Ann. N.Y. Acad. Sci. ISSN 0077-8923

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Issue: *The Year in Cognitive Neuroscience*

Understanding disgust

Hanah A. Chapman and Adam K. Anderson

Department of Psychology, University of Toronto, Toronto, ON, Canada

Address for correspondence: Hanah Chapman, Division of Humanities and Social Sciences, California Institute of Technology, 1200 E. California Blvd. MC-228-77, Pasadena, CA 91125. hchapman@caltech.edu

Disgust is characterized by a remarkably diverse set of stimulus triggers, ranging from extremely concrete (bad tastes and disease vectors) to extremely abstract (moral transgressions and those who commit them). This diversity may reflect an expansion of the role of disgust over evolutionary time, from an origin in defending the body against toxicity and disease, through defense against other threats to biological fitness (e.g., incest), to involvement in the selection of suitable interaction partners, by motivating the rejection of individuals who violate social and moral norms. The anterior insula, and to a lesser extent the basal ganglia, are implicated in toxicity- and disease-related forms of disgust, although we argue that insular activation is not exclusive to disgust. It remains unclear whether moral disgust is associated with insular activity. Disgust offers cognitive neuroscientists a unique opportunity to study how an evolutionarily ancient response rooted in the chemical senses has expanded into a uniquely human social cognitive domain; many interesting research avenues remain to be explored.

Keywords: disgust; distaste; morality; emotion; facial expression; interoception

Introduction

From unsavory foods to squalid restrooms, mutilations to moral depravity, the stimuli that evoke disgust are perhaps the most diverse of any human emotion. Nonetheless, these kinds of objects and events seem to trigger a common experience of revulsion and offence in human beings the world over.[1–3] Disgust has been recognized as a basic and universal human emotion at least since the time of Darwin,[4] but with the exception of pioneering work by Paul Rozin and his colleagues, disgust was largely ignored by the affective revolution that swept through psychology beginning in the 1980s. This trend of neglect has reversed in recent years, however, with an explosion of research on all aspects of disgust. Here we provide a review of recent and classic work on disgust, with an emphasis on what is known about its neural basis. We begin by describing a key evolutionary theory of disgust that makes sense of the heterogeneous assortment of disgusting stimuli, and that provides the conceptual foundation for much of modern disgust research.[1,5]

Disgust: origins and expansion or descent with modification

Disgust is perhaps best understood by analogy to a phylogenetic or evolutionary tree, with more specialized forms branching off from a root that is the "common ancestor" for all of the varied forms of disgust.[1] The ancestral process for disgust is thought to be distaste, a form of motivated food rejection triggered by the ingestion of unpleasant-tasting substances, prototypically those that are bitter.[1] The behavioral tendency of distaste is oral rejection, that is, spitting out the unpleasant substance. Distaste responses can be seen in adult humans[6] and neonates only a few hours old,[7,8] as well as nonhuman animals, including rats,[9] apes, and monkeys.[10] Because many toxins are bitter,[11] distaste has a clear and concrete adaptive function in motivating the avoidance of poisonous foods. Consistent with this basic adaptive role, the ability to detect and reject bitter substances seems to be very ancient: even sea anemones, which first evolved nearly 500 million years ago, will eject bitter foods from their gastrovascular cavity.[11] Interestingly, the relationship between bitterness and toxicity may

doi: 10.1111/j.1749-6632.2011.06369.x

Ann. N.Y. Acad. Sci. 1251 (2012) 62–76

represent a form of coevolved signaling between predators and prey.[11] Biological toxins likely evoked to defend prey species (including plants) against predation (including grazing). The bitter taste associated with toxins serves to warn to potential predators about the cost of consuming a particular prey species. Both sides benefit from this communication: the predator avoids ingesting more than a mouthful of the toxic prey, and the prey avoids extensive injury.

Although the terms *distaste* and *disgust* are often used interchangeably, the two systems are not identical.[1] In particular, although distaste is focused on the avoidance of toxins,[11] most forms of disgust serve to defend the organism against parasitic disease, including infection by microorganisms such as bacteria and viruses.[12,13] The problem of detecting and avoiding disease is rather more difficult than the problem of detecting and avoiding toxins, because it is in the parasite's interest to infect the host without being detected. Accordingly, parasites usually do not signal their presence in the same way that prey species may signal their toxicity. Instead, an organism that wishes to avoid infection must recognize and avoid stimuli that are reliably—but incidentally—associated with contamination by parasites.[14,15] Relevant cues may include certain types of odors (e.g., the smell of decay), as well as tactile and visual cues (e.g., slime, mold, worms, body products such as feces, certain insects, and sick conspecifics).[12] In species with the cognitive capacity to do so, it is also helpful to avoid objects that may have contacted a primary disease vector—that is, to avoid items that may be contaminated.[16] For example, the clothing or bedding of a person who has a skin infection may be almost as infectious as the diseased person themself.

The psychological features of disgust are consistent with a role in avoiding disease. Compared to distaste, disgust is less reliant on the sense of taste to diagnose potential threats[1] because many modalities can provide information about disease cues. Put more concretely, you do not need to eat a cockroach to be disgusted by it. Disgust also differs from distaste in that disgusting substances are much more contaminating than distasteful substances.[5] Although you may eat around a bitter and disliked vegetable on your plate, you are unlikely to do so if someone spits in your dinner. The property of contamination complements disgust's role in defending against infectious disease: microorganisms in particular can spread invisibly and easily from one substance to another, and a single organism can multiply exponentially to become a serious threat to health.[15] By contrast, toxins tend to be inert and may be harmless if sufficiently diluted.

In spite of the differences between distaste and disgust, the most basic forms of disgust share distaste's behavioral tendency of oral rejection.[1] Accordingly, disgust is thought to have originated from distaste; in other words, disgust is thought to be a branch off the distaste root. Consistent with this descent, the original forms of disgust—often referred to as "core" disgust—are believed to focus on defending against infection via the oral route.[1] From here, other branches developed as the function of disgust expanded to include defense against other types of threats.[1] Still closely tied to disease-avoidance, but less to oral incorporation, is disgust elicited by contact with unfamiliar, unhygienic, or diseased conspecifics, known as interpersonal disgust.[1] Somewhat less directly associated with disease, but still clearly related to biological fitness, are the various forms of sexual disgust.[1] These kinds of disgust may motivate the avoidance of sexual contact with partners who are undesirable from an evolutionary perspective, such as relatives, the very old or very young, and members of the wrong species or the wrong sex.[17] Finally, violations of the normal outer envelope of the body, such as injuries and blood, can also trigger disgust.[1] A number of diseases can spread through contact with blood, so this type of disgust could also serve a disease-avoidance function.[3] Disgust triggered by blood and injuries is sometimes grouped together with sexual disgust to form the category of "animal reminder" disgust, on the logic that these types of stimuli are disturbing because they remind us that humans are mortal animals.[1] Table 1 provides a summary of the stimulus triggers and hypothesized functions for distaste and different types of disgust.

Taken together, we refer to disgust elicited by the rather concrete assortment of stimuli just described as *physical disgust*. We use this umbrella term primarily for convenience, not because of any strong conviction that the various physical disgusts form a homogeneous group. In fact, few studies have directly compared different kinds of physical disgust in an effort to characterize differences and similarities between them.

Table 1. Varieties of distaste and disgust

Type	Example stimulus triggers	Hypothesized function
Distaste	Unpleasant tastes, especially bitter	Avoid toxins
Physical disgust		
Core disgust	Feces, vomit, rats, maggots, spoiled food	Avoid infection via oral route
Blood–injury	Injuries, blood, bodily deformities	Avoid infection
Interpersonal	Contact with diseased or unfamiliar individuals	Avoid infection
Sexual	Sexual contact with very old or very young, wrong sex, or wrong species	Avoid compromising reproductive fitness
Moral disgust	Violation of social and moral norms	Avoid unsuitable interaction partners

Accordingly, it is not clear whether we should expect substantial neural differences between disgust associated with different types of physical stimuli. An exception is research comparing core disgust to disgust triggered by blood and injuries (BI disgust). Core and BI disgust are associated with different psychophysiological correlates: core disgust is related to nausea and changes in the normal rhythm of stomach contractions,[18,19] whereas BI disgust is related to light-headedness and fainting, associated with changes in the cardiovascular system.[18,20] Core and BI disgust are also associated with different clinical phenomena: core disgust with OCD symptoms,[21] and BI disgust with blood–injection–injury phobia.[22,23]

Although distaste can evidently be seen in many nonhuman animals, it is less clear whether physical disgust exists beyond our own species.[5] On the one hand, many nonhuman animals do not seem to show the same aversion to disease vectors (e.g., feces) that humans do.[5] On the other hand, many species *do* show clear evidence of a variety of disease-avoidance behaviors.[24] It is not clear whether such behavior is accompanied by a subjective experience of disgust that is similar to what humans feel; nonetheless, some accompanying motivational state seems likely, and this may represent disgust in nonhuman animals.

Some of the confusion over disgust in nonhuman animals may be related to the different levels of disease risk faced by different species. In particular, some species may be more vulnerable to disease than others, and hence may have a greater need for disgust. For example, humans are omnivores: this lack of dietary specialization may lead to frequent exposure to dangerous foodstuffs.[5] By contrast, species with a highly specialized diet may simply never come into contact with foods that may carry disease. At the other end of the spectrum, species adapted for scavenging may have developed specialized mechanisms to deal with the challenges of eating rotten food. Humans' highly social lifestyle may also have encouraged the evolution of a sensitive disgust system: one of the costs of social life is increased risk of exposure to disease from conspecifics.[5,25] Animal species that are asocial, or that live in relatively isolated groups, may not need mechanisms to mitigate this risk.

There is one form of disgust that does seem unique to humans, namely disgust triggered by the violation of social norms and moral values.[1] For example, people who steal, lie, cheat, and harm others are all referred to as "disgusting."[3,26,27] Disgust's leap from the physical world of disease avoidance to the much more abstract sociomoral domain is quite striking, and may represent an example of exaptation,[1] an evolutionary process whereby a pre-existing system assumes a new functional role.[28–30] In the case of moral disgust, the new functional role may be motivating the avoidance of individuals who violate social norms, who accordingly may not be good partners for interaction.[1] It remains unclear whether there are particular types of moral transgressions that are most strongly tied to disgust.[31,32]

Although anger may seem like a more natural response to norm violations than disgust, it is worth considering that anger is an approach-related, strongly activating emotion.[33] Hence, it may represent a rather costly response to moral transgressions. By contrast, the withdrawal and avoidance

motivation associated with disgust may offer a lower-cost strategy.[32] Indeed, recent modeling work suggests that noncooperation is often a more efficient response to norm violation than is costly punishment.[34] That said, moral disgust is not without controversy:[35] some have argued that moral disgust may just be anger in disguise,[36] or that moral disgust may be limited to transgressions that remind us of physical disgust stimuli (e.g., gory murders).[13,37] We discuss the debate surrounding moral disgust in more detail below.

To summarize, disgust is believed to have expanded from an origin in distaste and the avoidance of toxins, through to avoidance of disease and other threats to biological fitness, and finally into the social and moral domain (Table 1).[1,5] The broad scope of disgust provides fertile ground for a number of cognitive neuroscience research questions, and in turn, cognitive neuroscience provides new avenues to test this theory of the evolution of disgust. A key question is whether the different forms of disgust are related to one another at the neural level, and on the flip side, how their differing functional roles are instantiated. Cognitive neuroscience research on disgust first began more than a decade ago, with work examining the neural basis of perceiving disgusted facial expressions.[38–40] More recent work continues to be heavily influenced by these early findings, so we will start our review of the cognitive neuroscience of disgust by considering the neural correlates of perceiving disgust expressions before going on to discuss distaste, physical disgust, and moral disgust. As we will see, the insula has been strongly implicated in perceiving as well as experiencing many forms of disgust. We therefore begin by providing a short overview of what is known about the insula.

Insular cortex: anatomy and function

Concealed beneath the overlying frontal, parietal, and temporal opercula, the human insula consists of five to seven gyri with substantial morphological variation between individuals (Fig. 1).[41,42] It is interconnected with a number of cortical regions, including anterior cingulate, frontal pole, and dorsolateral prefrontal cortex as well as primary and secondary somatosensory cortex and auditory cortex. The insula is also heavily connected with the amygdala and dorsal thalamus.[43–45]

Architectonic studies have revealed three major divisions of insula in most mammals: an anterior agranular section, a middle dysgranular section, and a posterior granular section.[46] In humans and great apes, there is an additional sector in the most anterior and ventral portion of the insula, at its junction with the orbitofrontal cortex.[47] This area, known as frontoinsular cortex, contains the distinctive von Economo neurons (VENs),[48] large bipolar neurons that are especially prominent in humans and great apes but not other primates.[47] VENs are selectively compromised in early-stage frontotemporal dementia, in which empathy, social awareness, and self-control deteriorate.[49]

The insula has been known to play a role in viscerosensation, olfaction, and gustation since Penfield's experiments.[50] Modern research has confirmed the important interoceptive function of the insula, and also suggests a posterior-to-mid-to-anterior functional gradient, from primary interoceptive representations in posterior insula, to a middle integration zone, and finally to an anterior region involved in high-level integration of homeostatic information with other cognitive and affective processes.[51] Indeed, the connectivity of the insula places it in an ideal position to integrate homeostatic information with information about the physical and social external environment. The role of the insula also seems to extend well beyond interoception, to include a wide variety of cognitive, affective, and social processes.[51] The sheer breadth of processes associated with insular activation, as well as the effects of VEN degeneration in frontotemporal dementia, have led to the suggestion that the insula, especially its most anterior sections, may underlie the human sense of self-awareness or consciousness.[51]

Perceiving disgusted facial expressions

Having completed this brief review of the insula, we now return to the cognitive neuroscience of disgust, beginning with what is known about perceiving disgust in others. Darwin was perhaps the first to recognize and describe a distinct facial expression associated with disgust.[4] The canonical disgust expression centers around movements of the mouth and nose, including raising of the upper lip and wrinkling of the nose.[4,52,53] Gape-like opening of the mouth may also be present, as well as lowering of the brows.[1] In addition to serving as a social signal, the disgust expression may provide egocentric benefits to the sender. In particular, some of the facial movements of disgust may serve to defend

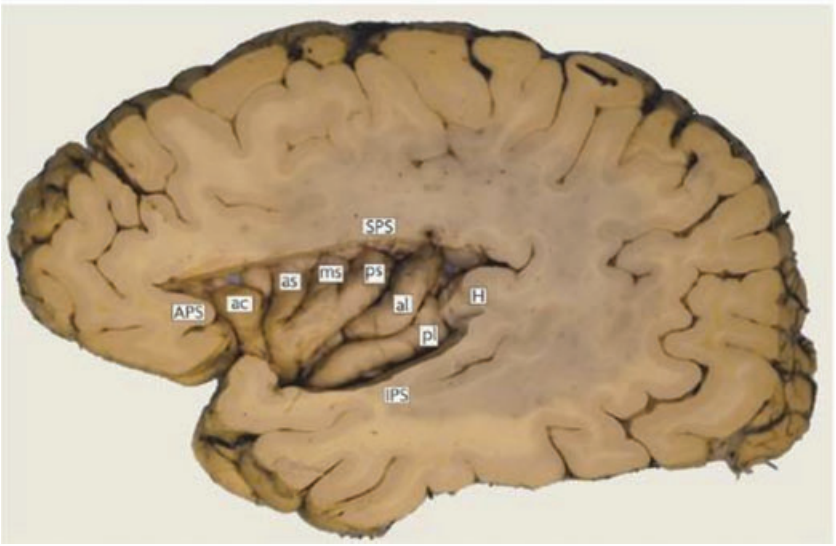

Figure 1. **Anatomy of the human insula. as, anterior short insular gyrus; al, anterior long insular gyrus; ac, accessory gyrus; APS, anterior peri-insular sulcus; H, Heschl's gyrus; IPS, inferior peri-insular sulcus; ms, middle short insular gyrus; ps, posterior short insular gyrus; pl, posterior long insular gyrus; SPS, superior peri-insular sulcus. Photograph is courtesy of Profs. A.D. Craig and Thomas Naidich;[51] reproduced with permission from Nature Publishing Group.**

the vulnerable mucous membranes of the eyes and nose from contact with contaminants.[1,54] Wrinkling the nose and raising the upper lip have the effect of decreasing the volume of the nasal cavities and reducing the amount of air that is inhaled through the nose.[54] Similarly, lowering the brows decreases the exposed surface of the eyes.[54] By contrast, the mouth opening that is sometimes seen in disgust may ready the individual to spit or vomit out any already-ingested food,[1] and increased salivation may help to flush contaminated material from the mouth.[1,55]

The canonical disgust expression is recognized cross-culturally, leading to the suggestion that disgust is one of the basic and universal human emotions.[56,57] Moreover, continuity of the upper lip raise across distaste, physical disgust, and moral disgust provides some of the only empirical evidence for the evolutionary expansion of disgust described above.[58] That said, there is debate as to how similar the expressions associated with distaste and the different forms of disgust really are.[59,60] One study has suggested that mouth gaping may be most strongly associated with distaste, whereas the upper lip raise may be more closely tied to forms of disgust that are removed from oral rejection (e.g., moral disgust).[59] However, this research examined recognition of posed facial expressions rather than measuring spontaneous expression production, and the validity of this approach for examining subtle differences in expression configuration is not clear. Moreover, only the canonical disgust expression, including the upper lip raise and/or nose wrinkle, is associated with activation of the anterior insula, which we will shortly see has been tied to many forms of disgust.[60]

In spite of this debate, the majority of neuroimaging research on disgust expression perception has not been concerned with potential differences among different types of disgust expressions. Rather, the most common question has been whether there are distinct neural substrates for perceiving different emotional expressions (e.g., disgust, fear, anger, etc.). The initial work on this question generated evidence that viewing the canonical disgust expression is associated with activation of the anterior insula, relative to viewing neutral facial expressions.[38–40,61] Although insular activation was also observed for fearful expressions, the insula responded most strongly to disgust when the two were directly compared (but see also Ref. 62). Consistent with these neuroimaging findings, one intracranial recording study in human epilepsy patients implanted with insular depth electrodes found a number of contacts that responded more strongly to facial expressions of disgust than to other emotions.[63]

A recent meta-analysis of 105 fMRI studies of facial expression perception confirms the association between disgust expression perception and activation of the anterior insula.[64] Angry expressions were also found to result in insular activation, but a direct comparison of the activation likelihood estimates for disgust and anger revealed a greater likelihood of activation for disgust.[64] There is some evidence that the anterior insula may provide information about disgust to other brain structures: under conditions of divided attention to disgust expressions, there is a reciprocal relationship between insular activity (reduced with divided attention) and amygdala activity (increased with divided attention).[61] Because the amygdala responds only to fearful expressions under full attention, information from insula may influence the breadth/narrowness of amygdala response tuning.[61]

An interesting extension of expression perception research is work that has examined whether the same brain regions are activated both when an individual perceives a disgusted facial expression and when they personally experience disgust. One study reported activation of the same regions of anterior insula both when subjects viewed videos of actors expressing disgust after smelling an unpleasant odor and when subjects personally experienced unpleasant odors delivered via an olfactometer.[65] Similarly, overlapping regions of anterior insula were activated when subjects viewed videos of actors tasting unpleasant liquids, when they personally tasted unpleasant liquids, and when they imagined physically disgusting events.[66] The results of these studies are important in the wider field of affective psychology and neuroscience, because they provide support for embodied or simulationist theories of facial expression perception. These theories argue that we understand the facial expressions, and indeed the emotions of others, by activating a similar emotion in ourselves.[67,68] Evidence for neural overlap between the perception of disgust expressions and the experience of disgust thus provides an important contribution to our understanding of emotion, empathy, and social communication.

To our knowledge, there have been no human neuroimaging studies of disgust expression production (as opposed to perception). However, a recent intracranial stimulation study in monkeys found that stimulation of ventral anterior insula resulted in facial grimacing, including curling of the upper lip and wrinkling of the nose, that resembled spontaneous responses to unpleasant stimuli.[69] These results suggest that anterior insula may participate in the production as well as the perception of disgust expressions. That said, a study of human patients implanted with insular depth electrodes did not report production of disgust expressions in response to stimulation of the ventral anterior insula, although two patients did report unpleasant sensations in the mouth and throat.[63]

Although the evidence just reviewed emphasizes the importance of the insula in perceiving disgust facial expressions, the basal ganglia have also been implicated, albeit less consistently. The early fMRI studies of disgust expression perception reported activation of the caudate, putamen, and globus pallidus in response to disgust facial expressions;[38–40,61] however, meta-analysis has not supported these findings.[64] There have been several reports of a specific impairment in recognizing disgust expressions in patients with disorders affecting the basal ganglia, such as Huntington's Disease (HD)[70,71] and Obsessive-Compulsive Disorder (OCD).[72] However, more recent results have been mixed. Some studies have replicated the early findings,[73,74] but others have failed to detect any deficit in disgust expression perception,[75] or have reported more general impairments in perceiving many emotional expressions.[76–78] One case report of a patient with a selective lesion of left basal ganglia and insula described a highly specific impairment in recognizing disgust expressions.[79] However, a comparable patient with a right-hemisphere lesion showed no deficit in disgust expression perception.[80] Thus, the involvement of the basal ganglia in disgust expression perception remains unclear.

In summary, neuroimaging work has strongly implicated the insula, particularly its anterior sectors, in perceiving disgust expressions. A caveat worth noting is that neuroimaging cannot demonstrate whether the insula is *necessary* for perceiving disgust. Given the sparse and mixed lesion evidence available to date, the question of necessity remains an open one.

Distaste

We now turn from perceiving disgust in others to considering the various forms of subjectively experienced disgust. We begin by examining the

neural substrates of distaste, given its apparent status as the precursor of disgust. As mentioned, the distaste response is strongly tied to gustatory sensation. Accordingly, distaste begins in the mouth with stimulation of taste receptor cells. Information from taste receptors is transmitted to the central nervous system via cranial nerves VII, IX, and X.[81] These projections synapse in the nucleus of the solitary tract and then continue to gustatory thalamus.[82] Thalamic efferents project to the anterior insula and overlying operculum,[83,84] whereas a second, less extensive projection terminates in postcentral gyrus.[85] The predominance of the insular projection suggests that the insula likely contains primary gustatory cortex.[86] However, the exact location of human primary gustatory cortex in the insula remains a topic of debate, and there may be multiple gustatory representations in human insula.[86] Some of the uncertainty likely stems from the fact that insular activity is by no means exclusive to taste: rather, the insula responds to a variety of inputs associated with feeding, including oral somatosensation,[87] olfaction,[88] and temperature.[89] Because it is difficult to control for all of these variables in human neuroimaging research, it remains challenging to pinpoint human primary gustatory cortex.[86]

Although the insula is evidently a multimodal region, there is some evidence for functional specialization both in the insula and in other taste-sensitive brain regions. In humans, the dorsal middle insula, as well as the amygdala, seem to respond to taste intensity, irrespective of pleasant or unpleasant valence.[90] By contrast, dorsal anterior insula and some regions of anterior obitofrontal cortex (OFC) have been found to respond preferentially to unpleasant (i.e., distasteful) stimuli, regardless of intensity.[90] In turn, pleasant tastes may be associated with activation of the insula more ventrally and OFC more laterally.[90] An interesting complement to these human neuroimaging findings is an intracranial stimulation study in macaques, which found that stimulation of the ventral anterior insula resulted in spitting out or throwing away preferred foods, as if they had become distasteful.[69] Single-neuron recordings from macaques also provide evidence that distinct cells in the anterior insula respond most strongly to particular pleasant and unpleasant tastes, but do not suggest a topographic organization of these cells (i.e., the location of a taste cell does not predict what taste it responds to).[91–93]

The take-home message here is that although the insula almost certainly has a way of representing distaste, it is clearly not—as a whole—a region that is selective for distasteful stimuli. Rather, the insula responds to both pleasant and unpleasant tastes, as well as other feeding-related stimuli, and likely codes for specific gustatory experiences in a distributed fashion.[91]

Physical disgust

In contrast to distaste, which is closely tied to gustatory sensation, physical disgust can be evoked by a much wider range of stimuli and via all sensory modalities. Cognitive neuroscientists have studied physical disgust using photographs,[94,95] films,[18,96,97] auditory stimuli,[39] autobiographical recall,[98] script-driven imagery,[66] and written vignettes.[99,100] A wide range of physical disgust stimuli have also been examined, most commonly including body products, such as feces and vomit; spoiled food; insects, such as roaches and worms; blood; injuries; and corpses. Although the stimulus triggers for physical disgust are quite distinct from the simple chemosensory stimuli used to study distaste, physical disgust stimuli are also strongly associated with activity in the anterior insula. For example, viewing disgusting photographs[94,95] and films,[18] imagining disgusting events,[66] and recalling disgusting experiences[98] have all been found to result in anterior insula activation, relative to neutral comparison conditions. Subjective ratings of disgust—but not fear—in response to disgusting photographs are correlated with activation of the anterior insula.[101] Similarly, subjective ratings of disgust in response to disgusting films are correlated with anterior insula activation.[18] Individual differences in the tendency to experience physical disgust (i.e., trait physical disgust) are also associated with the degree of activation of the anterior insula while viewing disgusting photographs.[102,103] That said, individual differences in trait anxiety are also associated with activation of the insula when subjects view fearful photographs.[102]

Although there have been occasional failures to replicate insular activation in response to physical disgust stimuli,[104,105] the association between bilateral insular activation and physical disgust has been confirmed in a recent meta-analysis of 83 neuroimaging studies of emotion, including 29 studies of physical disgust.[106] Smaller clusters of insular activity were also seen for happiness, fear, and sadness;

however, these activations were much smaller than for disgust, and the activation likelihood estimates for disgust were significantly stronger than for happiness, fear, or sadness. Naturally, the insula is not the only brain region associated with disgust. It is not uncommon to see amygdala activity in response to physical disgust, as well as the anterior cingulate and medial fontal gyrus.[106] Activation of these regions may represent nonspecific aspects of disgust experience, such as emotional arousal, withdrawal tendencies, and self-regulation.

The triggers for physical disgust encompass a remarkably diverse set of stimuli, and an obvious question is whether different subtypes of physical disgust stimuli are associated with distinct neural correlates in the insula or in other brain regions. As discussed above, there have been few empirical studies of behavioral and/or physiological differences and similarities between different types of physical disgust; thus, neuroimaging comparisons tend to be exploratory rather than hypothesis driven. An exception is the small handful of studies that have investigated differences between disgust evoked by stimuli such as body products, rotten food, and insects (e.g., core disgust) and disgust evoked by blood and violations of the outer body envelope (e.g., BI disgust). Core and BI disgust are known to be associated with different physiological responses[18,19,20] as well as with different clinical phenomena.[21,22,23] In spite of these differences, core and BI disgust seem to result in partly overlapping activation in the anterior insula, perhaps reflecting a common disgust experience.[18,95,97,107] There are also differences in insular activation between core and BI disgust, with core disgust activating a ventral anterior region more strongly, and BI disgust activating a more dorsal mid-insular area. The characteristic psychophysiological effects of core and BI disgust on the stomach and cardiovascular system, respectively, are also represented differentially in the insula.[18] Differences between core and BI disgust have also been reported in other brain regions, although the exact areas have been somewhat inconsistent across studies, perhaps due to methodological differences.[18,95,97,107]

Less is known about the neural correlates of sexual disgust as compared to other forms of physical disgust. One study has contrasted the neural responses to written scenarios describing incest and scenarios describing core disgust stimuli.[100] The authors found stronger activation of the anterior insula in response to the incest relative to the core disgust stimuli.[100] However, this study is somewhat unusual in that it did not find significant insular activation in response to the core disgust stimuli compared to neutral, perhaps because written stimuli were used, as compared to the films or photographs used in most neuroimaging studies of physical disgust. The only other study to investigate sexual disgust did use photographs as stimuli, but found no insular activation to either sexual disgust photographs or core disgust photographs, compared to neutral photographs.[108] This latter study comes from a group that has performed a number of neuroimaging studies of physical disgust, sometimes finding insular activity[94,101,109] and other times not.[104,107,108] Accordingly, it is somewhat difficult to interpret their null results on insular activation in response to sexual disgust stimuli; indeed, it is difficult to interpret null results in any neuroimaging study. The relationship between sexual disgust and other forms of physical disgust thus remains an open avenue for further exploration. It seems likely to be an interesting one, given recent findings that tie disapproval of homosexuality to trait physical disgust and political conservatism.[110,111]

A final question is whether physical disgust is indeed related to its supposed precursor, distaste, at the neural level. To our knowledge, only one study has directly compared the neural correlates of tasting unpleasant liquids and experiencing physical disgust.[66] To induce distaste, subjects drank bitter quinine solutions, whereas to induce physical disgust, subjects imagined disgusting incidents (e.g., ingesting vomit). A common region of anterior insula/frontal operculum was active in both conditions, suggesting that physical disgust and distaste are indeed supported by at least partially overlapping neural substrates.

Is insular activation specific to disgust?

The results described so far suggest an important role for the insula, especially its anterior regions, in perceiving disgust expressions as well as experiencing physical disgust and distaste. Moreover, there is some evidence that strong activation of the insula may be particularly characteristic of disgust: the two recent meta-analyses described above, one concentrating on facial expressions[64] and the other including a wider range of emotional stimuli,[106]

both showed stronger activation of the insula for disgust as compared to other emotional conditions. In spite of these findings, however, it seems unlikely that there is a unique, one-to-one mapping between activation of the anterior insula and disgust. Some of the results described above begin to hint at this: for example, the insula responds to a wide range of feeding-related stimuli beyond distaste, including oral somatosensation,[91] olfaction,[88] and ingestive motor activity.[86,91] Beyond this, the insula, including its anterior regions, responds to a variety of interoceptive stimuli including heartbeat,[112] stomach and bladder distention,[113,114] sexual arousal,[115] and itch,[116] among many others.[51] Lest researchers of a more cognitive bent feel left out, the insula is also activated by a variety of more traditionally cognitive phenomena, including goal-directed attention,[117] cognitive control and performance monitoring,[118] risk and uncertainty,[119,120] and perceptual decision making.[51,121]

Findings such as these lead us to believe that although the insula may be very important in disgust and distaste, it is not specific to these states. This position may initially seem difficult to reconcile with the meta-analytic results pointing to at least some degree of insular selectivity for disgust.[64,106] We suggest two possible explanations for the discrepancy. One possibility is that among the emotions, disgust may be particularly strongly associated with visceral changes, consistent with its apparent origins in defending against ingestion of toxic or contaminated foods. Indeed, taste itself may represent an interoceptive rather than an exteroceptive sense.[122] Given that the insula seems to play a key role in interoception,[123] heightened insular activity in response to disgust may simply reflect disgust's strong visceral component.

A second, related, but perhaps more mundane possibility is that disgust *per se* may not have a stronger visceral component than other emotions. Rather, the stimuli that are used to evoke disgust in the laboratory may simply be more effective at causing visceral changes than the stimuli that are used to evoke other emotions. On this view, more effective stimulus triggers for other emotions could also result in insular activity. This latter possibility could be tested by using more compelling comparison stimuli as a contrast to disgust.

We wish to note that our arguments against insular specificity to disgust are directed against a more traditional, "locationist" notion of specificity. In other words, what we disagree with is the idea that the insula as a whole, or even a specific region of it, is uniquely activated by disgust. We do believe that the insula must have a way of representing disgust and distaste as states that are distinct from other emotional and motivational experiences. However, this representation is likely a distributed one within the insula and may well extend beyond the insula. We also do not mean to suggest that past research linking the insula more broadly to disgust is uninformative; rather, it serves to highlight the insula as a region to focus on in more targeted analyses.

Sociomoral disgust

Most researchers will probably find the received view of how physical disgust evolved to be quite plausible,[1] and many may also accept an important—although perhaps not unique—role for the insula in distaste and physical disgust. Understandably, however, some may be more skeptical of sociomoral disgust. Is sociomoral "disgust" really related to more basic forms of disgust, or is it just a compelling metaphor used to condemn antisocial behavior?[13,124] Even if one can accept that sociomoral disgust is derived from physical disgust, maybe it is only triggered by transgressions that contain reminders of physical disgust, such as bloody murders and depraved sexual crimes?[37]

These questions remain unresolved in the behavioral literature. On the one hand, there is evidence that sociomoral disgust is indeed a genuine form of disgust, and that it is not limited to transgressions that involve physical disgust stimuli. For example, both adults and children call moral transgressions disgusting,[26,32,125] and match them to disgusted facial expressions,[36,58,125] even when the transgressions do not reference physical disgust. Moral transgressions result in raising of the upper lip,[58,126] a characteristic element of the disgust expression, as do physical disgust and distaste.[58] The upper lip raise in response to transgressions is correlated with self-reported disgust, but not anger or contempt.[58] Individuals who are higher in trait physical disgust make more severe judgments about moral transgressions than do their low-physical-disgust counterparts,[127] an effect that is not accounted for by more general differences in trait negative affect. Finally, experimentally induced distaste[128] and physical

disgust[129,130] cause changes in moral judgments about issues that do not concern physical disgust.

On the other hand, concerns have been raised about some of these findings,[35,131] and conflicting evidence also exists. For example, moral disgust seems to be relatively insensitive to the intent of a perpetrator and the degree of harm resulting from a transgression,[37,132] factors that are generally considered to be important in moral reasoning. Experimentally induced disgust and individual differences in trait disgust may also have a stronger influence on moral judgments about transgressions that contain reminders of physical disgust stimuli, such as sexually promiscuous behavior, relative to transgressions that contain no such reminders.[133] Measurement issues could explain some of the divergent results: self-reports of moral disgust seem to be quite sensitive to how questionnaire measures are phrased.[32,134] Similarly, different studies use quite dramatically different "moral" stimuli, which could have distinct relationships to moral disgust.

Moral disgust thus remains a contentious topic. Neuroimaging could potentially inform the debate by revealing whether moral and physical disgust have a common neural substrate. However, neuroimaging studies of moral disgust present their own challenges. For example, imagine a case where anterior insula activity was detected when subjects made judgments about moral transgressions (for example, Ref. 135). Could this represent sociomoral disgust, and provide evidence that moral disgust is indeed related to physical disgust? Given that the insula is not a unique substrate for disgust,[51] this is a rather questionable reverse inference.[136]

The inference would be somewhat stronger if a direct comparison between sociomoral and physical disgust in the same subjects revealed common insular activity. A handful of studies have now used this kind of design. However, two of these are somewhat difficult to interpret, as they did not find insular activation in response to the physical disgust conditions, perhaps because written rather than visual stimuli were used.[99,100] The only other study did find insular activation in response to a sexual disgust condition (even though written vignettes were used).[137] However, this study did not find insular activity in response to purely moral stimuli, such as descriptions of harm and dishonesty, relative to neutral stimuli. Once again though, the null result for sociomoral disgust is difficult to interpret. The disgusting sexual scenarios were rated as more emotionally arousing than the sociomoral stimuli;[137] it is possible that more arousing sociomoral transgressions could have resulted in activation of the anterior insula. Indeed, very difficult and emotional moral dilemmas, such as whether to kill a crying baby to save an entire village from enemy soldiers, have been found to cause activation of the anterior insula.[135] Similarly, actions that are judged to be morally wrong, as well as controversial moral transgressions, result in increased insular activation relative to actions that are judged to be not wrong and noncontroversial transgressions.[138]

These findings suggest that future work could potentially reveal overlapping activation of the anterior insula for both moral transgressions and physical disgust. However, any such overlap could still represent more generic similarities between moral cognition and physical disgust, such as emotional arousal or uncertainty, rather than a shared disgust experience *per se*. Accordingly, it is likely that neuroimaging studies will provide converging, rather than conclusive, evidence in the debate over moral disgust. It will also be very important for future studies in this area to use moral and physical disgust stimuli that are carefully controlled for spurious differences on dimensions, such as emotional arousal, so as not to confound comparisons of interest.

If moral disgust does indeed prove to be related to physical disgust, then neural differences between moral and physical disgust may also be very interesting. For example, moral disgust is triggered by much more abstract and social stimuli than most forms of physical disgust. Accordingly, moral disgust may involve brain regions that play a role in social cognitive processing, such as dorsal medial prefrontal cortex[139] and temporoparietal junction,[140,141] as well as regions involved in more basic forms of disgust such as insula and perhaps basal ganglia.

Outstanding questions and future directions

Behavioral and cognitive neuroscience studies have considerably increased our understanding of disgust—in all its forms—in recent years. In particular, there is now evidence that distaste and various forms of physical disgust are indeed related to one another at the neural as well as the behavioral levels, as proposed by Paul Rozin and his colleagues many years ago.[1,5] Nonetheless, relative to other emotions

such as fear and sadness, the study of disgust remains in its infancy. One area in particular need of further study is the degree of similarity between different forms of disgust. For example, an influential typology of disgust groups BI disgust and sexual disgust together to form the category of "animal reminder" disgust, which is believed to be rooted in anxiety over human mortality.[1] Neuroimaging studies could inform our understanding of the structure of disgust by revealing commonalities and differences in the neural processing of various disgust stimuli. These kinds of studies may be especially valuable for moral disgust, whose relationship to physical disgust remains a topic of intense debate.[35,36,58]

Neuroimaging comparisons of different types of disgust would likely benefit from the application of more advanced techniques, such as connectivity analyses and multivoxel pattern analysis, which afford analysis of the distributed representations supported by the anterior insula. Beyond functional neuroimaging, electroencephalography (EEG) may also prove a useful tool, especially for investigating sociomoral disgust. In particular, although anger is closely associated with approach motivation and increased EEG alpha power in the left relative to right hemispheres,[33] disgust is believed to be associated with withdrawal motivation[1] and perhaps increased alpha power in the right hemisphere.[142] This raises the possibility that sociomoral disgust may also be associated with increased right hemisphere alpha power and with a stronger tendency to withdraw from rather than approach transgressors.[32]

Another potential research direction is to examine the neural substrates underlying the perception that an object is contaminated or contaminating, a property that is unique to disgusting stimuli.[1,5] To our knowledge, no neuroimaging study has yet investigated contamination. Improved understanding of contamination could have important clinical implications, because excessive contamination concerns feature prominently in some forms of obsessive-compulsive disorder.[143] Speculatively, contamination may involve a memory component, because history of contact is the defining feature of contamination. In this way, the study of contamination could form a bridge between disgust research and the wider field of memory research. Similarly, there is a small but growing literature on the cognitive effects of disgust (for example, Refs. 144–146), but no studies have yet examined the influence of disgust on such processes as attention and memory at the neural level.

A final, and rather different direction is to examine the potential relationship between distaste, disgust, and pain. For example, concentrated bitter solutions can produce a painful burning sensation and result in activation of the trigeminal nerve, which carries nociceptive information to the central nervous system.[147,148] In our own research, we have found that the facial expression produced in response to distaste closely resembles the facial response to pain.[149] Moreover, BI disgust is, by definition, closely tied to the perception of physical injury. How are pain and disgust related at the neural level? Is blood-injury disgust more closely related to pain than core disgust? How does pain influence disgust, and vice versa? Finally, how does disgust toward another's injuries influence empathetic responses to their suffering? These questions remain to be examined.

Conclusion

Scientific knowledge of disgust has expanded far beyond what Darwin might have foreseen when he provided the first empirical description of this emotion more than one hundred years ago. Recent research has provided important support for classic theoretical work, especially for the idea that specialized forms of disgust—including core, BI, and perhaps also sociomoral disgust—are related to one another and descended from distaste, an ancient motivational response rooted in the chemical senses.[1] Exciting new directions have also emerged, including functional neuroimaging work that has increased not only our understanding of disgust, but also of empathy, social cognition, and emotion, more broadly. We are confident that many more promising research directions exist, to be suggested by future findings and creative research yet to be done.

Conflicts of interest

The authors declare no conflicts of interest.

References

1. Rozin, P., J. Haidt & C. McCauley. 2000. Disgust. In *Handbook of Emotions*. M. Lewis & J. Haviland-Jones, Eds.: 637–653. Guilford Press. New York.
2. Haidt, J., P. Rozin, C. McCauley & S. Imada. 1997. Body, psyche, and culture: the relationship between disgust and morality. *Psychol. Develop. Soc.* **9:** 107–131.

3. Curtis, V. & A. Biran. 2001. Dirt, disgust, and disease. Is hygiene in our genes? *Perspect. Biol. Med.* **44:** 17–31.
4. Darwin, C. 1872/1998. *The Expression of the Emotions in Man and Animals*. Oxford University Press. Oxford.
5. Rozin, P. & A. Fallon. 1987. A perspective on disgust. *Psychol. Rev.* **94:** 23–41.
6. Greimel, E., M. Macht, E. Krumhuber & H. Ellgring. 2006. Facial and affective reactions to tastes and their modulation by sadness and joy. *Physiology and Behavior* **89:** 261–269.
7. Peiper, A. 1963. *Cerebral Function in Infancy and Childhood*. Consultants Bureau. New York.
8. Steiner, J. 1973. The gustofacial response: observation on normal and anencephalic newborn infants. In *Fourth Symposium on Oral Sensation and Perception.* J.F. Bosma, Ed.: 254–278. U.S. Department of Health, Education and Welfare. Bethesda, MD.
9. Grill, H. & R. Norgren. 1978. The taste reactivity test. I. Mimetic responses to gustatory simuli in neurologically normal rats. *Brain Res.* **143:** 263–279.
10. Berridge, K. 2000. Measuring hedonic impact in animals and infants: microstructure of affective taste reactivity patterns. *Neurosci. Biobehav. Rev.* **24:** 173–198.
11. Garcia, J., W.G. Hankins, D.A. Denton & J.P. Coghlan. 1975. The evolution of bitter and the acquisition of toxiphobia. In *Olfaction and Taste*, Vol. V.D.A. Denton & J.P. Coghlan, Eds.: 39–45. Academic Press. New York.
12. Curtis, V., R. Aunger & T. Rabie. 2004. Evidence that disgust evolved to protect from risk of disease. *Proc. R. Soc. B.: Biol. Sci.* **271**(Suppl 4): S131–133.
13. Oaten, M., R. Stevenson & T. Case. 2009. Disgust as a disease-avoidance mechanism. *Psychol. Bull.* **135:** 303–321.
14. Schaller, M. & J.H. Park. 2011. The behavioral immune system (and why it matters). *Curr. Direct. Psychol. Sci.* **20:** 99–103.
15. Pinker, S. 1997. *How the Mind Works*. WW Norton. New York.
16. Rozin, P., L. Millman & C. Nemeroff. 1986. Operation of the laws of sympathetic magic in disgust and other domains. *J. Personal. Soc. Psychol.* **50:** 703–712.
17. Fessler, D.M.T. & C.D. Navarrete. 2003. Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evol. Hum. Behav.* **24:** 406–417.
18. Harrison, N.A., M.A. Gray, P.J. Gianaros & H.D. Critchley. 2010. The embodiment of emotional feelings in the brain. *J. Neurosci.* **30:** 12878.
19. Stern, R.M., M.D. Jokerst, M.E. Levine & K.L. Koch. 2001. The stomach's response to unappetizing food: cephalic-vagal effects on gastric myoelectric activity. *Neurogastroenterol. Motility* **13:** 151–154.
20. Cisler, J., B.O. Olatunji & J. Lohr. 2009. Disgust, fear, and the anxiety disorders: a critical review. *Clin. Psychol. Rev.* **29:** 34–46.
21. Olatunji, B.O., N.L. Williams, D.F. Tolin, *et al*. 2007. The disgust scale: item analysis, factor structure, and suggestions for refinement. *Psychol. Assess.* **19:** 281–297.
22. Olatunji, B.O., K.M. Connolly & B. David. 2008. Behavioral avoidance and self-reported fainting symptoms in blood/injury fearful individuals: an experimental test of disgust domain specificity. *Journal of Anxiety Disorders* **22:** 837–848.
23. Olatunji, B.O., C.N. Sawchuk, P.J. de Jong & J.M. Lohr. 2006. The structural relation between disgust sensitivity and blood-injection-injury fears: a cross-cultural comparison of U.S. and Dutch data. *J. Behav. Ther. Exp. Psychiatr.* **37:** 16–29.
24. Hart, B.L. 1990. Behavioral adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* **14:** 273–294.
25. Cote, I.M. & R. Poulinb. 1995. Parasitism and group size in social animals: a meta-analysis. *Behav. Ecol.* **6:** 159–165.
26. Simpson, J., S. Carter, S.H. Anthony & P.G. Overton. 2006. Is disgust a homogeneous emotion? *Motivat. Emot.* **30:** 31–41.
27. Tybur, J.M., D. Lieberman & V. Griskevicius. 2009. Microbes, mating, and morality: individual differences in three functional domains of disgust. *J. Personal. Soc. Psychol.* **97:** 103–122.
28. Bock, W. 1959. Preadaptation and multiple evolutionary pathways. *Evolution* **13:** 194–211.
29. Mayr, E. & S. Tax. 1960. The emergence of evolutionary novelties. In *Evolution After Darwin.* Vol. 1: The Evolution of Life. S. Tax, Ed.: 349–380. Univ. Chicago Press. Chicago.
30. Gould, S. & E. Vrba. 1982. Exaptation: a missing term in the science of form. *Paleobiology* **8:** 4–15.
31. Rozin, P., L. Lowery, S. Imada & J. Haidt. 1999. The CAD triad hypothesis: a mapping between three moral emotions (contempt, anger, disgust) and three moral codes (community, autonomy, divinity). *J. Personal. Soc. Psychol.* **76:** 574–586.
32. Hutcherson, C.A. & J.J. Gross. 2011. The moral emotions: a social-functionalist account of anger, disgust, and contempt. *J. Personal. Soc. Psychol.* **100:** 719–737.
33. Carver, C.S. & E. Harmon-Jones. 2009. Anger is an approach-related affect: evidence and implications. *Psychol. Bull.* **135:** 183–204.
34. Ohtsuki, H., Y. Iwasa & M.A. Nowak. 2009. Indirect reciprocity provides only a narrow margin of efficiency for costly punishment. *Nature* **457:** 79–82.
35. Rozin, P., J. Haidt & K. Fincher. 2009. From oral to moral. *Science* **323:** 1179.
36. Gutierrez, R., R. Giner-Sorolla & M. Vasiljevic. 2012. Just an anger synonym? Moral context influences predictors of disgust word use. *Cogn. Emot.* **26:** 53–64.
37. Gutierrez, R. & R. Giner-Sorolla. 2007. Anger, disgust, and presumption of harm as reactions to taboo-breaking behaviors. *Emotion* **7:** 853–868.
38. Phillips, M.L., A.W. Young, C. Senior, *et al.* 1997. A specific neural substrate for perceiving facial expressions of disgust. *Nature* **389:** 495–498.
39. Phillips, M.L., A.W. Young, S.K. Scott, *et al*. 1998. Neural responses to facial and vocal expressions of fear and disgust. *Proc. Roy. Soc. Lond., Ser. B: Biol. Sci.* **265:** 1809.
40. Sprengelmeyer, R., M. Rausch, U.T. Eysel & H. Przuntek. 1998. Neural structures associated with recognition of facial expressions of basic emotions. *Proc. Roy. Soc. Lond., Ser. B: Biol. Sci.* **265:** 1927.

41. Naidich, T.P., E. Kang, G.M. Fatterpekar, *et al*. 2004. The insula: anatomic study and MR imaging display at 1.5 T. *Am. J. Neuroradiol.* **25:** 222.
42. Varnavas, G.G. & W. Grand. 1999. The insular cortex: morphological and vascular anatomic characteristics. *Neurosurgery* **44:** 127.
43. Augustine, J. 1996. Circuitry and functional aspects of the insular lobe in primates including humans. *Brain Res. Rev.* **22:** 229–244.
44. Mufson, E.J. & M. Mesulam. 1982. Insula of the old world monkey. II: afferent cortical input and comments on the claustrum. *J. Comparat. Neurol.* **212:** 23–37.
45. Mesulam, M. & E. Mufson. 1982. Insula of the old world monkey. III: efferent cortical output and comments on function. *J. Comparat. Neurol.* **212:** 38–52.
46. Mesulam, M. 1982. Insula of the old world monkey I. Architectonics in the insulo-orbito-temporal component of the paralimbic brain. *J. Comparat. Neurol.* **212:** 1–22.
47. Allman, J.M., N.A. Tetreault, A.Y. Hakeem, *et al*. 2010. The von Economo neurons in frontoinsular and anterior cingulate cortex in great apes and humans. *Brain Struct. Funct.* **214:** 495–517.
48. von Economo, C. & G. Koskinas. 1925. *Die Cytoarchitectonic der Hirnrinde des Erwachsenen Menschen.* Springer. Berlin.
49. Seeley, W.W., D.A. Carlin, J.M. Allman, *et al*. 2006. Early frontotemporal dementia targets neurons unique to apes and humans. *Ann. Neurol.* **60:** 660–667.
50. Penfield, W. & M.E. Faulk. 1955. The insula. *Brain* **78:** 445.
51. Craig, A. 2009. How do you feel-now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* **10:** 59–70.
52. Ekman, P. & W. Friesen. 1978. *Facial Action Coding System: A Technique for the Measurement of Facial Movement*. Consulting Psychologists Press. Palo Alto, CA.
53. Izard, C. 1971. *The Face of Emotion.* Appleton-Century-Crofts. East Norwalk. USA.
54. Susskind, J., D.H. Lee, A. Cusi, *et al*. 2008. Expressing fear enhances sensory acquisition. *Nat. Neurosci.* **11:** 843–850.
55. Angyal, A. 1941. Disgust and related aversions. *J. Abnormal Social Psychol.* **36:** 393–412.
56. Ekman, P., E. Sorenson & W. Friesen. 1969. Pan-cultural elements in facial displays of emotion. *Science* **164:** 86–88.
57. Izard, C.E. 1994. Innate and universal facial expressions: evidence from developmental and cross-cultural research. *Psychol. Bull.* **115:** 288–299.
58. Chapman, H.A., D.A. Kim, J.M. Susskind & A.K. Anderson. 2009. In bad taste: evidence for the oral origins of moral disgust. *Science* **323:** 1222–1226.
59. Rozin, P., L. Lowery & R. Ebert. 1994. Varieties of disgust faces and the structure of disgust. *J. Personal. Soc. Psychol.* **66:** 870–881.
60. von dem Hagen, E.A.H., J.D. Beaver, M.P. Ewbank, *et al*. 2009. Leaving a bad taste in your mouth but not in my insula. *Soc. Cogn. Affect. Neurosci.* **4:** 379–386.
61. Anderson, A.K., K. Christoff, D. Panitz, *et al*. 2003. Neural correlates of the automatic processing of threat facial signals. *J. Neurosci.* **23:** 5627–5633.
62. Winston, J.S., J. O'Doherty & R.J. Dolan. 2003. Common and distinct neural responses during direct and incidental processing of multiple facial emotions. *NeuroImage* **20:** 84–97.
63. Krolak Salmon, P., M.A. Henaff, J. Isnard, *et al*. 2003. An attention modulated response to disgust in human ventral anterior insula. *Ann. Neurol.* **53:** 446–453.
64. Fusar-Poli, P., A. Placentino, F. Carletti, *et al*. 2009. Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *J. Psychiatr. Neurosci.* **34:** 418.
65. Wicker, B., C. Keysers, J. Plailly, *et al*. 2003. Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron* **40:** 655–664.
66. Jabbi, M., J. Bastiaansen & C. Keysers. 2008. A common anterior insula representation of disgust observation, experience and imagination shows divergent functional connectivity pathways. *PLoS ONE* **3:** e2939.
67. Niedenthal, P.M., L.W. Barsalou, P. Winkielman, *et al*. 2005. Embodiment in attitudes, social perception, and emotion. *Personal. Soc. Psychol. Rev.* **9:** 184–211.
68. Niedenthal, P.M. 2008. Emotion concepts. In *Handbook of Emotion*. M. Lewis, J.M. Haviland-Jones & L.F. Barrett, Eds.: 587–600. Guilford. New York.
69. Caruana, F., A. Jezzini, B. Sbriscia-Fioretti, G. Rizzolatti & V. Gallese. 2010. Emotional and social behaviors elicited by electrical stimulation of the insula in the macaque monkey. *Curr. Biol.* **21:** 195–199.
70. Sprengelmeyer, R., A.W. Young, A.J. Calder, *et al*. 1996. Loss of disgust. *Brain* **119:** 1647–1665.
71. Gray, J.M., A.W. Young, W.A. Barker, A. Curtis & D. Gibson. 1997. Impaired recognition of disgust in Huntington's disease gene carriers. *Brain* **120:** 2029–2038.
72. Sprengelmeyer, R., A. Young, I. Pundt, *et al*. 1997. Disgust implicated in obsessive-compulsive disorder. *Proc. R. Soc. B: Biol. Sci.* **264:** 1767–1773.
73. Corcoran, K., S. Woody & D. Tolin. 2008. Recognition of facial expressions in obsessive-compulsive disorder. *J. Anxiety Disorders* **22:** 56–66.
74. Sprengelmeyer, R., U. Schroeder, A.W. Young & J.T. Epplen. 2006. Disgust in pre-clinical Huntington's disease: a longitudinal study. *Neuropsychologia* **44:** 518–533.
75. Parker, H., R. McNally, K. Nakayama & S. Wilhelm. 2004. No disgust recognition deficit in obsessive-compulsive disorder. *J. Behav. Ther. Exp. Psychiatr.* **35:** 183–192.
76. Johnson, S., J. Stout, A. Solomon, *et al.* 2007. Beyond disgust: impaired recognition of negative emotions prior to diagnosis in Huntington's disease. *Brain* **130:** 1732–1744.
77. Snowden, J., N. Austin, S. Sembi, *et al*. 2008. Emotion recognition in Huntington's disease and frontotemporal dementia. *Neuropsychologia* **46:** 2638–2649.
78. Milders, M., J.R. Crawford, A. Lamb & S.A. Simpson. 2003. Differential deficits in expression recognition in gene-carriers and patients with Huntington's disease. *Neuropsychologia* **41:** 1484–1492.
79. Calder, A., J. Keane, F. Manes, N. Antoun & A. Young. 2000. Impaired recognition and experience of disgust following brain injury. *Nat. Neurosci.* **3:** 1077–1078.
80. Straube, T., A. Weisbrod, S. Schmidt, *et al*. 2010. No impairment of recognition and experience of disgust in a patient

with a right-hemispheric lesion of the insula and basal ganglia. *Neuropsychologia* **48:** 1735–1741.
81. Beckstead, R.M. & R. Norgren. 1979. An autoradiographic examination of the central distribution of the trigeminal, facial, glossopharyngeal, and vagal nerves in the monkey. *J. Comparat. Neurol.* **184:** 455–472.
82. Beckstead, R.M., J.R. Morse & R. Norgren. 1980. The nucleus of the solitary tract in the monkey: projections to the thalamus and brain stem nuclei. *J. Comparat. Neurol.* **190:** 259–282.
83. Mufson, E.J. & M. Mesulam. 1984. Thalamic connections of the insula in the rhesus monkey and comments on the paralimbic connectivity of the medial pulvinar nucleus. *J. Comparat. Neurol.* **227:** 109–120.
84. Petrides, M. & D.N. Pandya. 1994. Comparative architectonic analysis of the human and the macaque frontal cortex. In *Handbook of Neuropsychology*, Vol. 9. F. Boller & J. Grafman, Eds.: 17–58. Elsevier. New York.
85. Pritchard, T.C., R.B. Hamilton, J.R. Morse & R. Norgren. 1986. Projections of thalamic gustatory and lingual areas in the monkey, macaca fascicularis. *J. Comparat. Neurol.* **244:** 213–228.
86. Small, D.M. 2010. Taste representation in the human insula. *Brain Struct. Funct.* **214:** 551–561.
87. Smith-Swintosky, V.L., C.R. Plata-Salaman & T.R. Scott. 1991. Gustatory neural coding in the monkey cortex: stimulus quality. *J. Neurophysiol.* **66:** 1156–1165.
88. Verhagen, J.V. & L. Engelen. 2006. The neurocognitive bases of human multimodal food perception: sensory integration. *Neurosci. Biobehav. Rev.* **30:** 613–650.
89. Kadohisa, M., E.T. Rolls & J.V. Verhagen. 2005. Neuronal representations of stimuli in the mouth: the primate insular taste cortex, orbitofrontal cortex and amygdala. *Chem. Sens.* **30:** 401–419.
90. Small, D., M. Gregory, Y. Mak, *et al*. 2003. Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron* **39:** 701–711.
91. Scott, T.R. & C.R. Plata-Salam·n. 1999. Taste in the monkey cortex. *Physiol. Behav.* **67:** 489–511.
92. Yaxley, S., E.T. Rolls & Z.J. Sienkiewicz. 1990. Gustatory responses of single neurons in the insula of the macaque monkey. *J. Neurophysiol.* **63:** 689.
93. Verhagen, J.V., M. Kadohisa & E.T. Rolls. 2004. Primate insular/opercular taste cortex: neuronal representations of the viscosity, fat texture, grittiness, temperature, and taste of foods. *J. Neurophysiol.* **92:** 1685.
94. Schienle, A., R. Stark, B. Walter, *et al*. 2002. The insula is not specifically involved in disgust processing: An FMRI study. *Neuroreport* **13:** 2023–2026.
95. Wright, P., G. He, N. Shapira, *et al*. 2004. Disgust and the insula: FMRI responses to pictures of mutilation and contamination. *Neuroreport* **15:** 2347–2351.
96. Stark, R., A. Schienle, M. Sarlo, *et al*. 2005. Influences of disgust sensitivity on hemodynamic responses towards a disgust-inducing film clip. *Int. J. Psychophysiol.* **57:** 61–67.
97. Benuzzi, F., F. Lui, D. Duzzi, *et al*. 2008. Does it look painful or disgusting? Ask your parietal and cingulate cortex. *J. Neurosci.* **28:** 923–931.
98. Fitzgerald, D.A., S. Posse, G.J. Moore, *et al*. 2004. Neural correlates of internally-generated disgust via autobiographical recall: a functional magnetic resonance imaging investigation. *Neurosci. Lett.* **370:** 91–96.
99. Moll, J., R. de Oliveira-Souza, F. Moll, *et al*. 2005. The moral affiliations of disgust: a functional MRI study. *Cogn. Behav. Neurol.* **18:** 68–78.
100. Schaich Borg, J., D. Lieberman & K.A. Kiehl. 2008. Infection, incest, and iniquity: investigating the neural correlates of disgust and morality. *J. Cogn. Neurosci.* **20:** 1529–1546.
101. Stark, R., M. Zimmermann, S. Kagerer, *et al*. 2007. Hemodynamic brain correlates of disgust and fear ratings. *NeuroImage* **37:** 663–673.
102. Schaefer, A., V. Leutgeb, G. Reishofer, *et al*. 2009. Propensity and sensitivity measures of fear and disgust are differentially related to emotion-specific brain activation. *Neurosci. Lett.* **465:** 262–266.
103. Mataix-Cols, D., S.K. An, N.S. Lawrence, *et al*. 2008. Individual differences in disgust sensitivity modulate neural responses to aversive/disgusting stimuli. *Eur. J. Neurosci.* **27:** 3050–3058.
104. Stark, R., A. Schienle, B. Walter, *et al*. 2003. Hemodynamic responses to fear and disgust-inducing pictures: an FMRI study. *Int. J. Psychophysiol.* **50:** 225–234.
105. Schienle, A., A. Schafer, R. Stark, B. Walter & D. Vaitl. 2005. Relationship between disgust sensitivity, trait anxiety and brain activity during disgust induction. *Neuropsychobiology* **51:** 86–92.
106. Vytal, K. & S. Hamann. 2010. Neuroimaging support for discrete neural correlates of basic emotions: a voxel-based meta-analysis. *J. Cogn. Neurosci.* **22:** 2864–2885.
107. Schienle, A., A. Schafer, A. Hermann, *et al*. 2006. FMRI responses to pictures of mutilation and contamination. *Neurosci. Lett.* **393:** 174–178.
108. Stark, R., A. Schienle, C. Girod, *et al*. 2005. Erotic and disgust-inducing pictures-differences in the hemodynamic responses of the brain. *Biol. Psychol.* **70:** 19–29.
109. Schienle, A., A. Schafer, R. Stark, *et al*. 2005. Neural responses of OCD patients towards disorder-relevant, generally disgust-inducing and fear-inducing pictures. *Int. J. Psychophysiol.* **57:** 69–77.
110. Helzer, E.G. & D.A. Pizarro. 2011. Dirty liberals! Reminders of physical cleanliness influence moral and political attitudes. *Psychol. Sci.* **22:** 517–522.
111. Inbar, Y., D.A. Pizarro, J. Knobe & P. Bloom. 2009. Disgust sensitivity predicts intuitive disapproval of gays. *Emotion* **9:** 435.
112. Critchley, H.D., S. Wiens, P. Rotshtein, *et al*. 2004. Neural systems supporting interoceptive awareness. *Nat. Neurosci.* **7:** 189–195.
113. Mehnert, U., S. Boy, J. Svensson, *et al*. 2008. Brain activation in response to bladder filling and simultaneous stimulation of the dorsal clitoral nerve–an FMRI study in healthy women. *NeuroImage* **41:** 682–689.
114. Vandenbergh, J., P. DuPont, B. Fischler, *et al*. 2005. Regional brain activation during proximal stomach distention in humans: a positron emission tomography study. *Gastroenterology* **128:** 564–573.

115. Arnow, B.A., J.E. Desmond, L.L. Banner, *et al*. 2002. Brain activation and sexual arousal in healthy, heterosexual males. *Brain* **125:** 1014–1023.
116. Herde, L., C. Forster, M. Strupf & H.O. Handwerker. 2007. Itch induced by a novel method leads to limbic deactivations: Functional MRI study. *J. Neurophysiol.* **98:** 2347–2356.
117. Weissman, D.H., K.C. Roberts, K.M. Visscher & M.G. Woldorff. 2006. The neural bases of momentary lapses in attention. *Nat. Neurosci.* **9:** 971–978.
118. Cole, M.W. & W. Schneider. 2007. The cognitive control network: integrated cortical regions with dissociable functions. *NeuroImage* **37:** 343–360.
119. Huettel, S.A., C.J. Stowe, E.M. Gordon, *et al*. 2006. Neural signatures of economic preferences for risk and ambiguity. *Neuron* **49:** 765–775.
120. Paulus, M.P., C. Rogalsky, A. Simmons, *et al*. 2003. Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *NeuroImage* **19:** 1439–1448.
121. Binder, J., E. Liebenthal, E. Possing, *et al*. 2004. Neural correlates of sensory and decision processes in auditory object identification. *Nat. Neurosci.* **7:** 295–301.
122. Farb, N.A.S., Z.V. Segal & A.K. Anderson. Submitted. Attention-related modulation of primary interoceptive and exteroceptive cortices.
123. Craig, A. 2003. Interoception: the sense of the physiological condition of the body. *Current Opinion in Neurobiology* **13:** 500–505.
124. Bloom, P. 2004. *Descartes' Baby: How the Science of Child Development Explains What Makes us Human*. Basic Books. New York.
125. Danovitch, J. & P. Bloom. 2009. Children's extension of disgust to physical and moral events. *Emotion* **9:** 107–112.
126. Cannon, P.R., S. Schnall & M. White. 2011. Transgressions and expressions: affective facial muscle activity predicts moral judgments. *Soc. Psychol. Personal. Sci.* **2:** 325–331.
127. Jones, A. & J. Fitness. 2008. Moral hypervigilance: the influence of disgust sensitivity in the moral domain. *Emotion* **8:** 613–627.
128. Eskine, K.J., N.A. Kacinik & J.J. Prinz. 2011. A bad taste in the mouth. *Psychol. Sci.* **22:** 295–299.
129. Wheatley, T. & J. Haidt. 2005. Hypnotic disgust makes moral judgments more severe. *Psychol. Sci.* **16:** 780–784.
130. Schnall, S., J. Haidt, G.L. Clore & A.H. Jordan. 2008. Disgust as embodied moral judgment. *Personal Soc. Psychol. Bull.* **34:** 1096–1109.
131. Royzman, E. & R. Kurzban. 2011. Minding the metaphor: the elusive character of moral disgust. *Emot. Rev.* **3:** 269.
132. Young, L. & R. Saxe. 2011. When ignorance is no excuse: different roles for intent across moral domains. *Cognition* **120:** 202–214.
133. Horberg, E.J., C. Oveis, D. Keltner & A.B. Cohen. 2009. Disgust and the moralization of purity. *J. Personal. Soc. Psychol.* **97:** 963–976.
134. Nabi, R. 2002. The theoretical versus the lay meaning of disgust: implications for emotion research. *Cogn. Emot.* **16:** 695–703.
135. Greene, J.D., L. Nystrom, A. Engell, *et al*. 2004. The neural bases of cognitive conflict and control in moral judgment. *Neuron* **44:** 389–400.
136. Poldrack, R.A. 2006. Can cognitive processes be inferred from neuroimaging data? *Trend. Cogn. Sci.* **10:** 59–63.
137. Parkinson, C., W. Sinnott-Armstrong, P.E. Koralus, *et al*. 2011. Is morality unified? Evidence that distinct neural systems underlie moral judgments of harm, dishonesty, and disgust. *J. Cogn. Neurosci.* **23:** 3162–3180.
138. Schaich Borg, J., W. Sinnott-Armstrong, V.D. Calhoun & K.A. Kiehl. 2011. Neural basis of moral verdict and moral deliberation. *Soc. Neurosci.* **6:** 1–16.
139. Mitchell, J.P. 2009. Inferences about mental states. *Philos. Trans. R. Soc. Lond.: Ser. B, Biol. Sci.* **364:** 1309–1316.
140. Saxe, R. & N. Kanwisher. 2003. People thinking about thinking people. The role of the temporo-parietal junction in "Theory of Mind". *NeuroImage* **19:** 1835–1842.
141. Young, L., F. Cushman, M. Hauser & R. Saxe. 2007. The neural basis of the interaction between theory of mind and moral judgment. *Proc. Natl. Acad. Sci. U.S.A.* **104:** 8235–8240.
142. Davidson, R.J., P. Ekman, C.D. Saron, *et al*. 1990. Approach-withdrawal and cerebral asymmetry: emotional expression and brain physiology. I. *J. Personal. Soc. Psychol.* **58:** 330–341.
143. Berle, D. & E.S. Phillips. 2006. Disgust and obsessive-compulsive disorder: an update. *Psychiatry* **69:** 228–238.
144. Charash, M., D. McKay & N. Dipaolo. 2006. Implicit attention bias for disgust. *Anxiety* **19:** 353–364.
145. Buodo, G., M. Sarlo & D. Palomba. 2002. Attentional resources measured by reaction times highlight differences within pleasant and unpleasant, high arousing stimuli. *Motivat. Emot.* **26:** 123–138.
146. Cisler, J., B. Olatunji, J.M. Lohr & N.L. Williams. 2008. Attentional bias differences between fear and disgust: implications for the role of disgust in disgust-related anxiety disorders. *Cognit. Emot.* **23:** 675–687.
147. Liu, L. & S.A. Simon. 1998. Responses of cultured rat trigeminal ganglion neurons to bitter tastants. *Chem. Sens.* **23:** 125–130.
148. Lim, J. & B.G. Green. 2007. The psychophysical relationship between bitter taste and burning sensation: evidence of qualitative similarity. *Chem. Sens.* **32:** 31–39.
149. Chapman, H.A., D. Lee, J. Susskind, *et al*. The face of distaste. In review.