The neural correlates of moral aversion and physical disgust using biographical memory

Kate Hardwick, B.Sc.

Perception and Action Research Centre (PARC)

Department of Cognitive Science
Macquarie University, Sydney, Australia

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Summary

Moral thinking in humans is one aspect of behaviour that might set us apart from other species. Where did it come from? Why do we have morals? These are questions many philosophers, psychologists, anthropologists and more recently, neuroscientists are attempting to answer. One dominant hypothesis in the literature is that moral thinking has evolved from what is termed the basic emotion of *physical disgust*. A typical disgust response carries with it certain behavioural responses that aid in the avoidance of infection or disease. These behaviours include a characteristic facial expression, and other rejection behaviours such as gagging and nausea. Thus, if moral thinking has in fact evolved from our typical disgust response, we would expect some overlap in behavioural and neural responses to immoral and disgusting stimuli. The topic of this thesis is first, to evaluate the literature on moral cognition and review the evidence concerning the evolution of moral aversion from physical disgust. Second, in a carefully designed experiment using biographical memory, I test the hypothesis that there are differences between moral aversion and physical disgust. The results show some overlap as well as some differences in neural activity. I then conclude that because of the differences in neural activity, more evidence is needed to support the hypothesis that moral aversion has evolved from physical disgust.

Statement

This work has not been submitted for a higher degree to any other University or institution. I indicate in the thesis that sources of information used and the extent to which the work of others has been utilized. Ethics approval was obtained from the Human Research Ethics Committee (HREC) protocol number: 5201400104.

Signature:

Kate Hardwick

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Literature review

Abstract

Moral aversion is the act of deliberately avoiding malevolent individuals or frowning upon moral infractions. This aversion response in humans, functions to maintain one's social integrity. The basic emotion disgust arises when humans come into contact with disgusting items, such as fouled meat and bodily products. Often these disgusting items are riddled with disease or potentially infectious agents. This basic aversion of disgusting things aids in avoiding potential disease or infection. One dominant and controversial hypothesis in the disgust literature is that moral aversion has evolved from the disgust response. In the following paper, I review the literature concerning the evidence in support of this hypothesis as well as addressing some counter arguments. I conclude that there is not enough evidence to support the idea that moral aversion has evolved from disgust. Further, I provide some suggestions for future research that might add to this discussion.

One fascinating, and possibly unique, phenomenon of human social cognition is the ability to 'know' right from wrong. We call this morality. Even though moral codes vary from one culture to the next, morality seems ubiquitous (Adolphs, 2009b). The basic emotion *disgust* tends to keep us safe from disease and contamination, whereas aversion of moral violators preserves us from social corruption. Moral aversion in this sense is defined as the reactions that result in avoidance, or a general aversion, of those who violate a culturally bound moral code. This is sometimes referred to as *moral disgust.* One field of research investigating the origins of moral aversion suggests that abhorrence of moral violations may have evolved from the basic emotion disgust (Chapman & Anderson, 2013; Haidt, Rozin, McCauley, & Imada, 1997; Rozin & Fallon, 1987). If moral aversion has in fact evolved from the disgust response, we may find some overlap between our behavioural reactions and neural responses that occur in response to moral violations and those that occur in response to things we find disgusting.

In the domain of the basic emotion *disgust*, it is argued that humans display typical behaviours that aid in the avoidance and rejection of disease causing items (Curtis & Biran, 2001; Tybur, Lieberman, Kurzban, & DeScioli, 2013). These behaviours include a characteristic disgusted facial expression, sometimes coupled with gagging and nausea. This aids in the general avoidance and rejection of potentially disease causing, or infectious substances. If, for example, you found meat in your fridge that was months old, the foul odour that emerges from the meat would indicate to you that the meat is inedible. Your face would probably scrunch up into the characteristic disgusted expression and you may even gag a little. If your friend were present, your disgusted reaction would signal to them that eating the meat is a bad idea, avoiding any need for your friend to experience the sight and smell of the meat directly. Thus, this typical disgust response carries useful health information to both the self, and to others in the vicinity. These reactions associated with the disgust response have presumably adapted to aid the survivability of the organism (Curtis & Biran, 2001).

Substances that generally confer a basic disgust response range from bodily products, smells, tastes and visual stimuli (Rozin & Fallon, 1987). Bodily excretions such as pus, urine, blood and excrement usually elicit disgust responses in humans. Similarly, foul odours such as decaying bodies and off meat also provoke a disgusted reaction. In addition, the sight of body envelope violations such as open wounds, mutilations and dead bodies, elicit disgust (Haidt et al., 1997; Rozin & Fallon, 1987). Altogether, these disgust elicitors reflect situations or

substances that may be deleterious to the survival of the self, which result in this automatic disgust response.

The emotion called *moral disgust,* which I refer to as moral aversion, reflects an aversive reaction to moral violators, which presumably functions to maintain social cohesion. Some researchers have suggested this moral aversion has evolved from the disgust response based on several lines of evidence (Chapman & Anderson, 2013; Haidt et al., 1997; Rozin & Fallon, 1987). First, facial expressions typically conveyed in response to physical disgust bear similar features to that conveyed in response to moral infractions (Chapman, Kim, Susskind, & Anderson, 2009). Second, cleansing rituals commonly observed in response to disgusting situations, are used to 'wash away sins' (Schnall, Benton, & Harvey, 2008; Zhong & Liljenquist, 2006). Finally, the use of metaphorical language associated with disgust in conjunction with morally questionable acts is suggested to show an evolutionary link between moral aversion and physical disgust (Chapman & Anderson, 2013; Haidt et al., 1997; Rozin & Fallon, 1987). However, unlike most disgust responses, moral cognition can involve complex decision-making processes. Thus, much of the research supporting this evolutionary link between moral aversion and physical disgust is quite controversial.

One issue with the suggestion that moral aversion has evolved from the disgust response is whether moral aversion is reflexive, like the disgust response. Complex reasoning and rational thought have been implicated in moral thinking, which might suggest that moral cognition differs from the reflexive disgust response. Several researchers suggest that moral judgements are guided by intuitive processes that are automatic (Chapman & Anderson, 2013; Haidt, 2001; Mikhail, 2007). In other words, they propose that when humans make moral judgements, these are automatic emotional responses, where thought and reasoning play only a post-hoc role in justifying these initial intuitive responses (Haidt, 2007). Thus, the proposition that moral aversion has evolved from the disgust response is driven by the idea that moral judgements are intuitive and automatic (Chapman & Anderson, 2013; Chapman et al., 2009; Haidt, 2001, 2007). This automaticity facilitates our avoidance of social harm, akin to the automatic disgust rejection mechanism that aids humans in avoiding potential disease.

In contrast to those researchers' who propose that moral aversion is predominantly an automatic intuitive response, others suggest that moral aversion typically requires rational thinking and reasoning (Gerrans & Kennett, 2010; Royzman & Sabini, 2001). Accordingly,

while emotions may play a role in aspects of moral judgement, many reactions to moral transgressions and dilemmas do not contain an affective component. Instead moral aversion sometimes relies on rational thought and complex reasoning. For example, hearing that a parent was imprisoned for stealing a loaf of bread from a wealthy baker for her starving children might evoke different thoughts than those to hearing it was stolen from a poor baker who also had starving children. Further debate surrounds this contention of intuitive emotional versus complex reasoning in moral aversion.

It seems important to note that decisions based on moral dilemmas and judgements of moral violators differ according to the situation at hand. The context in which these decisions are based are likely to influence these decisions. For example, stealing a loaf of bread to feed a starving family may not seem as morally reprehensible as stealing an expensive car for an impulsive joyride. Thus, moral codes are flexible depending on the context in which the transgressions occur. Another example of the contextual influence on moral codes is the culture in which those codes arise. For instance, some cultures allow women the choice of aborting their unborn child, whereas other cultures forbid this. This suggests that moral codes are not only context dependent but also heterogeneous.

Some researchers have addressed this issue of heterogeneity in studies concerning moral thinking, suggesting that the degree of moral reasoning, whether emotional or rational, depends on the experimental paradigm used to disambiguate the two (Monin, Pizarro, & Beer, 2007). On the one hand, proponents of the emotionalist view tend to employ paradigms aimed at judging others' moral infractions, which often contain emotional reactions. On the other hand, proponents of the rationalist view draw inferences from decisions made in conjunction with complicated dilemmas often employing complex reasoning. Further, Monin and colleagues (2007) suggest that moral thinking goes beyond mere decision-making processes in response to complicated dilemmas and moral violations. They touch on other aspects of morality they believe to be under-researched, such as moral temptation in the individual and moral self-image. These aspects of morality are linked to the psychology of the individual as the moral violator together with the choices and justifications humans make in these situations. Given this heterogeneity in moral thinking, for the purposes of this paper, I use moral aversion as previously defined, the aversive reaction one has to moral violators in response to a culturally bound moral code. I consider this moral aversion to be universal across humans.

These debates concerning the precise notion of morality, pose difficulty for evaluating the evolution of moral aversion from the disgust response. Disgust is considered a basic emotion; it functions to aid the organism's survival success by avoiding disease and ill health. However, although moral aversion may aid in avoiding malevolent individuals, it is difficult to evaluate its significance to survival. Moreover, rational thinking is unlikely to affect the automatic disgust response, whereas complex rational thought is more commonly implicated in moral thinking. Although, it might be possible that *post hoc* rational thought may modulate a disgust response, such as a disgusted response to a nasty skin disease and then told it is not contagious. However, rational thought in response to automatic disgusted responses is yet to be tested. This discrepancy in automaticity and rational thinking in these types of reactions could imply that moral cognition might not recruit disgust response mechanisms.

The initial aim of this paper is to review in detail the literature concerning the neural and behavioural data linking morality and the basic emotion of disgust. Some of the questions I will address are: (1) Is there sufficient evidence to suggest that moral aversion has evolved from physical disgust; and (2) are there different behavioural and neural mechanisms subserving moral aversion and physical disgust? In an attempt to resolve these questions, I will discuss the mental mechanisms of morality. To do this, I will draw from literature on the neural correlates of moral decision-making, as well as behavioural data exploring morally laden decisions. Furthermore, the current research exploring the 'intuitive-emotional versus rational-reason' debate in moral cognition may aid in elucidating solutions to this enquiry. I will then suggest some future directions for research that might help to better understand the complex nature of morality. Finally, I conclude that further empirical and theoretical research is required in this contentious and exciting topic.

2. The domains of disgust

Several competing theories have been proposed to explain the various types of stimuli, or domains, that universally elicit disgust in humans. On the one hand, Rozin and colleagues argue for five domains of disgust eliciting stimuli (Haidt, McCauley, & Rozin, 1994; Rozin & Fallon, 1987; Rozin, Haidt, & McCauley, 2008; Rozin, Lowery, Imada, & Haidt, 1999). These are: distaste (rejection of bitter foods), core disgust (open wounds and spoiled food), animal reminder disgust (animals and their products), interpersonal disgust and moral disgust

(Rozin et al., 2008). On the other hand, Tybur and colleagues (2013) argue for four distinct domains: toxin avoidance, pathogen, sexual and moral disgust.

There is considerable debate concerning the soundness of the domains of disgust proposed by Rozin and colleagues' such as animal reminder disgust (Bloom, 2004; Royzman & Sabini, 2001; Tybur et al., 2013). They argue that humans are universally disgusted by animals because they remind us of our animal nature which in turn, reminds us that we are mortal. This is not necessarily true of all cultures. For example, Hindus revere cows; Buddhists believe in animal reincarnation and many cultures own and love their animal pets y(Royzman & Sabini, 2001). Similarly, whereas cockroaches evoke disgusted responses in many Westerners, other cultures eat them as a delicacy (Mbah C. E. & Elekma, 2007). Thus, these types of disgust cannot be considered universal as they are culturally specified. Therefore, because of this universal inconsistency of animal reminder disgust, I will primarily focus on the four domains proposed by Tybur and colleagues (2013).

The first domain of disgust described by Tybur and colleagues (2013) is termed toxin avoidance, which is also referred to as distaste. Humans generally produce an aversive reaction to sour or bitter tasting substances. This adaptive response aids in the avoidance of ingesting toxins, as toxins generally taste bitter (Glendinning, 1994). This distaste response, or oral rejection of bitter tasting foodstuffs, is seen very early in development and is considered the precursor to the more developed disgust response seen in children older than seven years old (Danovitch & Bloom, 2009).

The second domain of disgust is pathogen disgust. This type of disgust is evolutionarily adaptive and arises later in development. Pathogen disgust forms part of the first line of defense against infection and disease. Thus, items such as petrified meat and dairy products, body envelope violations (e.g., open wounds) and bodily products generally evoke disgust in humans. The likelihood that these products are carrying pathogens is high, thus minimal contact with items such as these, poses an evolutionary advantage in survival (Curtis & Biran, 2001; Tybur, Lieberman, & Griskevicius, 2009).

The third domain is sexual disgust. This aids in the avoidance of potentially 'unfit' mates, who might be considered of low sexual value. For example, most healthy humans find the thought of incest relations as especially disgusting (Borg, Lieberman, & Kiehl, 2008). This is

likely due to the high costs of mating with kin because the same genetic mutations tend to be carried by close relatives. These mutations are presumably inherited by the offspring of close relatives (Bittles & Neel, 1994; Charlesworth & Charlesworth, 1999). Sexual disgust may also emerge in response to sexual thoughts of pre or post reproductive individuals such as children and the elderly. Thus, sexual disgust is likely an adaptive mechanism that functions in choosing sexual mates of appropriate quality and health.

Finally, Tybur and colleagues suggest the fourth domain is moral disgust. Moral disgust is an abhorrence of acts ranging from stealing, lying and cheating to racism, chauvinism and exploitation of others. This type of moral disgust is proposed to safeguard oneself or one's community from malevolent individuals promoting social cohesion (Adolphs, 2003).

In sum, all four of these domains of disgust seem separable and distinct. While they commonly demonstrate an aversion or rejection mechanism, it raises a question about how distinct these avoidance strategies are in fact. It is possible that sexual disgust varies across cultures and as mentioned previously, morals are inherently defined by cultural norms. Thus, distaste and pathogen disgust are presumably the prime candidates of universal disgust responses. These are the types of disgust that I will refer to when speaking of the basic emotion disgust, which I use interchangeably with the physical disgust.

3. The proposed link between the basic emotion disgust and moral aversion

There are several lines of research that support the hypothesis that moral disgust has evolved from the basic emotion disgust. First, when we refer to an individual's behaviour that is morally questionable, we tend to use language that we would normally associate with disgusting items or events; for instance, 'her behaviour was nauseating' or 'he's a rotten egg' (Danovitch & Bloom, 2009; Rozin & Fallon, 1987). Second, the prototypical disgusted facial expression, described by Ekman and Friesen (1971), is sometimes expressed in response to moral transgressions (Chapman et al., 2009). Finally, the influence of cleanliness signals, generally associated with purifying contaminated items, appear to affect decision making in the moral domain (Helzer & Pizarro, 2011; Schnall, Benton, et al., 2008; Zhong & Liljenquist, 2006).

3.1 The use of metaphor for physical disgust and moral aversion

Several researchers argue that the use of disgust metaphorical language in conversations concerning immoral behaviours is evidence for the hypothesis that moral thinking has

evolved from the basic emotion disgust (Chapman et al., 2009; Haidt et al., 1997; Rozin & Fallon, 1987; Rozin et al., 1999). For example, we often speak of political transgressions as revolting and exploitative tactics as disgusting. Further, in Japanese, French, Spanish, Russian, Hebrew and Bengali, there is a word that describes both gross things and immoral people or events (Haidt et al., 1997). This use of metaphorical language regarding moral transgressions and physical disgust is used as evidence that moral disgust evolved from physical disgust.

However, although we commonly refer to malevolent individuals as disgusting, sickening or revolting, this may merely provide evidence that aversion of any such negative person or event involves the use of metaphorical language (Bloom, 2004; Nabi, 2002; Pizarro, Inbar, & Helion, 2011; Royzman & Sabini, 2001). Someone whom we think is morally reprehensible could just as easily be referred to as an idiot or an ignoramus, which is also common, but not related to disgust. Thus, given the breadth of the use of metaphorical language in descriptions not related to disgust or morality (e.g., 'he drowned in a sea of grief' or 'clear as mud') the use of metaphors does not provide strong evidence that moral aversion evolved from physical disgust. Further, despite the fact that this metaphorical symbolism for disgust and moral aversion occurs cross-culturally (Haidt et al., 1997), metaphorical representations not related to disgust and moral aversion also occur cross-culturally (Royzman & Sabini, 2001; Rozin et al., 2008).

Other research programs have explored the use of the 'disgusted' facial expressions in the moral domain. As previously described, there is a prototypical facial expression associated with the basic emotion of disgust and is said to be universally recognised (Ekman & Friesen, 1971). A number of researchers found that participants, when asked which facial expression matches an immoral scenario, participants tended to choose the disgust expression over an angry or sad expression (Danovitch & Bloom, 2009; Ekman & Friesen, 1971; Hutcherson & Gross, 2011).

Further support for the hypothesis that moral aversion evolved from physical disgust investigated this dual use of facial expressions. In their study (Chapman et al., 2009) facial expressions were analysed using facial electromyography when participants tasted sour and bitter tasting concoctions while viewing disgusting pictures. The facial expressions during these disgusting conditions were then compared with the facial expressions during an

ultimatum game manipulated to provide unfair offers. The researchers found that the more unfair the offer, the more the participants' facial expression resembled that which occurred in response to the physically disgusting conditions. They concluded that because of the use of the same facial expression in both the disgusting conditions as well as the moral condition, that aversion of moral violators has co-opted the evolutionarily adaptive disgust response. However, this particular study was later challenged (Royzman & Kurzban, 2011a, 2011b). It was argued that an alternative interpretation of Chapman's and colleagues (2009) results is that the use of the disgusted facial expression in response to immoral behaviour might merely imply a metaphorical use of the disgusted facial expression (Royzman & Kurzban, 2011b). Given this possible alternative explanation, these data do not provide strong evidence that moral aversion evolved from physical disgust.

3.2 Cleanliness reminders and 'washing away sins'

Several experiments have been conducted testing physical cleansing behaviours subsequent to immoral behaviour (for a review see (Chapman & Anderson, 2013)). When individuals contact potentially contaminated items, a common reaction is the washing of hands, clothes or the items themselves. These cleansing behaviours presumably function to minimise pathogenic or infectious qualities of the contaminant. Consistent with physical cleansing of disgusting items, some people associate cleansing rituals with purifying the 'soul'. The physical cleansing of oneself has religious affiliations and has been long reported to wash away 'sins' (Chapman et al., 2009; Rozin & Fallon, 1987). Further, individuals with obsessive compulsive disorder (OCD) will wash their hands excessively for fear of contamination and also tend to wash excessively in response to moral transgressions (Elliott & Radomsky, 2013). Several lines of evidence support the belief that as one can wash dirt from their body, one might also be able to *purify the soul* by washing away sinful, or immoral behaviour.

Zhong and Liljenquist (2006) investigated the link between cleansing rituals and the impact cleansing actions have on moral infractions. Participants were asked to recall and then write about their own past moral transgressions. Following this recall and write procedure, participants were asked to choose from a list their preferred grocery products. The results showed that participants were more likely to choose cleaning products over non-cleaning products. Further, following the recalling and writing about moral transgressions, participants performed a word completion task (filling in missing letters from a word string). These results

indicated that participants were more likely to complete the words with cleansing words than non-cleansing words. The authors argued that this link between cleansing of dirt and cleansing of the soul is indicative of the link between moral aversion and physical disgust. An alternative supposition is a metaphorical extension of cleansing rituals associated with pathogen avoidance and 'washing away' a guilty conscience.

Other researchers (Helzer & Pizarro, 2011) investigated the effects of cleansing products on political attitudes. The researchers placed a hand-sanitiser, labeling it a 'purity reminder', in clear view of an area where researchers conducted a survey. The survey contained questions directed to undergraduates regarding political positions in three domains: moral, social and fiscal. Across all three political domains, they found that the presence of the purity reminder influenced participants into more conservative political attitudes (i.e., less open-minded) as compared with the group without the sanitiser in view. They speculated that the presence of the purity reminder influenced participants into more conservative attitudes and proposed a link between cleansing rituals and decision-making in the moral domain. One concern with this speculation is that fiscal and social attitudes, both of which are devoid of moral implication, were similarly affected as with the moral attitudes. Thus, it does not rule out the possibility that many types of judgements are affected by 'physical purity'.

In contrast to Helzer and Pizarro's study (2011), a study performed by Schnall and colleagues (2008) found the opposite effect. They primed their experimental participants with several purity synonyms and control participants with neutral words. Following priming, they asked their participants to rate four morally questionable scenarios. They found the cleansing word priming influenced participants into less severe moral judgements. These inconsistent findings between both studies make it difficult to evaluate the hypothesis that physical purity, commonly related to physical disgust, is closely linked to morality.

In sum, the use of disgust language in association with moral transgressions may simply be explained by metaphor rather than suggesting a fundamental overlap in the underpinnings of disgust and moral aversion. Further, the use of similar facial expressions in response to immoral and disgusting things might also be explained by the use of metaphorical expression. Finally, the studies on 'washing away a guilty conscience' do not provide consistent evidence for the hypothesis that moral aversion evolved from physical disgust. To further investigate

the hypothesis that moral aversion evolved from physical disgust, I now turn to the literature exploring their neural correlates.

4. Disgust, morality and the brain

Several neuroimaging studies have investigated the neural correlates linked to processing different types of disgust-eliciting stimuli (Calder et al., 2007; Fitzgerald et al., 2004; Jabbi, Bastiaansen, & Keysers, 2008; Klucken et al., 2012; Phillips et al., 2004; Stark et al., 2007; Wicker et al., 2003). Moreover, several neuroimaging studies have investigated the link between physical disgust and moral aversion including decision-making in the moral domain (Borg et al., 2008; Moll, de Oliveira-Souza, Eslinger, et al., 2002; Moll, de Oliveira-Souza, et al., 2005; Parkinson et al., 2011). Although the literature exploring the neural correlates of decision-making in the moral domain is sparse compared with those examining the basic emotion disgust, preliminary evidence shows that there is some common neural activity. However, distinct neural activity is also observed when processing these different types of stimuli.

4.1 The neural correlates of disgust

Many researchers investigating the basic emotion disgust show consistent activation in the anterior insula (AI). This area has also been found to be activated in studies using disgusted facial expressions (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Phillips et al., 2004; Stark et al., 2007); disgusting scenes (Moll, de Oliveira-Souza, Eslinger, et al., 2002); when participants feel disgust (Fitzgerald et al., 2004); imagined and observed disgust (Jabbi et al., 2008) and in meta-analyses of research investigating the neural underpinnings of emotions (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Vytal & Hamann, 2010). Despite the AI's neural correlation with disgusting stimuli, one review (Craig, 2009) describes numerous behaviours that show activation in the AI which are unrelated to disgust. Activation in the AI has been shown in conditions using interoceptive stimuli such as itches, hunger and thirst, and exteroceptive stimuli such as recognising emotions and attentional demands. Moreover, the AI is linked to other tasks involving conscious awareness, music perception and time keeping. Although the AI may be unequivocally established in processing disgusting stimuli, its role in tasks unrelated to disgust suggests that it is not disgust specific.

The amygdala has also been linked to processing disgust related stimuli (Anderson et al., 2003; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Moll, de Oliveira-Souza,

Eslinger, et al., 2002). The amygdala's involvement in processing disgust expressions presumably stems from non-conscious or sensory experience that acts as a threat detection mechanism (Pessoa & Adolphs, 2010). Anderson and colleagues (2003) demonstrated this by superimposing disgusted faces onto houses. When asked to attend to the house, participants showed a strong response in the amygdala and when asked to attend to faces displaying disgust, strong activation in the insula was observed. Another study has confirmed amygdala activation when processing disgust-related stimuli (Borg et al., 2008).

Further brain regions involved with disgusting stimuli were identified in two recent meta-analyses of emotion literature. They identified subcortical regions, specifically the caudate and putamen (Lindquist et al., 2012; Vytal & Hamann, 2010) correlated with disgust. Researchers investigating the neural substrates involved in processing emotionally evocative stimuli suggest that subcortical structures in negatively valenced emotions are bottom-up mechanisms that send projections to higher cortical regions (Etkin, Egner, & Kalisch, 2011; Ochsner & Gross, 2005). These cortical regions are presumably involved in the conscious evaluation of an emotion. Thus, the conscious evaluation of disgusting stimuli probably activates regions in the neocortex. This is consistent with activation found in response to disgust-related stimuli in the medial prefrontal cortex, frontal operculum and temporal lobe (Borg et al., 2008; Jabbi et al., 2008; Jabbi, Swart, & Keysers, 2007).

Altogether, these results show that the neural correlates of disgust tend to be found in subcortical structures and cortical regions. If moral aversion has evolutionarily exapted the disgust response, I would predict that the neural underpinnings of responses to disgusting things would show marked overlap with those responses to moral violators. Although strong neural overlap between moral aversion and physical disgust may not be the sole predictor of the evolutionary link between the two, it is one way to probe evolutionary questions concerning behaviour.

4.2 The neural correlates of morality

In contrast to the basic emotion disgust, moral aversion has received less attention in the brain imaging literature, however, a growing number of researchers have taken on this task. Studies have investigated the neural correlates of moral aversion (Parkinson et al., 2011), reactions to moral dilemmas (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001) and decision-making processes concerning honesty that involve moral cognition (Greene & Paxton, 2009).

Further evidence regarding the neural substrates involved with aspects of moral cognition come from lesion studies (Koenigs et al., 2007).

Parkinson and colleagues (2011) investigated neural activity in response to different types of moral transgressions. They provided participants with sample scenarios in the third person in three moral domains: disgusting (acts of incest), harmful and dishonest events. Although the authors found overlap in the dorsomedial prefrontal cortex across conditions, distinct neural activity was also observed. This study provides evidence that different types of moral violations are differentially processed in the brain. The differences in activity between the conditions could be due to the different types of emotions produced when considering immoral events. Alternatively, differences in neutral activity could reflect different cognitive processes, such as 'self' or 'other' representations.

In another study, Greene and colleagues (2001) investigated the neural correlates of the affective (personal) and cognitive (impersonal) components using moral dilemmas. In the impersonal condition, participants had to choose whether to flip a switch that would kill one person, but save five people. The personal condition differed where flipping the switch was replaced with pushing someone to his death, in order to save the five people. The neural activity differed between conditions. Brain regions associated with emotion processing within the temporal and prefrontal cortices were active in the personal condition. Whereas brain areas associated with working memory in the parietal and frontal cortices responded in the impersonal condition. This demonstrates that the brain responds differentially to different types of morally laden stimuli.

In sum, there is some evidence pointing to overlapping circuits in the domain of moral cognition and the basic emotion disgust, particularly when emotional components are present in the moral stimuli.

4.3 Overlap of neural correlates of disgust and immoral stimuli

Some researchers have explicitly investigated whether an overlap exists during the processing of immoral and disgusting stimuli. Moll et al (2005) conducted an experiment that investigated the basic emotion disgust and the moral emotion of indignation. They did this by presenting morally aversive and disgusting statements to participants. Indeed they found

overlapping neural activation in both of these conditions, which included bilateral orbitofrontal cortex (OFC), right inferior frontal gyrus and inferior temporal gyrus. However, these results are difficult to interpret as the disgusting stimuli contained immoral facets and similarly, the immoral stimuli contained disgusting facets.

Another study conducted by the same research team (Moll, de Oliveira-Souza, Bramati, et al., 2002) presented sentences to participants that contained neutral (the elderly sleep more at night), morally unpleasant (the judge condemned the innocent man) and non-moral unpleasant (he licked the dirty toilet) content. They found medial OFC activity in the morally unpleasant condition and lateral OFC and amygdala activity in the non-moral unpleasant condition.

Adding further complexity, differences in neural activity are observed in response to different types of stimuli. In this study, instead of sentences Moll, de Oliveira-Souza, Eslinger, et al. (2002) presented pictures depicting moral violations. These included physical assaults or abandoned children, and non-moral aversive stimuli were bodily lesions or dangerous animals. The morally unpleasant pictures revealed activity in the medial OFC, medial frontal gyrus and superior temporal sulcus (STS). Whereas the non-moral condition resulted in middle frontal gyrus, amygdala and AI activity.

These two latter studies demonstrate that pictures and sentences depicting disgust reveal activity in subcortical regions, as well as in higher order emotion processing centres in the PFC. Whereas activity in response to moral transgressions activate only cortical structures. This absence of neural activity in subcortical regions in response to moral infractions might indicate the morally laden reactions recruit higher order brain regions for conscious evaluation. More widely distributed neural activity was observed with the observation of pictures than was observed in response to sentences. The differences in brain activity across studies might be due to different types of stimuli (i.e., reading sentences vs. viewing pictures). The saliency of the stimuli may have varied such that visual stimuli might induce different arousal levels as compared with reading sentences. Therefore, it seems important to note that stimuli differences as well as the moral and disgusting content are variables in neural activity across studies investigating moral aversion.

Finally, Borg and colleagues (2008) explored whether a difference exists between pathogen, moral or incest aspects of disgust. They tested males with statements of acts on, or performed with, a sister. Presentations included statements such as: you eating your sister's scab (pathogen), you burglarising your sister's home (moral) and you watching your sister masturbate (incest). They found activation in a common neural network of brain regions for the moral and pathogen disgust conditions in subcortical structures and the PFC. However, the disgust condition yielded significantly more brain activity than the moral condition. This might be due to the salience of the threat of infection or disease, which could be more deleterious to the survivability of the organism.

The threat of moral violators might be less salient than the threat of infection or disease evidenced by greater neural activity in the disgust condition. Moreover, they found distinct neural activity where pathogen disgust showed greater activity in the amygdala and moral disgust showed greater activity in the medial PFC and bilateral temporoparietal junction (TPJ). The amygdala functions as a threat detection mechanism sending projections to higher brain regions in the cortex for conscious evaluation (Ochsner & Gross, 2005). Thus, information regarding immoral acts might not represent an immediate threat. This might explain the PFC activity in the moral condition illustrating the importance of executive function in moral cognition.

Altogether, these results suggest that there is some overlap in neural activity between physical disgust and moral aversion. Although, much evidence points to distinct neural activity when processing disgusting things and moral aversive stimuli. Moreover, different types of paradigms used in moral conditions evoke different patterns of neural activity. This raises questions about the extent to which these findings reflect a fundamental overlap in the physical disgust and moral domain. Disgust reactions are likely adaptive, functioning to reduce exposure to infectious or disease causing stimuli. This evolutionarily adapted function might explain the widespread neural activity in subcortical and cortical structures. In contrast, observing moral violators or hearing about moral infractions is presumably less threatening to survival, which might explain responses in higher cortical structures. Furthermore, differences in neural activation might be explained by whether the research paradigm tests the cognitive or affective component of moral cognition.

5. Affective versus cognitive morality

Philosophers have argued for centuries about the roots of morality. This dates back to the 16th century when David Hume suggested that reason is the slave of emotions. In essence, Hume argued that human judgements are guided by emotions and rarely engage rational thought. Immanuel Kant disagreed, arguing that humans predominantly engage critical thought and rational reasoning in judgements concerning moral permissibility (as cited in (Monin et al., 2007)). This debate continues, and despite this philosophical tradition arguing for either emotion or reason in guiding human thought, the use of scientific paradigms has helped elucidate facets of this debate.

The moral psychologist Jonathon Haidt has proposed the *Social Intuitionist Model* of morality (Haidt, 2001). This article highlighted that an undue focus on rationality and reason in moral judgement existed at the expense of intuitive and emotional influences in these judgements. He suggested that many moral judgements occurring in everyday life are more likely to consist of intuitive responses. These intuitive responses are then followed by an *ex post facto* reasoning process that serves only to justify this initial response. Following this article, various research programs have set out to investigate the affective component in moral cognition, using the basic emotion disgust in particular.

5.1 Induced basic disgust affects moral ratings

There are a number of behavioural and neurological experiments that have investigated the link between moral disgust and the emotion disgust by inducing physical states of disgust. This inducement of disgust modulates participants' reactions to moral transgressions (Schnall, Haidt, et al., 2008; Wheatley & Haidt, 2005). This effect, they propose, illustrates that moral cognition is emotionally and intuitively driven. The effects that induced disgust has on decision-making processes in moral dilemmas are also used as evidence for the evolution of moral aversion from the disgust response.

One study tested whether hypnotically-induced disgust contributes to moral judgement (Wheatley & Haidt, 2005). Participants were hypnotised into feeling physically ill when they read the words *often* or *take*. Once out of hypnosis, participants performed a task rating moral dilemmas such as shoplifting, eating one's dead dog and cousins partaking in incest relations. They rated these acts on two scales: how disgusting and how morally wrong. Embedded

within some of these dilemmas were the target hypnotic words, ‘often’ or ‘take’. They found that the dilemmas that contained the target hypnotic word were viewed as more morally wrong as well as more disgusting. The authors argued that visceral, or gut feelings, influence moral decisions. This, according to the researchers, showed evidence of the inherent affective response in moral decision-making. However, an alternative interpretation of their initial finding might be that hypnotically induced disgust generates a negative mood which might also be induced by other emotions.

In another study Schnall, Haidt, et al. (2008) induced disgust in four ways: a disgusting odour (fart spray), a dirty environment in which to complete the experiment, recalling a disgusting event and using disgusting excerpts from films. Following each of the disgust inducements, participants were asked to rate the permissibility of four morally questionable scenarios. They found that participants rated the moral judgements significantly less permissible when disgust was induced. In their final experiment they induced sadness. This was conducted to test whether these greater impermissibility ratings were specific to disgust or a general negative valence. Those in the sadness condition rated immoral scenarios significantly more permissible than in the disgust condition. They speculated that moral judgements were harsher due to the inducement of the basic emotion of disgust because disgust is inherently linked with moral aversion, whereas other emotions such as sadness are not. These results are difficult to interpret.

First, the researchers controlled for the possibility that any negative emotion might yield the same results, but the choice of sadness is problematic. Researchers, Lench and Darbor (2014) investigated perceived risk when participants experienced either anger or sadness. Those participants experiencing sadness perceived more risk than those experiencing anger who perceived less risk. These results indicate that the type of negative emotion, whether it is disgust, anger or sadness, influences judgements differently.

Second, in their latter three experiments, Schnall et al. (2008b) take into account participants’ ‘Private Body Conciousness’ (PBC) rating. This is a rating scale that determines how individuals differ in their gut reactions to aversive stimuli. Those who rate high on this scale are more sensitive to internal bodily experiences than those who rate low. The results found that only those who rated high on this scale found moral transgressions to be less permissible than those who rated low on this scale. In fact, those who rated low on this scale did not rate

moral transgressions as less permissible than the control subjects. Thus the causal link between disgust and morality might have been due to the stimulus.'

Another group of researchers tested ratings on moral dilemmas (the same four dilemmas as used in Schnall, Haidt, et al. (2008)) in the presence of a disgusting tasting drink (Eskine, Kacinik, & Prinz, 2011). The researchers found that the bitter tasting drink influenced participants into harsher moral judgements compared with those who drank a sweet tasting concoction. As previously mentioned, it is possible that drinking a bitter tasting drink merely puts one into an aversively reactive mood, and that when in this type of mood, people make harsher judgements of any kind. Without appropriate controls, it is difficult to interpret these data clearly. Thus, disgust may still be linked with moral aversion, although other emotions may also have such a link.

In sum, by placing someone in a negative mood by inducing either disgust or anger is likely to affect all sorts of evaluations. Thus, there is no evidence for a stronger link between moral aversion and disgust than moral aversion and anger.

6. Future directions for research

Given that the study of the neural correlates of morality is relatively recent, the time is now here to instigate tighter controls to decrease confounding effects. For example, neuroimaging studies that assess the link between moral transgressions and physical disgust should exclude any suggestion of things that could be construed as disgusting. Often studies attempting to disambiguate the two domains fall into this trap, unknowingly using morally aversive stimuli containing physically disgusting traits (Moll, de Oliveira-Souza, et al., 2005). Another example of a potential confound is found in the behavioural literature and concerns experimenter bias. Thus, experimental paradigms examining the evolutionary link between moral judgements and the basic emotion of disgust could use investigators blind to the purposes of the study. Central to these ideas is the elimination of ambiguity between moral aversion and physical disgust.

Tybur and colleagues (Tybur et al., 2013) researchers argue for four distinct domains of disgust: toxin, pathogen, sexual and moral. Thus, another approach to delineate the evolutionary link between moral aversion and physical disgust could be to investigate each of these domains of disgust. The neural correlates of these domains may shed light on common

and distinct neural pathways in the different types of disgust. Similarly, that moral aversion contains affective and cognitive appraisal mechanisms indicates that various types of mechanisms play a role in moral judgements and thus, moral aversion. Moreover, aspects related to the moral self and the morality of others implies that moral cognition is heterogeneous. Disambiguating the behavioural and neural responses to the different aspects of moral cognition leaves much scope for further research in this area.

Moral judgements are cognitively controlled as well as emotionally driven. Currently, moral judgements asked of participants might not reflect the breadth of moral transgressions humans are commonly exposed. For example, the famous trolley dilemmas are frequently used to evoke moral judgements, such as, 'is it ok to flip a switch that saves 5 people, but kills one' versus 'is it ok to push a man in front of a trolley, killing him, but saving 5 others' (Greene et al., 2009; Greene et al., 2001; Mikhail, 2007). Similarly, other experimenters use questions such as "how morally wrong is it to eat your already-dead dog?" Although these are effective stimuli to probe moral cognition, these are not common dilemmas humans are faced with in everyday life (Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). Thus, perhaps the use of moral dilemmas that more accurately reflect decisions we make in everyday life may help to elucidate the universal mechanisms of moral cognition. These could include for instance, perceptions of politicians who use taxpayer's money for their own gain, or reactions to morally offensive behaviours such as racism, cheating and lying.

Finally, one intriguing aspect of moral cognition is that moral norms are fundamentally shaped by culture and context. Interesting to note is that one researcher has stated that killing a person is considered morally wrong in all cultures (Haidt, 2007). However, this is a false statement illustrated by cultures who perform honour killings and institutions that implement the death penalty. Thus, there does not seem to be moral violations that are absolute across cultures. Even though moral 'rights' and 'wrongs' diverge across cultures, presumably, behavioural and neural responses to those culturally bound rights and wrongs are consistent across humans. This is reflected by the fact that all societies have moral codes (Adolphs, 2009a). Cross-cultural studies may provide exciting new avenues to understand the cultural differences in moral cognition.

Conclusion

The feeling of disgust is an evolutionarily adapted mechanism that functions to avoid or reject potential disease and contamination. Although moral aversion might function to reject or avoid contact with malevolent individuals, the evolutionary link between these two avoidance strategies remains unresolved. There are some methodological issues with studies that have been used to suggest that moral aversion has evolved from physical disgust where tighter controls could eliminate these issues. Further, the use of disgust language with reference to moral transgressions might only serve to highlight the diversity and complexity of expression in language used as metaphor. Thus, this use of metaphor might show a linguistic link rather than an evolutionary link.

While some overlap is observed in investigations examining the neural correlates of moral aversion and physical disgust, differences are also apparent. Moral judgements appear to recruit processing regions in the higher cortex, while disgust shows activity in both subcortical and cortical regions. This lack of neural activity in subcortical regions in response to moral transgressions could be used as evidence against the hypothesis that moral aversion evolved from physical disgust. Moreover, aspects of moral cognition sometimes require complex decision-making processes of deliberate thought and reasoning, whereas disgust responses are automatic. This might also suggest that moral aversion is not evolutionarily linked to disgust.

Finally, to answer the questions defined at the start of this review: (1) Is there sufficient evidence to suggest that moral aversion has evolved from physical disgust? The evolutionary link between moral aversion and physical disgust does not appear to be strong, nonetheless, the absence of evidence does not mean evidence of absence. Given the infancy of the neuroscientific exploration of moral cognition, much research is needed in this area to further elucidate the complexity of moral cognition and its relation to physical disgust. (2) Are there different behavioural and neural mechanisms subserving moral aversion and physical disgust? The behavioural differences are reflected by the fact that disgust responses are automatic, whereas moral judgements sometimes require complex thought and deliberation. On the other hand, there appears to be similarities in neural circuits subserving moral cognition and physical disgust as well as differences. These differences likely arise from the varying paradigms used to probe emotional or rational components of moral cogntion. Much more

research is needed into this exciting area linking the basic emotion disgust and moral aversion.

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Research article

Abstract

Moral aversion toward individuals whose behaviour is malevolent, serves as a rejection mechanism to maintain social cohesion. The disgust response on the other hand, is a rejection mechanism that serves to keep us safe from infectious or disease causing stimuli. To investigate the hypothesis that moral aversion has evolved from physical disgust, we examined the overlap between responses to moral aversion and physical disgust. We trained participants to remember faces paired with biographies of physically disgusting vignettes (disgusting faces) and immoral vignettes (immoral faces). We used neutral vignettes as a control for biographical memory and unknown faces as a control for the presentation of the stimulus (faces presented in the scanner). Once the participants were trained on these biographies, we examined the neural activity using functional Magnetic Resonance Imaging (fMRI). When we controlled for biographies, the results showed that biographies of disgusting vignettes reveal activity in the left temporopolar region. When we controlled for the presentation stimuli (unknown faces) we found overlap in the disgusting and immoral vignettes in the left premotor cortex. Further, distinct neural activity was found for the immoral faces and the disgusting faces. Given the differences in neural activity found between these conditions, we conclude that further research is necessary to support the hypothesis that moral aversion has evolved from physical disgust.

The disgust response in humans is an evolutionarily adapted rejection mechanism that functions to keep us safe from infection and disease (Curtis & Biran, 2001; Rozin & Fallon, 1987; Tybur, Lieberman, Kurzban, & DeScioli, 2013). When one is faced with a dead and decaying animal corpse, infested with maggots and wreaking a foul odour, behavioural responses might include gagging and nausea, as well as the classic disgusted facial expression. It is the decaying matter of corpses that are riddled with microorganisms, which could pose a fatal threat to the health of one that made contact with the corpse. Thus, these typical responses to disgusting things aid the avoidance and rejection of items that may be carrying pathogens (Curtis & Biran, 2001).

Moral aversion is defined as aversive reactions to moral transgressions which likely results in the rejection of malevolent individuals. This rejection of moral violators presumably functions to maintain social cohesion. One dominant hypothesis in the disgust literature suggests that moral aversion has exapted (an evolved trait originally serving one function provides the foundation for a new function) the typical disgust response. In other words, the evolutionarily adapted behavioural responses to *disgusting* items has provided the foundation for behavioural mechanisms to form a new ability, *moral aversion*. The topic of this paper is to assess the similarity and differences between physical disgust and moral aversion. First, we critically review the evidence that has been used to argue for an evolutionary exaptation of moral aversion from the physical disgust response. Second, we present the results of a carefully designed study examining the neural underpinnings of both physical disgust and moral aversion.

Several lines of evidence have been used to support the hypothesis that while physical disgust keeps us safe from infection and disease, moral aversion keeps us safe from social corruption, and therefore relies on similar foundations (Chapman & Anderson, 2012, 2013; Haidt, Rozin, McCauley, & Imada, 1997; Rozin & Fallon, 1987). First, researchers have shown that people use metaphors when describing both pathogen related disgust and moral transgressions. Examples include ‘her behaviour is nauseating’ or ‘the legislation just passed is sickening’. There are claims that the use of metaphorical language for both physically disgusting things and moral transgressions demonstrates an evolutionary link (Chapman & Anderson, 2013; Haidt et al., 1997; Rozin & Fallon, 1987; Rozin, Haidt, & McCauley, 2008).

However, the use of metaphor is ubiquitous in language (Royzman & Sabini, 2001). Phrases such as 'clear as mud' and 'it's raining men' illustrate this point. Therefore, the use of disgust language in relation to moral transgressions might simply reveal the dynamic properties of language *per se,* rather than demonstrate an evolutionary link between physical disgust and moral aversion. When referring to physically disgusting things, such as finding faeces on the floor of a public toilet, participants used statements such as, 'grossed out' and 'repulsed' whereas, words such as, 'disgust' and 'disgusted' were used in response to events that trigger anger that were either annoying or irritating (Nabi, 2002). The wide-spread use of metaphorical language has been used to argue that the use of metaphor does not provide strong evidence for the link between physical disgust and moral aversion (Royzman & Sabini, 2001).

Another line of evidence that has been argued to link morality and disgust comes from observations that the prototypical disgusted facial expression is sometimes present when reacting to moral transgressions (Chapman, Kim, Susskind, & Anderson, 2009; Danovitch & Bloom, 2009). One study analysed facial expressions using facial electromyography during the experience of physical disgust and then again when reacting to unfair offers in an ultimatum game (Chapman et al., 2009). The authors found similar facial muscular activation to both physical disgust and the unfair offers and claim that this provides evidence for the evolution of moral aversion from physical disgust. However, others have argued that metaphor is not limited to language (Royzman & Kurzban, 2011a, 2011b). Although facial expressions can signal an internal bodily state, they can also be used metaphorically such as when a child pokes his tongue out when angry or upset. On balance, it seems that disgusted facial expressions in response to unfair offers does not provide strong evidence for the evolutionary link between moral and physical disgust.

Data suggesting links between cleansing behaviours and moral transgressions have also been interpreted as support for the exaptation of moral aversion from physical disgust. Cleansing behaviours, for example, hand washing following a toilet break, generally function to reduce the risk of infection and disease (Curtis & Biran, 2001). However, sometimes these behaviours are observed in reaction to immoral acts (Zhong & Liljenquist, 2006). A number of studies have tested the effects of physical cleansing, cleaning products and the presence of hand sanitisers on moral judgements (Helzer & Pizarro, 2011; Schnall, Benton, & Harvey, 2008; Zhong & Liljenquist, 2006). The results for these studies have been inconsistent, where

some have found cleanliness indicators to provoke harsher moral judgements (Helzer & Pizarro, 2011) whereas others found cleanliness reminders to provoke less severe judgements (Schnall et al., 2008). These ambiguous behavioural results make it difficult to evaluate the relationship between cleansing practices in both physical disgust and moral aversion.

Neuroimaging studies investigating the neural correlates of disgust causing stimuli and moral aversion have added to the debate on the exaptation of moral aversion from physical disgust. If moral aversion has in fact evolved from the disgust response, we predict that people experiencing disgust and moral aversion should use similar brain areas. There have been several studies that attempt to test this hypothesis using fMRI (J. Borg, Lieberman, & Kiehl, 2008; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Moll, de Oliveira-Souza, Eslinger, et al., 2002; Moll, de Oliveira-Souza, et al., 2005; Parkinson et al., 2011). Thus far, there is some evidence for the prediction that disgust and moral aversion elicit similar brain activation. Although, there is also evidence that neural responses to disgusting things differs from neural responses to immoral acts. This could be due to the paradigm used to disambiguate the two. We now review these studies to provide the foundation for the experiment in this paper.

Moll and colleagues have conducted two studies exploring the neural correlates of responses to moral and non-moral (physically disgusting) stimuli, one using sentences (Moll, de Oliveira-Souza, Bramati, et al., 2002) and the other using pictures (Moll, de Oliveira-Souza, Eslinger, et al., 2002). Although there was similar neural activity in response to both moral and disgusting conditions, there were also distinct activation differences between the conditions. Disgusting conditions evoked considerably more widespread neural activity than moral conditions. Immoral sentences produced activity in the medial orbitofrontal cortex (OFC) whereas disgusting sentences evoked activity in the lateral OFC and the amygdala (Moll, de Oliveira-Souza, Bramati, et al., 2002). Pictures of immoral acts produced more widespread activity than immoral sentences, including the medial OFC, medial frontal gyrus and superior temporal sulcus (STS) whereas disgusting pictures revealed activation in the middle frontal gyrus, anterior insula (AI) and amygdala (Moll, de Oliveira-Souza, Eslinger, et al., 2002). Across the two studies, immoral conditions predominantly evoke activity in cortical regions whereas disgusting stimuli evokes more widespread activity in subcortical structures, as well as in cortical regions. This might reflect a higher evaluative component

when reacting to immoral acts as compared with automatic disgust responses typical of threat detection in the amygdala (Pessoa & Adolphs, 2010).

In another fMRI study on disgust versus moral aversion, J. Borg et al. (2008) examined the neural responses to pathogen disgust and moral aversion using first person statements such as, 'you eating your sister's scab' and 'you burglarising your sister's home'. They found activity in the moral condition in the temporopareital junction and medial prefrontal cortex (PFC), whereas in the disgust condition, activity was observed in the amygdala. Consistent with the above results (Moll, de Oliveira-Souza, Bramati, et al., 2002; Moll, de Oliveira-Souza, Eslinger, et al., 2002), physically disgusting stimuli seems to activate more primitive subcortical structures, whereas moral violations show activity in the more recently evolved cortex.

These studies have all used statements or pictures depicting immoral acts (J. Borg et al., 2008; Moll, de Oliveira-Souza, Bramati, et al., 2002; Moll, de Oliveira-Souza, Eslinger, et al., 2002; Parkinson et al., 2011) that suffer from the same limitation or confound: insufficient control over the experimental stimuli. In their experiment, Moll, de Oliveira-Souza, et al. (2005), the sentences used in disgusting conditions contained moral components and immoral sentences contained disgusting components which confounded their stimuli. In another study (Moll, de Oliveira-Souza, Eslinger, et al., 2002) the pictures in disgusting conditions contained stimuli which commonly induce fear, which might account for activity in the amygdala. Further, we cannot be sure whether participants presented with third person statements of immoral acts and disgusting behaviours were taking the perspective of the perpetrator or the victim (Parkinson et al., 2011). This makes it difficult to determine whether the results are due to the differences in the disgust conditions or because of the confounded stimuli.

In the present experiment we used a single set of faces which we trained participants to associate with biographies representing immoral, disgusting or neutral individuals. We examined the behavioural and neural responses to these faces after extended training. Different participants had different face-biography pairs ensuring any differences between our conditions could only be due to the association with physically disgusting versus immoral vignettes.

There has been little research on moral aversion and disgust elicitation in the social domain. Moral violations are inherently social phenomena, such that human individuals are the sole inflictors of moral infractions, whereas contaminated items as well as diseased people can elicit disgust responses. Thus, here we attempted a different approach to investigate the neural correlates of disgust and morality that involved manipulations in the social domain. The present experiment set out to test the hypothesis that seeing the faces of physically disgusting people would result in differential neural activity compared to seeing faces of moral violators, when the category of individual was set by biographical memory. Our intention was to create disgusting vignettes that would cause participants to feel physically disgusted by those fictional characters due to their physically disgusting traits. In the immoral condition, we wanted to create vignettes that would cause participants to feel abhorrence to the moral violators because of their immoral behaviours.

We trained participants over several days to remember fictional people. Vignettes of either physically disgusting characteristics, individuals who are inherently immoral, or neutral people (i.e., a control condition) were presented to participants. Our other control condition was pictures of novel faces that were not part of the training paradigm. We examined the neural response using functional Magnetic Resonance Imaging (fMRI) when participants were presented with just the faces of these fictional individuals and a novel set of faces (hereafter called unknowns) displaying neutral, happy and disgusted facial expressions. The use of these different identities paired with facial expressions meant that the stimuli were consistent across all vignette conditions.

Based on the literature reviewed above, we expected some similarities in neural activity in the prefrontal cortex in response to faces paired with immoral vignettes (hereafter 'immoral faces') and faces paired with disgusting vignettes (hereafter 'disgusting faces). We also predicted that disgusting faces would evoke neural responses in the insula and amygdala, whereas we expected immoral faces to recruit activity in the medial OFC and STS. Disgusting individuals are more likely to be carriers of disease causing pathogens presenting a greater threat than moral violators. Therefore, we expected to find more widespread activity in the brain to disgusting individuals than moral violators.

We use a novel paradigm that allows us to avoid the stimulus confounds that raise difficulties for interpretation of the results of previous studies. We designed vignettes that avoided

overlap between the types of disgust. Our immoral vignettes did not have any physical disgust components, and, conversely, our physical disgust vignettes had no immoral components (see appendix I for complete stimulus set). We also had neutral vignettes that contained all the same types of components (name, gender, occupation, family information and characteristics) without any disgust or immoral elements. These carefully controlled stimuli ensured that any differences in response to faces could only be due to the experimental manipulation. Immoral vignettes, as they are created in this paradigm, contain a sense of agency. Agency implies that an act is deliberate which is what makes a nasty act an immoral act (Moll et al., 2007). We did not want to confound our disgusting stimuli with vignettes that contained a sense of agency as these could be construed as both immoral and physically disgusting. Thus, our disgusting vignettes indicated an unawareness of disgustingness, or at least a lack of agency over their disgustingness.

We initially did a whole brain analysis but controlled for the problem of Type I error due to multiple comparisons by including a cluster-level restriction (Lieberman & Cunningham, 2009). We followed this up with an ROI analysis of the insula, the inferior frontal gryus and superior temporal gyrus regions identified in the literature. Based on previous studies of disgusted facial expressions and physical disgust, we selected the anterior insula as a key ROI (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Jabbi, Bastiaansen, & Keysers, 2008; Wicker et al., 2003). Based on previous moral aversion studies, we selected the STS and IFG (J. Borg et al., 2008; Moll, de Oliveira-Souza, Bramati, et al., 2002; Moll, de Oliveira-Souza, Eslinger, et al., 2002). We examined the response in all ROIs for disgust and moral aversion conditions relative to our neutral condition and the unknown faces to test for links between moral and physical disgust. We also conducted a behavioural experiment to test for effects of our training on classification of facial expressions.

Materials and Methods

Participants and ethics

Twenty seven Macquarie University undergraduate and postgraduate students, (18 female), aged between 18 and 43 years (Mean age, 27 yrs; SD, 7 yrs), participated in this experiment. Four participants' data were removed prior to analysis: one due to excessive movement in the scanner, one fell asleep during scanning, one due to technical difficulties in the scanner and the final participant did not respond according to the instructions. Macquarie University Human Research Ethics Committee approved the experiment. Written and informed consent

was obtained from all participants and they were reimbursed $130AU in total, for eight days of participation.

Stimuli

Eight fictional vignettes (four * male and four * female) were generated to represent individuals who had: (i) disgusting attributes, (ii) immoral behaviours and (iii) 'normal' characteristics, (24 vignettes in total; see appendix I for complete stimulus set). The vignettes were 50 words in length and contained information about the fictional character's occupation, personal habits and general lifestyle. For example:

1. ***Immoral:*** Alex works for a charity accepting cash donations. He is paid for his charity work but at the end of each day he pockets as much of the charity's donations he thinks he can get away with. He cheats on his girlfriend regularly, and lies to her about it.
2. ***Physically disgusting:*** Ted is a cleaner in a large office building and suffers from a severe skin disease. Bloody scabs and pus ooze from his skin where office workers often find the debris of his skin disease on their desks. His wife treats his skin disease each night without any effect.
3. ***Neutral:*** Leonard does shiftwork in a factory canning fruit and vegetables. He owns a radio control helicopter that he flies once or twice a month in the local park. He lives by himself with his pet cat and two pet goldfish and often gets takeaway pizza from the local pizzeria.

We selected 24 individuals' faces from the Karolinska Directed Emotional Faces database (KDEF) (Lundqvist & Flykt, 1998), one to be paired with each vignette. A set of eight novel faces were used as a further control in the fMRI and behavioural task, thus 32 target faces (16 x Male and 16 x Female) were used in total. A 33rd face was designated as a target throughout the scanning period in a task designed to maintain attention. We used faces that were similar in age and appearance so that we could counterbalance vignettes over the 32 faces chosen for the experiment. This was performed to control for effects of the faces. The sex of the vignette-face pair was counterbalanced such that for half of the participants a particular vignette was female and for the other half it was male (e.g., Alex the male charity worker became Amanda the female charity worker). This counterbalancing of faces corresponding with the vignettes,

as well as the sex, was performed to ensure that there were no facial and gender confounds that could contribute to the results.

Experimental protocol

Subjects participated in 5 consecutive days of training sessions in which they were asked to memorise the identities of the 24 fictional individuals. Arousal measures and subjective rating scales of the vignettes (without the faces) were taken on the first day of the experiment. We also took arousal measures and subjective ratings on the final day of the experiment. Participants also undertook fMRI scanning and a behavioural task after the final training day. These are outlined in the following:

Day 1 – Heart rate, subjective rating and training

Participants read the vignettes while their heart rate was taken (AD Instruments Dual Bio Amp and PowerLab 8/30, using LabChart 7.Ink v7.3.7 software, raw data were analysed with Matlab). This was performed to measure the arousal level caused by the vignette content. Participants were asked to read to themselves from three power-point slides the three conditions in blocks (i.e., one slide of all of the disgusting vignettes, another slide all of the immoral vignettes and the other slide all of the neutral vignettes). The order in which the blocks were read was counterbalanced across participants. Their heart rate was taken from the point they began reading a block to the point they stopped reading that block. The neutral condition was used as the baseline to control for reading effects. Participants were then asked to rate each vignette on three questions: (i) how immoral, (ii) how disgusting and (iii) how appealing they found the individuals on a scale from 1-7 (1 = not at all, 7 = highly) (J. Borg et al., 2008). Finally, participants were shown the neutral expressions of the individuals that corresponded with the vignettes. They were provided with A4 sheets of paper, each containing a colour picture (16x8cm) featured above the vignette. They were permitted to write and draw on the A4 sheets anything that might help them remember those identities.

Days 2-5 – Training

Participants spent half an hour each day memorising the 24 individuals with the same A4 representations provided the day before. To further help them memorise the characters, they were given a ‘match the face to the vignette task’. They were also given the multiple-choice

questions, which were to be tested on day 6 for practice. During practice, participants used the A4 sheets as references to ensure their answers were correct.

Day 6 – Multiple choice questionnaire

Participants undertook a multiple choice questionnaire mentioned above (288 questions), to ensure they had remembered, with at least 90% accuracy, the faces paired with immoral, physically disgusting and neutral vignettes. All participants performed above 95%. Multiple-choice questions were presented on a computer using customized software (Presentation package, version 16.5). The software recorded participants' responses, which was then compared with correct responses.

Day 7 – Scanning task

During scanning, participants passively viewed the faces of the 24 learned individuals as well as the unknown faces of neutral, happy and disgusted facial expressions. The faces were displayed using customized software (Presentation package, version 16.5) compatible with the MRI scanner using a projector onto a screen at the rear of the scanner with a resolution of 1280x800p. To ensure attention was maintained throughout the scanning, participants were asked to press a button when they saw a specified target face indicated at the start of each run (the same face throughout).

Day 8 - Heart rate, subjective rating and behavioural task,

Participants' heart rates were obtained in the same manner as day one. They were then asked to rate the individuals on the rating scale as in day one (i.e., three separate questions: how disgusting, how morally wrong and how appealing do you find these individuals).

To test whether participants' behaviour was modulated by the biographical memories of disgusting and immoral vignettes, we asked participants to classify the emotional expressions of the 32 identities as quickly as possible. Participants were presented single faces showing either disgusted or happy facial expressions for each of the learned individuals, as well as the novel faces seen during scanning. The images were displayed using customized software (Presentation package version 16.5), which presented the face and beneath the face were the written words positive (left hand side) and negative (right hand side). They then performed the same task where the words were switched to minimise the effect of handedness in participants. They were asked to Using a standard keyboard, participants pressed on the

numeric keys '1' and '0' for the corresponding words. The software recorded the response for accuracy and reaction time (RT).

fMRI Data Acquisition

Scanning was performed on a Siemens Verio 3T scanner, combined with a 32-channel receiver only head coil (Erlanger, Germany) at Macquarie Medical Imaging, Macquarie University Private Hospital, Sydney, Australia. Functional imaging was implemented with T2*-weighted echo planar imaging (EPI). One scan volume was obtained every 3 seconds (TR) and consisted of 171 slices (slice thickness 2.4mm, TE = 32 ms, isotropic voxel size 2.4x2.4x2.4, SNR > 100, slice angle ~ 20°). Transverse sections were taken with the aim to capture insula and frontal brain regions.

fMRI protocol

A block design was implemented to present the stimuli. Blocks consisted of happy, disgusted and neutral faces of the immoral, disgusting, neutral and unknown individuals (12 conditions in total). To maintain attention during scanning, participants were shown a novel target face before each run and were required to press a button when that face appeared psuedorandomly throughout the blocks. Each block contained 8 presentations of the different faces within that condition (e.g., immoral happy) as well as the novel target face, for 1500ms with an inter-trial interval of 500ms (i.e., 18s blocks). Blocks of up to 30s have been used in previous fMRI designs that use (Baron, Gobbini, Engell, & Todorov, 2011; Matthews & Jezzard, 2004; Moll, de Oliveira-Souza, Eslinger, et al., 2002). Blocks were presented two times per run with a fixation cross (18s) at the beginning and end of each run and after eight consecutive blocks (28 blocks, including rest block fixation crosses, per run). Participants viewed 6 runs in total (approximately 53 minutes scanning).

Data analysis

fMRI images were pre-processed using Statistical Parametric Mapping (SPM8 Wellcome Department of Cognitive Neurology, London UK; http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). Images were realigned and registered to the mean of the participant's brain. Images were then normalized to the EPIii template and then smoothed with a 2.4mm Gaussian kernel. A three (facial expressions) x four (vignette type) ANOVA was used to test for the effects of facial expressions (happy, disgusted and neutral) and vignette types (immoral, disgusting, neutral and unknown) using SPM. For each of the

participants, the rest condition (fixation cross) was subtracted from each of the 12 conditions, which made up the contrasts in the first level analysis. Data from each participant was pooled in a second level analysis where conditions (facial expressions and vignettes) were contrasted against each other. The neutral expressions were used as a baseline for the facial expression condition and the neutral vignettes and unknowns were used as separate baselines in the vignette condition. Behavioural data and rating scales were analysed using two-way ANOVAs in a statistical package (Minitab 16.Ink). Heart rate data was analysed with MATLAB version 7.11.0 (R2010b) and statistically analysed using statistical software (Minitab 16.Ink). We used templates from the 'wfu_ pickatlas' (version 3.0.4)(Lancaster et al., 2003; Maldjian, Laurienti, Kraft, & Burdette, 2003) in SPM to identify ROIs in this analysis.

Results

The aim of the present experiment was to investigate the similiarities and the differences between neural activity and behavioural responses to physical disgust and moral aversion using biographical memory. The experimental design includes neutral vignettes to control for biographical knowledge about an individual, as well as the phases of the training. Another control measure we used were unknown faces, which were intended to control only for the physical stimulus, which was the presentation of the faces. Thus, using both analyses allows us to identify first, the activation due to the characteristics of the vignettes (disgusting or immoral); and second, the activation due to the training and biographical knowledge about the faces.

Heart rate measures

To ensure the level of arousal was consistent across the vignette types, heart rates were measured while participants read blocks of the vignettes (immoral, disgusting and neutral) on the first and final day of experimentation. The average times to read the blocks and the standard deviation on the first day were: neutral vignettes (100 ± 26s), disgusting vignettes (108 ± 22s) and immoral vignettes (109 ± 28s). The average heart rate for each block was: neutral 71 ± 13bpm, disgusting 70 ± 12bpm and immoral 70 ± 12bpm, (d = 0.07). A one-way ANOVA revealed there were no differences in heart rates when participants read the vignette blocks on the first day ($F_{(2,54)} = 0.05$, $p = 0.953$). With respect to heart rate variability, inspection of the variation measured by the standard deviations of the heart rates did not differ.

The average times to read the blocks and the standard deviation on the final day were: neutral vignettes (81 ± 27s), disgusting vignettes (88 ± 28s) and immoral vignettes (89 ± 26s). The average heart rate for each block was: neutral 72 ± 8bpm, disgusting 72 ± 9bpm and immoral 71 ± 8bpm, (d = 0.07). A one-way ANOVA revealed there were no differences in heart rates when participants read the vignette blocks on the final day ($F_{(2,54)} = 0.03$, $p = 0.972$). As in the first day, heart rate variability did not differ.

Behavioural measures

To investigate whether subjective reports from participants reflected the expected degree of immorality and disgustingness, ratings for each of the vignettes were taken on the first and the final day of the experiment. T-tests revealed that the ratings did not differ from the first to the final day; therefore, data were pooled to obtain average ratings for each of the three questions relating to the three vignette types (see Figure 1). Mean ratings for each of the questions were submitted to a 2 factor repeated-measures ANOVA with the factors of question (how disgusting, how morally wrong, how appealing) and vignette type (immoral, disgusting, neutral). There were significant main effects of rating ($F_{(2.63)} = 39.20$, $p < 0.001$), vignette type ($F_{(3,248)} = 106.02$, $p < 0.001$), and an interaction ($F_{(3,248)} = 367.54$, $p < 0.001$). Post hoc tests (Student Newman Keuls) revealed that all comparisons were significantly different except, there was no difference between the participants' ratings of how disgusting they found the disgusting and immoral vignettes.

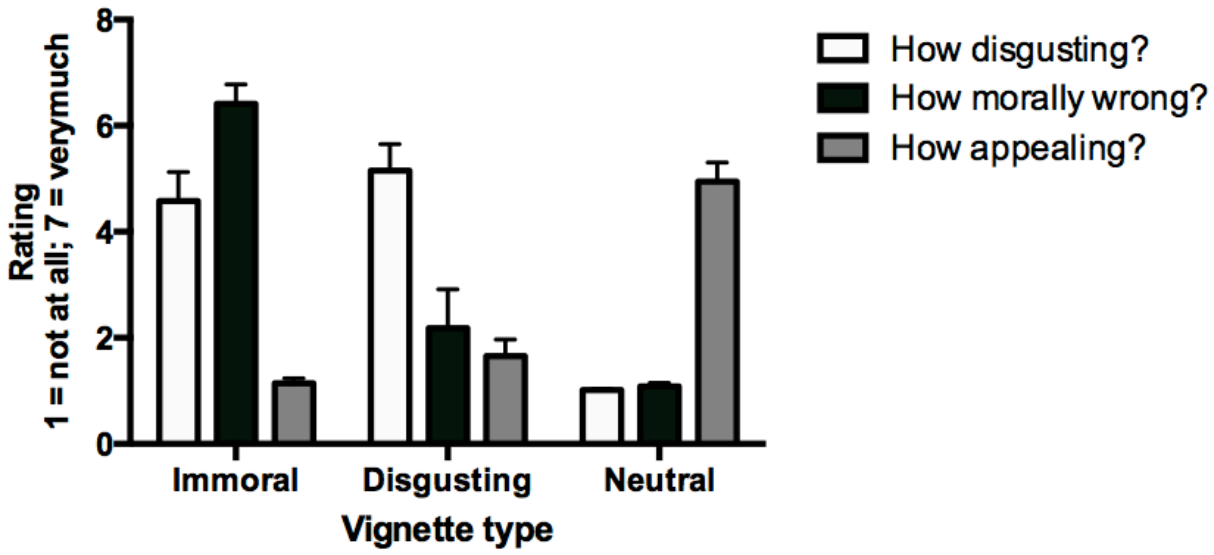

Figure 1. Participants' ratings of the immoral, disgusting and neutral vignettes using a Likert scale (1 = not at all, 7 = highly) on the first and final day of the experiment. T-tests revealed there were no significant differences between the ratings on the different days; thus, data were pooled to obtain the mean ratings. A two-way ANOVA revealed significant differences between all conditions except for how disgusting participants found the immoral and the disgusting vignettes. Error bars represent SEM.

In the behavioural task, participants categorised as quickly and accurately as possible via a button press, happy facial expressions (positive) and disgusted facial expressions (negative) for all four vignette conditions (immoral, disgusting, neutral and unknown). The aim of this task was to investigate whether biographical information about the vignettes paired with the faces affected the time taken to categorise emotional expressions. Data points that were inaccurate were removed prior to analysis of reaction times (RTs) and the first 5 trials were removed to allow for practice. Accuracy for all participants was above 90%.

Mean correct RTs for each of the conditions (Figure 2) were submitted to a two factor repeated-measures ANOVA with the factors of facial expression (positive, negative) and vignette type (immoral, disgusting, neutral, and unknown (no vignette)). There were no significant main effects of expression ($F_{(1,248)} = 0.79$, $p = 0.37$), or vignette type ($F_{(3,248)} = 0.08$, $p = 0.97$) and no interaction ($F_{(3,248)} = 0.55$, $p = 0.648$).

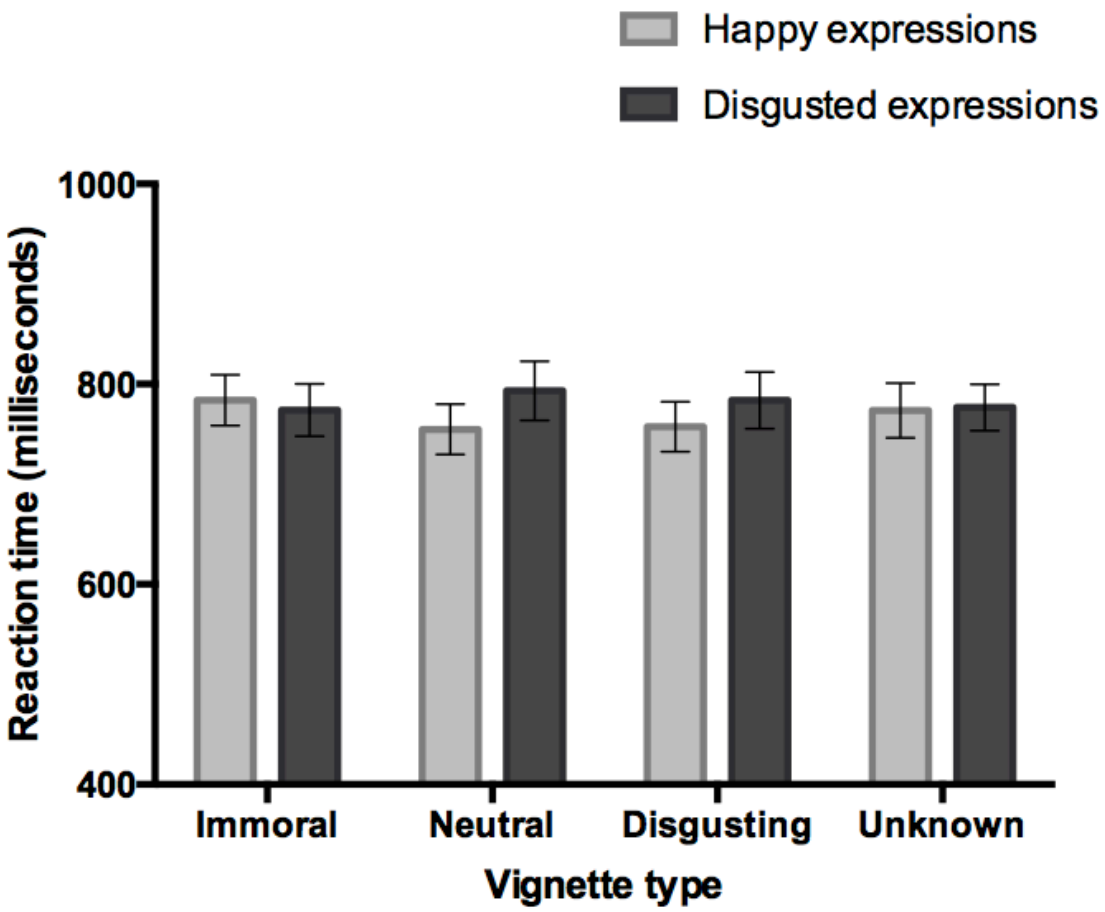

Figure 2. Behavioural results exhibiting correct reaction times to recognising facial expressions as positive (happy) or negative (disgusted). A two-way ANOVA revealed there were no significant differences between the reaction times across vignette types. Error bars represent SEM.

Imaging results

We performed a whole brain analysis of facial expressions collapsed across vignettes and of vignettes collapsed across facial expressions. We report only the collapsed conditions due to the numerous individual comparisons, which are shown in the appendix II. Because we did not have enough power, we did not perform a conjunction analysis. We performed an uncorrected cluster based analysis with a minimum of 10 contiguous voxels and set the threshold at $p < 0.01$. We did this based evidence that studies examining social cognition show small effect sizes, thus we placed a greater focus on activity in contiguous voxels (Lieberman & Cunningham, 2009). Here, we first present the results of the analysis of facial expressions before moving on to the main findings of the effect of vignettes in response to faces. Finally, as becomes clear below, because our whole brain analyses failed to find activation in regions identified repeatedly in the literature as being associated with disgust and responses to immoral acts, we conducted an additional ROI analysis of key regions to thoroughly test our hypotheses. Contrary to our prediction, we saw no significant insula activity in response to disgusted facial expressions, disgusting vignettes nor the immoral vignettes. In the immoral vignettes minus neutral vignettes analysis, no neural activity reached significance. To explore our dataset we extracted the beta weights from the peak activations drawn from the facial expression minus neutral expression contrasts, and the vignette type minus the unknowns, separated by condition. These are shown in appendix III.

Facial expressions

To investigate regional activation due to facial expression type, vignettes were collapsed across facial expressions. In separate analyses, neutral expressions were subtracted from happy and disgusted expressions, see table 1.

Disgusted – Neutral Faces

This subtraction showed a range of activity, the greatest activation was in bilateral middle occipital gyri. There was also activity in bilateral fusiform gyri as well as the caudal portion of the right superior temporal gyrus. Table 1 shows the neural activity in response to facial expressions with Brodmann areas, MNI coordinates, z-scores and cluster sizes. Figure 3 (A) shows the regional activation of disgusted expressions overlaid on a T1 template.

Happy – Neutral

The major portion of activity in this analysis was observed in the occipital cortex. Specifically, the right cuneus showed significant activity as well as regions in the lingual gyrus of the middle occipital gyrus, see table 1. Figure 3 (B) depicts the neural activity of both happy expressions overlaid on a T1 template.

Brain region	Hemisphere	Brodmann Area	MNI coordinates x	y	z	Z-scores	Cluster size (voxels)
Disgusted expressions - neutral expressions							
Superior temporal gyrus	right	**22**	*49*	*-35*	*8*	3.23	62
Fusiform gyrus	left	**37**	*-47*	*-71*	*-2*	3.88	126
Fusiform gyrus	right	**37**	*52*	*-57*	*-4*	3.54	148
Middle occipital gyrus	left	**18**	*-28*	*-83*	*3*	3.35	212
Middle occipital gyrus	right	**18**	*32*	*-86*	*-2*	3.02	148
Fusiform gyrus	left	**37**	*-49*	*-62*	*10*	2.77	19
Happy expressions - neutral expressions							
Cuneus	right	**18**	*16*	*-95*	*15*	3.27	192
Middle occipital gyrus	left	**18**	*-18*	*-95*	*12*	2.93	59
Middle occipital gyrus	left	**19**	*-28*	-81	5	2.69	12

Table 1. Each facial expression (happy, disgusted and neutral) was collapsed across vignettes. Whole brain analysis was performed using cluster thresholding at $p < 0.01$, with a minimum of 10 contiguous voxels.

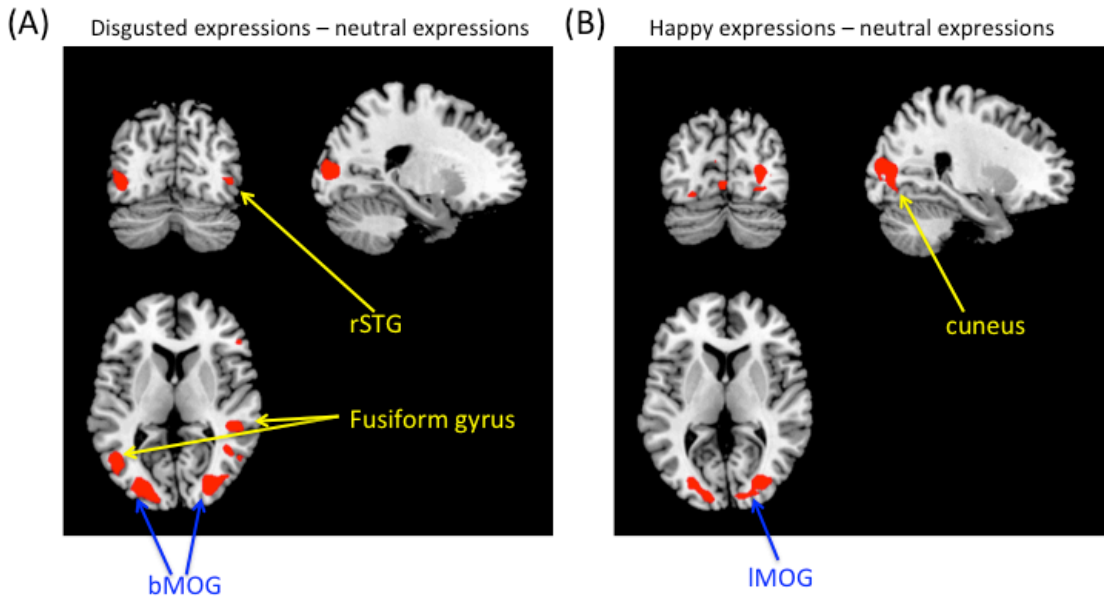

Figure 3. Activation clusters within facial expressions collapsed across vignette types. (A) disgusted expressions – neutral expressions revealed activity in the right superior temporal gyrus (rSTG), bilateral fusiform gyri and bilateral middle occipital gyri (MOG); (B) happy expressions – neutral expressions revealed activity in the right cuneus and left MOG, for MNI coordinates and cluster size see table 1.

Vignettes types

In order to investigate the neural activity associated with vignettes type, we analysed the effect of vignettes collapsed across facial expressions. In separate analyses, we used neutral vignettes and unknown faces as controls for subtraction from both the disgusting and immoral vignette conditions. The aim of the design is that neutral vignettes control for biographical knowledge about an individual, and all aspects of the training. The use of the unknown faces provides another type of control, one in which there is only control for the physical stimulus (the presentation of a face). Thus, using both analyses allows us to identify: (1) activation due to the characteristics of the vignettes (disgusting or immoral); and (2) activation due to the training and biographical knowledge about the faces, see table 2. In other analyses, we subtracted the collapsed facial expressions of the immoral from disgusting vignettes which revealed no significant activation. Whereas, in the subtraction analyses of the immoral and disgusting vignettes showed marked differences modulated by the expression, See Appendix II.

Disgusting vignettes

There was significant activity in the disgusting vignettes minus neutral vignettes in the left anterior superior temporal gyrus (STG) in the temporopolar region. We emphasise that the only difference between these conditions (disgusting vs neutral) is that the faces were previously associated with different types of biographical information.

Wider spread activity was observed in the disgusting vignettes minus unknown faces analysis which was laterlised to the left hemishpere. The largest activation was observed in the left dorsal anterior cingulate cortex (dACC), extending into the left premotor region. Further activity was detected in the left temporal lobe, both in the middle temporal gyrus and temporopolar area. There was activity in the left hippocampal region of the inferior frontal gyrus and a small cluster of activation in the left dorsolateral prefrontal cortex (PFC). Finally, an area in the precuneus in the occipital lobe was active, see table 2. Figure 4 depicts the regional activation overlaid on a T1 template (disgusting minus neutral vignettes (A) and disgusting minus unknowns (B)).

Immoral vignettes

In the immoral vignettes minus neutral vignettes subtraction analysis, no significant activations survived the thresholded cluster analysis. In the immoral vignette minus unknown

faces analysis significant activity was observed in the left premotor cortex as well as a cluster in the right posterior portion of the STG, see table 2. Figure 5 depicts the neural activation overlaid on a T1 template.

Neutral vignettes

No premotor activity was observed in the neutral vignettes minus unknowns analysis. The only brain region that survived correction was in the left dorsal anterior cingulate (data not shown, see appendix II for results of all contrasts we conducted).

Brain region	Hemisphere	Brodmann Area	MNI coordinates			Z-score	Cluster size (voxels)
			x	*y*	*z*		
Disgusting vignettes - neutral vignettes							
Temporopolar	left	**38**	*-49*	*18*	*-9*	2.83	21
Disgusting vignettes - unknown vignettes							
Dorsal anterior cingulate cortex	left	**32**	*-4*	*13*	*51*	4.01	294
Premotor cortex	left	**6**	*-1*	*6*	*68*	3.16	
Premotor cortex	left	**6**	*-11*	*1*	*75*	3.07	
Temporopolar	left	**38**	*-49*	*20*	*-7*	3.61	83
Retrosubicular	left	**48**	*-49*	*18*	*22*	2.78	29
Dorsolateral PFC	left	**46**	*-30*	*54*	*24*	2.58	11
Middle temporal gyrus	left	**21**	*-42*	*-45*	*5*	2.68	11
Immoral vignettes - unknown vignettes							
Premotor cortex	left	**6**	*-6*	*10*	*51*	3.69	196
Superior temporal gyrus	right	**22**	*54*	*-38*	*3*	2.75	33

Table 2. Significant areas of activation in subtraction analyses for each vignette type (immoral, disgusting, neutral and unknown), collapsed across facial expressions. Whole brain analysis was performed using cluster thresholding at $p < 0.01$, with a minimum of 10 contiguous voxels.

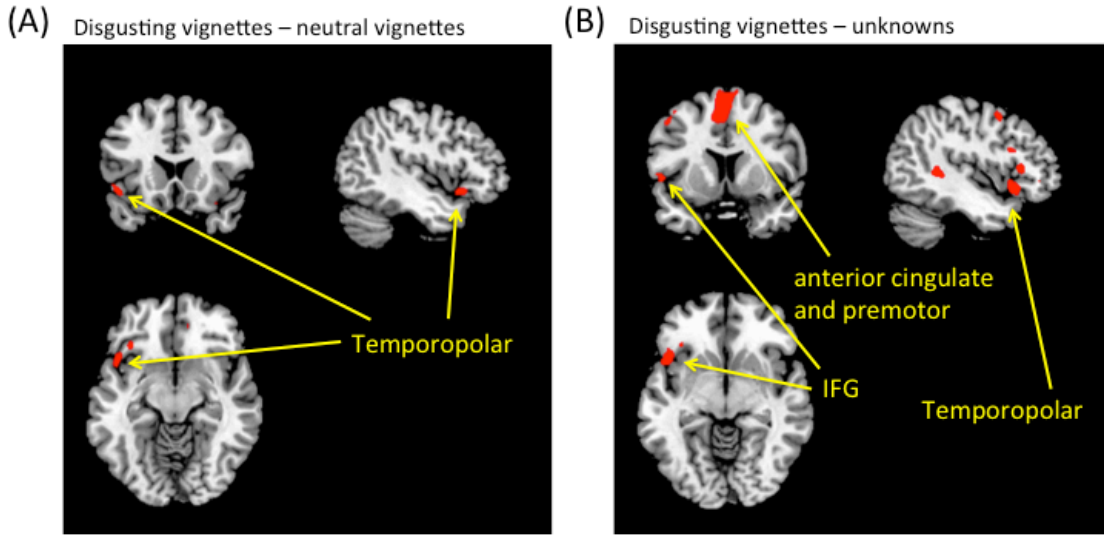

Figure 4. Activation clusters for disgusting vignettes collapsed across facial expressions (A) disgusting vignettes – neutral vignettes revealed activity in the left temporopolar region (B) disgusting vignettes – unknowns revealed activity in the left dorsal anterior cingulate which extended into the left premotor cortex, left temporopolar region, left inferior frontal gyrus (IFG), left precuneus, left dorsolateral prefrontal cortex and left middle temporal gyrus. For MNI coordinates and cluster size see table 2.

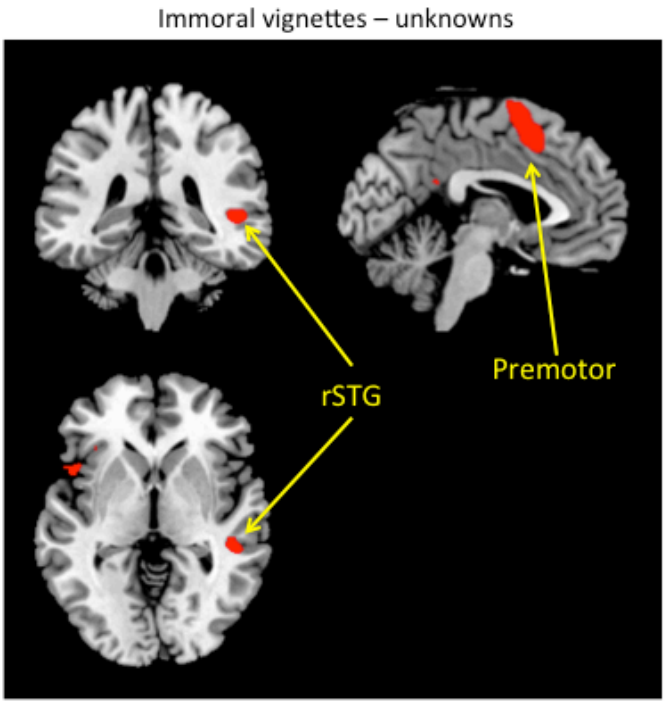

Figure 5. Activation clusters for immoral vignettes - unknowns collapsed across facial expressions. There was activity in the left premotor cortex and the right superior temporal gyrus (rSTG); for MNI coordinates and cluster size see table 2.

ROI analysis

In addition to the whole brain analysis presented above, we wanted to examine the effect of our conditions in specific *a priori* regions of interest (ROIs) that have been identified in the literature. As our whole brain analysis used a cluster-based correction, it is possible that activations in these key areas did not survive correction. We therefore did a targeted ROI analysis in which we used a small volume correction to explore this further. The ROIs were: bilateral superior temporal gyri (STG), bilateral inferior frontal gyri (IFG) and bilateral insula. These regions were selected based on the emotional judgment literature (superior temporal gyrus (STS) and inferior frontal gyrus (IFG) (Bzdok et al., 2011; Bzdok et al., 2012)) and the disgust literature (insula; (Jabbi et al., 2008; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Phillips et al., 1997). We used templates from 'wfu_pickatlas' (version 3.0.4)(Lancaster et al., 2003; Maldjian et al., 2003) to identify ROIs in this analysis. See table 3 for activation clusters.

Disgusting vignettes – neutral vignettes

We tested in each of the conditions all three ROIs whether there was a difference between disgusting and neutral vignettes. The only difference found was in the IFG, see table 3 (A).

Disgusting vignettes – unknowns

Wider spread activity was observed in the disgusting vignettes minus unknowns analysis. Two regions in the STG showed significant activation in the left temporoploar region and activity was observed in the left IFG.

Immoral vignettes – unknowns

In the immoral vignettes minus unknowns analysis, the only ROI showing statistical significance was the right STG, see table 3.

Disgusted expressions – neutral expressions

In the disgusted expressions minus neutral expressions, there was only significant activation in the ROI of the posterior portion of the right STG. Contrary to our prediction and previous literature, we did not find significant insula activity in this condition, See table 3 (B).

Brain region	Hemisphere	Brodmann Area	MNI coordinates x	y	z	Z-scores	Cluster size (voxels)
(A) Vignette type							
Disgusting vignettes - neutral vignettes							
Inferior frontal gyrus	left	**47**	*-49*	*20*	*-9*	2.79	13
Disgusting vignettes - unknown vignettes							
Temporopolar	left	**38**	*-49*	*18*	*-9*	3.44	14
Temporopolar	left	**38**	*-49*	*20*	*-7*	3.61	55
Inferior frontal gyrus	left	**48**	*-49*	*18*	*22*	2.78	23
Immoral vignettes - unknown vignettes							
Superior temporal gyrus	right	**22**	*52*	*-38*	*5*	2.71	13
(B) Facial expressions							
Disgusted expressions - neutral expressions							
Superior temporal gyrus	right	**22**	49	-35	8	3.23	40

Table 3. Each vignette type (immoral, disgusting, neutral and unknown) was collapsed across facial expressions. A region of interest (ROI) analysis was performed using brain regions: *a priori* regions selected from the literature were the superior temporal gyrus (STG), inferior frontal gyrus (IFG) and insula, of activation $p < 0.01$, with a minimum of 10 contiguous voxels.

Discussion

The aim of this study was to examine the similarities as well as the differences between moral aversion and physical disgust. We investigated the neural correlates of biographical memory associated with physically disgusting attributes and immoral characteristics using basic emotional expressions of happy and disgust. We obtained subjective reports about the vignettes and we examined behavioural and neural responses using fMRI to the faces paired with the vignette types.

Behavioural measures

The behavioural task did not find any differences in participants' reaction times to categorise happy and disgusted expressions of immoral faces, disgusting faces, neutral faces and unknown faces. In light of the subjective ratings, which showed strong differences, this was unexpected and there are a few potential explanations for this. First, the lack of statistical significance when participants responded to the disgusted and happy facial expressions might be because we compared two different types of negative vignettes. This could reflect the idea that it takes a similar amount of time to react to faces paired with negatively valenced information. This could support the idea that people respond to physically disgusting people similarly to morally aversive people. Or it could suggest that negative information in a vignette is processed similarly, not necessarily specific to disgusting and immoral information. We did not include a further negative control for this, so we cannot conclude which of these options is correct. Another reason for the lack of statistical significance could be because participants were asked to classify a positive (happy) and negative (disgusted) expression. The need to compute happy into positive and disgusting into negative might have created noise in the data.

In contrast, participants' subjective ratings of the vignettes showed significant differences concerning the evaluation of immoral vignettes and disgusting vignettes. Disgusting vignettes were not rated as morally wrong, which suggests that participants knew that the disgusting characteristics were not a deliberate choice. In contrast, participants found immoral individuals as disgusting as they found the disgusting individuals. The failure to find a difference in disgust ratings between immoal and disgusting faces reflects on metaphorical use of language whereas finding a difference in morality ratings between immoral and disgusting faces reflects on the success of the experimental manipulation. This could lend support to the hypothesis that metaphorical language associated with disgust is used when

referring to moral violators (Royzman & Sabini, 2001). Language associated with disgusting words is often used metaphorically when referring to immoral behaviour. However, this use of metaphor does not seem to be strong evidence for the evolution of moral aversion from physical disgust. It may rather demonstrate that the use of linguistic negative metaphor is common when referring to irritating or annoying events (Bloom, 2004; Nabi, 2002; Royzman & Sabini, 2001).

Neuroimaging results

We discuss only the analyses of both controls (neutral vignettes and unknowns) subtracted from immoral and disgusting conditions and the neutral expressions subtracted from both the happy and disgusted expressions. For the complete set of subtraction analyses see Appendix II. The neuroimaging results revealed that when collapsed across facial expressions, (i) viewing the immoral faces showed activity in the premotor cortex and the right STG; (ii) viewing disgusting faces produced more widespread activity with the largest activations in the left dorsal anterior cingulate cortex (dACC) which extended into the left premotor cortex as well as left temporopolar regions and left inferior frontal gyrus (IFG); (iii) pooled across vignette types, disgusted facial expressions showed the largest activation in bilateral middle occipital gyrus (MOG), bilateral fusiform gyrus and superior temporal gyrus (STG) and; (iv) pooled across vignette types, happy expressions showed activation in the cuneus and MOG. Altogether, these results suggest that neural representations to immoral faces are different from that of neural representations to disgusting faces with the exception of activity in the premotor cortex. Furthermore, activity evoked by disgusting faces revealed more widespread activity than did immoral faces. Finally, neural responses to disgusted expressions exhibited more widespread neural activity than happy facial expressions. Due to the lack of significant activation in classic areas identified in the literature, we conducted an additional ROI analysis. However, we still did not find activation in the insula while viewing disgusted facial expressions nor for the disgusting faces.

Neural activity in response to vignettes

The most intriguing part of this experiment, is that neural responses to both the disgusting individuals and moral violators relative to unknown faces revealed activity in the left premotor cortex. It might have been possible that this simply reflected an effect of the training. However, in the neutral vignettes minus unknowns, there was no premotor activity

(see appendix II). This means that activity in the premotor region cannot be due to biographical knowledge or our task *per se*.

The premotor cortex has been shown to contain mirror neurons that fire both when undertaking an action as well as when observing that same action (Keysers, 2011; Kohler et al., 2002). It has been suggested that the firing of neurons in this region when both viewing and actively expressing an emotion, might help the observer to understand the emotions of others, which are important in social interactions (Keysers, 2011). However, in the present experiment, the emotional expressions were collapsed across vignettes which means responses to emotional expressions are cancelled out in this type of subtraction analysis. Therefore, mimicking, or understanding emotional expressions does not explain this premotor activity. This premotor activity seems to be representing something about the biographical memory of negatively valenced information.

The activity in the premotor region, might suggest that negative semantic knowledge of an individual is represented in the premotor cortex. Negative events, people or feelings often engage more attention, as well as deliberation, than their positive counterparts (Rozin & Royzman, 2001). Therefore, negative semantic knowledge about an individual might suggest the importance of understanding the emotional state of negatively valenced individuals that does not require understanding an emotional expression *per se*. This could reflect a need to understand the social significance when viewing the faces of disgusting and immoral people, or simply negatively valenced people. This idea is supported by the fact that the neutral vignettes minus unknowns did not show premotor activity.

Moving now to other neural responses to the vignettes, a significant cluster of activation in the temporopolar region in the left hemisphere was observed in response to disgusting faces. This occurred in both the most rigorous contrast with neutral vignette faces and in the second control with the unknown faces. In the disgusting minus neutral vignette faces contrast, this temporopolar activity was the only region showing significant activity. Thus, something of the disgusting biographical information appears to be represented here. The temporal pole is strongly connected with the amygdala and orbitofrontal cortex (Olson, Ploaker, & Ezzyat, 2007). The amygdala plays a role in threat detection, whereas the orbitofrontal cortex is involved in social evaluative tasks (Bzdok et al., 2011; Pessoa & Adolphs, 2010). It has been suggested that the temporal pole integrates visceral information and complex visual stimuli

(Olson et al., 2007). Because the vignettes contained aspects of vomiting, bad smells and disease, memories of these aspects might have been implicitly recalled. This might explain the activity found in this disgusting minus neutral contrast. This could also explain the temporopolar activity in the disgusting minus unknown condition, where the same difference exists (disgusting information compared to no information). Particularly as neither the immoral nor the neutral vignettes relative to the unknowns showed this response.

Activity in the left temporopolar region has been implicated in retrieving the name of familiar people as well as retrieving semantic information about that person (Hanley, 2011; Tranel, 2009). Presumably participants were retrieving names and knowledge in the disgusting condition in a way they were not able to do in the unknown condition. Tsukiura, Namiki, Fujii, and Iijima (2003) found bilateral temporal pole activity when names of pleasant people were recalled immediately after a learning paradigm. Names recalled after a two-week delay showed activity only in the left temporal pole (Brodmann area 38). Thus, activity found in the present paradigm to disgusting individuals might reflect the retrieval of names relative to emotional salience, and this may be why it also shows up in the well-controlled disgusting minus neutral contrast.

If temporal pole activity is involved with recollection of semantic information about familiar people, it is surprising that activity in this region was not observed in the immoral minus neutral contrast. This might imply that sematic information and possibly the need to remember names of disgusting vignettes is more salient than that about morally aversive vignettes. One interpretation of this is that avoiding disgusting people might be evolutionarily adaptive, while avoidance of immoral people could reflect a developmental rejection mechanism.

There was a large region in the dACC that responded in the disgusting minus unknown contrast. Todorov, Gobbini, Evans, and Haxby (2007) found this region activated when participants viewed faces paired with disgusting behaviours. Similarly, C. Borg, de Jong, Renken, and Georgiadis (2013) found regions in the same area in response to disgusting food and bodily products. The activity seen in the present study in response to disgusting people could reflect an evaluative mechanism. Carretie, Albert, Lopez-Martin, and Tapia (2009) hypothesise that the ACC integrates information from emotional centres such as the amygdala and sends outputs to executive and motor areas in the PFC. Thus, this activity could represent

a form of evaluation of the disgusting stimuli, and demonstrates that our vignette training was very effective for the disgusting individuals.

A smaller, but nonetheless notable, region in the middle temporal gyrus was activated in response to disgusting faces. This region has also been found to activate in perspective taking paradigms (Ruby & Decety, 2004), suggesting our activity could reflect a degree of perspective taking. Some participants did report feeling 'sorry' for the people described in the disgusting vignettes (pers. com.), and such empathic concern is a form of perspective taking. Cognitive empathy has been shown to activate a diverse number of brain regions including the insula and regions surrounding this structure (Fan, Duncan, de Greck, & Northoff, 2011; Lamm, Decety, & Singer, 2011) in the frontal gyrus and frontal operculum.

Small clusters of activation were found in response to the disgusting faces in the inferior frontal gyrus, and frontal operculum. This is consistent with a study that showed activity in these regions to disgusting transgressions, but not to harmful or dishonest transgressions (Parkinson et al., 2011). Moreover, activity in the frontal operculum has been shown in relation to the mental imagery of disgusting things (Jabbi et al., 2008). The frontal operculum is functionally connected to the AI, and is likely involved in processing inner body feelings (Craig, 2009). Activity seen in the present study in the frontal operculum might reflect imagined disgust when recalling disgusting aspects of the vignettes. Otherwise, it could reveal empathic concern for the disgusting faces. As mentioned previously, some participants reported feeling sorry for the disgusting vignettes, but they also reported 'feeling disgusted' by the disgusting vignettes. Therefore, participants may have been feeling disgusted, but also empathic toward those that were disgusting. This is consistent with research conducted by Jabbi, Swart, and Keysers (2007) who found that the degree of empathic concern that a participant showed for others predicted the amount of frontal operculum activity when viewing pleasant and unpleasant emotions. Thus, observation of disgusted facial expressions, mental imagery of disgusting things as well as own feelings of disgust, tend to show activation in the frontal operculum. This might explain the results observed in the present experiment.

Turning now to the results of the immoral vignettes, neural activity in the superior temporal gyrus (STG) has been implicated in theory of mind tasks and understanding the emotional states of others (Adolphs, 1999). We observed BOLD responses in the right STG in response

to immoral faces compared with unknowns. This activity in the STG is consistent with other research finding responses here to socially salient information (Christianson, Saisa, & Silfvenius, 1995). This saliency effect might be associated with acknowledging malevolent individuals one might prefer to avoid. This is also consistent with a study that revealed lateralisation of the right hemisphere when processing biographical information of malicious behaviours paired with a face (Christianson et al., 1995). In the present study, there was right lateralised activity in the STG evoked with immoral individuals, which is in contrast to the left lateralised activity in response to disgusting people. This could indicate that immoral faces are processed differently in the brain to disgusting faces.

Neural activity in response to facial expressions

Most surprisingly, we did not see insula activity when participants viewed the disgusted faces collapsed across vignette type. The anterior insula (AI) has been implicated in processing disgusted facial expressions (Anderson et al., 2003; Phillips et al., 2004; Stark et al., 2007; Wicker et al., 2003), disgusting scenes (Moll, de Oliveira-Souza, Eslinger, et al., 2002), the feeling of disgust (Fitzgerald et al., 2004) as well as imagined and observed disgust (Jabbi et al., 2008). The lack of AI activity in the present study might be explained by the biographical knowledge participants had about the individuals. This is the first study, to our knowledge, to investigate the neural correlates of physically disgusting people learned over time. Thus, this learned information about disgusting traits might modulate insula activity to disgusted expressions.

To elucidate this potential explanation further, activity in the anterior insula probably reflects sensory and interoceptive effects of disgust related stimuli (Craig, 2009). Insula activity might therefore attenuate when one has knowledge of an individual. This learned knowledge might weaken overall sensory information by sending projections to higher cortical structures that are involved in evaluating visually evocative stimuli such as regions in the PFC. An alternative explanation for the lack of AI activity to disgusted expressions in our study could, however, be habituation in the insula. We used a block design to maximise our power to detect effects, but one limit of this design is the possibility of neural activity attenuating with repeated exposure to the same stimuli (Grill-Spector, Henson, & Martin, 2006). Because participants were repeatedly exposed to disgusted faces, as well as disgusting vignettes, this might explain the lack of AI activity here. In the future, one way to get around this limitation might be to implement an event-related design, which could bypass this attenuating effect. In

addition, one study showed neural activity was augmented with the presentation of dynamic emotional expressions as compared to static pictures (van der Gaag, Minderaa, & Keysers, 2007). Thus, using moving images of emotional expressions might also bypass this attenuating effect.

The BOLD responses in the middle occipital gyri (MOG) were significant for both disgusted and happy facial expressions, although bilateral MOG activity was observed only in response to disgusted facial expressions. Authors of a meta-analysis investigating the role of regions active in perspective-taking and false-belief formation (Schurz, Aichhorn, Martin, & Perner, 2013) found MOG activity in both perspective taking and false belief paradigms. Activity in the MOG in the current experiment could represent the biographical information known about the identities of the people. This is presumably because we collapsed across vignettes types, whereby three out of the four conditions contained biographical information. Thus, the impact of biographical information could influence these results. This could be explained by the fact that participants reported putting themselves in the place of the fictional vignettes; thus, some participants may have been taking the perspective of the fictional individuals.

On the other hand, some participants reported finding it difficult to believe that the face of the fictional person matched the description of the vignette. For example, one participant who reported finding one of the faces attractive, found it difficult to believe they could be malevolent (pers. com.). Thus, it is unknown whether participants took the perspective of the fictional people, or struggled with forming a belief about the person, both possibilities of which could explain activity in the MOG.

In sum, the neural activity in response to the disgusting vignette faces show activation patterns consistent with perspective taking and emotional centres in the temporal and frontal cortices. The wider-spread activity seen for the disgusting vignettes might reflect that the emotional reaction serves as a harm avoidance strategy, which is consistent with the view that the disgust response is evolutionarily adaptive. In contrast, immoral individuals did not evoke the widespread activity seen in response to disgusting people. This could be interpreted as evidence that immoral individuals do not pose as big a threat as disgusting people, which would suggest that further evidence is needed to infer the evolution of moral aversion from the disgust response. Alternatively, it could be that the effect of immorality is subtler than physical disgust, and our paradigm was not sensitive enough to detect this effect.

Variability among participants

Most moral transgressions are culturally and contextually defined, where moral judgements usually depend on varying factors such as religious background, country of origin, social group and the context in which the transgression has occurred (Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). The country of origin of the subject pool recruited in the present experiment varied (French, German, Indian, Australian, English and Chinese). Although, overall there was little variability between participants' rating of either the disgusting or the immoral vignettes, some variability was evident in personal communications. One participant expressed that the person stealing from a charity was extremely abhorrent, while another pondered over whether this person may be justified in stealing from a charity. Similarly, concerning the disgusting vignettes, one relayed that it was difficult to imagine the bad smell of a person thus it was difficult to feel disgusted. However, another reported that the vignettes containing any foul smelling component elicited a great sense of disgust. One risk when averaging neural responses across participants is that individual variability is lost. We discussed with several people our choice of vignettes, and altered them accordingly. However, perhaps a more rigorous pilot study to find consistencies among participants' opinions of immoral and disgusting acts might have helped to tailor the vignettes. This could also reduce the confound of cultural context and social standing of the individual participants.

Conclusion

The present study was the first to use biographical information related to immoral and disgusting behaviour to examine the neural response to moral aversion and physical disgust using fMRI. Other studies have used a range of stimuli, from pictures of scenes or faces to phrases and sentences. The novel aspect of this experiment is that, unlike other studies, we have used identical stimuli (faces) in the scanner. Any neural differences can therefore be interpreted as due to our training on the vignettes. We found activity in response to faces paired with disgusting vignettes that other researchers have found in response to actual disgusting stimuli. With regards to the evidence of similarities and differences between immoral and disgusting conditions, mostly we found that the neural underpinnings were different for immoral faces and disgusting faces. While this does not exclude the proposal that moral aversion has exapted the disgust response, it does suggest that more work is needed to shed light on that proposition. Although, we did find some evidence for activation of the

premotor cortex in response to both immoral and disgusting individuals relative to the unknowns. This premotor activity, to our knowledge, has not been shown in response to biographical memory of negatively valenced information. This could reflect the importance of attending to negative people perhaps to evaluate potential threat. Although questions of an evolutionary nature of behaviour are difficult since behaviour does not fossilize, neural activity in response to different traits is one way to probe these questions. The differences we found in neural activity to disgusting and immoral faces might suggest that the neural underpinnings of immoral behaviour and disgusting traits differs. Therefore, more work is necessary to support the hypothesis that moral aversion has evolved from physical disgust.

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Appendices

Appendix I: Vignette stimuli

Immoral vignettes

4. Alex works for a charity accepting cash donations. He is paid for his charity work but at the end of each day he pockets as much of the charity's donations he thinks he can get away with. He cheats on his girlfriend regularly, and lies to her about it.
5. Tim works for a bank and provides large loans to people knowing they can't pay it back and will probably end up bankrupt. He receives very big bonuses because of his exploitation of these people. He is married and regularly seeks prostitutes for sex. He has no close friends.
6. Rachel is a politician. She accepts bribes from large corporations and has deliberately changed some policies so that these large corporations pay less tax. She goes on extravagant shopping sprees and puts it on her business expense account. She also takes month long holidays claiming it as an expense.
7. Bob owns and runs a mechanic workshop. He has no business qualifications, nor mechanical qualifications. When he receives cars, he often returns them unrepaired still charging them. When customers confront him about this, he uses violent tactics to intimidate them into inaction. His girlfriend left because of his abuse.
8. Margaret is a prosecutor in a criminal court. She has let one of her family members escape punishment and she knows he is continuing to con people into buying pharmaceuticals harmful to their health. She has one child that she gave up for adoption because it cried too much.
9. Brenda is in the people trafficking business. She employs several boat owners to bring refugees to Australia to work in her factory. She gets her illegal immigrant workers to work 16 hours a day for 50c an hour. She lies to her husband about how she gets her income.
10. Greg owns a strip club with illegal workers. He often beats them to get what he wants. He 'pays' them with heroine and cocaine to get hem addicted so that they work harder to feed their habit. He provides them with very poor living conditions. He has one daughter.

11. Colleen is a corrupt police detective. She often receives large sums of money from high profile criminals to keep them safe from any police investigation. She spends this money on her excessive cocaine addiction that costs around $1500AU per week. She has one child that lives with his father.

Neutral vignettes

1. Rhonda works as a secretary in a small law firm. She owns a dog that she walks in a park close by. She is married to a grocer and they have two children who are both at school. She has two friends who occasionally pop over for a cuppa.
2. Matthew works as a legal aid in a large law firm. He and his wife take walks around the local area and occasionally purchase a coffee from their local café. He and his wife are known in the community as a quiet but friendly couple who like to walk.
3. Leonard does shiftwork in a factory canning fruit and vegetables. He owns a radio control helicopter that he flies once or twice a month in the local park. He lives by himself with his pet cat and two pet goldfish and often gets takeaway pizza from the local pizzeria.
4. Ben works in a local carpenters workshop as an apprentice and performs general maintenance and carpentry duties on site. He has two friends that he regularly drinks with on a Friday or Saturday night. He lives in an apartment with one room mate he found through a mutual friend.
5. Julia works as a managing director of a national bank working around 50 hours a week. In her free time she likes watching television soapies and going to the movies. She and her husband enjoy dinner out with friends occasionally and at home she maintains a small vegetable patch.
6. Paul owns a local bar and bistro. He keeps the books and keeps the bar maintained for business. He likes cars and car racing and would like to buy a sports car in the near future. He likes playing video games and lives in an apartment with his girlfriend.
7. Amy has recently finished her security apprenticeship and now works in the security branch of a shopping centre. She would like to marry and have two to three children with her husband and she is happy to become a housewife. She likes watching television and playing with her cat.

8. Audrey works for an international organization researching global food security. She works 40 hours a week Monday to Friday and enjoys watching YouTube videos when she arrives home. She has a daughter who is 7 years old and shares custody with her former husband who she remains friends with.

Disgusting vignettes

1. Ted is a cleaner in a large office building and suffers from a severe skin disease. Bloody scabs and pus ooze from his skin where office workers often find the debris of his skin disease on their desks. His wife treats his skin disease each night without any effect.
2. Maree works for a university, is pregnant and experiences severe morning sickness. She vomits regularly and carries a vomit bag around with her in public, it smells badly of vomit. Sometimes people smell vomit on her breath but don't say anything because they know about her morning sickness.
3. Rick works in sewerage maintenance and lives an alternative lifestyle whereby his daily hygiene activities are not so important. He does not know he has this pooey smell that he gets from his job. He has a girlfriend who tolerates the smell as she works at the same sewerage plant.
4. Janet works for a financial institution and cares deeply for her dog. She reciprocates kissing and licking her dog, even when the dog has dog food around its mouth and it has been seen licking its genitals. Colleagues smell the dog on her and avoid her because of this.
5. Michael has had a flatulence problem from early childhood. He is sometimes unaware of his constant breaking wind, which has a foul stench that he is used to, but really grosses out others. He works in a fish factory where the fish smell can overpowers the strong flatulent smell.
6. Luke is an electrician and has grown up with very few rules. He picks his nose and eats it. He doesn't wear deodorant and rarely showers so he smells like a homeless person. He has very bad back acne where blood oozes through his t-shirt that he can't see.
7. Leah owns a cafe with her husband and has personal habits that she doesn't know people find gross. She scratches her butt and smells her fingers, she doesn't wash her

hands after finishing on the toilet. She wipes ear wax on couch arms and farts and burps at will.

8. Geraraldine is a sickly woman and was made redundant from the legal profession. She leaves meat products out which become infested with maggots which she feeds to her dog. She rarely showers and has a particularly pungent body odour. She hoards everything from empty milk bottles to cockroach baits.

Vignettes to control for gender effects: change of sex vignettes

Immoral vignettes

1. Amanda works for a charity accepting cash donations. She is paid for her charity work but at the end of each day she pockets as much of the charity's donations she thinks she can get away with. She cheats on her boyfriend regularly, and lies to him about it.
2. Tamara works for a bank and provides large loans to people knowing they can't pay it back and will probably end up bankrupt. She receives very big bonuses because of her exploitation of these people. She is single and regularly seeks escorts for sex. She has no close friends.
3. Richard is a politician. He accepts bribes from large corporations and has deliberately changed some policies so that these large corporations pay less tax. He visits brothels and strip clubs and puts it on his business expense account. He also takes very long holidays claiming it as an expense.
4. Bethany owns a hairdresser and beauty salon. She has no business, or beauty or hairdressing qualifications. When the customers complain about the really bad job she does, she yells at them and threatens to call the police if they've refused to pay. Her boyfriend left because of her abuse.
5. Quentin is a prosecutor in a criminal court. He has let one of his family members escape punishment even though he knows he is continuing to con people into buying shonky pharmaceuticals that either don't work or are potentially harmful to their health. He has no children by choice.
6. Brendan is in the people trafficking business. He employs several boat owners to bring refugees to Australia to work in his factory. He gets his illegal immigrant workers to work 16 hours a day for 50c an hour. He lies to his wife about how he gets his income.

7. Paula owns a strip club and employs illegal immigrants because they have no rights. She beats them often and ‘pays’ them with heroine and cocaine to get hem addicted so that they work harder to feed their habit. She has two daughters that she is grooming for her industry.
8. Mark is a corrupt police detective. He often receives large sums of money from high profile criminals to keep them safe from any police investigation. He spends this money on his excessive cocaine addiction that costs around $1500AU per week. He has one child that lives with his mother.

Neutral vignettes

1. Raymond works as a secretary in a small law firm. He owns a dog that he walks in a park close by. He is married to a hairdresser and they have two children who are both at school. He has two friends who occasionally pop over for a cuppa.
2. Rebecca works as a legal aid in a large law firm. She and her husband take walks around the local area and occasionally purchase a coffee from their local café. she and her husband are known in the community as a quiet but friendly couple who like to walk.
3. Lara does shiftwork in a factory canning fruit and vegetables. She owns an exercise bike that she rides once or twice a month. She lives by herself with her pet cat and two pet goldfish and often likes to get takeaway pizza from the local pizzeria below her apartment.
4. Belinda works in a local artists workshop as an apprentice as well as performs general maintenance duties. She has two close friends that she regularly drinks with on a Friday or Saturday night. She lives in an apartment with one room mate that she found through a mutual friend.
5. Jason works as a managing director of a national bank working around 50 hours a week. In his free time he likes watching television dramas and going to the movies. He and his wife enjoy dinner out with friends occasionally and at home he maintains a small vegetable patch.
6. Penny owns a local bar and bistro. She keeps the books and keeps the bar maintained for business. She likes cars and car racing and would like to buy a sports car in the

near future. She likes playing video games and lives in an apartment with her boyfriend.

7. Adam has recently finished his security apprenticeship and now works in the security branch of a shopping centre. He would like to marry and have two to three children with that wife and he is happy to become a househusband. He likes watching television and playing with his cat.
8. Colin works for an international organization researching global food security. He works 40 hours a week Monday to Friday and enjoys watching YouTube videos when he arrives home. He has a daughter who is 7 years old and shares custody with his former wife who he remains friends with.

Disgusting vignettes

1. Tanya is a cleaner in an office building and suffers from a severe skin disease. Bloody scabs and pus ooze from her skin. Office workers often find the debris of her skin disease on their desks, like blood droplets, dead skin and scabs. She treats her skin each night.
2. Martin works for a university, and has unusual stomach ulcers causing him to vomit regularly. He carries a vomit bag around with him, even in public, and it smells badly of vomit. Sometimes people smell vomit on his breath but don't say anything because they know about his condition.
3. Renee works in the local sewerage plant with her boyfriend and she doesn't know she has a very pooey stench from her job. She lives a lifestyle where her hygiene activities aren't important, so she usually has grubby fingernails and unwashed hair. She also doesn't wash her clothes often.
4. John works for a financial institution and cares deeply for his dog. He reciprocates kissing and licking his dog, even when the dog has dog food around its mouth and it has been seen licking its genitals. Colleagues smell the dog on him and so avoid talking to him.
5. Michelle has had a flatulence problem from early childhood. She is sometimes unaware of her constant breaking wind, which has a foul stench that she is used to, but really grosses out others. She works in a fish factory where the fish smell can sometimes overpower the fart smell.

6. Lena is a receptionist in a mechanic workshop and has grown up with very few rules. She picks her nose and eats it. She doesn't wear deodorant and rarely showers so she sometimes smells like a homeless person. She also has severe gingivitis so she has very bad breath.
7. Nick owns a cafe with his wife and has habits that he doesn't know people find gross. He scratches his butt and smells his fingers and he doesn't wash his hands after finishing on the toilet. He wipes ear wax on couch arms and farts and burps at will.
8. George is a sickly man and was made redundant from the legal profession. He hoards everything because he can't let things go, from empty milk bottles and rotting food to expired cockroach baits. His house is riddled with all sorts of creep crawly's; bed bugs, cockroaches, lice and fleas.

Appendix II: Results of specific contrasts

Appendix II. Substraction analyses, brain regions and MNI coordinates; neut, neutral; imm, immoral; unk, unknown; first abbrev. facial expression second abbrev. vignette type.

	Contrasts	Key: Frontal lobe, Temporal lobe, Occipital lobe, parietal lobe, cingulate, insula, basal ganglia, N/A
	Faces	**Faces**
1	Disgusted - neut	L Inf Temp Gyr, R&L Mid temp gyr, L&R Mid occip gyr, R sup temp gyr, L fusiform gyr _47 _71 _2; 52 _57 _4;_28 _83 3; 49 _35 8; 32 _86 _2;_49 _62 10;_42 _45 _19
2	Disgusted - Hap	0
3	Hap - neut	R cuneus 0.001, L Middle occip gyr, L Inf temp gyr 16_95 15;_18_95 12;_28_81 5;_47_71_2;
4	Hap - disgusted	R Mid front gyr 23 39_14;
5	neut - Disgusted	R Inf parietal lobule, L cing gyr 49_45 41;_4_30 41
6	neut - Hap	0
	Vignettes	**Vignettes**
7	Imm - neut	R lat ventricle, L sub gyral 35_23_14;_37 25_12
8	Imm - Disgusting	0
9	Imm - unk	L premotor, R sup temp gyr, _6 10 51; 54_38 3
10	neut - Imm	0
11	neut - Disgusting	0
12	neut - unk	L dorsal anterior cingulate _4 15 48
13	Disgusting - Imm	0
14	Disgusting - neut	L STG, L IFG _49 18_9;_35 30_9
15	Disgusting - unk	L dorsal anterior cingulate, 2xL premotor, L temp pole, L retrosubicular, L dl PFC, L mid temp gyr _4 13 51;_1 6 68;_11 1 75;_49 20_7;_49 18 22;_30 54 24;_42_45 5
16	unk - Imm	L Med Front gyr, R Sup Front gyr, _6 39 29;32 22 56; 25 20 65
17	unk - Disgusting	R Inf parietal lobule, L Med front gyr 40_40 46;59_33 53;_6 42 29
18	unk - neut	L Med front gyr _6 42 27
	Contrasting Facial expressions	**Contrasting Facial expressions**
19	Hap Imm - neut Imm	R IFG, R Med front gyr, R sup Front gyr, R IFG 42 22_16; 6 46 17;18 54 36;47 44_14
20	Hap Imm - Disgusted Imm	0
21	neut Imm - Hap Imm	0
22	neut Imm - Disgusted Imm	L Caudate, L STG, postcentral gyr, L subgyral _11 13_7;_59_14 3;_40_23 27;_49_18 22
23	Disgusted Imm - neut Imm	R Mid occ gyr Lx2 Mid occ gyr, L Fusiform gyr, R&L STG, R Cuneus, L Inf temp gyr, R&L IFG, _20_88 8;_42_45_19;32_86_2;44_35 8;16_95 17;_44_74_2;_52_50 8;42 22 8;_35 20_9
24	Disgusted Imm - Hap Imm	R Sup front gyr, R Mid temp gyr, R subgyral, L Extra nuclear 13_14 77;42_50 5;37_30 0;_32 6_7
25	Hap neut - neut neut	L Mid temp gyr _52_28_16
26	Hap neut - Disgusted neut	0
27	neut neut - Hap neut	L extranuclear _18_42 17
28	neut neut - Disgusted neut	0
29	Disgusted neut - neut neut	L Mid temp gyr, L Mid front gyr, R Inf temp gyr, L Supramarginal gyr, L extra nuclear, R ITG, R subgyral _52 _28 _16; _28 27 48; _52 _47 5; 59 _14 _24; _59 _52 29; _32 15 _9; 59 _21 _21; 13 46 _12;
30	Disgusted neut - Hap neut	0
31	Hap Disgusting - neut Disgusting	R Insula 0.001, R IFG, R Mid occ gyr, L claustrum, R lentiform nucleus 42_18 20;56 10 34;28_78 8;_35_21 22;_35_9 8;37_4 0;25 8 5
32	Hap Disgusting - Disgusted Disgusting	R IFG, R sup front gyrx2, R IFG, L Med front gyr 54 3 17;8 54 32;13 56 24;47 22_2;_11 46_14
33	neut Disgusting - Hap Disgusting	L Mid temp gyr, L Mid front gyr, L extra nuc, L Inf par lob, L precuneus, _52_28_16;_32 27 48;_32 15_9;_56_35 48;_6_62 44;20 27 63;59_11_26;32 20 58;54_47 44;_1_28 5
34	neut Disgusting - Disgusted Disgusting	R inf parietal lobule, R Mid temp gyr, L IFGx2, R extranuclear, R Mid front gyr 54_47 44;61_23_9;_37 15_9;1_26 5;_35 15_21;32 30 41
35	Disgusted Disgusting - neut Disgusting	R Mid temp gyr 0.000, L Lat ventricle 52_59_4;_8 15 17;28_78 5;_42_11 22;_44_9 12;_8_9 24;61 3 36;_52_62_7;20_23 48
36	Disgusted Disgusting - Hap Disgusting	0
37	Hap unk - Disgusted unk	R extranuclear, R cuneus, R Inf TG, R IFG, R Mid TG 25_26 10;13_71 17;59_14_21;32 32_2;54_26_19;
38	Hap unk - neut unk	R subgyr, L IFG 30 3 -28; -37 18 -12
39	neut unk - Hap unk	L extranuc, L STG, L cing gyr, L STG, L Postcentral gyrus, L subgyr x3, _23_18 8;_37_42 10;_16_33 27;_44 22 0;_40 _21 27;_23 32 27;_32_9 29;_32 3 20
40	neut unk - Disgusted unk	L Thalamus, L subgyr, _23_21 10;_25 15 24;_23 32 24

Appendix II. Substraction analyses, brain regions and MNI coordinates; neut, neutral; imm, immoral; unk, unknown; first abbrev. facial expression second abbrev. vignette type.

41	Disgusted unk -neut unk	**L IFG, L subgyr, R IFG** _40 15_21;42_18_16;32 20_16
42	Disgusted unk - Hap unk	**0**

Appendix II. Substraction analyses, brain regions and MNI coordinates; neut, neutral; imm, immoral; unk, unknown; first abbrev. facial expression second abbrev. vignette type.

	Contrasting Vignettes	Contrasting Vignettes
43	Hap Imm - Hap neut	**Rx2 Sup front gyr, R IFG,** 18 58 24: 42 25_14; 18 51 34
44	Hap Imm - Hap Disgusting	**0**
45	Hap Imm - Hap unk	**L STG, R Sup front gyr** _44_38 5;18 54 36
46	Hap neut - Hap Imm	**0**
47	Hap neut - Hap Disgusting	**0**
48	Hap neut - Hap unk	**0**
49	Hap Disgusting - Hap Imm	**L Lat ventricle, R sup front gyr, R precentral gyr** _32_52 3;6_9 77;11_26 77
50	Hap Disgusting - Hap neut	**R IFG, Parahippocampal Gyr, L Mid front gyr** 56 6 17; 28_21_16;_32 42_16
51	Hap disgusting - Hap unk	**L STG, L&R Sup front gyr, L IFG, L angular gyr, L brainstem** _42_40 5;_8 10 53;_49 18_7;11 6 72;_32_62 34;_1_38_21
52	Hap unk - Hap Imm	**R subgyrx2** 37_40 0;35_66 5
53	Hap unk - Hap neut	**L Mid front gyr, R insula, R Mid temp gyr, L Extranuc, L subgyr, L caudate** _6 42 27;40_23_2;61_21_12;_18_40 17;_40_11_14;_16 20 3
54	Hap unk - Hap Disgusting	**Lx2 Mid fron gyr, Rx2 Mid temp gyr, Rx2 inf parietal lobule, L postcentral gyr, R mid front gyr, R precuneus** 59_33 53;23 22 63;_32 27 51;64_23_14;_52_33_14;47_40 39;_56_35 51;6 39 27;44_54 56;8_54 51
55	neut Imm - neut neut	**0**
56	neut Imm - neut Disgusting	**L subgyr, R precentral gyrus, R insula, L STG** _42_11 22;61 3 34;42_18 22;_56_9 8
57	neut Imm - neut unk	**0**
58	neut neut - neut Imm	**0**
59	neut neut - neut Disgusting	**L extranuc, L insula** _11 22 15;_47_9 12
60	neut neut - neut unk	**0**
61	neut Disgusting - neut Imm	**Rx2 sup front gyr, Lx2&Rx2 Mid fron gyr, L mid temp gyr, L supramarginal gyr, R ant cing, L inf par lobule,** 20 27 60;_32 27 48;_52_45 0;_56_52 29;8 42 10;32 22 56;_56_35 48;1 42 34;4_26 5;_6_62 44;_6 42 22
62	neut Disgusting - neut neut	**Lx2 Mid temp Gyr, L Mid front gyr, R Inf temp gyr, L supramarginal gyr, L extra nuclear, R Inf temp gyr,** _52_28_16;_28 27 48;_52_47 5;59_14_24:_59_52 29;_32 15_9;59_21_21;13 46_12
63	neut disgusting - neut unk	**L Inf fron gyr, L STG, L sup front Gyr** _42 15_12;_52_50 8;_8 3 75
64	neut unk - neut Imm	**R Mid front gyr, R sup front gyr, R ant cing** 1 42 29;32 22 53;6 46 12
65	neut unk - neut neut	**L Mid front gyr, L Med front gyr, R sub gyr, R mid front gyr, L sub gyr** _25 27 48;_4 42 29;23_21 48;32 22 51;_23 10 44
66	neut unk - neut Disgusting	**L Sub-gyr** _25 10 32
67	Disgusted Imm - Disgusted neut	**R Mid temp gyr, L Inf front gyr, R STG** 37_42 3;_35 20_9;44 18_24
68	Disgusted Imm - Disgusted Disgusting	**R Inf front gyr, L extra nuc, L sub gyr, L Inf front gyr, R sup front gyr, L Inf front gyr,** 42 22 5;_30 6_9;37_30 0;_37 15_21;13 54 29;_28 25_12
69	Disgusted Imm - Disgusted unk	**L med front gyr, L Sub-gyr, L Inf front gyr, R insula, L&R sug-gyr, L lingual gyr, L Mid front gyr, R thalamus,** _6 13 51;_23_50 41;_35 25_9;30 20 3;_47 18 22;44 20 15;_25_78_9;_35 3 39;13_18 0;35 32_2;35_59_31
70	Disgusted neut - Disgusted Imm	**0**
71	Disgusted neut - Disgusted Disgusting	**R Sup front gyr** 11 51 32
72	Disgusted neut - Disgusted unk	**Lx2 sub-gyr,** _47 18 20;_28 34 22
73	Disgusted Disgusting - Disgusted Imm	**L extra nuc, L caudate, R sub-gyr** _8_11 24;_11 15_7;35_57 8
74	Disgusted Disgusting - Disgusted neut	**R&L lat vent,** 8 8 20;_8 6 22;
75	Disgusted disgusting - Disgusted unk	**R culmen, R sub-gyr, L extra nuc, L culmen** 30_57_31;25 22 15;_8 3 24;_6_40_28
76	Disgusted unk - Disgusted Imm	**R&L anguglar gyr, R precentral gyr, L Med front gyr,** 47_69 34;_35_78 32;56 1 8;_8 56 8
77	Disgusted unk - Disgusted neut	**R&L STG, R Inf front gyr, L precuneus,** 66_26 10;32 20_16;_35_81 34;_37 15_24
78	Disgusted unk - Disgusted Disgusting	**R Mid temp gyr, L Inf front gyr, R Lat vent** 61_23_12;_37 15_21;35_14_19

Appendix III: Percent signal change graphs

Beta weights were extracted from the peak activations drawn from the facial expression – neutral expression contrasts, and vignettes from the unknowns.

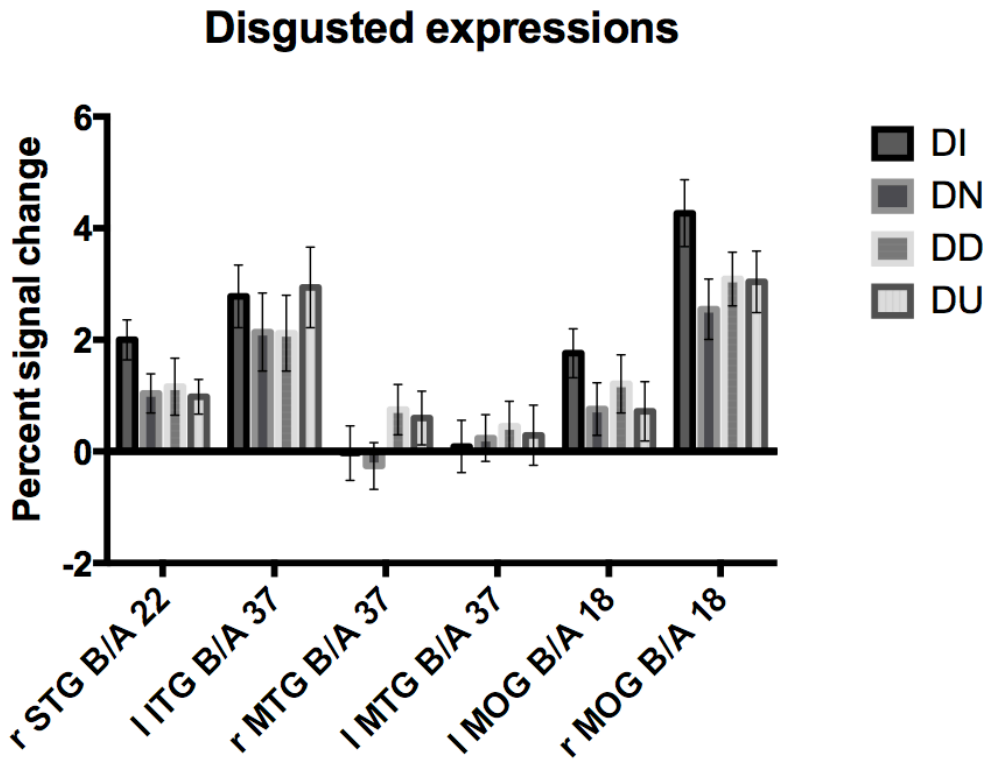

Figure 6. The effect of condition on activity of disgusted facial expressions minus neutral expressions for each vignette type. DI, disgusted face of immoral individual; DN, disgusted face of neutral individual; DD, disgusted face of disgusting individual; DU, disgusted face of unknown individual; r, right; l, left; superior temporal gyrus, STG; inferior temporal gyrus, ITG; middle temporal gyrus, MTG; middle occipital gyrus, MOG; B/A Brodmann area. Error bars represent SE.

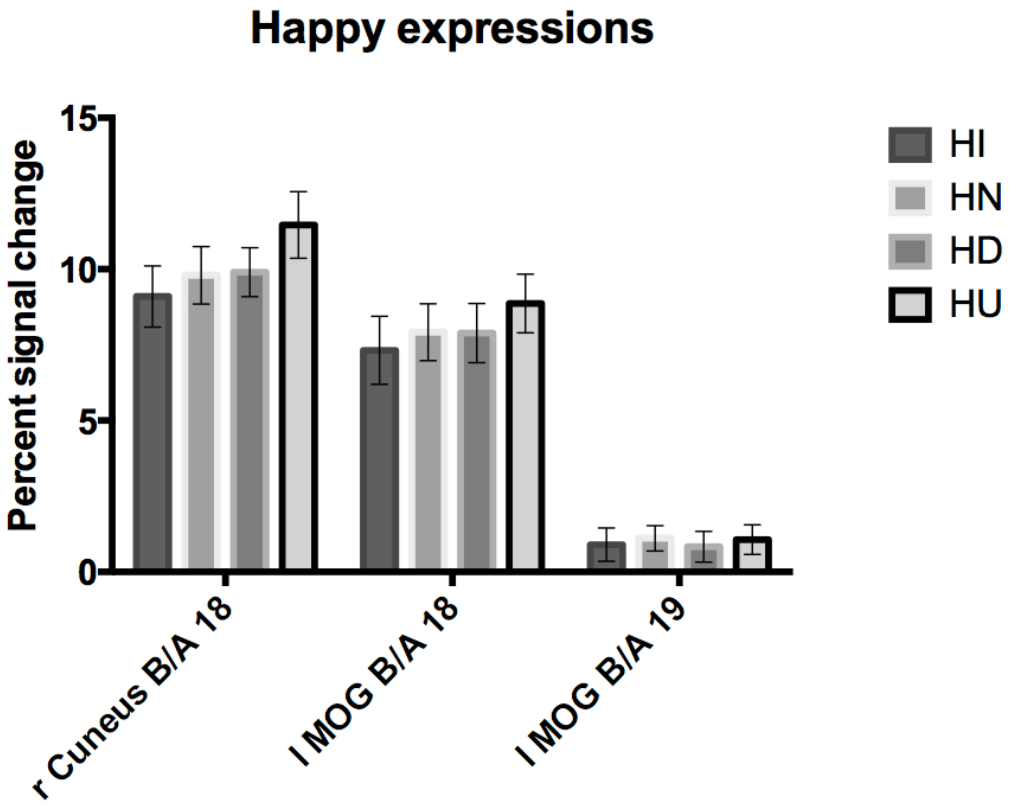

Figure 7. The effect of condition on activity of happy facial expressions - neutral expressions for each vignette type. NI, happy face of immoral individual; HN, happy face of neutral individual; HD, happy face of disgusting individual; HU, happy face of unknown individual; r, right; l, left; middle occipital gyrus, MOG; B/A, Brodmann area. Error bars represent SE.

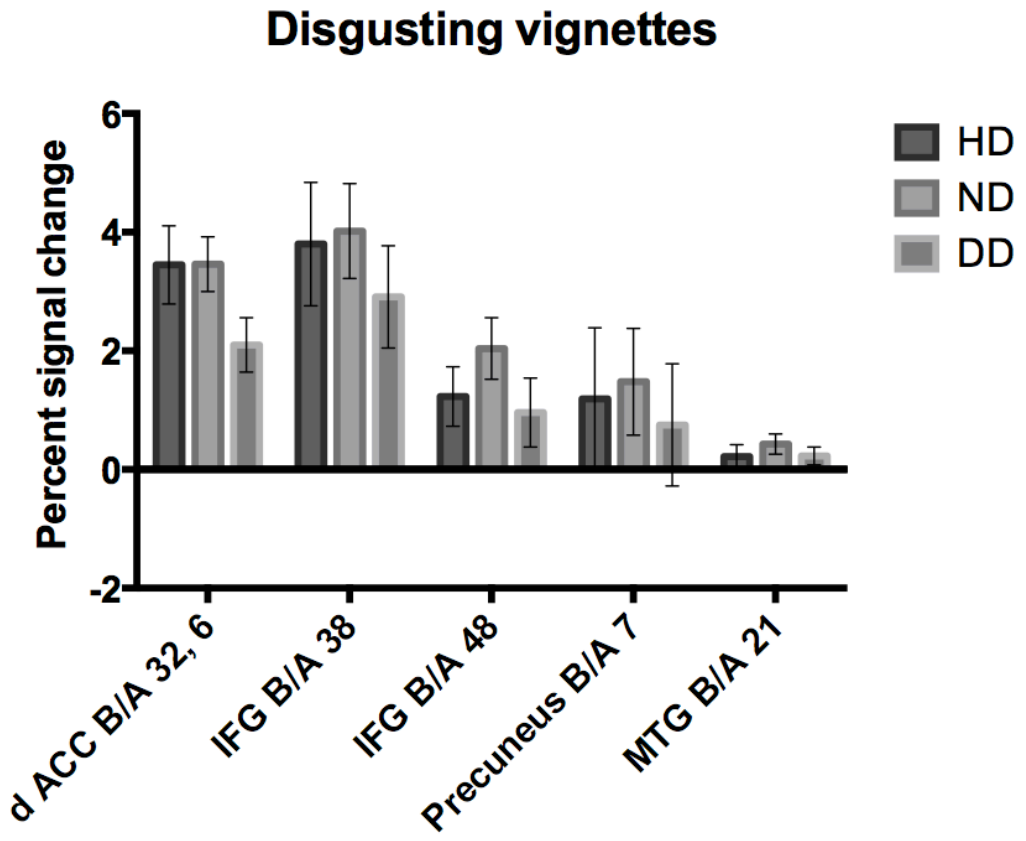

Figure 8. The percent signal change of disgusted vignettes - unknowns for each facial expression. Happy face of disgusting individual, HD; neutral face of disgusting individual, ND; disgusted face of disgusting individual DD; dorsal anterior cingulate cortex, d ACC; inferior frontal gyrus, IFG; middle temporal gyrus, MTG; B/A Brodmann area. Error bars represent SE.

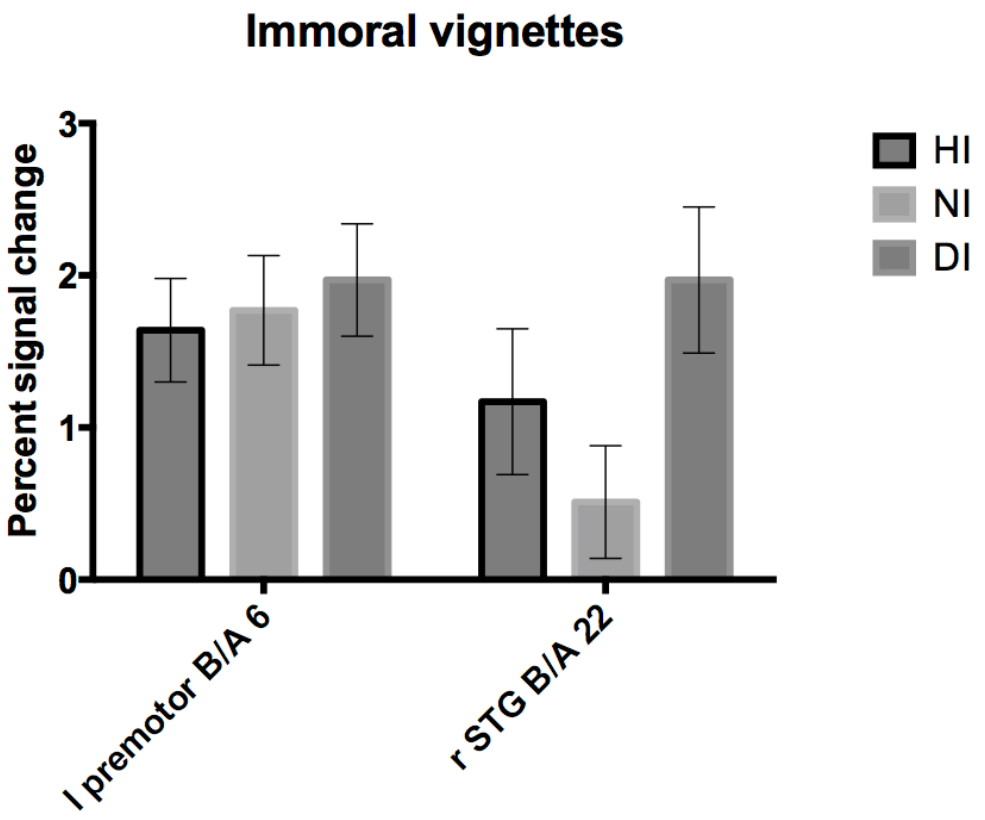

Figure 9. Activity for immoral vignettes - unknown individuals for each facial expression. HI, happy face of immoral individual; NI, neutral face of immoral individual; DI, disgusted face of immoral individual; r, right; l, left; IFG; superior temporal gyrus, STG; B/A Brodmann area. Error bars represent SEM.

Appendix IV: Ethics Approval

Office of the Deputy Vice-Chancellor (Research)

Research Office
C5C Research HUB East, Level 3, Room 324
MACQUARIE UNIVERSITY NSW 2109 AUSTRALIA

Phone **+61 (0)2 9850 4194**
Fax +61 (0)2 9850 4465
Email ethics.secretariat@mq.edu.au

5 March 2014

Associate Professor Mark Williams
Department of Cognitive Science
Faculty of Human Sciences
Macquarie University NSW 2109

Dear Associate Professor Williams

RE: *The neural correlates of physical disgust and moral aversion using biographical memory*

Thank you for submitting the above application for ethical review. Your application was considered by the Macquarie University Human Research Ethics Committee (HREC (Medical Sciences)) at its meeting on 27 February 2014.

I am pleased to advise that ethical and scientific approval has been granted for this project to be conducted at:

- Macquarie University

This research meets the requirements set out in the *National Statement on Ethical Conduct in Human Research* (2007) (the *National Statement*).

This letter constitutes ethical and scientific approval only.

Details of this approval are as follows:

Reference No: 5201400104

Approval Date: 27 February 2014

The following documentation has been reviewed and approved by the HREC (Medical Sciences):

Documents reviewed	Version	Date
Macquarie University Ethics Application Form	2.3	July, 2013
Morally Aversive Vignettes		
Neutral Vignettes		
Physically Disgusting Vignettes		
Rating scale of aversion: Biographical vignettes		
Advertisement		
Macquarie University Participant Information and Consent Form entitled *fMRI using facial stimuli*	2	31/10/2013

Please ensure that in all future correspondence with the HREC all documentation includes a version number and date.

Standard Conditions of Approval:

1. Continuing compliance with the requirements of the *National Statement,* which is available at the following website:

http://www.nhmrc.gov.au/book/national-statement-ethical-conduct-human-research

2. This approval is valid for five (5) years, subject to the submission of annual reports. Please submit your reports on the anniversary of the approval for this protocol.

3. All adverse events, including events which might affect the continued ethical and scientific acceptability of the project, must be reported to the HREC within 72 hours.

4. Proposed changes to the protocol must be submitted to the Committee for approval before implementation.

It is the responsibility of the principal investigator to retain a copy of all documentation related to this project and to forward a copy of this approval letter to all personnel listed on the project.

Should you have any queries regarding your project, please contact the Ethics Secretariat on 9850 4194 or by email ethics.secretariat@mq.edu.au

The HREC (Medical Sciences) Terms of Reference and Standard Operating Procedures are available from the Research Office website at:

http://www.research.mq.edu.au/for/researchers/how_to_obtain_ethics_approval/human_research_ethics

The HREC (Medical Sciences) wishes you every success in your research.

Yours sincerely

Professor Tony Eyers
Chair, Macquarie University Human Research Ethics Committee (Medical Sciences)

Cc. Ms Kate Hardwick, Department of Cognitive Science

This HREC is constituted and operates in accordance with the National Health and Medical Research Council's (NHMRC) *National Statement on Ethical Conduct in Human Research* (2007) and the *CPMP/ICH Note for Guidance on Good Clinical Practice*.