings across morality studies may be due to the different types of modalities being implicated in the individual paradigms.

Acknowledgements

This work was funded by an ARC Discovery Early Career Research Award (DE130100120), Heart Foundation Future Leader Fellowship (100458), and an ARC Discovery Grant

(DP130100559) awarded to Pascal Molenberghs and an Australian Postgraduate Award awarded to Robert Eres. We gratefully acknowledge the research interns who assisted with finding and sorting relevant papers.

References

Berridge, K. C., & Kringelbach, M. L. (2013). Neuroscience of affect: brain mechanisms of pleasure and displeasure. Curr Opin Neurobiol, 23(3), 294-303. doi: 10.1016/j.conb.2013.01.017

Berthoz, S., Grèzes, J., Armony, J. L., Passingham, R. E., & Dolan, R. J. (2006). Affective response to one's own moral violations. *Neuroimage, 31*(2), 945-950. doi: http://dx.doi.org/10.1016/j.neuroimage.2005.12.039

Boccia, M., Dacquino, C., Piccardi, L., Cordellieri, P., Guariglia, C., Ferlazzo, F., . . . Giannini, A. M. (2016). Neural foundation of human moral reasoning: an ALE meta-analysis about the role of personal perspective. *Brain Imaging and Behavior*, 1-15. doi: 10.1007/s11682-016-9505-x

Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., & Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure and Function, 217*(4), 783-796. doi: 10.1007/s00429-012-0380-y

Cáceda, R., James, G. A., Ely, T. D., Snarey, J., & Kilts, C. D. (2011). Mode of effective connectivity within a putative neural network differentiates moral cognitions related to care and justice ethics. PLoS One, 6(2), e14730. doi: 10.1371/journal.pone.0014730

Carter, R. M., & Huettel, S. A. (2013). A nexus model of the temporal–parietal junction. *Trends Cogn Sci, 17*(7), 328-336. doi: http://dx.doi.org/10.1016/j.tics.2013.05.007

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain, 129*, 564-583. doi: 10.1093/brain/awl004

Cikara, M., Farnsworth, R. A., Harris, L. T., & Fiske, S. T. (2010). On the wrong side of the trolley track: neural correlates of relative social valuation. Social cognitive and affective neuroscience. doi: 10.1093/scan/nsq011

Cooper, J. C., Kreps, T. A., Wiebe, T., Pirkl, T., & Knutson, B. (2010). When giving is good: ventromedial prefrontal cortex activation for others' intentions. *Neuron, 67*(3), 511-521. doi: 10.1016/j.neuron.2010.06.030

Cushman, F., Murray, D., Gordon-McKeon, S., Wharton, S., & Greene, J. D. (2012). Judgment before principle: engagement of the frontoparietal control network in condemning harms of omission. Soc Cogn Affect Neurosci, 7(8), 888-895. doi: 10.1093/scan/nsr072

Decety, J., Cacioppo, S. (2012). The speed of morality: a high-density electrical neuroimagingstudy. Journal of Neuro*physiology*, 108, 3068–72.

Decety, J., Michalska, K.J., Kinzler, K.D. (2012). The contribution of emotion and cognition to moral sensitivity: a neurodevelopmental study. *Cerebral Cortex*, 22, 209–20.

Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012). A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience, 24*(8), 1742-1752. doi: 10.1162/jocn_a_00233

Dominguez, J. F., Taing, S. A. & Molenberghs, P. (2016). Why do some find it hard to disagree? An fMRI study. *Frontiers in Human Neuroscience, 9*, 718. doi: 10.3389/fnhum.2015.00718.

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-Based Activation Likelihood Estimation Meta-Analysis of Neuroimaging Data: A Random-Effects Approach Based on Empirical Estimates of Spatial Uncertainty. *Human Brain Mapping, 30*(9), 2907-2926. doi: 10.1002/hbm.20718

Eickhoff, S. B., Nichols, T. E., Laird, A. R., Hoffstaedter, F., Amunts, K., Fox, P. T., . . . Eickhoff, C. R. (2016). Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *Neuroimage, 137*, 70-85. doi: http://dx.doi.org/10.1016/j.neuroimage.2016.04.072

Eres, R., Louis, W. R., & Molenberghs, P. (2016). Why do people pirate? A neuroimaging investigation. *Social Neuroscience*, 1-13. doi: 10.1080/17470919.2016.1179671

Fourie, M. M., Thomas, K. G., Amodio, D. M., Warton, C. M., & Meintjes, E. M. (2014). Neural correlates of experienced moral emotion: an fMRI investigation of emotion in response to prejudice feedback. Soc Neurosci, 9(2), 203-218. doi: 10.1080/17470919.2013.878750

Garrigan, B., Adlam, A. L., & Langdon, P. E. (2016). The neural correlates of moral decision-making: A systematic review and meta-analysis of moral evaluations and response decision judgements. Brain and Cognition, 108, 88-97

Greene, J., & Haidt, J. (2002). How (and where) does moral judgment work? *Trends Cogn Sci, 6*(12), 517-523.

Greene, J. D., Morelli, S. A., Lowenberg, K., Nystrom, L. E., & Cohen, J. D. (2008). Cognitive Load Selectively Interferes with Utilitarian Moral Judgment. *Cognition, 107*(3), 1144-1154. doi: 10.1016/j.cognition.2007.11.004

Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M., & Cohen, J. D. (2001). An fMRI Investigation of Emotional Engagement in Moral Judgment. *Science, 293*(5537), 2105-2108. doi: 10.1126/science.1062872

Harada, T., Itakura, S., Xu, F., Lee, K., Nakashita, S., Saito, D. N., & Sadato, N. (2009). Neural correlates of the judgment of lying: A functional magnetic resonance imaging study. *Neurosci Res, 63*(1), 24-34. doi: 10.1016/j.neures.2008.09.010

Harenski, C. L., & Hamann, S. (2006). Neural correlates of regulating negative emotions related to moral violations. Neuroimage, 30(1), 313-324. doi: 10.1016/j.neuroimage.2005.09.034

Hauser, M., Cushman, F., Young, L., Kang-Xing Jin, R., & Mikhail, J. (2007). A Dissociation Between Moral Judgments and Justifications. *Mind & Language, 22*(1), 1-21. doi: 10.1111/j.1468-0017.2006.00297.x

Heekeren, H. R., Wartenburger, I., Schmidt, H., Prehn, K., Schwintowski, H. P., & Villringer, A. (2005). Influence of bodily harm on neural correlates of semantic and moral decision-making. Neuroimage, 24(3), 887-897. doi: 10.1016/j.neuroimage.2004.09.026

Hutcherson, C. A., Montaser-Kouhsari, L., Woodward, J., & Rangel, A. (2015). Emotional and Utilitarian Appraisals of Moral Dilemmas Are Encoded in Separate Areas and Integrated in Ventromedial Prefrontal Cortex. J Neurosci, 35(36), 12593-12605. doi: 10.1523/jneurosci.3402-14.2015

Immordino-Yang, M. H., McColl, A., Damasio, H., & Damasio, A. (2009). Neural correlates of admiration and compassion. Proceedings of the National Academy of Sciences, 106(19), 8021-8026. doi: 10.1073/pnas.0810363106

Kédia, G., Berthoz, S., Wessa, M., Hilton, D., & Martinot, J. L. (2008). An agent harms a victim: a functional magnetic resonance imaging study on specific moral emotions. J Cogn Neurosci, 20(10), 1788-1798. doi: 10.1162/jocn.2008.20070

Kim, M. J., Loucks, R. A., Palmer, A. L., Brown, A. C., Solomon, K. M., Marchante, A. N., & Whalen, P. J. (2011). The structural and functional connectivity of the amygdala: From normal emotion to pathological anxiety. Behav Brain Res, 223(2), 403-410. doi: 10.1016/j.bbr.2011.04.025

Kliemann, D., Young, L., Scholz, J., & Saxe, R. (2008). The influence of prior record on moral judgment. *Neuropsychologia, 46*(12), 2949-2957. doi: 10.1016/j.neuropsychologia.2008.06.010

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature*, 399(6732), 148-151.

Koechlin, E., & Hyafil, A. (2007). Anterior prefrontal function and the limits of human decision-making. *Science*, 318(5850), 594-598.

Koenigs, M., Young, L., Adolphs, R., Tranel, D., Cushman, F., Hauser, M., & Damasio, A. (2007). Damage to the prefrontal cortex increases utilitarian moral judgements. *Nature, 446*(7138), 908-911. doi: 10.1038/nature05631

Kohn, N., Eickhoff, S. B., Scheller, M., Laird, A. R., Fox, P. T., & Habel, U. (2014). Neural network of cognitive emotion regulation — An ALE meta-analysis and MACM analysis. *Neuroimage, 87*, 345-355. doi: http://dx.doi.org/10.1016/j.neuroimage.2013.11.001

Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Prog Neurobiol, 72*(5), 341-372. doi: 10.1016/j.pneurobio.2004.03.006

Li, W., Mai, X., & Liu, C. (2014). The default mode network and social understanding of others: what do brain connectivity studies tell us. *Front Hum Neurosci, 8*, 74. doi: 10.3389/fnhum.2014.00074

Luo, Q., Nakic, M., Wheatley, T., Richell, R., Martin, A., & Blair, R. J. (2006). The neural basis of implicit moral attitude--an IAT study using event-related fMRI. *Neuroimage, 30*(4), 1449-1457. doi: 10.1016/j.neuroimage.2005.11.005

Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2001). Remembering familiar people: the posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience, 104*(3), 667-676.

Mendez, M. F. (2009). The Neurobiology of Moral Behavior: Review and Neuropsychiatric Implications. *CNS spectrums, 14*(11), 608-620.

Mercadillo, R. E., Diaz, J. L., Pasaye, E. H., & Barrios, F. A. (2011). Perception of suffering and compassion experience: brain gender disparities. Brain Cogn, 76(1), 5-14. doi: 10.1016/j.bandc.2011.03.019

Michl, P., Meindl, T., Meister, F., Born, C., Engel, R. R., Reiser, M., & Hennig-Fast, K. (2012). Neurobiological underpinnings of shame and guilt: a pilot fMRI study. Social Cognitive and Affective Neuroscience. doi: 10.1093/scan/nss114

Moll, J., de Oliveira-Souza, R., Bramati, I. E., & Grafman, J. (2002a). Functional networks in emotional moral and nonmoral social judgments. *Neuroimage, 16*, 696-703.

Moll, J., de Oliveira-Souza, R., Eslinger, P. J., Bramati, I. E., Mourao-Miranda, J., Andreiuolo, P. A., & Pessoa, L. (2002b). The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. *J Neurosci, 22*(7), 2730-2736. doi: 20026214

Moll, J., Zahn, R., de Oliveira-Souza, R., Krueger, F., & Grafman, J. (2005a). Opinion: the neural basis of human moral cognition. *Nat Rev Neurosci, 6*(10), 799-809. doi: 10.1038/nrn1768

Moll, J., de Oliveira-Souza, R., Moll, F. T., Ignacio, F. A., Bramati, I. E., Caparelli-Daquer, E. M., & Eslinger, P. J. (2005b). The moral affiliations of disgust: a functional MRI study. Cogn Behav Neurol, 18(1), 68-78.

Molenberghs, P., Bosworth, R., Nott, Z., Louis, W. R., Smith, J. R., Amiot, C. E., . . . Decety, J. (2014a). The influence of group membership and individual differences in psychopathy and perspective taking on neural responses when punishing and rewarding others. Human Brain Mapp*ing, 35*(10), 4989-4999. doi: 10.1002/hbm.22527

Molenberghs, P., Gapp, J., Wang, B., Louis, W. R., & Decety, J. (2014b). Increased Moral Sensitivity for Outgroup Perpetrators Harming Ingroup Members. *Cereb Cortex*. doi: 10.1093/cercor/bhu195

Molenberghs, P., Johnson, H., Henry, J. D., & Mattingley, J. B. (2016). Understanding the minds of others: A neuroimaging meta-analysis. *Neurosci Biobehav Rev, 65*, 276-291. doi: 10.1016/j.neubiorev.2016.03.020

Molenberghs, P., Ogilvie, C., Louis, W. R., Decety, J., Bagnall, J., & Bain, P. G. (2015). The neural correlates of justified and unjustified killing: an fMRI study. *Soc Cogn Affect Neurosci*. doi: 10.1093/scan/nsv027

Parkinson, C., Sinnott-Armstrong, W., Koralus, P. E., Mendelovici, A., McGeer, V., & Wheatley, T. (2011). Is morality unified? Evidence that distinct neural systems underlie moral judgments of harm, dishonesty, and disgust. J Cogn Neurosci, 23(10), 3162-3180. doi: 10.1162/jocn_a_00017

Phelps, E. A. (2006). Emotion and cognition: insights from studies of the human amygdala. *Annu Rev Psychol, 57*, 27-53. doi: 10.1146/annurev.psych.56.091103.070234

Robertson, D., Snarey, J., Ousley, O., Harenski, K., DuBois Bowman, F., Gilkey, R., & Kilts, C. (2007). The neural processing of moral sensitivity to issues of justice and care. Neuropsychologia, 45(4), 755-766. doi: 10.1016/j.neuropsychologia.2006.08.014

Schaich Borg, J., Sinnott-Armstrong, W., Calhoun, V. D., & Kiehl, K. A. (2011). Neural basis of moral verdict and moral deliberation. Soc Neurosci, 6(4), 398-413. doi: 10.1080/17470919.2011.559363

Schleim, S., Spranger, T. M., Erk, S., & Walter, H. (2010). From moral to legal judgment: the influence of normative context in lawyers and other academics. Social Cognitive and Affective Neuroscience. doi: 10.1093/scan/nsq010

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience & Biobehavioral Reviews, 42*, 9-34. doi: http://dx.doi.org/10.1016/j.neubiorev.2014.01.009

Sergerie, K., Chochol, C., & Armony, J. L. (2008). The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews, 32*(4), 811-830. doi: 10.1016/j.neubiorev.2007.12.002

Sevinc, G., & Spreng, R. N. (2014). Contextual and Perceptual Brain Processes Underlying Moral Cognition: A Quantitative Meta-Analysis of Moral Reasoning and Moral Emotions. *PLoS One, 9*(2), e87427. doi: 10.1371/journal.pone.0087427

Shackman, A. J., Salomons, T. V., Slagter, H. A., Fox, A. S., Winter, J. J., & Davidson, R. J. (2011). The integration of negative affect, pain and cognitive control in the cingulate cortex. *Nature Reviews Neuroscience, 12*(3), 154-167. doi: 10.1038/nrn2994

Shenhav, A., & Greene, J. D. (2014). Integrative moral judgment: dissociating the roles of the amygdala and ventromedial prefrontal cortex. The Journal of Neuroscience, 34(13), 4741-4749. doi: 10.1523/jneurosci.3390-13.2014

Sinke, C. B., Sorger, B., Goebel, R., & de Gelder, B. (2010). Tease or threat? Judging social interactions from bodily expressions. Neuroimage, 49(2), 1717-1727. doi: 10.1016/j.neuroimage.2009.09.065

Smith, L. J., Anand, P., Benattayallah, A., & Hodgson, T. L. (2015). An fMRI investigation of moral cognition in healthcare decision making. Journal of Neuroscience, Psychology, and Economics, 8(2), 116-133. doi: 10.1037/npe0000038

Takahashi, H., Yahata, N., Koeda, M., Matsuda, T., Asai, K., & Okubo, Y. (2004). Brain activation associated with evaluative processes of guilt and embarrassment: an fMRI study. Neuroimage, 23. doi: 10.1016/j.neuroimage.2004.07.054

Tamir, D. I., & Mitchell, J. P. (2011). The Default Network Distinguishes Construals of Proximal versus Distal Events. J Cogn Neurosci, 23(10), 2945-2955. doi: 10.1162/jocn_a_00009

Van Overwalle, F. (2009). Social Cognition and the Brain: A Meta-Analysis. *Human Brain Mapping, 30*(3), 829-858. doi: 10.1002/hbm.20547

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *Neuroimage, 48*(3), 564-584. doi: http://dx.doi.org/10.1016/j.neuroimage.2009.06.009

Verdejo-Garcia, A., Contreras-Rodriguez, O., Fonseca, F., Cuenca, A., Soriano-Mas, C., Rodriguez, J., ... de la Torre, R. (2014). Functional alteration in frontolimbic systems relevant to moral judgment in cocaine-dependent subjects. Addict Biol, 19(2), 272-281. doi: 10.1111/j.1369-1600.2012.00472.x

Yarkoni, T. (2009). Big correlations in little studies: Inflated fMRI correlations reflect low statistical power—Commentary on Vul et al.(2009). *Perspectives on Psychological Science*, *4*(3), 294-298.

Young, L., & Dungan, J. (2012). Where in the brain is morality? Everywhere and maybe nowhere. *Soc Neurosci, 7*(1), 1-10. doi: 10.1080/17470919.2011.569146

Young, L., & Koenigs, M. (2007). Investigating emotion in moral cognition: a review of evidence from functional neuroimaging and neuropsychology. *Br Med Bull, 84*, 69-79. doi: 10.1093/bmb/ldm031

Young, L., Nichols, S., & Saxe, R. (2010). Investigating the Neural and Cognitive Basis of Moral Luck: It's Not What You Do but What You Know. *Review of Philosophy and Psychology, 1*(3), 333-349. doi: 10.1007/s13164-010-0027-y

Young, L., & Saxe, R. (2008). The neural basis of belief encoding and integration in moral judgment. *Neuroimage, 40*(4), 1912-1920. doi: 10.1016/j.neuroimage.2008.01.057

Young, L., & Saxe, R. (2009). An fMRI investigation of spontaneous mental state inference for moral judgment. *Journal of Cognitive Neuroscience*, 21(7), 1396-1405. doi: 10.1162/jocn.2009.21137

Young, L., Scholz, J., & Saxe, R. (2011). Neural evidence for "intuitive prosecution": the use of mental state information for negative moral verdicts. *Soc Neurosci, 6*(3), 302-315. doi: 10.1080/17470919.2010.529712

Zahn, R., de Oliveira-Souza, R., Moll, J. (2011). *The neuroscience of moral cognition and emotion.* In: Decety, J., Cacioppo, J.T., editors. The Oxford Handbook of Social Neurosciene. Oxford: University Press, pp. 477–90.

Figure 1. Global result of the meta-analysis displayed on coronal, axial and sagittal slices and a rendered (shell) image using MRIcroGL.

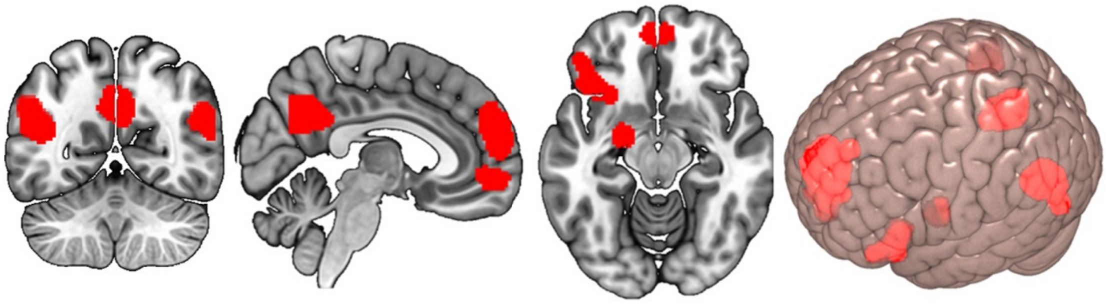

Figure 2. Individual meta-analyses for each of the eight modalities. Significant clusters are displayed on coronal, axial and sagittal slices and a rendered (shell) image using MRIcroGL.

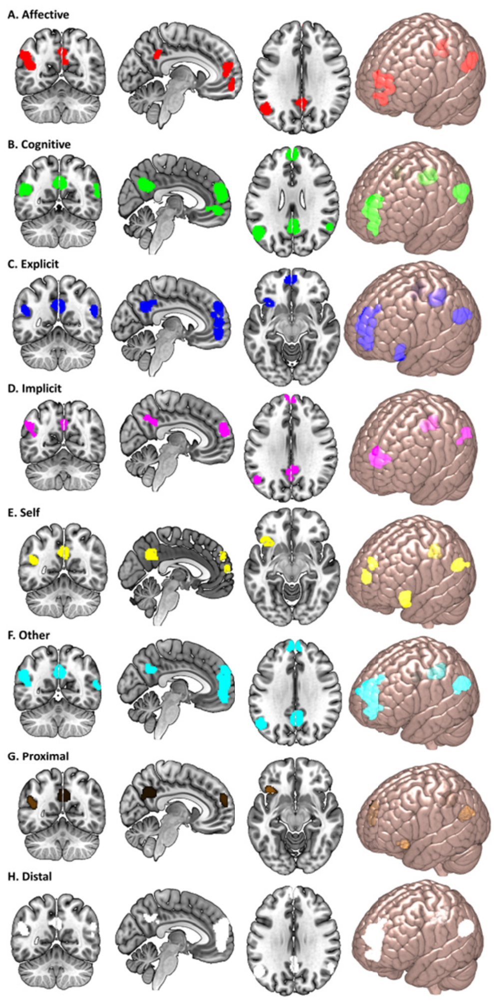

Figure 3. Conjunction meta-analyses for each of the four broad domains. Significant clusters are displayed on coronal, axial and sagittal slices and a rendered (shell) image using MRIcroGL.

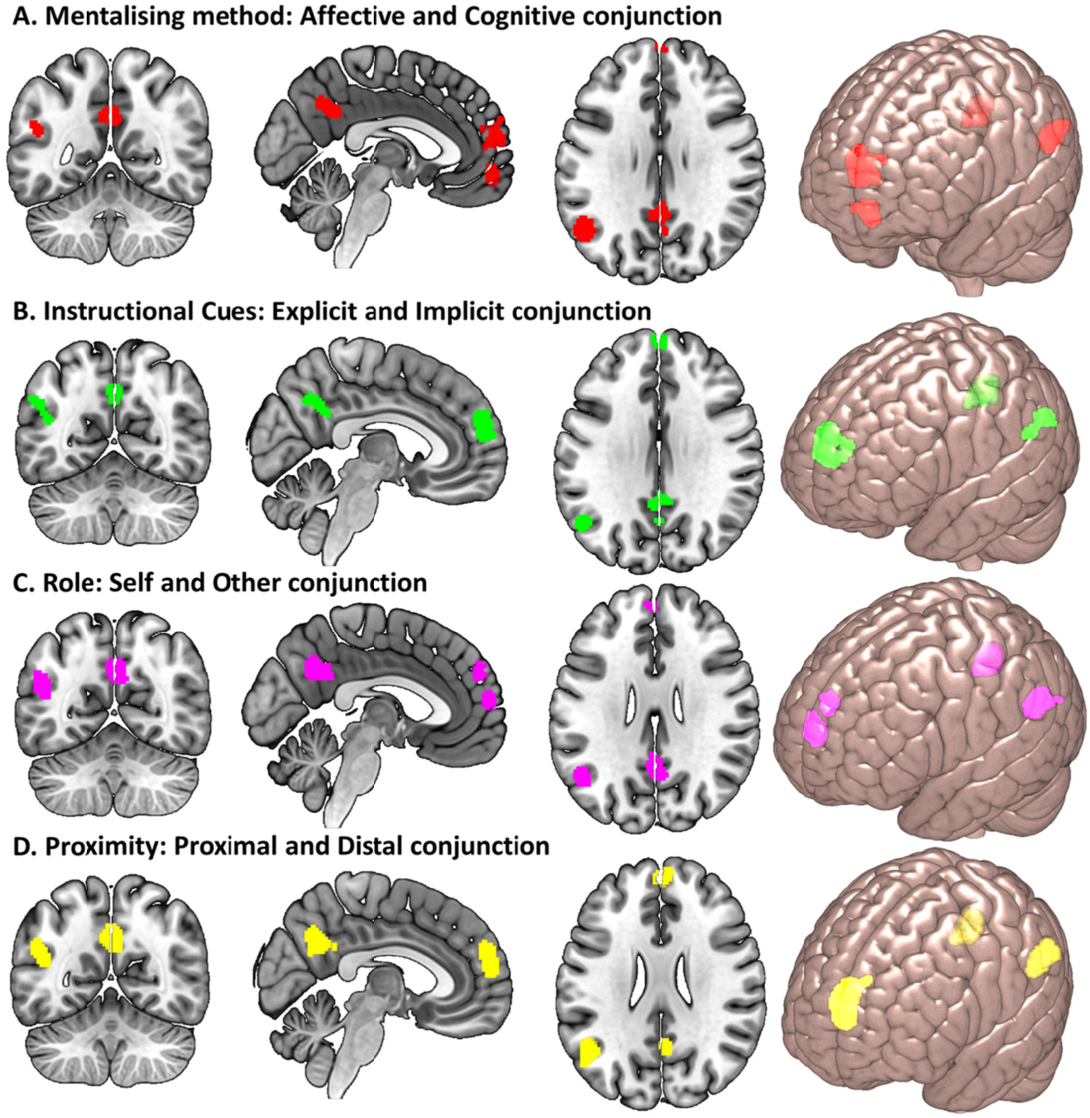

Figure 4. Contrast analyses for each modality dyad. Significant clusters are displayed on coronal, axial and sagittial slices and a rendered (shell) image using MRIcroGL.

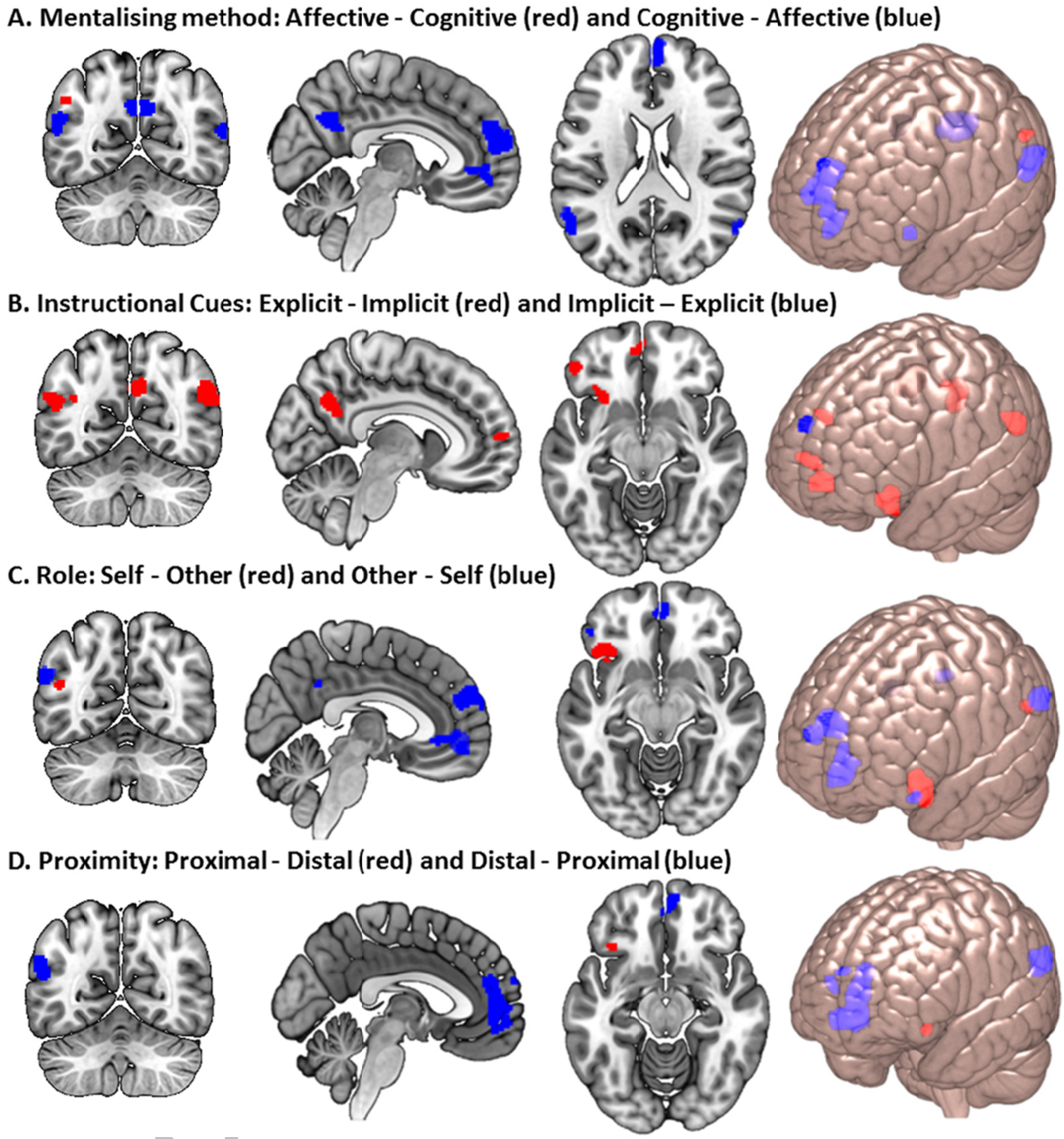

Table 1.

Examples of studies used in meta-analysis for each of the different modalities.

Reference	N	Contrast	Task
Cognitive, Explicit, Proximal, Self			
Hutcherson et al. (2015)	26	Utilitarian > Emotional	Participants were presented statements that were utilitarian or emotional in nature. Participants needed to rate how costly/beneficial and appalling/appealing they found the statements. Explicitly told to consider themselves in the scenarios. Utilitarian responses were compared against emotional responses.
Molenberghs et al. (2014a)	48	Intentional Harm > Neutral	Participants were required to shock or reward ingroup and outgroup members based on their performance on a questionnaire-like task.
Cognitive, Explicit, Proximal, Other			
Schleim et al. (2011)	40	Moral > Neutral	Participants read scenarios that were understandable from legal, moral and neutral point of views. Responses were made based on whether the scenarios were legally or morally right.
Cáceda et al. (2011)	16	Care > Neutral Justice > Neutral	Justice and care based moral scenarios relating to a fictional character were compared against neutral scenarios. Participants were required to make responses about the information in each scenario.
Cognitive, Explicit, Distal, Self			
Schaich Borg et al. (2011)	26	Wrong > Not Wrong	Participants read scenarios depicting morally wrong behaviours, morally neutral behaviours,

			and morally ambiguous behaviours. Participants were required to make a button-press response to indicate whether the behaviour was morally right or wrong.
Smith et al. (2015)	30	Medical judgments > Non-Medical judgments	Participants were required to make fair/unfair judgments in a money allocation task. Responses were based on participant point of view of what is fair in medical and non-medical scenarios.
Cognitive, Explicit, Distal, Other			
Parkinson et al. (2011)	38	Harmful > Neutral Dishonest > Neutral Disgust > Neutral	Participants read scenarios that depicted harm, dishonest, and disgust moral situations. Participants were required to make wrong/not wrong decisions based on the scenarios of other people.
Heekeren et al. (2005)	12	Moral > Semantic	Moral and semantic decision were made through a series of statements containing bodily harm or not.
Cognitive, Implicit, Proximal, Self			
Michl et al. (2014)	14	Guilt > Neutral Shame > Neutral	Participants were required to imagine themselves in scenarios that were either neutral, guilt-laden or shame-laden.
Takahashi et al. (2004)	19	Guilt > Neutral Embarrassment > Neutral	Short sentences detailing neutral, guilt and embarrassing information were given to participants. Participants were required to make a rating of how guilty or embarrassed they felt in the presented situations.
Cognitive, Implicit, Proximal, Other			
Luo et al. (2006)	29	Incongruent > congruent	An implicit association task was used to assess

			legal/illegal actions paired with good and bad animals.
Sinke et al. (2010)	14	Colour > Emotion	Videos of two actors engaging in social situations were presented to participants. Videos were overlayed with a colour dot. Participants were required to make a judgment on the colour of the dot (ignore the moral content) or identify whether the interaction was threatening or teasing.
Cognitive, Implicit, Distal, Other			
Robertson et al (2007)	16	Moral > Neutral	Ethical and non-ethical business problems were presented to participants. Participants subsequently responded by button-press if they could identify an important issue or information in the scenario.
Young and Saxe (2009)	14	Moral > Non-moral	Participants read scenarios regarding a protagonist's action on another person. Actions were either morally salient or non-morally salient.
Affective, Explicit, Proximal, Self			
Molenberghs et al. (2014b)	48	Intentional Harm > Control	Participants viewed ingroup and outgroup members harming or interacting with each other.
Shenhav & Greene (2014)	34	Integrative > emotional Emotional > integrative	Participants read scenarios depicting morally salient events. Participants are required to rate which scenario was more appropriate. Researchers manipulated the utilitarian decision, emotional assessment and an integrative moral judgment without participants' awareness.
Affective, Explicit, Proximal, Other			

Kedia et al. (2008)	35	Other > Self	Participants read stories with differing target emotions. Either self-anger, other-anger, guilt, or compassion. Participants read and made a button press response to signal their response. Comparisons were made between other agent and self.
Verdejo-Garcia et al. (2014)	14	Moral > Neutral	Participants viewed sketched cartoons and listened to corresponding dilemmas. Moral dilemmas depicted an imaginary third person completing an action and participants had to respond by raising their finger whether the action was morally right or wrong.
Affective, Explicit, Distal, Self			
Moll et al. (2002a)	7	Moral > Non-Moral	Participants read scenarios that were either moral or non-moral and asked to make covert emotional judgments as to whether they were morally right or wrong. Comparisons were made between right and wrong decisions.
Moll et al. (2001)	9	Moral > Non-Moral	Moral and non-moral statements were presented to participants. Participants were required to make right/wrong moral judgments.
Affective, Explicit, Distal, Other			
Cushman et al. (2012)	35	Omission > Action	Participants were presented with moral scenarios in which a person either took action or did nothing.
Cikara et al. (2010)	18	Saving High warmth+ High competence > other three conditions	Authors employed an adapted trolley paradigm by presenting a picture of one person (sacrifice) followed by five people (survivors). The moral salience of images was manipulated through warmth and competence of sacrifice

			and survivors. Participants were asked to rate how morally acceptable the sacrifice was.
Affective, Implicit, Proximal, Other			
Mercadillo et al. (2011)	24	Compassion > Neutral	Participants viewed high compassion eliciting images and non-compassion images. Participants were instructed to view images only and allow themselves to naturally feel emotions toward the stimuli. Comparisons were made between compassion and control images.
Moll et al. (2005b)	13	Moral > Non-moral	Pairs of statements were presented to participants depicting emotional and neutral scenarios. Statements were construed in such a way that participants passively witnessed the scenarios. Scenarios depicted morally salient and non-moral but emotional events. Comparisons were made between moral emotions and basic emotions.
Affective, Implicit, Distal, Self			
Immordino et al. (2009)	13	Moral > Neutral	Participants viewed emotionally salient narratives. No responses were made; participants had to just allow themselves to feel the emotions towards the text. All narratives elicited either pain related or non-pain related social emotions.
Fourie et al. (2014)	22	Prejudice > Neutral	Participants told they provided low-prejudice scores on a measure and were then asked to complete an IAT inside the MRI scanner. Emotional reactions were recorded in response to programmed feedback about IAT performance.

Affective, Implicit, Distal, Other			
Harenski et al. (2006)	10	Implicit moral > Implicit Social	Participants viewed moral and non-moral images and were required to either watch the images passively or regulate their emotions. No button-press responses were made. Images related to other people in distanced situations (e.g. male harming a female).
Moll et al. (2002b)	7	Moral > Non-moral	Participants viewed emotionally salient images that contained either moral or non-moral content. No button-press responses were made. Images were not pertaining to the self but instead moral images focused on harm doing to others.

Supplementary Table 1

Studies included in the ALE meta-analysis. In the condition column, C represent cognitive tasks and A represents affective tasks. E represents explicit tasks, and I represents implicit tasks. P represent proximal and D distal distance. S represents self-related and O other-related moral tasks.

Author	Date	x	y	z	N	Condition
Hutcherson et al.	2015	9	35	52	26	C E P S
		-39	26	-8		
Eslinger et al.	2009	-28	52	0	9	C E P S
		36	-40	55		
		28	-56	-25		
		28	52	0		
		-36	-40	60		
		-28	-48	-15		
		32	8	65		
		12	-72	60		
		44	12	40		
Eslinger et al.	2009	36	-32	-10	9	C E P S
		-48	-8	5		
		-24	-12	-20		
		-40	20	-25		
		20	-14	-5		
Eslinger et al.	2009	0	60	10	9	C E P S
		-12	36	55		
		0	-60	35		
		-56	-60	10		
		60	-64	15		
		-40	20	-25		
Eslinger et al.	2009	-12	44	45	9	C E P S
		-36	20	45		
		-36	24	-15		

		-56	-56	5		
		-24	-84	-40		
		32	-100	0		
		0	-20	5		
		-12	44	45		
		-24	-12	-25		
Pujol et al.	2008	3.72	-44.97	26.69	10	C E P S
		7.04	-57.51	30.12		
		6.03	-54.76	36.59		
		-3.83	-48.18	27.14		
		2.6	-52.93	21.9		
		3.73	-51.45	26.21		
		-0.55	-55.51	28.93		
		2.65	-40.51	28.51		
		-0.7	-53.36	17.51		
		0.33	-54.84	13.16		
Molenberghs et al.	2014a	-3	53	28	48	C E P S
		-48	23	-8		
		45	29	-8		
		57	-25	-5		
Molenberghs et al.	2015	9	-49	55	48	C E P S
		6	-85	-5		
		-33	20	-11		
		36	17	-20		
		-36	-46	-14		
Schleim et al.	2011	-4.02	54.31	32.69	40	C E P O
		-36.11	15.03	50.57		
		-47.08	-56.3	23.08		
		-35.14	-57.97	27.52		
		-1.61	-58.71	29.26		
		37.51	-68.2	-39.94		

Cáceda et al.	2011	8	-60	32	16	C E P O
		-30	-22	20		
		0	-51	28		
		-59	-43	10		
		-56	-42	28		
		3	51	23		
Cáceda et al.	2011	3	-51	28	16	C E P O
		-15	-71	44		
		-62	-51	21		
		-48	-45	28		
		53	-48	21		
		48	-40	20		
		3	51	23		
Harrison et al.	2012	0	-58	34	73	C E D S
		-12	54	32		
		-46	-62	24		
		-64	-12	-26		
		38	28	-22		
		64	-10	-8		
		-20	-22	-20		
		62	-8	-32		
		0	-20	34		
		-2	-8	6		
		-12	8	10		
Schaich Borg et al.	2011	-3	30	51	26	C E D S
		0	51	30		
		-6	45	21		
		-18	57	36		
		18	54	42		
		-12	63	21		
		-39	12	54		
		51	9	51		
		-39	12	30		
		-33	18	-9		
		39	27	0		

		-45	42	-9		
		33	45	-18		
		-45	24	-18		
		48	18	-15		
		48	9	-39		
		-48	-9	-21		
		-57	-42	0		
		-51	-75	21		
		-42	-69	51		
		-6	-78	-6		
		-9	-87	9		
		-36	-90	18		
		45	-87	0		
		-45	-52	-21		
		-30	-39	-21		
		-24	-21	-15		
		33	-15	-12		
		-9	-18	-18		
		12	-21	-18		
		-3	-30	-18		
		3	-18	-30		
Smith et al.	2015	45	-58	10	30	C E D S
		-18	-79	34		
		39	-79	16		
		6	11	13		
		-6	17	7		
		21	-25	70		
		12	44	52		
		21	-55	55		
		-51	4	46		
		42	-31	16		
Parkinson et al.	2011	-3.05	45.83	22.31	38	C E D O
		7.92	8.85	28.02		
		-12.33	25.1	53.65		
		32.7	46.68	29.46		

		-30.99	39.22	33.52		
		-47.16	-57.99	16.52		
		-57.77	-42.33	35.32		
		45.07	-60.52	-38.59		
Parkinson et al.	2011	-13.61	40.01	40.99	38	C E D O
		16.85	30.73	54.84		
		-41.67	26.94	40.52		
		-47.93	-54.54	41.97		
		62.25	-54.25	38.94		
		-2.66	-48.62	33.89		
Parkinson et al.	2011	-21.33	48.62	30.19	38	C E D O
		-3.12	58.49	19.94		
		8.7	62.37	14.87		
		-24.08	15.77	-22.54		
		-44.35	38.39	2.46		
		35.24	16.31	-31.45		
		-27.44	-5.91	-36.03		
		-44.38	-46.1	-17.2		
		-20.72	-4.12	-17.27		
		21.39	-1.95	-19.33		
		-3.12	36.59	15.38		
		-1.65	-42.55	29.91		
		-0.99	-15.05	2.52		
		41.91	-63.2	-32.66		
Parkinson et al.	2011	3.4	57.66	22.15	38	C E D O
Heekeren et al.	2005	55	7	-24	12	C E D O
		-54	5	-26		
		-6	54	-14		
		4	55	-8		
		6	-50	26		
		3	58	12		
		-56	-62	18		
		58	-60	22		

Reniers et al.	2012	-28.84	35.83	31.58	24	C E D O
		-3.25	53.09	8.15		
		-7.74	56.19	-4.41		
		-57.62	-37.89	48.33		
		-2.49	-33.13	50.28		
		-53.39	-42.96	39.79		
		-29.05	-78.39	-7.54		
		0.91	-65.16	-28.41		
		14.06	-75.78	-16.38		
Takahshi et al.	2008	14	-90	-8	15	C E D O
		-40	32	-20		
		-50	18	-24		
		-48	0	48		
		-52	26	14		
		6	58	14	15	C E D O
		-54	-64	30		
Greene et al.	2004	1.61	-28.19	34.03	41	C E D O
		-22.82	53.26	-0.5		
		31.17	54.3	-3.77		
		-13.35	-66.43	39.19		
		9.46	-66.48	48.89		
		40.61	-41.46	39.17		
		2.48	-69.17	8.94		
		-53.79	-72.23	2.36		
		59.72	-58.13	9.11		
		18.26	62.32	2.38		
		-3.8	-27.14	34.02		
		-39.48	-43.95	28.45		
		70.42	-30.44	6.19		
Hayashi et al.	2014	6	35	-8	37	C E D O
		27	20	52		
		3	-58	34		

		45	-64	25		
		-9	-55	34		
		-39	-76	37		
Hayashi et al.	2014	36	-73	-8	37	C E D O
		9	-85	-5		
		-54	-16	52		
Hayashi et al.	2014	63	-25	37	37	C E D O
		42	-61	10		
		-9	-28	46		
Hayashi et al.	2014	57	26	25	37	C E D O
		54	26	1		
		30	11	-8		
		48	-25	-5		
		18	-88	4		
		-6	59	34		
		-48	29	7		
		-30	17	-14		
		-39	11	25		
		-57	2	-14		
		-63	-19	-5		
		-33	-88	-8		
Bahnemann et al.	2010	-2	50	-14	25	C E D O
		-44	10	46		
		-46	36	-12		
		-8	48	36		
		2	-56	30		
		-56	-14	-16		
		54	6	-28		
		-58	-38	-4		
		62	-38	-2		
		-54	-64	28		
		58	-64	32		

Yoder & Decety	2011	58	-32	24	40	C E D O
		-52	6	4		
		-54	-32	22		
		-12	-28	42		
		14	-28	40		
		-22	-56	68		
		14	-4	74		
		-20	-12	-10		
		38	-10	-18		
Young et al.	2007	56	-52	30	10	C E D O
		4	-62	38		
		-42	-62	26		
		2	52	28		
		2	58	12		
		0	46	-2		
Young et al.	2007	56	-54	28	17	C E D O
		0	-54	32		
		-52	-58	26		
		2	60	28		
		-4	56	8		
		0	54	-28		
Cope et al.	2010	-51	3	39	23	C E D O
		-18	63	21		
		-54	15	0		
		-48	45	3		
		-51	42	-9		
		-39	-3	-36		
		-54	-45	-15		
		-18	-15	-21		
		-42	-51	54		
		-30	-66	51		
		-27	-72	57		
		-3	48	-3		

Takahashi et al.	2004	-6	-95	12	19	C I P S
		2	-85	6		
		-16	49	9		
		4	57	16		
		-44	-61	20		
Michl et al.	2014	-27.6	-87.7	19.13	14	C I P S
		4.75	-84.7	14.92		
		7.49	-75.36	-23.03		
		-5.29	-34.62	0.05		
		-44.6	17.92	-21.29		
		-7.75	10.61	70.69		
		39.66	21.41	-23.07		
		-57.2	23.87	8.59		
		4.83	50.48	48.61		
		1.25	71.99	26.37		
Luo et al.	2006	48.47	6.32	-12.76	29	C I P O
		-2.46	12.65	-22.6		
		-20.81	6.55	62.36		
		37.29	6.05	42.36		
		-16.14	14.24	6.61		
		-33.21	-11.58	18.42		
		-8.07	-62.88	30.91		
		20.58	0.02	1.78		
		-2.91	11.9	26.78		
Luo et al.	2006	24.72	-5.67	-13.41	29	C I P O
		-5.74	59.41	-15.97		
Luo et al.	2006	2.96	4.5	62.15	29	C I P O
		-51.59	-28.12	14.76		
		46.77	-36.18	15.01		
		-50.62	-15.87	7.93		
		-34.74	-21.05	66.44		
		-41.31	-10.86	61.06		
		-30.58	-1.45	57.71		

		-36.05	-19.53	48.39		
		23.64	-6.74	-13.29		
Robertson et al.	2007	8.14	-47.52	33.59	16	C I P O
		-31.03	-17.95	19.01		
		3.41	55.53	22.36		
		-62.3	-50.49	17.16		
		71.67	-52.15	15.04		
Robertson et al.	2007	5.55	70.74	24.18	16	C I P O
		3.04	64.84	-4.33		
		71.71	-51.83	18.37		
		-62.26	-50.18	20.49		
		10.51	-47.02	50.31		
		2.81	62.01	-23.1		
Sinke et al.	2010	-49	-14	49	14	C I P O
		49	-14	51		
		-24	2	5		
		23	2	5		
		-3	-76	13		
		5	-72	13		
		-8	-72	-9		
		3	-75	-7		
		1	-5	56		
		-2	-29	54		
		57	-4	24		
		48	-43	45		
Harada et al.	2009	42	30	-18	10	C I D O
		-54	27	0		
		60	36	15		
		12	66	30		
		-12	66	27		
		-18	54	39		
		-9	36	60		
		12	27	66		

		-30	-93	21		
		51	-66	15		
		-45	-81	18		
		15	-99	3		
Harada et al.	2009	0	39	54	10	C I D O
		63	27	9		
		15	18	69		
		-24	0	-27		
		42	33	-18		
		33	-81	18		
		42	-48	-27		
		-45	-84	6		
		-12	-102	12		
		0	-87	-12		
Harada et al.	2009	45	14	-3	10	C I D O
		36	17	-8		
		-39	17	-8		
		-30	47	17		
		-12	18	60		
		-12	23	49		
		-3	9	55		
Harada et al.	2009	6	-72	33	10	C I D O
		-6	60	6		
		0	51	-3		
		-12	15	66		
		-21	48	21		
		42	33	30		
		-27	39	33		
		-36	15	48		
		3	36	-3		
		-51	-66	9		
		57	-66	18		
		39	-63	21		
		-45	33	-18		

Harada et al.	2009	-8	44	46	18	C I D O
		-48	16	-34		
		-50	16	16		
		-52	26	-10		
		-46	6	50		
		-36	24	44		
		-56	-42	0		
		32	-86	-36		
		14	8	0		
Robertson et al.	2007	8.14	-47.52	33.59	16	C I D O
		-31.03	-17.95	19.01		
		3.41	55.53	22.36		
		-62.3	-50.49	17.16		
		71.67	-52.15	15.04		
Young & Saxe	2009	54	-52	16	14	C I D O
		-4	62	32		
		-52	-70	26		
		0	46	44		
		2	62	16		
		4	50	-4		
Young & Saxe	2009	50	-70	18	14	C I D O
		6	-62	24		
		-58	-66	22		
		0	54	30		
		0	60	18		
		4	52	-8		
Sommer et al.	2009	0	52	36	12	A E P S
		-42	-62	22		
		50	14	-28		
		6	-60	38		
		60	22	18		
		10	-4	6		

Molenberghs et al.	2014b	-48	-73	-2	48	A E P S
		-48	-64	4		
		-57	-25	28		
		48	-73	-2		
		51	-61	4		
		48	-64	-8		
		-12	-25	40		
		-57	8	34		
		-51	8	12		
		-24	-10	52		
		-15	-28	4		
		27	17	-17		
		30	5	-20		
		24	-4	-14		
		-21	-7	-14		
		-36	23	-14		
		-27	20	-14		
Shenhav & Greene	2014	60	-28	22	39	A E P S
		0	36	-12		
		-36	6	-8		
		30	-46	72		
Shenhav & Greene	2014	0	52	38	39	A E P S
De Achava et al.	2013	70.58	-28.13	19.41	13	A E P S
		-39.98	14.7	1.36		
		42.15	8.61	0.57		
		5.61	25.24	19.72		
		-61.42	-27.92	5.95		
		29.56	46.33	37.39		
		-3.02	7.77	17.11		
		3.32	59.26	16.39		
		-13.32	31.24	62.03		
		5.23	50.81	-5.22		
		8.15	-87.91	26.38		

		-9.9	59.48	-3.58		
		5.9	-65.58	24.21		
Greene et al.	2001	2.14	58.53	8.64	9	A E P S
		-2.58	-52.36	39.86		
		49.84	42.41	17.26		
		-50.19	-65.16	31.85		
		55.57	-56.9	22.51		
Shenhav & Greene	2010	-42	4	6	34	A E P S
		-2	-60	-4		
		52	-2	40		
		8	6	62		
		-46	-62	-10		
		8	-30	48		
		-30	-12	-30		
		54	8	-2		
		-56	-34	24		
		26	48	36		
		64	-36	26		
		-42	-86	18		
Shenhav & Greene	2010	6	-74	0	34	A E P S
		-20	-22	-2		
		-46	-66	20		
		-38	-22	26		
		-16	-28	62		
		28	-36	36		
Shenhav & Greene	2010	-46	-10	-22	34	A E P S
		8	-64	24		
		-4	56	-12		
		-14	-14	6		
		-42	-60	18		
		-52	30	0		
		52	-54	26		

Harenski et al.	2008	12	45	-12	28	A E P S
		-6	-54	9		
		12	-48	3		
		-51	-72	24		
		54	-66	33		
		21	-33	-18		
		-24	36	51		
		-12	-72	60		
		-21	6	69		
		0	-12	-15		
Sommer et al.	2014	6	52	56	16	A E P S
		56	54	28		
		54	52	22		
		32	20	12		
		30	20	10		
		4	58	42		
Sommer et al.	2014	8	58	24	16	A E P S
		14	20	64		
		54	2	22		
		30	20	12		
		56	52	32		
		52	54	20		
		14	30	6		
		34	38	12		
		36	10	14		
		2	60	54		
		16	12	14		
Harrison et al.	2008	-9	50	17	22	A E P S
		3	-51	30		
		-50	-57	28		
		53	-57	28		
		48	28	-11		
		24	-74	-29		

		-45	25	-16		
		-31	-71	-30		
Decety & Porges	2011					
		12	20	10	22	A E P S
		-6	12	8		
		-38	22	26		
		-14	42	46		
		-52	36	10		
		-38	-68	28		
		6	-32	-8		
		10	-20	18		
		-6	-18	18		
		34	36	-10		
		-32	40	-10		
Majdandzic et al.	2012	6	40	-2	40	A E P O
		42	10	14		
		-22	28	-14		
		-6	-40	40		
		-12	2	68		
		38	-24	4		
		8	16	30		
Kédia et al.	2008	12	48	6	35	A E P O
		8	46	33		
		8	3	3		
		27	12	-29		
		22	1	-20		
		-23	4	-16		
		-15	-2	0		
		-7	3	4		
		1	-62	37		
		57	-59	16		
		-52	-71	14		
		-49	-70	26		
Verdejo-Garcia et al.	2014	-6	54	38	14	A E P O

		-34	26	-22		
		0	28	22		
		4	-58	32		
		50	-60	32		
		-48	-66	28		
		16	-98	16		
		-60	-16	-20		
Li et al.	2015	-48	39	-12	24	A E P O
		-9	21	57		
		-39	-54	42		
		42	33	21		
Schaich Borg et al.	2006	-12	51	-9	28	A E D S
		-15	72	-6		
		-6	-72	-3		
		51	-75	9		
		-54	-72	6		
		-63	-51	21		
		-42	48	30		
Moll et al.	2001	-29.18	63.95	10.87	10	A E D S
		-36.83	45.76	0.48		
		-11.33	-56.51	30.33		
		-22.66	-13.41	-1.75		
		45.28	62.52	3.02		
		59.06	6.93	-29.81		
		-49.28	-60.98	19.1		
		5.18	59.22	-7.17		
		29.07	-76.55	-25.52		
		48.44	-60.63	-28.55		
Moll et al.	2002a	-10.12	49.1	-22.72	7	A E D S
		-35.01	19.15	-31.66		
		-49.6	-41.47	-1.88		
Prehn et al.	2008	-8	42	-18	23	A E D S
		-40	28	-22		

		-42	12	-38		
		-64	-12	-28		
		50	10	-34		
		32	-68	34		
Greene et al.	2004	1.25	39.15	19.53	41	A E D S
		-29.32	54.19	-1.6		
		35.57	52.71	1.92		
		35.51	19.45	-9.36		
		0.44	-24.46	28.08		
		1.84	-68.09	43.58		
		51.44	-52.16	38.92		
		-43.61	-57.82	41.1		
		-38.99	16.21	-5.53		
Greene et al.	2004	2.54	-77.48	12	41	A E D S
		54.98	-5.46	-12.83		
		-58.45	-5.86	-10.85		
		-61.32	-47.92	10.16		
		50.99	-35.82	7.05		
		-54.69	-5.2	30.48		
		-3.2	-23.12	-3.36		
		-2.11	6.53	3.77		
		-51.66	8.56	16.74		
Greene et al.	2004	1.08	60.86	10.66	41	A E D S
		-2.58	-48	40.55		
		-25.07	15.32	-15.76		
		-0.98	-5.16	4.91		
		0.14	-16.86	6.04		
		-56.37	-7.54	-17.45		
		-27.23	-8.71	-20.07		
		1.62	-16.07	37.32		
		53.81	-3.96	-19.68		
		27.88	-4.05	-19.23		
		-0.99	26.51	10.74		
		51.2	-48.51	20.63		

		-47.1	-58.64	21.07		
		23.92	-68.11	-3.86		
Zahn et al.	2008	-30	33	-12	24	A E D S
		-24	57	9		
		-12	-51	0		
		-18	-27	0		
		33	-57	-27		
		21	-30	-3		
		6	-42	60		
Chiong et al.	2013	50	-60	26	15	A E D S
		0	-78	42		
		8	60	-4		
Chiong et al.	2013	-4	34	-14	15	A E D S
		56	-64	26		
		4	-58	24		
		-20	4	-12		
Cushman et al.	2012	24	56	16	35	A E D O
		6	41	40		
		39	23	37		
		-45	8	43		
		-60	-31	-8		
		57	-34	-8		
		-6	-43	40		
		-51	-52	31		
		51	-61	37		
Greene et al.	2004	28.8	-62.88	40.37	41	A E D O
		-31.7	-59.8	42.21		
		47.81	11.66	21.46		
		-50.48	10.36	24.38		
		-2.75	-28.52	30.78		
		43.41	33.98	19.33		
		47.63	-51.01	-5.95		
		-42.01	-59.84	-3.55		

Cikara et al.	2010	-16	62	13	18	A E D O
		-10	44	39		
Cikara et al.	2010	-33	-85	26	18	A E D O
Cikara et al.	2010	-13	49	0	18	A E D O
FeldmanHall et al.	2013	-2	54	-4	35	A E D O
		-12	46	6		
		6	30	-6		
		-2	60	26		
FeldmanHall et al.	2013	56	-2	-14	35	A E D O
		56	-52	14		
		-40	-58	16		
		50	-16	-14		
		64	-56	10		
		-54	-6	46		
Chiong et al.	2013	-32	-60	44	15	A E D O
		40	-58	46		
		-36	14	30		
		46	38	14		
		-26	-72	30		
		8	0	52		
		44	20	40		
		4	26	48		
Cope et al.	2010	-3	54	-9	31	A E D O
		-9	57	0		
		-15	27	-18		
		-60	-57	-6		
		-54	-51	-12		
		-57	-69	0		
		-63	-42	-12		

		-63	-48	-3		
		-24	-9	-33		
		-24	-45	-9		
		-21	-54	-3		
		-57	-60	33		
		-45	-63	48		
		-12	-72	57		
		-9	-66	63		
		-6	-54	72		
		-33	-60	57		
		-21	-63	66		
		-30	-78	42		
		-3	48	6		
Berthoz et al.	2006	-6	-54	50	12	A I P O
		32	-76	-30		
Schaich Borg et al.	2008	-9	54	36	50	A I P O
		-6	54	-15		
		-45	9	54		
		63	-9	42		
		-42	-6	60		
		-36	-12	51		
		-48	12	-42		
		-42	32	-14		
		48	12	-42		
		-69	-36	0		
		-60	-12	-12		
		54	-12	54		
		51	-18	60		
		-21	-57	72		
		-6	-51	33		
		9	-87	0		
		-13	-84	0		
		-3	-12	39		
		21	0	-12		
		-15	-30	-3		

		-6	0	12		
		24	-3	-15		
		-24	-5	-15		
FeldmanHall et al.	2012	14	38	28	14	A I P O
		-26	-2	-26		
		28	-8	-28		
		28	-64	-10		
Moll et al.	2005	58.33	29.29	2.73	13	A I P O
		-48.42	20.58	18.85		
		-34.76	61.52	-3.36		
		-7.49	67.94	17.95		
		4.04	22.66	-19.22		
		-13.24	23.77	-17.92		
		-22.95	25.96	-16.85		
		25.68	29.53	-15.79		
		-12.2	38.77	-18.3		
		6.44	-6.18	-6.33		
		-28.43	11.18	-25.38		
		-33.47	-14.62	-2.57		
		67.92	-13.27	-16.76		
		-43.55	-11.83	-29.57		
		15.95	-86.56	-40		
		-24.06	-85.85	-41.63		
Moll et al.	2005	21.35	46.95	-12.96	13	A I P O
		-30.48	45.91	-9.73		
		58.38	32.89	6.85		
		60.13	-6.25	-33.01		
		-29.53	13.2	-26.68		
		-2.98	63.89	31.73		
Avram et al.	2014	-6	56	22	16	A I P O
		-3	-52	31		
		-3	-58	40		
		-42	-55	19		

		12	56	22		
Finger et al.	2006	74	2	-21	16	A I P O
		-61	12	-4		
		-71	-50	-11		
		-1	71	35		
		-10	-3	70		
Basile et al.	2011	1.97	63.15	81.02	22	A I P O
		-11.92	45.2	4.59		
Mercadillo et al.	2011	52	22	18	24	A I P O
		-40	20	-12		
		-58	12	16		
		36	-6	48		
		-36	-2	44		
		-48	26	18		
		-46	-24	40		
		30	-58	60		
		-22	-66	58		
		52	-70	10		
		-48	-80	14		
		-4	6	46		
		62	-34	22		
		-32	28	-4		
Wagner et al.	2011	0	-62	30	13	A I P O
		-16	58	24		
		0	60	16		
		-36	12	-22		
		-48	-60	26		
		-66	-14	-14		
		42	6	-42		
		-46	8	-40		
		2	-34	-2		
		0	-48	-6		

Cope et al.	2010	-12	45	18	50	A I P O
		-12	54	6		
		-3	42	-9		
		-60	-18	-27		
		-57	-60	39		
Wagner et al.	2011	36	32	-4	18	A I P O
		-10	42	34		
Yu et al.	2013	0	34	16	24	A I P O
Akitsuki et al.	2009	0	20	50	26	A I P O
		8	24	48		
		-40	-8	48		
		44	-2	50		
		10	16	28		
		36	52	14		
		34	-80	32		
		36	-84	10		
		-40	-84	-6		
		32	-86	-14		
		24	-94	-4		
		8	-64	-4		
		16	-92	-14		
		44	-42	-22		
		24	-78	-8		
Avram et al.	2014	-15	50	37	16	A I P O
		-33	-85	4		
		-22	-25	-8		
		17	6	-82		
		3	59	28		
Fehse et al.	2014	-28	-56	38	18	A I P O
		18	-56	32		
		28	-60	42		
		48	8	24		

Kédia et al.	2008	-3.21	57.76	12.16	35	A I P O
		1.77	-54.36	41.1		
		-50.17	-60.59	34.76		
Akitsuki et al.	2009	-20	42	46	26	A I P O
		2	-74	46		
		-10	64	-8		
Sinke et al.	2010	-4	19	57	14	A I P O
		13	35	50		
		5	12	58		
		-4	29	44		
		8	52	31		
		-44	34	9		
		48	31	15		
		41	9	26		
		-42	22	0		
		33	21	-11		
		-45	-56	11		
		51	-48	7		
		-60	-34	28		
		50	-31	25		
		-39	-33	-15		
		35	-34	-17		
		45	10	-19		
		30	-36	45		
		5	-51	33		
		44	-2	-8		
		40	-61	-5		
		45	-59	17		
		-64	-16	-18		
Wang et al.	2014	-40	18	48	22	A I P O
		4	-36	70		
		-4	-16	40		
		4	-22	40		

		0	-36	28		
		-14	-60	36		
		12	52	-10		
		-42	-58	38		
		48	-60	52		
		-36	40	-14		
		-64	-16	-18		
FeldmanHall et al.	2012	-44	-74	0	14	A I D S
		46	-68	2		
		54	22	6		
		46	-18	62		
		-30	10	-18		
		26	10	-18		
		16	40	26		
		10	-12	10		
		28	32	-8		
Immordino et al.	2009	-28.12	23.35	1.43	13	A I D S
		43.21	7.34	-1.57		
		-1.94	25.31	20.96		
		7.88	22.78	27.76		
		-1.68	-41.69	27.58		
		1.72	-60.2	36.08		
		-53.42	-60.71	33.71		
		1.07	-2.69	-3.22		
		1.01	-19.58	-11.63		
		-2.6	-35.47	-43.61		
Fourie et al.	2014	-2.98	34.34	25.68	22	A I D S
		-3.21	49.05	10.79		
		-6.45	39.15	8.46		
		-2.98	34.34	25.68		
		-39.01	21.52	-6.05		
		-2.74	-16.4	34.06		
		0.53	-68.69	25.73		
		3.34	-22.69	0.96		

Harenski et al.	2010	-27	-45	-15	30	A I D O
		-15	-36	-12		
		-63	-39	-9		
		-54	-75	6		
		-48	12	39		
Harenski et al.	2006	63	27	9	10	A I D O
		-21	-6	-15		
		-12	39	54		
		-9	30	63		
		9	57	18		
		9	69	21		
		30	-45	-12		
Harenski et al.	2006	-15	54	39	10	A I D O
		3	-63	15		
		-6	51	21		
		-9	27	63		
		18	-3	27		
Harenski et al.	2006	-51	-66	30	10	A I D O
		-15	-45	24		
Avram et al.	2013	-6	47	21	16	A I D O
		-6	47	16		
		3	-43	28		
		1	-62	41		
		-33	20	52		
		-45	-64	34		
		-48	-52	22		
		-3	-64	19		
Moll et al.	2002b	7.3	62.21	-9.75	7	A I D O
		19.19	43.65	-13.71		
		45.83	-46.09	23.85		
		48.96	-65.51	11.15		
		48.79	-53.68	-0.11		

		-43.94	-71.26	12.18		
Moll et al.	2002b	7.28	59.87	-11.75	7	A I D O
		9.75	46.86	9.66		
		19.14	45.47	-17.25		
		19.37	-10.8	-10.57		
		-16.28	-9.76	-8.95		
		51.63	5.71	-19.48		
		49.98	-64.86	6.58		
		-47.21	-72.54	10.12		
		44.24	-47.7	-16.31		
		-40.07	-47.25	-18.28		
		12.66	-52.53	48.58		
		-42.11	-82.46	-15.88		

Supplementary Table 2

Significant clusters revealed by the ALE analysis of 123 fMRI studies in which a measure of morality was administered.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	16168	-1.9	54.5	15.8	2	60	14	vmPFC
2	6816	-49.1	-62.7	23	-48	-60	24	Left TPJ
3	6600	1.1	-55.7	32.8	2	-58	34	dmPFC
4	4032	-39.5	25.2	-13.1	-36	20	-10	Left lOFC
5	2928	52.9	-57.3	24.8	54	-56	26	Right TPJ
6	1280	-21.2	-7	-15.9	-22	-6	-16	Amygdala

Supplementary Table 3

Significant clusters revealed by the individual ALE analysis of **affective** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	3488	-48.1	-60.1	26.1	-44	-58	20	Left TPJ
2	3352	-3.7	53.6	13.6	0	60	12	vmPFC
3	2888	0.6	-56.2	34.8	0	-56	40	Precuneus
4	936	-2	55.5	-9.2	-4	54	-10	dmPFC

Supplementary Table 4

Significant clusters revealed by the individual ALE analysis of **cognitive** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	7104	-0.5	56.4	22	0	54	28	vmPFC
2	4464	1.9	-55.9	32.2	2	-58	32	Precuneus
3	3976	-51.8	-60.9	23.7	-50	-60	26	Left TPJ
4	2088	0.6	51.4	-6.4	2	52	-6	dmPFC
5	1120	56.6	-57.1	22.9	56	-54	28	Right TPJ

Supplementary Table 5

Significant clusters revealed by the individual ALE analysis of **explicit** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	9024	-1.4	54.8	13.4	2	58	12	dmPFC
2	4992	1.4	-55.9	32.6	2	-58	32	vmPFC
3	4368	-48.6	-61.5	24.4	-48	-60	24	Left TPJ
4	2784	54.2	-57.3	25.6	54	-56	26	Right TPJ
5	2032	-35.1	21.9	-14.5	-34	20	-12	Left lOFC

Supplementary Table 6

Significant clusters revealed by the individual ALE analysis of **implicit** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	4472	-0.1	57	21.2	2	58	18	dmPFC
2	1992	1.7	-53.9	34.5	8	-48	34	Precuneus
3	1184	-49.8	-61.5	30.4	-50	-62	34	Left TPJ

Supplementary Table 7

Significant clusters revealed by the individual ALE analysis of **self** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	

1	3096	0.6	-56.9	32.1	2	-60	36	Precuneus
2	2904	-37.8	22	-12.3	-36	22	-12	Left lOFC
3	2144	-46.1	-61.2	22.3	-46	-60	22	Left TPJ
4	1136	2.1	59	13.9	2	60	12	dmPFC
5	888	-3.7	52.8	33.4	-2	52	30	dmPFC

Supplementary Table 8

Significant clusters revealed by the individual ALE analysis of **other** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	11856	-0.9	54.7	14.5	2	58	26	dmPFC
2	4080	2.3	-55.1	33.1	2	-56	32	vmPFC
3	3648	-50.7	-61.5	26.9	-52	-64	28	Left TPJ
4	784	56.6	-55.6	15.1	56	-54	16	Right TPJ

Supplementary Table 9

Significant clusters revealed by the individual ALE analysis of **proximal** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	4504	1.7	-56	32.5	0	-54	30	Precuneus
2	3936	0.1	55.8	25.3	2	58	16	dmPFC
3	2552	-46.5	-62	24.2	-44	-60	20	Left TPJ
4	1352	-36.8	23.2	-13	-36	22	-12	Left lOFC

Supplementary Table 10

Significant clusters revealed by the individual ALE analysis of **distal** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	10792	-1.3	54.8	11.5	0	52	-6	dmPFC
2	3488	-50.7	-60.8	25.7	-52	-62	28	Left TPJ
3	2952	0.8	-55.9	33.7	2	-58	34	Precuneus
4	928	55.1	-54.5	25.2	56	-54	28	Right TPJ

Supplementary Table 11

Significant clusters revealed by the conjunction analysis between **affective** and **cognitive** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	1760	-48.3	-60.6	24.9	-46	-58	22	Left TPJ
2	1720	0.7	-55.6	34.5	0	-58	38	Precuneus
3	1520	0.6	58.1	16.1	0	60	12	dmPFC
4	648	-1.6	54.9	-9	-2	54	-8	vmPFC
5	56	-5.1	47.7	21.1	-6	46	20	dmPFC

Supplementary Table 12

Significant clusters revealed by the conjunction analysis between **explicit** and **implicit** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	2672	0.7	57.1	20.5	2	58	16	dmPFC
2	1440	0.4	-55.1	35.1	0	-58	40	Precuneus
3	776	-49.2	-61.6	27.6	-50	-62	32	Left TPJ
4	8	2	-64	28	2	-64	28	Precuneus

Supplementary Table 13

Significant clusters revealed by the conjunction analysis between **self** and **other** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
1	2160	0.7	-56.5	32.9	2	-60	36	Precuneus
2	1208	-48	-60.2	23.9	-50	-60	24	Left TPJ
3	1056	2.1	58.9	14.1	2	60	14	dmPFC
4	568	-3.7	52.8	32	-2	52	30	dmPFC

Supplementary Table 14

Significant clusters revealed by the conjunction analysis between **proximal** and **distal** morality tasks.

Cluster	Volume (mm^3)	Weighted	Peak MNI	Anatomical location

		X	Y	Z	X	Y	Z	
1	2688	0.7	56.8	21.4	2	58	16	dmPFC
2	2160	1	-56.8	33.5	2	-58	32	Precuneus
3	1736	-47.6	-61.1	25.1	-46	-58	22	Left TPJ

Supplementary Table 15

Significant clusters revealed by the contrast analysis between **affective** and **cognitive** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
Affective – Cognitive Contrast								
1	80	-50.6	-61	37	-50	-62	38	Left TPJ (Angular Gyrus)
Cognitive – Affective Contrast								
1	3528	0.3	55.5	23	1.3	52	26	vmPFC
2	1912	2.5	-57.6	31.5	4	-58	32	Precuneus
3	1256	-55.8	-60.6	21.5	-58	-58	18	Left TPJ
4	680	1.9	47	-4.4	4	42	-2	dmPFC
5	352	58.2	-61.6	16.1	60	-62	16	Right TPJ (supramarginal gyrus)
6	88	-32.5	17.8	-10.2	-32	20	-10	Left lOFC

Supplementary Table 16

Significant clusters revealed by the contrast analysis between **explicit** and **implicit** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
Explicit – Implicit Contrast								
1	2112	53.8	-58.3	28.5	53.5	-58.9	32.2	Right TPJ
2	1136	4.1	-57	30	2	-56	28	Precuneus
3	1064	-49.9	-61	24.1	-52	-60	22	Left TPJ
4	728	-5.8	54.6	-5.9	-9	52	-6	dmPFC
5	560	-33.3	23	-16.3	-34	26	-16	Left lOFC
6	280	3.5	58.2	7.5	4	58	6	dmPFC
7	200	-47.6	39.9	-10.2	-46	42	-8	Left lOFC
8	184	-2.1	50	34.8	-2	48	34	vmPFC
9	80	-6	-42.1	40.7	-6	-40	42	Precuneus
Implicit – Explicit Contrast								
1	136	-3.4	66	32.7	-4	68	32	dmPFC

Supplementary Table 17

Significant clusters revealed by the contrast analysis between **self** and **other** morality tasks.

Cluster	Volume (mm^3)	Weighted	Peak MNI	Anatomical location

		X	Y	Z	X	Y	Z	
Self – Other Contrast								
1	1528	-39.1	23.3	-12.5	-42	22	-16	Left lOFC
2	96	-45.3	-63.7	20.5	-46	-64	20	Left TPJ
Other – Self Contrast								
1	2368	-1.4	51	-2.2	-4	51	-2	dmPFC
2	1904	2.8	58.2	24.9	2	58	26	dmPFC
3	752	-55.1	-64	27.1	-58	-64	26	Left TPJ
4	288	56.9	-54.9	13.3	56	-52	12	Right TPJ
5	224	7.8	-48.2	32.2	10	-50	30	Precuneus
6	88	-47.5	37.1	-14.2	-50	38	-12	vmPFC

Supplementary Table 18

Significant clusters revealed by the contrast analysis between **proximal** and **distal** morality tasks.

Cluster	Volume (mm^3)	Weighted			Peak MNI			Anatomical location
		X	Y	Z	X	Y	Z	
Proximal – Distal Contrast								
1	56	-37.4	25.2	-13.7	-40	26	-12	Left lOFC
Distal – Proximal Contrast								
1	4304	-1.3	51.9	0.8	-2.5	52.1	-1.9	vmPFC
2	1032	-55.2	-61.9	26.2	-58	-62	26	Left TPJ
3	160	7.5	63.4	14.4	8	66	16	dmPFC
4	64	-1.2	63	22.8	2	64	22	dmPFC

Included Studies References

Akitsuki, Y., & Decety, J. (2009). Social context and perceived agency affects empathy for pain: an event-related fMRI investigation. *Neuroimage*, 47(2), 722-734. doi: 10.1016/j.neuroimage.2009.04.091

Avram, M., Gutyrchik, E., Bao, Y., Poppel, E., Reiser, M., & Blautzik, J. (2013). Neurofunctional correlates of esthetic and moral judgments. *Neurosci Lett*, 534, 128-132. doi: 10.1016/j.neulet.2012.11.053

Avram, M., Hennig-Fast, K., Bao, Y., Pöppel, E., Reiser, M., Blautzik, J., . . . Gutyrchik, E. (2014). Neural correlates of moral judgments in first- and third-person perspectives: implications for neuroethics and beyond. *BMC Neuroscience*, 15(1), 1-11. doi: 10.1186/1471-2202-15-39

Bahnemann, M., Dziobek, I., Prehn, K., Wolf, I., & Heekeren, H. R. (2010). Sociotopy in the temporoparietal cortex: common versus distinct processes. *Soc Cogn Affect Neurosci*, 5(1), 48-58. doi: 10.1093/scan/nsp045

Basile, B., Mancini, F., Macaluso, E., Caltagirone, C., Frackowiak, R. S., & Bozzali, M. (2011). Deontological and altruistic guilt: evidence for distinct neurobiological substrates. *Hum Brain Mapp*, 32(2), 229-239. doi: 10.1002/hbm.21009

Berthoz, S., Armony, J. L., Blair, R. J., & Dolan, R. J. (2002). An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain*, 125(Pt 8), 1696-1708.

Berthoz, S., Grèzes, J., Armony, J. L., Passingham, R. E., & Dolan, R. J. (2006). Affective response to one's own moral violations. *Neuroimage*, 31(2), 945-950. doi: http://dx.doi.org/10.1016/j.neuroimage.2005.12.039

Buckholtz, J. W., Asplund, C. L., Dux, P. E., Zald, D. H., Gore, J. C., Jones, O. D., & Marois, R. (2008). The neural correlates of third-party punishment. Neuron, 60(5), 930-940. doi: 10.1016/j.neuron.2008.10.016

Cáceda, R., James, G. A., Ely, T. D., Snarey, J., & Kilts, C. D. (2011). Mode of effective connectivity within a putative neural network differentiates moral cognitions related to care and justice ethics. *PLoS One*, 6(2), e14730. doi: 10.1371/journal.pone.0014730

Chiong, W., Wilson, S. M., D'Esposito, M., Kayser, A. S., Grossman, S. N., Poorzand, P., . . . Rankin, K. P. (2013). The salience network causally influences default mode network activity during moral reasoning. *Brain*, 136(Pt 6), 1929-1941. doi: 10.1093/brain/awt066

Cikara, M., Farnsworth, R. A., Harris, L. T., & Fiske, S. T. (2010). On the wrong side of the trolley track: neural correlates of relative social valuation. *Soc Cogn Affect Neurosci*. doi: 10.1093/scan/nsq011

Cope, L. M., Borg, J. S., Harenski, C. L., Sinnott-Armstrong, W., Lieberman, D., Nyalakanti, P. K., . . . Kiehl, K. A. (2010). Hemispheric Asymmetries during Processing of Immoral Stimuli. *Frontiers in Evolutionary Neuroscience*, 2, 110. doi: 10.3389/fnevo.2010.00110

Cushman, F., Murray, D., Gordon-McKeon, S., Wharton, S., & Greene, J. D. (2012). Judgment before principle: engagement of the frontoparietal control network in condemning harms of omission. *Soc Cogn Affect Neurosci*, 7(8), 888-895. doi: 10.1093/scan/nsr072

de Achaval, D., Villarreal, M. F., Salles, A., Bertomeu, M. J., Costanzo, E. Y., Goldschmidt, M., . . . Guinjoan, S. M. (2013). Activation of brain areas concerned with social cognition during moral decisions is abnormal in schizophrenia patients and unaffected siblings. *J Psychiatr Res*, 47(6), 774-782. doi: 10.1016/j.jpsychires.2012.12.018

Decety, J., & Porges, E. C. (2011). Imagining being the agent of actions that carry different moral consequences: an fMRI study. *Neuropsychologia*, 49(11), 2994-3001. doi: 10.1016/j.neuropsychologia.2011.06.024

Eslinger, P. J., Robinson-Long, M., Realmuto, J., Moll, J., deOliveira-Souza, R., Tovar-Moll, F., . . . Yang, Q. X. (2009). Developmental frontal lobe imaging in moral judgment: Arthur Benton's enduring influence 60 years later. *J Clin Exp Neuropsychol*, 31(2), 158-169. doi: 10.1080/13803390802298064

Fehse, K., Silveira, S., Elvers, K., & Blautzik, J. (2015). Compassion, guilt and innocence: An fMRI study of responses to victims who are responsible for their fate. *Soc Neurosci*, 10(3), 243-252. doi: 10.1080/17470919.2014.980587

FeldmanHall, O., Dalgleish, T., Thompson, R., Evans, D., Schweizer, S., & Mobbs, D. (2012). Differential neural circuitry and self-interest in real vs hypothetical moral decisions. *Soc Cogn Affect Neurosci*. doi: 10.1093/scan/nss069

Feldmanhall, O., Mobbs, D., & Dalgleish, T. (2014). Deconstructing the brain's moral network: dissociable functionality between the temporoparietal junction and ventro-medial prefrontal cortex. *Social Cognitive and Affective Neuroscience*, 9(3), 297-306. doi: 10.1093/scan/nss139

Finger, E. C., Marsh, A. A., Kamel, N., Mitchell, D. G., & Blair, J. R. (2006). Caught in the act: the impact of audience on the neural response to morally and socially inappropriate behavior. *Neuroimage*, 33(1), 414-421. doi: 10.1016/j.neuroimage.2006.06.011

Fourie, M. M., Thomas, K. G., Amodio, D. M., Warton, C. M., & Meintjes, E. M. (2014). Neural correlates of experienced moral emotion: an fMRI investigation of emotion in response to prejudice feedback. *Soc Neurosci*, 9(2), 203-218. doi: 10.1080/17470919.2013.878750

Greene, J. D., Nystrom, L. E., Engell, A. D., Darley, J. M., & Cohen, J. D. (2004). The neural bases of cognitive conflict and control in moral judgment. *Neuron*, 44(2), 389-400. doi: 10.1016/j.neuron.2004.09.027

Greene, J. D., Sommerville, R. B., Nystrom, L. E., Darley, J. M., & Cohen, J. D. (2001). An fMRI Investigation of Emotional Engagement in Moral Judgment. *Science*, 293(5537), 2105-2108. doi: 10.1126/science.1062872

Han, H., Glover, G. H., & Jeong, C. (2014). Cultural influences on the neural correlate of moral decision making processes. Behav Brain Res, 259, 215-228. doi: 10.1016/j.bbr.2013.11.012

Harada, T., Itakura, S., Xu, F., Lee, K., Nakashita, S., Saito, D. N., & Sadato, N. (2009). Neural correlates of the judgment of lying: A functional magnetic resonance imaging study. *Neurosci Res*, 63(1), 24-34. doi: 10.1016/j.neures.2008.09.010

Harenski, C. L., & Hamann, S. (2006). Neural correlates of regulating negative emotions related to moral violations. *Neuroimage*, 30(1), 313-324. doi: 10.1016/j.neuroimage.2005.09.034

Harenski, C. L., Antonenko, O., Shane, M. S., & Kiehl, K. A. (2008). Gender differences in neural mechanisms underlying moral sensitivity. *Social cognitive and affective neuroscience*, 3(4), 313-321. doi: 10.1093/scan/nsn026

Harenski, C. L., Antonenko, O., Shane, M. S., & Kiehl, K. A. (2010). A functional imaging investigation of moral deliberation and moral intuition. *Neuroimage*, 49(3), 2707-2716. doi: 10.1016/j.neuroimage.2009.10.062

Harrison, B. J., Pujol, J., López-Solà, M., Hernández-Ribas, R., Deus, J., Ortiz, H., . . . Cardoner, N. (2008). Consistency and functional specialization in the default mode brain network. *Proceedings of the National Academy of Sciences*, 105(28), 9781-9786. doi: 10.1073/pnas.0711791105

Harrison, B. J., Pujol, J., Soriano-Mas, C., Hernandez-Ribas, R., Lopez-Sola, M., Ortiz, H., . . . Cardoner, N. (2012). Neural correlates of moral sensitivity in obsessive-compulsive disorder. *Arch Gen Psychiatry*, 69(7), 741-749. doi: 10.1001/archgenpsychiatry.2011.2165

Hayashi, A., Abe, N., Fujii, T., Ito, A., Ueno, A., Koseki, Y., . . . Mori, E. (2014). Dissociable neural systems for moral judgment of anti- and pro-social lying. *Brain Res*, 1556, 46-56. doi: 10.1016/j.brainres.2014.02.011

Heekeren, H. R., Wartenburger, I., Schmidt, H., Prehn, K., Schwintowski, H. P., & Villringer, A. (2005). Influence of bodily harm on neural correlates of semantic and moral decision-making. *Neuroimage*, 24(3), 887-897. doi: 10.1016/j.neuroimage.2004.09.026

Hutcherson, C. A., Montaser-Kouhsari, L., Woodward, J., & Rangel, A. (2015). Emotional and Utilitarian Appraisals of Moral Dilemmas Are Encoded in Separate Areas and Integrated in Ventromedial Prefrontal Cortex. *J Neurosci*, 35(36), 12593-12605. doi: 10.1523/jneurosci.3402-14.2015

Immordino-Yang, M. H., McColl, A., Damasio, H., & Damasio, A. (2009). Neural correlates of admiration and compassion. *Proceedings of the National Academy of Sciences*, 106(19), 8021-8026. doi: 10.1073/pnas.0810363106

Kahane, G., Wiech, K., Shackel, N., Farias, M., Savulescu, J., & Tracey, I. (2012). The neural basis of intuitive and counterintuitive moral judgment. Social cognitive and affective neuroscience, 7(4), 393-402. doi: 10.1093/scan/nsr005

Kédia, G., Berthoz, S., Wessa, M., Hilton, D., & Martinot, J. L. (2008). An agent harms a victim: a functional magnetic resonance imaging study on specific moral emotions. *J Cogn Neurosci*, 20(10), 1788-1798. doi: 10.1162/jocn.2008.20070

Li, X., Yang, J., Li, P., & Li, H. (2016). Individual differences in moral judgment competence are related to activity of the prefrontal cortex when attributing blame to evil intention. *Soc Neurosci*, 11(4), 438-448. doi: 10.1080/17470919.2015.1093960

Luo, Q., Nakic, M., Wheatley, T., Richell, R., Martin, A., & Blair, R. J. (2006). The neural basis of implicit moral attitude--an IAT study using event-related fMRI. *Neuroimage*, 30(4), 1449-1457. doi: 10.1016/j.neuroimage.2005.11.005

Majdandžić, J., Bauer, H., Windischberger, C., Moser, E., Engl, E., & Lamm, C. (2012). The Human Factor: Behavioral and Neural Correlates of Humanized Perception in Moral Decision Making. *PLoS One*, 7(10), e47698. doi: 10.1371/journal.pone.0047698

Marsh, A. A., Finger, E. C., Fowler, K. A., Jurkowitz, I. T., Schechter, J. C., Yu, H. H., . . . Blair, R. J. (2011). Reduced amygdala-orbitofrontal connectivity during moral judgments in youths with disruptive behavior disorders and psychopathic traits. *Psychiatry Res*, 194(3), 279-286. doi: 10.1016/j.pscychresns.2011.07.008

Mercadillo, R. E., Diaz, J. L., Pasaye, E. H., & Barrios, F. A. (2011). Perception of suffering and compassion experience: brain gender disparities. *Brain Cogn*, 76(1), 5-14. doi: 10.1016/j.bandc.2011.03.019

Michl, P., Meindl, T., Meister, F., Born, C., Engel, R. R., Reiser, M., & Hennig-Fast, K. (2012). Neurobiological underpinnings of shame and guilt: a pilot fMRI study. *Social Cognitive and Affective Neuroscience*. doi: 10.1093/scan/nss114

Molenberghs, P., Bosworth, R., Nott, Z., Louis, W. R., Smith, J. R., Amiot, C. E., . . . Decety, J. (2014a). The influence of group membership and individual differences in psychopathy and perspective taking on neural responses when punishing and rewarding others. *Human Brain Mapping*, 35(10), 4989-4999. doi: 10.1002/hbm.22527

Molenberghs, P., Gapp, J., Wang, B., Louis, W. R., & Decety, J. (2014b). Increased Moral Sensitivity for Outgroup Perpetrators Harming Ingroup Members. *Cereb Cortex*. doi: 10.1093/cercor/bhu195

Molenberghs, P., Ogilvie, C., Louis, W. R., Decety, J., Bagnall, J., & Bain, P. G. (2015). The neural correlates of justified and unjustified killing: an fMRI study. *Soc Cogn Affect Neurosci*. doi: 10.1093/scan/nsv027

Moll, J., Eslinger, P. J., & Oliveira-Souza, R. (2001). Frontopolar and anterior temporal cortex activation in a moral judgment task: preliminary functional MRI results in normal subjects. *Arq Neuropsiquiatr*, 59(3-b), 657-664.

Moll, J., de Oliveira-Souza, R., Bramati, I. E., & Grafman, J. (2002a). Functional networks in emotional moral and nonmoral social judgments. *Neuroimage,* 16, 696-703.

Moll, J., de Oliveira-Souza, R., Eslinger, P. J., Bramati, I. E., Mourao-Miranda, J., Andreiuolo, P. A., & Pessoa, L. (2002b). The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. *J Neurosci*, 22(7), 2730-2736. doi: 20026214

Moll, J., de Oliveira-Souza, R., Moll, F. T., Ignacio, F. A., Bramati, I. E., Caparelli-Daquer, E. M., & Eslinger, P. J. (2005). The moral affiliations of disgust: a functional MRI study. *Cogn Behav Neurol*, 18(1), 68-78.

Parkinson, C., Sinnott-Armstrong, W., Koralus, P. E., Mendelovici, A., McGeer, V., & Wheatley, T. (2011). Is morality unified? Evidence that distinct neural systems underlie moral judgments of harm, dishonesty, and disgust. *J Cogn Neurosci*, 23(10), 3162-3180. doi: 10.1162/jocn_a_00017

Prehn, K., Wartenburger, I., Mériau, K., Scheibe, C., Goodenough, O. R., Villringer, A., . . . Heekeren, H. R. (2008). Individual differences in moral judgment competence influence neural correlates of socio-normative judgments. *Social cognitive and affective neuroscience*, 3(1), 33-46. doi: 10.1093/scan/nsm037

Pujol, J., Reixach, J., Harrison, B. J., Timoneda-Gallart, C., Vilanova, J. C., & Perez-Alvarez, F. (2008). Posterior cingulate activation during moral dilemma in adolescents. *Hum Brain Mapp*, 29(8), 910-921. doi: 10.1002/hbm.20436

Reniers, R. L., Corcoran, R., Vollm, B. A., Mashru, A., Howard, R., & Liddle, P. F. (2012). Moral decision-making, ToM, empathy and the default mode network. *Biol Psychol*, 90(3), 202-210. doi: 10.1016/j.biopsycho.2012.03.009

Robertson, D., Snarey, J., Ousley, O., Harenski, K., DuBois Bowman, F., Gilkey, R., & Kilts, C. (2007). The neural processing of moral sensitivity to issues of justice and care. *Neuropsychologia*, 45(4), 755-766. doi: 10.1016/j.neuropsychologia.2006.08.014

Schaich Borg, J., Hynes, C., Van Horn, J., Grafton, S., & Sinnott-Armstrong, W. (2006). Consequences, Action, and Intention as Factors in Moral Judgments: An fMRI Investigation. *J Cogn Neurosci*, 18(5), 803-817. doi: 10.1162/jocn.2006.18.5.803

Schaich Borg, J., Lieberman, D., & Kiehl, K. A. (2008). Infection, incest, and iniquity: investigating the neural correlates of disgust and morality. *J Cogn Neurosci*, 20(9), 1529-1546. doi: 10.1162/jocn.2008.20109

Schaich Borg, J., Sinnott-Armstrong, W., Calhoun, V. D., & Kiehl, K. A. (2011). Neural basis of moral verdict and moral deliberation. *Soc Neurosci*, 6(4), 398-413. doi: 10.1080/17470919.2011.559363

Schleim, S., Spranger, T. M., Erk, S., & Walter, H. (2010). From moral to legal judgment: the influence of normative context in lawyers and other academics. *Social Cognitive and Affective Neuroscience*. doi: 10.1093/scan/nsq010

Schneider, K., Pauly, K. D., Gossen, A., Mevissen, L., Michel, T. M., Gur, R. C., . . . Habel, U. (2013). Neural correlates of moral reasoning in autism spectrum disorder. *Soc Cogn Affect Neurosci*, 8(6), 702-710. doi: 10.1093/scan/nss051

Shenhav, A., & Greene, J. D. (2010) Moral Judgments Recruit Domain-General Valuation Mechanisms to Integrate Representations of Probability and Magnitude. *Neuron*, 67(4), 667-677. doi: 10.1016/j.neuron.2010.07.020

Shenhav, A., & Greene, J. D. (2014). Integrative moral judgment: dissociating the roles of the amygdala and ventromedial prefrontal cortex. *J Neurosci*, 34(13), 4741-4749. doi: 10.1523/jneurosci.3390-13.2014

Sinke, C. B., Sorger, B., Goebel, R., & de Gelder, B. (2010). Tease or threat? Judging social interactions from bodily expressions. *Neuroimage*, 49(2), 1717-1727. doi: 10.1016/j.neuroimage.2009.09.065

Smith, L. J., Anand, P., Benattayallah, A., & Hodgson, T. L. (2015). An fMRI investigation of moral cognition in healthcare decision making. *Journal of Neuroscience, Psychology, and Economics, 8*(2), 116-133. doi: 10.1037/npe0000038

Sommer, M., Meinhardt, J., Rothmayr, C., Dohnel, K., Hajak, G., Rupprecht, R., & Sodian, B. (2014). Me or you? Neural correlates of moral reasoning in everyday conflict situations in adolescents and adults. Soc Neurosci, 9(5), 452-470. doi: 10.1080/17470919.2014.933714

Sommer, M., Rothmayr, C., Dohnel, K., Meinhardt, J., Schwerdtner, J., Sodian, B., & Hajak, G. (2010). How should I decide? The neural correlates of everyday moral reasoning. *Neuropsychologia*, 48(7), 2018-2026. doi: 10.1016/j.neuropsychologia.2010.03.023

Takahashi, H., Kato, M., Matsuura, M., Koeda, M., Yahata, N., Suhara, T., & Okubo, Y. (2008). Neural Correlates of Human Virtue Judgment. *Cerebral Cortex*, 18(8), 1886-1891. doi: 10.1093/cercor/bhm214

Takahashi, H., Yahata, N., Koeda, M., Matsuda, T., Asai, K., & Okubo, Y. (2004). Brain activation associated with evaluative processes of guilt and embarrassment: an fMRI study. *Neuroimage*, 23. doi: 10.1016/j.neuroimage.2004.07.054

Verdejo-Garcia, A., Contreras-Rodriguez, O., Fonseca, F., Cuenca, A., Soriano-Mas, C., Rodriguez, J., ... de la Torre, R. (2014). Functional alteration in frontolimbic systems relevant to moral judgment in cocaine-dependent subjects. *Addict Biol*, 19(2), 272-281. doi: 10.1111/j.1369-1600.2012.00472.x

Wagner, U., N'Diaye, K., Ethofer, T., & Vuilleumier, P. (2011). Guilt-specific processing in the prefrontal cortex. *Cereb Cortex*, 21(11), 2461-2470. doi: 10.1093/cercor/bhr016

Wang, T., Mo, L., Mo, C., Tan, L. H., Cant, J. S., Zhong, L., & Cupchik, G. (2014). Is moral beauty different from facial beauty? Evidence from an fMRI study. *Social cognitive and affective neuroscience*. doi: 10.1093/scan/nsu123

Yoder, K. J., & Decety, J. (2014). The Good, the Bad, and the Just: Justice Sensitivity Predicts Neural Response during Moral Evaluation of Actions Performed by Others. *The Journal of Neuroscience*, 34(12), 4161-4166. doi: 10.1523/jneurosci.4648-13.2014

Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. *Proc Natl Acad Sci U S A*, 104(20), 8235-8240. doi: 10.1073/pnas.0701408104

Young, L., & Saxe, R. (2009). An fMRI investigation of spontaneous mental state inference for moral judgment. *J Cogn Neurosci*, 21(7), 1396-1405. doi: 10.1162/jocn.2009.21137

Yu, H., Hu, J., Hu, L., & Zhou, X. (2014). The voice of conscience: neural bases of interpersonal guilt and compensation. *Soc Cogn Affect Neurosci*, 9(8), 1150-1158. doi: 10.1093/scan/nst090

Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E. D., & Grafman, J. (2009). The Neural Basis of Human Social Values: Evidence from Functional MRI. *Cerebral Cortex*, 19(2), 276-283. doi: 10.1093/cercor/bhn080