A Proximal Perspective on Disgust

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Abstract

The functional basis of disgust in disease-avoidance is widely accepted, however there is disagreement over what disgust is. This is a significant problem, as basic questions about disgust require knowing if single/multiple forms/processes exist. We address this issue with a new model with one form of disgust generated by multiple processes: (1) Pure disgust experienced during gastrointestinal-illness; (2) Somatosensory disgust, elicited by specific cues that activate the pure disgust state. (3) Anticipatory disgust, elicited by associations between distance cues for (2) and requiring threat evaluation. (4) Simulated disgusts, elicited by imagining (2&3) and frequently involving other emotions. Different contamination processes interlink (1-4). The implications of our model for fundamental questions about disgust (e.g., emotion status; continuation into animals) are examined.

Keywords: disgust, emotion, gustation, olfaction, pain, state, somatosensation

Introduction

One of Tinbergen's most enduring contributions to the life sciences has been to identify the four basic questions we should ask about any behavior (Tinbergen, 1963). These questions move from proximal causation, to development, and then to evolution and function - ultimate causation. Disgust researchers have been very successful at addressing issues of ultimate causation, with broad agreement that disgust functions to facilitate disease avoidance (e.g., Curtis & Biran, 2001; Fleischmann & Fessler, 2011; Marzillier & Davey, 2004; Oaten, Stevenson & Case, 2009; Rozin, Haidt & McCauley, 2016; Tybur et al., 2013). This functional perspective is now well supported empirically and the aim of this manuscript is not to critique it, but rather to focus on Tinbergen's first two questions. These have unfortunately garnered far less attention and so there is much disagreement over what disgust is, most notably as to whether there is one or multiple types of disgust, or one or multiple forms of process to generate a common disgust state (e.g., Chapman & Anderson, 2013; Marzillier & Davey, 2004; Olatunji et al., 2008; Rozin & Fallon, 1987; Simpson et al., 2006; Tybur et al., 2009). This is a major conceptual problem because several important questions about disgust cannot be effectively addressed without some idea of the answer. One such question concerns disgust's status as an emotion, with one influential theory cleaving disgust in two, with one part as an emotion and the other not (Rozin & Fallon, 1987). Beyond this there are several other important questions concerning disgust's developmental trajectory, its neural basis and its continuity into animals, all of which depend upon knowing if there is one disgust or many. In this manuscript we start by demonstrating that there are currently few clear answers to what disgust is. The remainder focuses on our answer to this question, and its broader implications for understanding disgust.

What is disgust?

There have been two main approaches to the what question. The first has categorised cues that elicit disgust (e.g., Angyal, 1941; Curtis & Biran, 2001; Olatunji et al., 2008; Rozin & Fallon, 1987; Tybur et al., 2009). This approach is closely allied to the question of function, which has either driven or accompanied categorisation.

Currently, there are three elicitor categorisation models. The oldest, developed by Rozin and colleagues (Rozin & Fallon, 1987; Rozin et al., 2016), divides disgust into five domains each with its own functional basis: (a) distaste covering oral responses to bitter and sour tastants (function: protect body); (b) core disgust, for preventing oral incorporation of body products (e.g., feces), certain foods (e.g., rotten) and certain animals (e.g., maggots; function: protect body and soul); (c) animal reminder disgust, which serves to remind us of our animal origins and hence our mortality (e.g., mangled body; function protect body and soul); (d) interpersonal contamination (e.g., avoiding sick people; function, protect body, soul, and social order); and (e) sociomoral disgust (e.g., defrauding a helpless person: function, protect social order).

There have been several attempts to validate these categories. Developmentally, there is support for the early presence of distaste relative to the other disgusts (e.g., Ganchrow, Steiner & Daher, 1983; Steiner, 1979). Individual differences in distaste are related to disgust sensitivity for elicitors of core and animal reminder disgust, but not to sociomoral disgust (Herz, 2011). Similarly, developmental evidence suggests that core, animal reminder, and sociomoral disgusts occur, in that order, progressively later in development, but whether this means they involve qualitatively different emotional states (i.e., different disgusts) is not established (Stevenson et al., 2010). There seems to be little support for the theoretical underpinning of animal reminder disgust (Kollareth & Russell, 2016). Interpersonal disgust may not be uniquely different from the preceding categories, although some recent cross-cultural research suggests it may not induce disgust at all (Han, Kollareth & Russell, 2016). It has been noted that the sick face associated with illness - and hence avoidance of sick people, which is a type of interpersonal disgust - may differ from the disgust face associated with bad smells or tastes (Widen et al., 2013). While this may suggest a dissociation, it does not cleanly map onto the categories under consideration here (i.e., there is no bad smell and taste domain), nor for that matter does other work examining distinct subtypes of disgust-related facial expression (Rozin, Lowery & Ebert, 1994). For sociomoral elicitors, this is the most contentious category, with uncertainty as to whether this represents disgust, some metaphorical usage or the involvement of other emotions (Case, Oaten & Stevenson, 2012; Nabi, 2002; Simpson et al., 2006; Yoder, Widen & Russell, 2016).

Olatunji et al., (2008) have suggested a revised version of Rozin's scheme, with three main categories - core, animal-reminder and contamination disgust. This structuring seems to reflect a consistent pattern of individual differences across cultures (Olatunji et al., 2009). In addition, the categories of distaste and sociomoral disgust are presumably still included, although this is not made explicit. These two categories are not covered in the individual differences measure that forms the basis for the other categories (distaste not being considered as part of the emotion of disgust and because a satisfactory factor solution for sociomoral disgust could not be obtained).

Contamination disgust is identified as a specific category in Olatunji et al.'s, (2008) revised scheme. Contamination occurs when there has been contact between a neutral item (e.g., a shoe) and a disgust inducing elicitor (e.g., feces), rendering the contaminated object disgusting (Rozin & Nemeroff, 1990). To some theorists, contamination is of special significance, with Rozin and Fallon (1987) claiming that the separation between the category of distaste and the other categories of disgust is dependent on the presence of contamination with the latter but not with the former. Contamination has also been important to functional accounts of this emotion (Oaten et al., 2010), principally because it represents an implicit form of germ theory. Currently, it is unclear what relationship contamination has to disgust, namely whether it is a type of disgust or an accompanying feature. It is also unclear if there are one or multiple forms of contamination process. Some forms may require the development of specific cognitive skills for their emergence (e.g., Rozin, Fallon & Augustoni-Ziskind, 1985), while others could depend solely upon observing contact (e.g., Brown & Harris, 2012).

The most recent categorisation-based theory suggests a more circumscribed model composed of three domains (Tybur et al., 2013), with contamination a notable absence. The three-domain model is derived from theoretical considerations of function and from a factor analysis of self-report individual difference data (Tybur, Lieberman & Griskevicius, 2009). The three disgust domains are pathogen (e.g., feces), sexual (e.g., incest avoidance) and sociomoral. Each domain represents a different function, pertaining respectively to disease avoidance, quality of sexual partners, and quality of other people. The question again here is whether these domains actually reflect different disgusts. There is some evidence for a difference between sexual and pathogen disgusts, based upon greater gender difference on self-report disgust measures for the sexual category, as well as divergent correlations with other self-report measures (Tybur et al., 2009; Olatunji et al., 2012). Evidence for a discrete sociomoral category has the same problems identified earlier for Rozin & Fallon's (1987) scheme (e.g., see Olatunji et al., 2012), and as we noted above the three-domain model is silent on the nature of contamination.

There is a second way in which disgust categorisation has been examined. This involves focussing on the range of emotions that different disgust eliciting cues generate. In common with other emotions and states, disgust may occur in tandem with fear, anger, pity, sadness, shame and embarrassment. This led Marzillier and Davey (2004; and see Simpson et al., 2006 for a similar idea) to suggest a distinction between simple and complex disgusts - noting that this approach does not accommodate contamination. In this view, there is no intention to think of differences in disgust *per se*, but rather differences in the number and type of emotions that are elicited. This scheme crudely maps onto those above, in that sociomoral elicitors typically engage a much broader range of emotions, notably anger, than disgusts elicited by say bad smells or tastes. Many animal cues that engender disgust such as rats and spiders, also generate fear (Muris et al., 2008; Tucker & Bond, 1997; Ware et al., 1994), and thus disgust at animals may be complex in the sense that it involves fear-disgust blends. Similarly, interpersonal disgusts may utilise complex blends including feelings of pity and sadness (Marzillier & Davey, 2004). This perspective suggests one disgust, but one that involves varying degrees of interaction with other emotions.

It is then unclear what disgust is. There is little agreement over how many disgusts there are and no agreement over how contamination fits into this picture. We suggest a new perspective is needed.

Overview

A diagrammatic summary of the model is presented in Figure 1, with four processes that all give rise to the same disgust feeling state (see Table 1 for summary properties and features).

Pure disgust

An important feature of an emotion or state, which contributes to making it one thing rather than another, is the way it feels. Arguably, the purest feeling state of disgust is generated during gastrointestinal illness. It is characterised by nausea, an aversive bodily sensation localised to the oral-gastric region, which signals gastrointestinal threat and the imminence of its solution in vomiting. This feeling state can be broken down into three components – its negative affect, its bodily locus and the feeling that vomiting is imminent (i.e., nausea). A further issue of importance here is whether equating gastric sickness to pure disgust means that pure disgust cannot be termed an emotion. Rather than examine this here we discuss the broader question of disgust's status as an emotion at the end of the manuscript.

Somatosensory disgust

Somatosensory disgust is characterised by a distinct bodily locus, nausea, and negative affect. It is modular (i.e., in considering disgust in animals, different sensory cues could be 'plugged-into' or 'un-plugged from' the brain circuits underpinning disgust) and present early in development. While occurring automatically in response to certain cues - via a dedicated neural link to the same brain circuitry underpinning pure disgust - this process is modulated by bodily threat assessment. Somatosensory disgust occurs: (a) in the mouth, with any of the following senses either alone or in combination – gustation with certain tastants, retronasal (via the posterior nares) olfaction with certain odorants, and via somatosensation with certain textures; (b) orthonasally (via the anterior nares) from smelling certain odorants; and (c) via bodily somatosensation, with certain textures. The somatosensory system is intimately linked to both taste and smell perception, as it assists bodily localisation by binding taste to the tongue and smell to either the mouth (flavor) or nose (sniffing/smelling).

Anticipatory disgust

Anticipatory disgust first emerges in infancy. During weaning the infant passively learns associations between the sensory components of food - what they see, hear, smell and touch - and its flavor in the mouth. They also passively acquire sensory associations between the visual and auditory appearance of objects, and their smell and feel, an on-going process, which includes experiences during toilet-training, and with other bodily products.

Post-weaning, looking at a food should allow an infant to anticipate what it might be like to eat. Anticipating oral contact with something that signals an unpleasant experience can result in disgust. This occurs via two parallel paths, both of which are necessary for anticipatory disgust to occur. First, via the passively acquired sensory associations that link back to pure disgust (e.g., perception of visual slimy texture automatically activates a representation of slimy texture, which then automatically activates brain areas underpinning pure disgust). Second, via the degree of bodily threat, which is instantiated as a visceral feeling, substituting for the lack of direct physical contact between the elicitor and observer, which only occurs with somatosensory disgust.

In some cases, anticipatory disgust cues may overlap with fear-inducing cues, with the latter resulting from dedicated neural detection and response systems for things like spiders and snakes. For example, the slimy visual appearance of snakes *may* predict how these animals might feel, resulting in anticipatory disgust. As these animals can also be fear provoking, this may combine with the anticipatory disgust to produce a hybrid experience. In other cases, there may be anticipated disgust - such as towards a slimy looking object - and in addition that object may also generate somatosensory disgust via smell. Cues such as feces, urine, and vomit are all examples of combined anticipatory and somatosensory disgusts. A rather different scenario emerges when seeing mutilated bodies. This may involve a far more extensive hybrid of anticipatory disgust (e.g., visual texture cues), empathetic pain, surprise, fear and anxiety.

In sum, anticipatory disgusts involve the automatic activation of sensory associations back to pure disgust, a visceral feeling of imminent bodily threat, but without a specific bodily locus. Anticipatory disgust can either occur alone (e.g., a slimy-looking food), in combination with a somatosensory disgust (e.g., seeing and smelling feces), or with other drive states (i.e., empathetic pain), or with one or more emotions (e.g., fear).

Simulated disgust

Most people have seen a large range of body forms and products, injuries, dead animals, etc. Even if these have not been seen directly, they may have been viewed in photographs or film. They will also have experienced somatosensory and anticipatory disgusts and will be cogent of the sensory associates of somatosensory disgust (e.g., if something *looks* slimy it will probably feel that way). These experiences form the basis for simulated disgusts, which occur intentionally, in the physical absence of the inducing object (i.e., you *hear*, you *read*, you *imagine*, etc) and generally with lower levels of bodily threat, as the whole process is a simulation.

Simulating disgust is not difficult. We suggest this as much disgust research is based upon answers to self-report questionnaires, which probably involve recalling and/or imagining each scenario. Simulated disgust may induce negative affect, a feeling of bodily threat (viscerality) and nausea. It differs qualitatively from somatosensory disgust as somatosensory stimulation is absent, and from both anticipatory and somatosensory disgust as there is no external eliciting object *other than* written or spoken words. Consequently, bodily threat should be lower for simulated disgust in comparison to the others. Intentionality is a further differentiating feature. Simulated disgusts generally involve intention to form a simulation, with the process being under conscious control. Anticipatory and somatosensory disgusts are respectively less intentional. A further distinction from anticipatory disgust is the range of emotions that may accompany simulated disgust. Emotions can be generated *de novo* in mental simulations (e.g., imagining an affect-laden experience is a widely used experimental means of inducing emotion). The resultant emotions such as shame, pity, anger, humiliation and so forth may then co-occur with simulated disgust, making the experience more affectively potent.

Contamination

Contamination occurs when a neutral object becomes imbued with the capacity to induce disgust. Three processes can generate contamination, and these act to link pure, somatosensory, anticipatory and simulated disgusts. All three processes are fundamentally connected by a common reliance on associative learning between a disgust state and a neutral object. The first process links pure disgust to somatosensory disgust. The pure disgust experienced during gastrointestinal illness can become associated with a food's flavor (including each individual sensory component), and its smell. Smelling or eating the illness-paired food results in somatosensory disgust, while its appearance - often already linked to its flavor - allows the anticipation of its disgust-inducing properties.

The second process links somatosensory and anticipatory disgust to simulated disgust. It occurs when a neutral cue is perceived to come into physical contact with a somatosensory disgust cue. In this case the neutral cue is experienced simultaneously with somatosenory and/or anticipatory disgust. When that disgust-paired neutral cue is later experienced alone, it can generate a form of simulated disgust, in which the somatosensory or anticipatory disgust cue can be recalled/imagined.

The third process occurs wholly in the mind. Here, the disgust-eliciting cue is simulated, as is the contact with a neutral target object (e.g., imagine your toothbrush being used to scrub clean a pus filled sore). This allows for violations of causality, as events physically separate in time or space can be imagined contemporaneously, generating phenomena such as backward contamination.

Evidence

Pure disgust

Emotions and states each have their own unique feeling (e.g., Barrett et al., 2007). Disgust has been reported to possess at least three types of feeling, which individually are shared with other emotions and states, but together define the way disgust feels: negative affect (e.g., Angyal, 1941), nausea/retching (e.g., Rozin, Haidt & Fincher, 2009; Davey, 1994) and viscerality – feeling of imminent or actual bodily contact (e.g., Verstaen et al., 2016). Together, and as others have noted (Royzman & Sabini, 2001; Royzman, Leeman & Sabini, 2008; Royzman et al., 2014), this feeling state occurs in its purest form when experiencing gastrointestinal illness, reflecting disgust's probable phylogenetic origin as a threat-detector for ingestible toxins (Chapman & Anderson, 2013; Darwin, 1872/1998; Glendinning, 2007; Herz, 2011; Rozin, Haidt & McCauley, 2016; Schienle, Arendasy & Schwab, 2015).

An important aspect of pure disgust is its neural correlates, as these may allow it to be distinguished from non-disgust states. Although the neural correlates of gastrointestinal illness have not been studied a closely related phenomenon has - virtual motion-induced nausea. We suggest it is highly related because nausea resulting from motion-induction, chemotherapy, and illness, can all support conditioned taste aversions (e.g., Arwas, Rolnick & Lubow, 1989; Bernstein, 1978; De Silva & Rachman, 1987). This suggests both functional and experiential similarity across these different nausea inducers.

The virtual motion procedure has revealed phasic activity in three brain areas that precede increasing reports of nausea - basal ganglia (putamen), locus coeruleus and amygdala (Napadow et al., 2013). Sustained activity in several other brain areas, including the anterior insula, primary and secondary somatosensory cortex, orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), ventral tegmental area (VTA), nucleus accumbens (NA) and ventromedial prefrontal cortex, is associated with increasing nausea (Napadow et al., 2013). We note four things about these activations. First, that OFC, ACC, VTA, NA, anterior insula and amygdala activation are all known to be associated with affect generation (e.g., Carlezon & Thomas, 2009; Vogt, 2005). Second, that brain areas associated with evaluating bodily threat relevance are active, notably the anterior insula and ACC (e.g., Craig, 2003), and with direct anterior insula stimulation also generating sensations of nausea (Penfield & Faulk, 1955) and oral-gastric displeasure (Krolak-Salmon et al., 2003). Third, activity in primary and secondary somatosensory cortices, with the former known to underpin somatosensory perception, relating here to increased oesophageal and gastrointestinal activity (e.g., Coen et al, 2007). Fourth, that nausea's direct antecedents involve brain areas involved in: (1) fear and threat-related processing (i.e., amygdala, locus coeruleus); (2) sites known to generate nausea when stimulated in animals (amygdala; Robinson & Mishkin, 1968); and (3) areas responsible for habitual motor patterns (putamen) that may underpin aversive withdrawal. We suggest that together, this pattern of neural activation is both necessary and sufficient to generate pure disgust.

Somatosensory disgust

The somatosensory system plays a key role in anchoring gustatory, olfactory and of course tactile disgust to specific bodily locations, generating a located bodily feel. For olfaction, somatosensory cues may dictate whether an odor is perceived as coming from inside (flavor) or outside (smell) the body (e.g., Green, 2002; von Bekesy, 1964). For gustation, somatosensation underpins binding of taste sensation to the tongue (e.g., Green, 2002; Todrank & Bartoshuk, 1991). In general, tactile sensations are detected by mechanoreceptors in the skin (Guinard & Mazzucchelli, 1996) and feed information to the primary and secondary somatosensory cortex, and to the posterior insula and anterior cingulate cortex (e.g., Case et al., 2016). These brain areas are organised into two processing streams, one dealing with sensory feel and location (especially primary somatosensory cortex), and the other with affective reaction (Morton, Sandhu & Jones, 2016).

We suggested that the gustatory, olfactory and tactile sensations that evoke disgust do so because there are dedicated neural pathways linking their detection to the same brain sites active during pure disgust (see Mzrahi, 2018, for a related proposal). There have been no specific investigations of this hypothesis, although it is already clear that there are overlaps between brain areas active during gustatory and olfactory somatosensory disgust - OFC, amygdala, anterior cingulate cortex, anterior insular, basal ganglia, primary and secondary somatosensory cortices (Haase, Cerf-Ducastel & Murphy, 2009; Rolls, Kringelbach & de Araujo, 2003; Seubert et al., 2010; Small et al., 2003; Wicker et al., 2003; Zald, Hagen & Pardo, 2002) and the brain areas identified earlier associated with nausea, which we labelled as pure disgust.

The main evidence base so far is limited to showing a consistent mapping between perceiving particular stimuli and demonstrating negative affect. In neonates, bitter and sour tastants evoke a facial expression that is readily recognised by adults as indicating dislike/disgust (e.g., Ganchrow, Steiner & Daher, 1983). This expression also shares substantial similarity to that observed in infant and adult great apes, when exposed to the same stimuli (Steiner et al., 2001). In adult humans, sampling bitter and sour tastants, and concentrated salts (and sweeteners), can yield a similar facial expression (Bredie, Tan & Wendin, 2014; Weiland, Ellgring & Macht, 2010). The presence of this reaction to bitter and sour tastants in neonates, and in many primates, suggests these responses arise from a dedicated neural link between receptors and brain areas responsible for generating pure disgust.

Functionally, bitter tastes are indicative of plant-based toxins. In rats, there is a substantial correlation between a chemicals LD_{50} value and the degree of neural activity it evokes in primary taste processing areas. This suggests that the more bitter it is (i.e., greater neural activity) the more toxic it is (Scott & Mark, 1987). Sour tastants are associated with microbial decay. For extremely high concentration tastants, their ingestion may be harmful (e.g., hypernatremia).

For olfaction, the dominant view (Engen, 1988; Moncrieff, 1966; Rozin, Haidt & McCauley, 2016) has been that hedonic reactions are mainly learned. However, there are now several reasons to challenge this view. First, certain vertebrates rely on olfactory-based defences (e.g., skunks, common tree snakes, hoatzins, opossums, vultures). Most of these smell of decay (e.g., opossums, skunks), feces (e.g., tree snakes, hoatzins) or vomit (e.g., vultures). As humans also find these smells repulsive, this would suggest that there are certain classes of odorant that smell foul to other vertebrates. It would be a risky strategy to rely upon a chemical defence if it were of uncertain effectiveness, and such effectiveness presumably relies upon the ability to repel all potential predators. This suggests that some odorants may be repulsive by virtue of their chemical features mimicking odorants that repel primarily because they signal disease-causing agents (i.e., decay, feces).

A second line of evidence comes from studies linking the structural features of odorants to human hedonic reactions. Khan et al., (2007) found that indicators of small molecular size are predictive of less pleasant smells, a finding that has now been replicated several times (e.g., Haddad et al., 2010; Poncelet et al., 2010). These smaller molecules are not only liked less than larger more complex ones (Kermen et al., 2011) but they are also characterised by particular classes of chemical structure, notably indoles, amines and sulphur containing compounds like thiols (Zarzo, 2011). These types of molecule are often the end product of organic decay processes (Keller et al., 2017; Zarzo, 2011), and interestingly thiols are found in abundance in the foul secretion of skunks - the only vertebrate chemical defence agent to be analysed in detail (Wennig et al., 2010).

Humans and other primates are especially sensitive to thiols and indoles, relative to other comparable molecular classes. It has been suggested that this is because they are characteristic markers of decay (Laska et al., 2007; Kamiya & Ose, 1984) as well as being volatile constituents of feces (Chappuis et al., 2015). That certain structural features of an odorant predict its likely hedonic reaction - including in children (Poncelet et al., 2010) - would seem to favor the idea that the olfactory system, like the gustatory system, has dedicated neural links that result in negative affect in response to certain chemicals. This conclusion is also consistent with the finding that human neonates tend to respond to decay odors (fishy/rotten) with disgust-like facial expressions (Steiner, 1979; Soussignan et al., 1997) and adults respond faster to unpleasant odorants such as indole (Bensafi et al., 2002).

The idea of dedicated neural links sub-serving affective responses to certain tactile stimuli, while plausible, has not been explored. Adults and children find similar tactile sensations in the mouth and on the body surface, disgusting (Skolnick, 2013; Boquin et al., 2014). In the mouth, slimy sensations evoke disgust, and people link such sensory qualities to decay and bad smells (Martins & Pliner, 2006). Child 'picky eaters' find slimy foods in their mouth particularly disgusting and react in the same way when just handling them (e.g., Nederkoon et al., 2015). These children are also more likely to gag when asked to sample a food they reportedly dislike and also evidence more aversive responses to bodily tactile stimuli (e.g., touching slime) than non-picky eaters (Coulthard & Jahota, 2016). Studies of tactile responses to areas other than the mouth have been limited to adults and suggest that sensory characteristics associated with microbial decay (i.e., slimy, sticky, gooey) are the most effective stimuli at inducing tactile-driven disgust (e.g., Oum et al., 2011).

There is little data as yet to indicate whether tactile disgust cues emerge early in development. However, during toilet training, it has been noted that one of the key drivers of toileting readiness is when children (aged around 18M) manifest a strong dislike for the slimy/gooey feeling of being wet or soiled (Kaerts et al., 2012; Yeager et al., 1999). It is also unclear whether there is any continuity of tactile disgust cues into animals. Tactile cues are important drivers of grooming behavior in many mammals (Greer & Capecchi, 2002; Sachs, 1988). We surveyed people who work and study great apes. Chimpanzees do not like the feeling of feces on their fur and make great efforts to remove it (Case et al., Submitted). Great apes (and perhaps other mammals too) may possess a disgust-like response to bodily contact with stimuli that have textures that induce disgust in humans.

People consume bitter, sour and slimy foods, eat putrid cheese, and contact the bodily products of other people (e.g., sexual encounters, caring for infants; Case, Repacholi & Stevenson, 2006; de Jong, van Overveld & Borg, 2013; Rozin, 1976a; Stevenson & Repacholi, 2005). If these stimuli automatically elicited a full-strength disgust response, then presumably many of these important behaviors would not occur. The fact that they do suggests some form of modulation. We suggest this is substantially based on an evaluation of bodily threat, a notion akin to that proposed by Sparks et al., (2018) in relation to risk assessment and disgust. This evaluation results in either the amplification of disgust (threat) or its reduction (safety; see Herz & von Clef, 2001, for an example). An analogous and well documented process occurs for pain, with threat evaluation modulating its intensity and unpleasantness (e.g., Jackson, Wang & Fan, 2014; Wiech et al., 2010).

While modulation is clearly relevant to somatosensory disgust - as the examples above suggest - it is not critical for its occurrence, as somatosensory disgusts are threatening by default. The elicitor has already contacted the body (i.e., threat is imminent) and has a propensity to be unpleasant via the dedicated neural link from specific receptors to brain areas subserving this response. In contrast, threat evaluation should be more important for anticipatory disgust, where there is no physical contact and no direct neural link to negative affect. For this reason, we defer a more detailed consideration of threat evaluation until then.

In sum, somatosensory disgust is triggered by specific gustatory, olfactory and tactile cues that have dedicated neural links to brain areas that evoke negative affect (and probably nausea too), and it also has a specific bodily location. This disgust response is modulated by a threat evaluation. Functionally, these disgust cues signal toxins and pathogens. Each cue-response is modular, such that different animal species should have sets of modules attuned to relevant behavioral and environmental risks (e.g., Gorilla's tolerance for bitter and sour tastes because of their folivorous diet [Gustafsson et al., 2014]). Indeed, it is important to note that we currently understand rather little about disgust's continuation into animals, even though this is an issue directly pertinent to understanding process and function in humans.

Anticipatory Disgust

Anticipatory disgust occurs at the prospect of contacting a physically present somatosensory disgust elicitor. This requires two processes - one mediated via sensory associations with somatosensory disgust that then automatically engage pure disgust and the other via an evaluation of bodily threat. A key issue is the extent to which anticipatory disgust can activate the same qualitative state as somatosensory disgust. Three approaches to this problem are considered.

The first is whether when people experience anticipatory disgust they report feeling negative affect, nausea and a visceral feeling of bodily threat. For negative affect there is widespread agreement that viewing disgusting objects is unpleasant (e.g., Kollareth & Russell, 2016; Rozin et al., 1999; Stevenson et al., 2011; Stevenson et al., 2015). Few studies have used nausea ratings, but those that do find higher ratings for anticipatory disgust stimuli than for control stimuli (Calder et al., 2007; Stevenson et al., 2012). An important caveat here is that almost all of the studies cited in this paragraph used pictorial disgust stimuli. Strictly speaking these cannot be anticipatory disgusts as the stimuli are not physically present. While pictures generate a similar visual state as looking at disgusting objects, they are not real, which may reduce feelings of bodily threat. While no study has measured feelings of bodily threat, pictures/films should be less effective inducers than their real counterparts.

A second approach is neuroimaging, to see if anticipatory disgust activates brain regions that overlap those of pure disgust. There have been several fMRI studies that use pictures of disgust-inducing cues (with the same caveat as noted above). Many pictorial disgust fMRI studies generate activity in the amygdala (e.g., Schienle et al., 2002; 2005; Stark et al., 2003; 2005; Moll et al., 2003), OFC (e.g., Lane et al., 1997; Paradiso et al., 1997; Schafer et al., 2005) and anterior insula (e.g., Wright et al., 2004; Jabbi et al., 2008). However, we could find only one that reported activation in the basal ganglia, and only then when examining correlations with self-reported disgust (Calder et al., 2007). No study reported primary or secondary somatosensory cortical activity, as would be expected. So, there are some similarities to the neural activity pattern characterising pure disgust, but pictures are not as potent a threat to the body as their real equivalent.

A third approach is to look to the example of pain. This is important because of the issue of bodily threat, which we suggest is a key component of anticipatory disgust. Anticipated and real pain produce overlapping patterns of neural activity (e.g., Fairhurst et al., 2012; Ogino et al., 2007; Ploghaus et al., 1999), as do anticipated (using pictures - so caveats above apply) and somatosensory disgust (e.g., Jabbi, Bastiaansen & Keysers, 2008; Wicker et al., 2003). The overlap for both pain and disgust, when contrasting real and anticipated states, occurs in the anterior insular cortex (Jabbi, Bastiaansen & Keysers, 2008; Singer & Lamm, 2011; Lamm, Decety & Singer, 2011; Wicker et al., 2003) - and especially so if there is greater personal bodily threat (e.g., anticipating oneself being injected in the hand vs. viewing someone else being injected; Decety & Grezes, 2006).

We suggest the anterior insula supports bodily threat evaluation. First, it is the neural correlate of visceral body-related feelings (e.g., Craig, 2003). Crucially, this feeling is not associated with a specific bodily location. Rather, specific locations are represented by activity in the primary somatosensory cortex, just as for externally induced pain (Lamm, Decety & Singer, 2011). Second, activity in the anterior insula is known to support aversive anticipatory arousal for pain (e.g., Ploghaus et al., 1999; Ogino et al., 2006), which is effectively an evaluation of a stimulus's threat potential to the body. Third, we noted earlier that pain is modulated by threat, with greater threat linked to more pain in both experimental and naturalistic settings (Jackson, Wang & Fan, 2014). Functional imaging suggests that the neural correlate of pain modulation resides in the anterior insula (Wiech et al., 2010). If there is an imminent threat to the body, the anterior insula integrates relevant information, resulting in a visceral feeling of threat whose intensity reflects its imminence. We also hypothesise that the anterior insula may then act to up (or down) regulate the activity of the brain areas that underpin pure disgust. Notably then, anterior insula lesions should impair a rather specific aspect of disgust - its threat evaluation capacity.

The idea that threat or risk estimation is strongly linked to disgust has been made before (e.g., Sparks et al., 2018), as has the idea that threat estimation can be instantiated as a feeling (see Loewenstein et al., 2001). In addition, and as we noted earlier, threat-driven response amplification is seen in pain (above) and in other states (Koteles & Whitthoft, 2017), suggesting by analogy that this type of process could also occur for disgust. However, there have been no direct investigations of whether bodily threat evaluations lawfully affect disgust, although several extant findings suggest this is likely. Habituation should diminish threat, and it certainly diminishes disgust (e.g., Rozin, 2008). The source of an elicitor (e.g., self vs. other) affects the magnitude of the disgust response, with source reflecting perceived disease threat (e.g., Stevenson & Repacholi, 2005). Bodily need should also modify threat estimation, so for example, hunger might be expected to lead to less disgust towards food that might otherwise induce disgust (e.g., Hoefling et al., 2009; Sacco, Young & Hugenberg, 2014) and sexual arousal should lead to reductions in disgust towards cues that might normally signal disease (e.g., Stevenson, Case & Oaten, 2011). Health-related anxiety increases evaluations of disease threat, and this translates into more intense disgust (e.g., Fan & Olatunji, 2013). These and other variables (e.g., physical proximity, risk expectation, context) will then act to amplify or dampen the anticipatory disgust response - to the extent that it is *felt* to be a threat. While threat evaluation can serve to unify this diverse range of moderating variables, it may be too procrustean. The possibility remains that multiple separate mechanisms may serve to up and down regulate disgust - but such an alternate model would come at the cost of parsimony.

We suggested that somatosensory disgust had dedicated neural links between cue detectors and brain areas sub-serving affective response. In contrast, anticipatory disgusts are passively learned sensory associations that emerge during development and which then automatically link a visual or auditory cue with a somatosensory disgust cue. The first anticipatory disgusts are probably acquired during weaning (between 6M and 18M), when the infant is first exposed to a range of liquid then solid foods, varying in physical appearance, texture, taste and smell, allowing them to learn the sensory properties and correspondences of new foods. Part of this learning involves forming associations between the external and internal attributes of flavor: (1) the appearance of food, its sound, and texture to touch, with its oral texture; (2) appearance of food with its flavor; and (3) the flavor with its orthonasal smell. This then allows the infant to anticipate that a particular food will have an unpleasant texture or flavor in the mouth, by simply looking at, touching and smelling it. Thus, viewing the food, can automatically generate a prediction of whether it will taste disgusting based on its sensory correlates. We suggest this mental prediction is represented as a feeling of disgust rather than that of (or in addition to) the food's flavor. There are three reasons for this. First, as the person is actively perceiving - for example looking at the somatosensory disgust cue - this is likely to make forming a mental image of its flavor, difficult. Second, mental imagery for taste, smell and flavor is poor (Stevenson & Case, 2005). Third, as the link between the visual/auditory cues and the somatosensory disgust cue is passively learned, it may be activated in a similarly passive manner, and so the link back to disgust may be rapid and unintentional - automatic. While it is important to stress that this developmental perspective has not been tested, it seems uncontroversial to suggest that the *link* between a food's appearance and its probable flavor results from prior learning and that the first opportunity for this occurs during weaning (Stevenson, 2009), but the nature of the resulting representation is less certain.

One probable manifestation of food-related anticipatory disgust in children (and in adults) is the avoidance of unfamiliar foods - neophobia. If food neophobia and anticipatory disgust are much the same, there should be an association between the degree of neophobia that an adult or child displays and their disgust sensitivity. Such associations, of moderate size, have been reported (Bjorklund & Hursti, 2004; Nordin et al., 2004; Al-Shawaf et al., 2015). A further and important observation is that when people are asked *why* they will not consume an unfamiliar food they say: (1) it will be disgusting (e.g., Martins & Pliner, 2005); and (2) they identify sensory properties, notably textural ones like sliminess, associated with somatosensory disgust (e.g., Boquin et al., 2014). This is especially so in picky eaters, who demonstrate a high degree of neophobia and indicate that many foods will invoke disgust from their smell, taste or tactile qualities (Nederkoon et al., 2015; Russell & Worsley, 2013).

A further issue is the continuity of anticipatory disgust into animals. As we noted earlier, many mammals avoid bitter or sour tastants and display facial expressions that in some cases are reminiscent of human responses to such tastes (e.g., Steiner et al., 2001). It has often been assumed that this is likely the full extent of the overlap between humans and animals, but we suggested earlier that the link is more substantial and may include certain odorants (for which there is already some evidence; Laska et al., 2007), as well as certain tactile stimuli. Here, we suggest a further extension to include what is presumably a common form of anticipatory disgust - neophobia. Neophobia is evident in primates, especially chimpanzees (e.g., Gustafsson et al., 2014), and rodents (e.g., Rozin, 1976b), but whether it conforms to the type of anticipatory disgust envisaged here is not known.

Using the same basic process of sensory association, it is possible to see how body products and decay-related stimuli can contribute to and/or engender an anticipatory disgust response. Three mechanisms are at work. First, body products and decaying organic matter often emit chemicals that can induce somatosensory disgust when smelled (Laska et al., 2007; Kamiya & Ose, 1984). Second, body products and decaying organic matter have physical properties that directly induce somatosensory disgust if they are touched or trodden in, most notably a slimy feel (Oum et al., 2011; Skolnick , 2013). Third, visual examination or auditory cues can reveal information about texture (e.g., in other domains see De Wijk et al., 2004; Zampini & Spence, 2004) that should anticipate somatosensory disgust. Toilet training affords the child many opportunities to learn cross-modal sensory associations between the sounds (e.g., defecation), appearance (e.g., visual texture/color), tactile properties (e.g., skin of the anal-genital region and from hand contact) and smell of feces. The resulting combination of anticipatory and somatosensory disgust - at the sight and smell of things like feces - should then evoke a more potent disgust response (i.e., additivity).

There are a number of disgust elicitors identified in the literature (e.g., Tolin et al., 1997) that are also known to be the target of specific fears (i.e., phobias), notably animals such as snakes, rodents and spiders (e.g., Sawchuk et al., 2002), and blood, injury, and mutilation phobias (e.g., Bienvenu & Eaton, 1998; Page, 1994). Perhaps not surprisingly, the tendency to develop all of these forms of specific phobias is substantially heritable (Kendler et al., 2001; Van Houtem et al., 2013). This may reflect a graded tendency for a near universal fear response to these types of stimuli, based upon dedicated neural detection and response systems - a parallel perhaps to somatosensory disgusts. As indicated earlier, not only are these stimuli fear provoking but they may also have visual characteristics that anticipate disgust on contact (i.e., visual texture indicative of sliminess – exposed intestines or snake scales), so there may be fear induced by sight of the animal or injury, combined with anticipatory disgust. The presence then of fear, anxiety (and empathetic pain in the case of injury) should increase the experienced negative affect well-beyond that generated by anticipatory disgust alone (see, Kupfer, 2018; Shenhav & Mendes, 2014). Moreover, the presence of fear and anxiety would also increase feelings of bodily threat, which would then lead to an amplification of anticipatory disgust.

In sum, anticipatory disgust occurs when: (1) a sensory correlate of a physically present somatosensory disgust cue is perceived, which then automatically activates brain regions sub-serving pure disgust; and (2) the somatosensory disgust cue is judged to be an imminent threat to the body. Anticipatory disgusts are dependent on sensory cross-modal learning for their emergence during development, unlike somatosensory disgusts, which are based upon dedicated neural links between receptor and brain areas sub-serving negative affect and disgust. Experientially, anticipatory disgusts should involve the same set of qualitative features as somatosensory disgust, namely negative affect, viscerality and nausea. Anticipatory disgusts like anticipatory pain lack a discrete bodily locus, and so both of these states should be reliant on bodily threat perception mediated by the anterior insula. Anterior insula activity should also serve to up or down regulate brain regions associated with the pure disgust response. The recruitment of other negative emotions and the presence of somatosensory disgust, may all serve to increase affective potency.

Simulated disgust

Mental simulation is a ubiquitous aspect of human cognition, involving recreations of motor actions, sensory and emotional states (Hesslow, 2002). Simulated disgust is an intentional act of the imagination driven either by self or other (e.g., thinking, reading or hearing about disgust) and is widely used in contemporary disgust research (i.e., questionnaires, vignettes). It involves the person imagining a somatosensory or an anticipatory disgust cue. It may also involve imagining being disgusted or showing disgust divorced from any particular eliciting cue (e.g., demonstrating disgust for someone in a daydream). Simulated disgust is distinct from anticipated disgust, in three ways. First, no somatosensory disgust elicitor is required for its activation. Second, there can be no threat of contact with the disgust elicitor, as there is no physical elicitor present, which may reduce the magnitude of anterior insula activation (i.e., minimal bodily threat). Third, for anticipatory disgust, mental content is feeling disgust and what is perceived (e.g., seeing dog feces), while for simulated disgust mental content is feeling disgust and what is imagined.

While simulated disgusts are likely then to be less potent than anticipatory and somatosensory disgusts, we suggest that it may be rare to experience this state on its own. Fear, sadness, pity, shame and anger, can each be generated solely from acts of the imagination and these can be as potent as those resulting from real situations (Oatley, 2016) - hence the widespread use of imagination as an experimental emotion induction technique (e.g., Gerrards-Hesse, Spies & Hesse, 1994). This is important, because these emotions may often accompany simulated disgust (e.g., moral violations, prejudice, horror; Cottrell & Neuberg, 2005; Russell & Giner-Sorolla, 2013; Ottaviani et al., 2013). While the presence of these emotions along with simulated disgust should inflate the degree of negative affect - this feeling being common to them all - it should not affect reports of viscerality or nausea, which are particular to disgust, unless these other emotions somehow generate a sense of bodily threat.

Although we know of no direct data, we suggest that simulated disgust in adults is common. Adults appear to have little difficulty in either recalling disgusting events or in simulating how disgusting something would be (e.g., Haidt, McCauley & Rozin, 1994).

Moreover, the process of simulation allows disgust to be extended into situations that are infrequently encountered. Two examples should suffice. First, having dirty underwear, not washing hands after using the toilet, and sleeping on soiled bedding are things that can be readily imagined about someone, but that are less likely to be observed. Second, one is more likely to hear about the sexual exploits of another person than to directly witness them. Finally, the flexibility of this process lends itself both to humour (e.g., Hemenover & Schimmack, 2007), as simulated disgust offers minimal threat, and also to story transmission via its emotionally arousing nature (Heath, Bell & Sternberg, 2001).

Contamination

Contamination occurs when a neutral object becomes imbued with the capacity to induce disgust. We suggested three processes that can generate contamination, which relate to the types of disgust outlined in our model. The first is conditioned taste aversions, in which non-disgust inducing stimuli - almost always a food - becomes associated with a gastrointestinal disturbance generating pure disgust - nausea, negative affect and viscerality. Animal studies indicate that oral based taste (Garcia & Koelling, 1966), retronasal odor (e.g., Bouton, Dunlap & Swartzentruber, 1987), oral texture (e.g., Ramirez, 1992) or their respective combinations - and in addition the sniffed smell of an oral based flavor (e.g., Capaldi, Hunter & Privitera, 2004) - can all serve as associates of pure disgust. Similar findings are observed in humans, with aversions found to the specific taste, smell (orthonasal and retronasal) and texture of foods (De Silva & Rachman, 1987; Logue, Ophir & Strauss, 1981).

Somatosensory disgust may be most strongly associated with the mouth as this location combines all of the eliciting senses of taste, smell and touch, relative to olfaction or touch alone - as well as the greatest threat to bodily integrity. Conditioned taste aversion learning seems to follow this same ordering of being most potently linked to flavor cues in the mouth and then to the smell of food. Once an association has been formed, the human literature suggests that the linked food comes to act as: (1) a somatosensory disgust (i.e., to its smell, taste, texture); (2) an anticipatory disgust, presumably based on pre-existing sensory associations, with its sight sufficient to induce feelings of nausea, negative affect and viscerality; and (3) as a simulated disgust (i.e., imagining it produces revulsion; De Silva & Rachman, 1987; Logue, Ophir & Strauss, 1981).

The second contamination process involves the direct observation of an affectively neutral object coming into physical contact with a somatosensory or anticipatory disgust cue. This has a powerful effect. For example, Rozin, Millman and Nemeroff (1986) had participants watch as they touched a sample of a previously liked fruit juice with what they described as a sterilized cockroach. Immediately after the cockroach was removed, participants judged the juice as undrinkable. Presumably the capacity to visualise and remember the contacting disgust elicitor underpins this contamination effect.

A further aspect of Rozin, Millman and Nemeroff's (1986), experiment was the minimal generalisation of disgust to a new juice sample of the same type as the contaminated one. This illustrates the importance of cognitive control over the spread of contamination. Participants were aware that there was no cockroach contact with the new juice sample – in contrast to behaviour observed with conditioned taste aversions, where any example of the aversive food can induce disgust. Where generalization with this second contamination process does occur, it is typically pathological, with contamination rapidly spreading to related objects (Rachman, 2006). Developmentally, direct physical contamination probably emerges after weaning, with the earliest evidence observed in 18-24M infants, with contact between a liked and a disliked food rendering the liked food inedible (e.g., Brown & Harris, 2012). Over time, the range of stimuli (i.e., disgust inducers) that can support physical contamination grows, moving from direct physical traces (i.e., somatosensory disgust) to anticipatory disgusts (Rozin, Fallon & Augustoni-Ziskind, 1985).

The third contamination process just involves mental simulation with the contaminant and the neutral object both being imagined. People seem readily capable of undertaking simulated contamination, as evidenced by the large number and variety of experimental tasks that require this approach (e.g., Fairbrother, Newth & Rachman, 2005; Rozin, Markwith & McCauley, 1994; Riskind & Maddux, 1994). Mechanistically, it likely involves holding in working memory a representation that explicitly connects the disgust elicitor and the contaminated object. Note how this mental process can *potentially* allow simulated contamination to violate causality (e.g., thinking that tomorrow a stranger will die in the hotel bed you are going sleeping in today, can render that bed disgusting *now*; Rozin et al., 1989; and see, Kim & Kim, 2011).

Discussion

This manuscript offers a proximal perspective on what disgust is. Fundamentally, we suggest that there is one disgust state with four processes that can generate it (see Table 1). This common disgust state is a set of feelings - negative affect, nausea and viscerality (actual and/or imminent bodily threat). The processes that generate it are primarily distinguished by: (1) the physical presence or absence of an elicitor (absent - pure and simulated disgust; present - somatosensory and anticipatory disgust); (2) the presence or absence of a discrete bodily location (absent - anticipatory and simulated disgust; present - pure and somatosensory disgust); and (3) the degree of threat to the body (in order from generally greatest to least; pure, somatosensory, anticipatory and simulated disgust). The extent to which negative affect, nausea and viscerality are present is especially dependent on bodily threat evaluation, the presence of other emotions and states, and whether multiple disgust eliciting cues are present.

An important feature of disgust is its capacity to make other things, which previously did not evoke a response, disgusting. Three contamination processes are envisaged that directly relate to the disgust processes in our model. These allow the creation of: (1) new somatosensory disgust cues, constrained by their relevance to the gastrointestinal system; (2) new anticipatory disgust cues, following an object's contact with a somatosensory disgust elicitor; and (3) new simulated disgust cues, by imagining contact between a neutral and a disgust eliciting object. Just as there is a transition from cognitively inflexible and automatic, to cognitively flexible and controlled, when moving from pure to simulated disgust processes, the same trend is evident in moving from conditioned taste aversions to simulated contamination processes.

Disgust is generally regarded as an emotion (Ortony & Turner, 1990), which is defined here as an object-orientated intentional affective state. Disgust is also widely regarded as a basic emotion, possessing a defined set of properties (Ekman, 1999). Determining what is included as an 'emotion' is a hard problem (Scarantino, 2012), with much argument over boundary conditions (e.g., Craig, 2003; is pain an emotion?). Whether disgust should be categorised among the emotions like fear and anger has also been debated (e.g., Royzman & Sabini, 2001). As we noted earlier, Rozin and Fallon, (1987) argued that everything *beyond* distaste (i.e., reactions to bitter and sour) constitutes disgust and is an emotion. In contrast, few emotion researchers have regarded pain as a basic emotion (Ortony & Turner, 1990), even though it has a distinct facial expression (Williams, 2002), the capacity to experience it is present from birth, and it is clearly affect laden. Perhaps this is because pain is very closely allied to somatosensory perception and is linked to a specific bodily location. This description sounds very much like pure and somatosensory disgust. Both have distinct bodily locations, either in or on the body (Fessler & Haley, 2006).

Avoiding terminology, we could say that pain and pure and somatosensory disgust are taxonomically more alike, than these last-mentioned forms of disgust and the basic emotions.

A further issue is the 'emotion' status of anticipatory and simulated disgust. If pure and somatosensory disgust are not emotions, then perhaps anticipatory or simulated disgust cannot be either, because we can anticipate and simulate pain but this is still not thought of as an emotion. Izard (2007) has suggested the existence of emotion-cognition complexes to account for the array of interactions that routinely occur between basic emotions and cognitions in adults. One could extend this idea to consider new forms of interaction between threat-based feelings, states such as pain and disgust, and other emotions. Thus alone, pain and disgust may be more state-like, but perhaps they can achieve a more emotion-like status when they interact with threat-based feelings and emotions.

Functionally disgust serves to keep us distant from disease (e.g., Curtis & Biran, 2001; Fleischmann & Fessler, 2011; Marzillier & Davey, 2004; Oaten, Stevenson & Case, 2009; Rozin, Haidt & McCauley, 2016; Tybur et al., 2013). For pure and somatosensory disgust, this link is clear. Pure disgust is envisaged to be synonymous with the feeling state of gastrointestinal illness and somatosensory disgust cues are linked to toxins, bacterial degradation products and microbe-friendly environments. For anticipatory disgust elicitors, much the same holds, as these are sensory associates of somatosensory disgust elicitors. For simulated disgust it becomes harder to tie this back to disease avoidance, making it functionally more flexible. For example, people can be shaped to think of certain things in a way that draws attention to their disgust-related properties - or equally that does not. On some occasions this may align with disease avoidance (e.g., poor hygiene), but it could equally reflect other social forces that have no direct connection to disease (e.g., manipulating out-group fear).

A significant area of contention in the literature has been the issue of moral disgust, and most notably whether it involves disgust at all (e.g., Case, Oaten & Stevenson, 2012; Nabi, 2002; Simpson et al., 2006; Yoder, Widen & Russell, 2016). The process model we propose is silent on whether certain forms of immoral behavior can induce disgust. This is because the model does not rely on specifying elicitor types - beyond those involved in somatosensory disgust - but rather focusses on process. Thus, if the requisite process is engaged, and in this case it would most likely be simulated disgust (i.e., hearing about a person's behavior), then disgust should be experienced.

As outlined earlier, a considerable amount of theorising and research has revolved around grouping elicitors into domains and then comparing them to discern their different properties. We suggest this line of enquiry is problematic. Setting aside the multiple forms of grouping and the ensuing lack of agreement over which might be correct, the more fundamental 'carving at the joints' may not always align with elicitor types, but rather with the cognitive processes that give rise to the disgust response, and whether that disgust response is common across processes. For some reason, possibly because of the focus on function, the study of elicitor groupings seems to have dominated thinking about disgust in a way that has not occurred for most other emotions and states.

Elicitor categories seem to be most meaningful for the somatosensory disgusts, arguably because of their modularity (e.g., see Peng et al., 2015). For example, bitter taste receptors are of lesser value to carnivores or folivorous animals, which consume, respectively, either none or very large quantities of secondary plant products. Similarly, olfactory signals of decay are of value to animals that consume rotting flesh, just as fecal odors are of high value for avoiding predators - but in each case with differing valence. Aversion to slimy feces-filled innards is of little use to a carnivore with its head inside the guts of its prey, but of great use to a social animal that needs to avoid its conspecifics feces.

Somatosensory disgust cues may then represent a coalition of disease-avoidant cues that are each 'plugged in' to pure disgust, with the repertoire dependent on ecological need. Beyond somatosensory disgusts, we suggest that a basic form of anticipatory disgust - neophobia - may be present in mice, rats and chimpanzees, but how extensive other forms of anticipatory disgust are, remains to be examined (but see, Sarabian, Ngoubangoye & Macintosh, 2017).

We made three claims about the neural basis of disgust. First, that the brain state observed during gastrointestinal illness reflects the purest neural correlate of the common felt experience of disgust - albeit based on induced virtual motion sickness. Second, that the primary somatosensory cortex is active for pure and somatosensory disgust, giving these states a specific bodily location, something not expected for anticipatory and simulated disgust. Third, while pure and somatosensory disgust represent actualised bodily threats, and so should be associated with activity in the anterior insula (Ploghaus et al., 1999; Ogino et al., 2006), the potential degree of bodily threat should dictate the degree of anterior insula activity for anticipatory and simulated disgusts. In turn, damage to these brain areas should produce particular forms of deficit. Lesions or drugs affecting the neural basis of nausea – amygdala, putamen, locus coeruleus (Napadow et al., 2013) - should impair the capacity to experience all forms of disgust, by diminishing its unique feel relative to other states and emotions. Lesions that affect somatosensory processing (i.e., parietal lobe) should reduce the sense of viscerality and hence the threat-value of somatosensory disgusts. Such lesions should have less impact on anticipatory and simulated disgust, which rely for bodily threat evaluation on the anterior insula. Lesions affecting the anterior insula should affect threat-evaluation and impair disgust amplification, notably for anticipatory and simulated disgust.

Our model also has implications for the development of disgust. From the perspective of developmental order, we suggest that: (1) the brain circuitry to support pure disgust is present at birth; (2) somatosensory disgusts appear at birth, or soon after; (3) the first anticipatory disgusts emerge at around 18M connected with weaning and toilet training; and (4) simulated disgust emerges last, dependent both upon the maturation of the cognitive processes necessary to support imagination and a body of disgust-experience to draw upon. The capacity for each type of contamination should emerge in line with this scheme. Key developmental processes should involve learning sensory associations and the formation of threat evaluation feelings.

In conclusion, we suggest that our model offers a new and more productive framework to approach important proximal questions about disgust's development, its neural basis, its continuity into animals, and its status as an emotion.

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Table 1: Summary properties and features of the processes that generate disgust

Property and features	Disgust generation process			
	Pure	Somatosensory	Anticipatory	Simulated
Eliciting stimulus present or absent when disgust occurs	Absent	Present	Present	Absent
Eliciting stimulus has discrete bodily location	Yes	Yes	No	No
Typical degree of bodily threat	Very high	High	Moderate	Low
Role of learning in generation process	None	None	Significant	Significant
Developmental appearance	Birth	Birth to toileting	Post-weaning	School age
Degree of intentional control over the disgust experience	Little	Some	Moderate	High
Related contamination process	CTA*	Explicit learning	Explicit learning	Imagined
Involvement of other emotions and states	None	None	Significant	Very significant
Occurrence in other mammals	Yes	Yes	Yes	No

*Conditioned taste aversion

Figure 1: Cues to disgust, and the processing steps involved in generating the associated feeling state and contamination, with hashed lines and boxes indicating, respectively, pathways and processes involving a greater learning component