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Evolution, Development, and the Emergence of Disgust

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Abstract: Evolutionary developmental psychology typically utilizes an evolutionary lens to explain various phenomena that occur throughout development. In this paper, I argue that the converse is also important: Developmental evidence can inform evolutionary theory. In particular, knowledge about the developmental origins of a psychological trait can be used to evaluate theoretical claims about its evolved function. I use the emotion of disgust as a case study to illustrate this approach. Disgust is commonly thought to be a behavioral adaptation for avoiding the ingestion of pathogens. Given this claim, disgust should be expected to develop at a time when humans are especially vulnerable to the dangers of ingesting pathogens, during the immediate post-weaning period from about 3 to 5 years of age. Despite a strong selective pressure at this point in development, research has suggested that the emotion of disgust and the recognition of the "disgust face" do not reliably emerge until later in ontogeny, at 5 years of age or after. Given the late developmental appearance of disgust, I re-evaluate claims about its adaptive role.

Keywords: disgust, evolution, development, adaptationism

Introduction

Imagine eating excrement, kissing a stranger covered in open sores, or painting a swastika on a Holocaust memorial. Despite the broad range of these behaviors, all trigger a common aversive reaction: the emotion of disgust (e.g., Tybur, Lieberman, Kurzban, and DeScioli, 2013). Because disgust is such a multifaceted emotion, there are multiple possible accounts of its evolutionary origins. The most widely accepted functional explanation is that disgust originally evolved to prevent the ingestion of pathogenic substances (e.g., Rozin, Haidt, and McCauley, 2008).[1] I evaluate this claim using evidence

[1] Although Rozin and colleagues often characterize disgust as being rooted in abstract ideas about the nature or origin of "offensive" substances, they also describe it as functioning to protect the body from disease and infection (e.g., Rozin et al., 2008, Table 47.1). Because protecting oneself from ingesting pathogens has obvious evolutionary significance, this survival-relevant function will be the focus of the present paper.

from developmental psychology and argue that this particular evolutionary account should be further scrutinized, as it is not consistent with the current developmental evidence.

In particular, I assert that it can be productive to apply a developmental lens to evolutionary theorizing. Specifically, one can evaluate a proposed functional explanation by: a) predicting what developmental patterns and processes would fit that explanation and b) examining the developmental evidence in that light. In the current paper, I use the case of disgust as a concrete example of how ontogenetic evidence can be used to examine claims about the evolved function of a trait. Several questions guide this analysis:

1) Fitness value: During what age range should the evolved function of a trait afford the greatest benefits for survival and/or reproduction?
2) Flexibility: Based on functional assumptions about the trait in question, should the evolved design include a fixed set of evolutionarily prepared elicitors that develop similarly across varying contexts, or should the content of the elicitors instead be variable and primarily shaped through learning mechanisms?[2]
3) Theory evaluation: Given the answers to the first two questions, does the evidence of the developmental trajectory and the flexibility of the eliciting content fit with the evolutionary hypothesis?

Combining Evolutionary and Developmental Approaches to Psychology

Evolutionary psychology has emphasized the importance of developmental processes since its advent, recognizing that "nothing about humans could possibly be immune from developmental intervention" (Tooby and Cosmides, 1992, p. 80). However, despite this theoretical emphasis, a focus on developmental processes has been slow to gain empirical traction, as the major advances in evolutionary psychology have historically been achieved by researchers studying only adults (although there are a few notable exceptions: e.g., Barrett and Broesch, 2012). This lack of developmental research is unfortunate, as it may have contributed to misguided accusations that evolutionary psychology assumes preformationism and ignores the crucial role of ontogenetic development in shaping the human mind (e.g., Buller, 2005; Buller and Hardcastle, 2000; Karmiloff-Smith, 2009; Karmiloff-Smith and Thomas, 2005; Lickliter and Honeycutt, 2003; Ploeger, van der Maas, and Raijmakers, 2008). A greater emphasis on development will likely be helpful in deflecting these criticisms in the future (see Bjorklund, 2003; Frankenhuis, Panchanathan, and Barrett, 2013).

[2] It is important to note that either possibility – biologically prepared content or content that is derived from socially transmitted knowledge or other environmental influences – could be a solution designed by natural selection. Following a core tenet of evolutionary psychology, I do not draw a dichotomy between "innate" and "learned" traits, but rather acknowledge that learning and cross-cultural diversity can be products of evolved adaptations (e.g., Barrett and Kurzban, 2012; Tooby and Cosmides, 1992, 2005; Tooby, Cosmides, and Barrett, 2003).

Although developmental psychology has also largely proceeded independently of evolutionary psychology, an increasing number of developmentalists are adopting strong evolutionary perspectives (e.g., Belsky, 1997; Belsky and Pluess, 2009; Bjorklund and Pellegrini, 2000; Causey, Gardiner, and Bjorklund, 2008; Ellis and Bjorklund, 2005; Geary, 2006; Geary and Bjorklund, 2000; King and Bjorklund, 2010; also see Konner, 2010). In particular, several researchers have underscored the importance of developmental plasticity and gene-environment interactions as crucial factors underlying the emergence of evolved psychological traits, showing that genotypes may support a range of possible phenotypes that are variably optimal depending on the particular environmental conditions in which an organism develops (e.g., Belsky, Houts, and Pasco Fearon, 2010; also see Belsky, 1997; Belsky and Pluess, 2009; Causey et al., 2008; Ellis and Boyce, 2008).

In addition, the emerging lens of evolutionary developmental psychology explicitly focuses on applying an evolutionary perspective to explain and make predictions about developmental phenomena. Evolutionary developmental psychology emphasizes that there are varying selection pressures at different points in development, and therefore children (and other altricial animals) at various ages will exhibit evolutionary adaptations that may differ from the adaptations that appear in adulthood (Bjorklund and Pellegrini, 2000; Galef, 1981; King and Bjorklund, 2010). Thus, evolutionary developmental psychology can offer functional explanations for developmental phenomena (Bjorklund and Pellegrini, 2000; Geary and Bjorklund, 2000; Hernández Blasi and Bjorklund, 2003).

Another way of approaching the integration of evolutionary and developmental perspectives is also possible: Developmental evidence can be used to evaluate theoretical claims about evolved functions. Therefore, not only can evolutionary theories help to make sense of development (as evolutionary developmental psychology emphasizes), but the converse is true as well: Developmental data can help to make sense of evolutionary accounts, which are often primarily based on evidence from adults. Accordingly, researchers can use developmental evidence to rule out, or at least call into question, certain functional explanations. This approach can also help to highlight developmental experiments that would provide evidence to support or challenge different accounts. Unfortunately, however, systematic attempts to pursue this strategy are lacking. In the remainder of the paper, I use the example of disgust to demonstrate and encourage the use of developmental evidence when assessing the plausibility of evolutionary hypotheses.

The "Oral Origins" Hypothesis of the Evolution of Disgust

Disgust can be defined as an emotional reaction that activates the parasympathetic nervous system, generates feelings of nausea and a characteristic facial expression, and results in the behavioral avoidance of a stimulus. This is importantly different from distaste, which is a phylogenetically ancient sensory response to toxins that requires gustatory contact. Indeed, disgust is thought by some to be a uniquely human emotion (Kelly, 2011; Rozin et al., 2008), potentially because it is cognitively complex or perhaps because humans encountered new survival pressures when their diets become more omnivorous or when they began living in dense groups.

A search for the evolved function of disgust has been a major focus of most disgust

researchers. Whereas some have argued for various unique evolutionary trajectories of disgust to account for the multiplicity of its current functions (Tybur, Lieberman, and Griskevicius, 2009; Tybur et al., 2013), I restrict my discussion to an investigation of the hypothesized initial function of disgust rather than subsequent exaptations. In particular, I focus on Rozin and colleagues' prominent claim that disgust initially evolved because it served as an effective mechanism for orally rejecting harmful substances (Rozin and Fallon, 1987; Rozin, Haidt, and Fincher, 2009; Rozin et al., 2008). I define an "Oral Origins" account of the function of disgust as the hypothesis that *disgust evolved because it allowed humans to avoid the ingestion of pathogens.*[3]

According to advocates of the Oral Origins hypothesis, humans may have had an increased risk of foodborne disease and infection due to their meat-heavy generalist diet. This would have made it especially advantageous to have a mechanism for the oral avoidance of infectious substances. Support for this proposal has primarily come from data indicating the overlap between neural, behavioral, and physiological correlates of disgust and distaste, and the observation that the disgust expression is functionally suited for orally expelling ingested substances and restricting the entry of external substances into the mouth (Chapman and Anderson, 2012; Darwin, 1872/1998; Jabbi, Bastiaansen, and Keysers, 2008; Rozin et al., 2008).

If disgust truly evolved as a food rejection system designed to protect the human body from infectious disease, then disgust should emerge by the developmental time at which humans are most susceptible to the dangers of ingesting pathogens (e.g., Haidt, Rozin, McCauley, and Imada, 1997; Stevenson, Oaten, Case, Repacholi, and Wagland, 2010). During the first 2 years of life, infants in traditional societies are almost exclusively breastfed and are usually carried and kept off of the ground, which protects them from ingesting harmful microbes (Hrdy, 2011; Sear, Mace, and McGregor, 2000). However, evidence suggests that children are especially vulnerable to pathogens during the immediate post-weaning period, before the immune system has fully developed (Dobson and Carper, 1996; Hewlett, 1991; Sear et al., 2000). The time of weaning varies by culture based largely on the timing of the mother's next birth, but children are generally weaned by 3 years of age (Hrdy, 2011; Konner, 2010; Kramer, 2005; Whiting and Edwards, 1992), which is notably much earlier than in other apes (Kennedy, 2005).

The post-weaning period from roughly 3 to 5 years of age is therefore a crucial time during which survival depends on the ability to avoid eating and drinking substances that pose infection risks. Recent public health studies provide information about the causes of

[3] This idea is related to, but distinct from, several other accounts of the evolution of disgust, which posit that disgust serves to motivate an increased avoidance of pathogens through all possible routes of infection, including skin surfaces and genitals (Chapman and Anderson, 2012; Curtis, 2011; Curtis, Aunger, and Rabie, 2004; Curtis and Biran, 2001; Curtis, de Barra, and Aunger, 2011; Davey, 1994; Kelly, 2011; Oaten, Stevenson, and Case, 2009; Siegal, Fadda, and Overton, 2011; Stevenson, Case, and Oaten, 2009; Tybur et al., 2013). The Oral Origins hypothesis departs from these hypotheses in that it focuses specifically on incorporating pathogens through the mouth rather than through other forms of physical contact. However, several of the considerations discussed in this paper also pertain to these broader conceptions of disgust as a more general pathogen avoidance mechanism.

death during these early years. Although these data are only available at a country level and for recent years, they can be used as a basis for educated guesses about the kinds of pathogens that posed the greatest threats to children during human evolutionary history. Overall, evidence shows that the oral ingestion of pathogens and parasites from feces and other contaminated substances is a major cause of death in childhood, underlying diarrheal diseases as well as hepatitis A, polio, streptococcal infections, tapeworm, and toxoplasmosis (see Curtis, 2011). Indeed, global assessments of the causes of deaths in young children demonstrate that diarrheal diseases are among the greatest causes of mortality, accounting for 18% of deaths in children under 5 years of age (Bryce, Boschi-Pinto, Shibuya, Black, and the WHO Child Health Epidemiology Reference Group, 2005).

Based on these considerations, the Oral Origins hypothesis predicts that disgust has the greatest adaptive potential in early childhood and should therefore emerge early in ontogeny. Additionally, it is reasonable to expect an early preparedness for experiencing disgust at a set of core elicitors, such as feces and rotting meat, since these have universally and historically posed a reliable disease threat when ingested.[4]

Criteria for Identifying Disgust

Before reviewing the developmental evidence, it is important to highlight a key methodological issue: the difficulty of measuring emotional experiences. The obscurity of others' phenomenological states is an issue that continues to plague philosophers of mind (e.g., Jackson, 1986; Nagel, 1974), and it also presents a major difficulty for psychologists, and perhaps especially developmentalists (Lewis, 2008). Because it is challenging to document the experience of disgust with the methods that are currently available to researchers, any attempt to identify the developmental emergence of disgust is complicated by the initial challenge of defining criteria for its empirical operationalization. Ideally, multiple convergent methods should be utilized; several of these are described below.

Researchers taking an evolutionary approach to emotion, most prominently Darwin (1872/1998), Ekman (1992), and Izard (1994), often use facial expressions to indicate the presence of an emotion. The Facial Action Scoring Technique (Ekman and Friesen, 1975) has been used as a metric for measuring the early emergence of emotions such as anger (Stenberg, Campos, and Emde, 1983) and also disgust (Stevenson et al., 2010). Therefore, one measurable sign that somebody is experiencing disgust is the "disgust face," an expression that involves a wrinkled nose, squinting eyes, and a gaping mouth. This facial expression also signifies distaste, however, and therefore it can only be taken as evidence of disgust when nothing unpleasant is being tasted.

Self-report is another commonly used method for identifying the presence of an emotion. Because children demonstrate an understanding of the word "yucky" by 2 years of age (Bretherton and Beeghly, 1982; Fenson et al., 1994), this raises the possibility of asking young children to identify "yucky" things in order to explore whether this adjective

[4] It should be noted, however, that coprophagy is not unusual among certain other animals, including great apes (Krief, Jamart, and Hladik, 2004).

extends beyond distasteful substances. However, it is possible that this would only reflect conceptual understanding rather than an underlying emotional reaction. Additionally, within the current disgust literature, self-reports from children have only been used to identify items as "good" or "bad" rather than specifically disgusting (e.g., Schmidt and Beauchamp, 1988; Stevenson et al., 2010), and therefore this evidence is not precise enough to demonstrate the presence of disgust.

Yet another way of measuring disgust is by examining physiological or neural indicators. For example, electrogastography has allowed researchers to measure gastric reactivity, with decreased stomach muscle contractions indicating greater disgust (e.g., Shenhav and Mendes, 2013). Additionally, fMRI has been used to explore neural correlates of disgust, often finding reliable activation in regions such as the anterior insula (e.g., Wicker et al., 2003; but see Schienle et al., 2006). However, measures such as these have not been used with children.

Behavioral avoidance has also been utilized as a measure of disgust due to its obvious functional relevance. However, avoidance alone is insufficient to demonstrate disgust, as various other mechanisms can produce functionally indistinguishable behavioral patterns. For example, other negative emotions such as fear and distress are operative in many avoidance responses (e.g., Gerull and Rapee, 2002). Additionally, avoidance may sometimes result from non-affective mechanisms. For example, inhibitory control allows children to suppress their motor responses and therefore avoid touching an appealing but forbidden toy (e.g., Carlson and Wang, 2007). Hesitancies to come into contact with certain objects can also be driven by intuitions or beliefs about their negative characteristics. For instance, human infants have natural tendencies to avoid touching potentially toxic plants, but it is not clear that this avoidance involves any particular emotional reaction (Wertz and Wynn, 2014). Finally, even though many other species faced with the threat of pathogens and parasites employ a range of behavioral strategies to avoid contact with common sources of infection like feces (Curtis et al., 2011; Hart, 1990; Hutchings, Kyriazakis, Anderson, Gordon, and Coop, 1998; Loehle, 1995), these evolved mechanisms are generally presumed to exist independently of a disgust response (e.g., Rozin et al., 2008). For these reasons, I argue that avoidance cannot definitively indicate the experience of disgust in the absence of other converging forms of evidence.

Finally, another important issue to address is that disgust may not emerge as a singular monolithic package, but might instead develop cumulatively, with various subcomponents arising at different points in development and only eventually forming one cohesive mechanism. Alternatively, it is also conceivable that children experience other functionally appropriate responses to pathogen vectors before acquiring disgust. Though a careful investigation of these issues is beyond the scope of the present discussion, these theoretical possibilities are in need of careful empirical investigation.

The Development of Disgust

Distaste has been documented in newborns by demonstrating mouth gaping in response to bitter substances (e.g., Rosenstein and Oster, 1988). However, a robust disgust response lags behind this considerably, and does not seem to be acquired by the onset of

weaning. On the contrary, developmental research has repeatedly shown that disgust is a relatively late-emerging emotion, possibly not fully coming online until middle childhood (e.g., Rozin and Fallon, 1987). This evidence will be briefly reviewed below.

Two-year-old children are often willing to put just about anything into their mouths, even objects that are considered highly disgusting by older children and adults (e.g., imitation feces), and young children are therefore generally regarded as completely lacking disgust (Rozin, Hammer, Oster, Horowitz, and Marmora, 1986). One study has found limited evidence of disgust toward oral elicitors as early as 2.5 years of age (Stevenson et al., 2010), but a close examination of these data raises questions about whether this research truly measured disgust rather than another avoidance mechanism (e.g., fear or inhibition), as the conclusions were primarily based on evidence of behavioral approach/avoidance. When taken through various revolting tasks, such as sniffing fecal and urinous odors and being asked if they wanted to touch live maggots or eat candy from the bottom of a new toilet, 2.5-year-olds avoided the items nearly half the time, and this increased to 75% by 6.8 years of age. However, children below the age of 6.8 made facial expressions of disgust to these same elicitors less than 20% of the time (much less frequently than smiling), which increased to about 40% by 6.8 years (Stevenson et al., 2010). Therefore, even though very young children tended to be unwilling to come into contact with disgusting stimuli, their behavioral avoidance and negative evaluations were not often accompanied by a disgust expression or another more specific indicator of disgust and therefore cannot be taken as clear evidence for the experience of disgust. Additionally, these data demonstrate that the disgust response becomes increasingly more pronounced in middle childhood.

A separate issue that has often been closely associated with disgust is that of contamination sensitivity. There is mixed evidence regarding the age at which this begins to develop (Rozin and Fallon, 1987; Siegal et al., 2011). Rozin and colleagues have found that children under the age of 7 do not reject substances that have come into contact with objects such as insects or used combs (Fallon, Rozin, and Pliner, 1984; Rozin, Fallon, and Augustoni-Ziskind, 1985). More recent research has suggested a much earlier onset of contamination sensitivity, as young as 3 years of age (Legare, Wellman, and Gelman, 2009; Siegal and Share, 1990). However, this early emergence may be largely due to cultural scaffolding, potentially through explicit teaching about germs, as children in Western countries have more robust hygiene-related behaviors than children in developing countries (Siegal et al., 2011). Additionally, although beliefs about contamination and feelings of disgust are often linked, there is some evidence that contamination sensitivity may be driven by ideas about magical contagion (Nemeroff and Rozin, 2000) or folk biological causal understandings (Legare et al., 2009) rather than emotional reactions. Most studies on contamination sensitivity have measured avoidance behavior rather than the disgust reaction per se, and therefore provide weak evidence for the emergence of disgust.

Although little is known about how particular disgust elicitors develop in childhood, there have been a few investigations of whether there is an evolutionarily prepared set of elicitors that universally elicit disgust in adults. Some studies have demonstrated widespread regularities, with several substances (e.g., feces, vomit) appearing to be cross-culturally recurrent elicitors of disgust (Curtis et al., 2004; Curtis and Biran,

2001). However, these are likely to develop as a result of prepared cultural learning rather than biological maturation (Curtis and Biran, 2001), possibly due to experiences such as toilet training (Rozin et al., 2008). Other cross-cultural evidence suggests that most elicitors of disgust vary widely around the world (Haidt et al., 1997; Herz, 2012; Rozin et al., 2008) and remain very plastic throughout adulthood (e.g., Case, Repacholi, and Stevenson, 2006). For example, food is used to establish cultural boundaries from very early in development (Mahajan and Wynn, 2012; Shutts, Kinzler, and DeJesus, 2013), and a range of different foodstuffs may be considered delicious or disgusting depending on one's particular cultural experiences (Herz, 2012). Although foods that are considered disgusting are often meat-based and/or fermented, and therefore potentially carry disease in the absence of knowledge to the contrary, even foods as innocuous as peanut butter and jelly sandwiches are considered revolting in certain places. Additionally, disgust is lacking in autistic children, who have impairments in social learning (Kalyva, Pellizzoni, Tavano, Iannello, and Siegal, 2010), as well as in feral children (Malson, 1964/1972). Furthermore, the fact that handwashing and hygiene campaigns have had to be instilled as major public health initiatives, and are often unsuccessful (Curtis, Danquah, and Aunger, 2009), suggests that disgust at fecal-oral contamination has not been evolutionarily prepared. Overall, therefore, it seems that disgust has been evolutionarily designed to have a great degree of flexibility in content, which is likely facilitated by a social learning mechanism of some kind. However, disgust is not entirely malleable, and it is noteworthy that many disease-causing substances are regularly considered to be repulsive. It is equally noteworthy that many of these substances (e.g., open sores) generally pose no threat of oral incorporation.

Most researchers believe that the facial expression of disgust is likely to be the most important mechanism of the cultural transmission and parental socialization of disgust (Curtis et al., 2011; Herz, 2012; Izard, 1994; Kelly, 2011; Oaten et al., 2009; Rozin and Fallon, 1987; Rozin et al., 2008; Stevenson et al., 2010; Widen and Russell, 2013). Indeed, some have suggested that recognizing the disgust face is the very foundation of developing disgust (Widen and Russell, 2013; also see Harris, 1989). If children are acutely attuned to others' disgust reactions in the first years of life, they should be able to obtain crucial information about the sources of dangerous pathogens from the context-specific facial reactions of local cultural authorities such as their parents.

Studies have demonstrated that adults' facial expressions of disgust effectively lead infants to learn that particular objects should be avoided (Hertenstein and Campos, 2004; Moses, Baldwin, Rosicky, and Tidball, 2001). However, these results are strongly influenced by ostensive cues that signal culture-relevant information, suggesting that the experimenters' pedagogical displays may have conveyed norms rather than eliciting shared emotional states (Egyed, Király, and Gergely, 2013). In addition, these studies tested disgust against positive emotions and therefore cannot demonstrate that disgust, rather than negative affect, led to the avoidance. Differential findings with anger or other negative emotions are needed before strong conclusions about the specificity of disgust can be made.

Indeed, recent evidence suggests that young children do not understand others' facial expressions of disgust as actually conveying disgust. The recognition of the characteristic disgust face appears late in ontogeny, considerably lagging behind the correct recognition of all other basic emotional expressions. Even as late as 7 years of age, most

children interpret a disgust expression as signaling anger (Widen and Russell, 2008, 2013). Because it takes many years before the facial expression of disgust is interpreted as conveying the disgust emotion, there may not be a straightforward way for children to observe what others in their culture consider disgusting until they reach middle childhood. This suggests that when very young children see an adult display a disgusted expression toward an object that should not be orally ingested, their learned avoidance is not occurring via the disgust emotion in particular. Of course, this inability to recognize disgust in others does not mean that children cannot themselves experience disgust, but rather that social learning about disgust elicitors will be hindered throughout early childhood.

Evaluating the Developmental Evidence

Integrating developmental and evolutionary perspectives allows for an evaluation of the Oral Origins hypothesis that goes beyond examining the apparent functional role that disgust plays during adulthood. In particular, this evolutionary account can be evaluated in terms of whether the developmental trajectory of disgust is consistent with its hypothesized functional benefits. Recalling the three questions posed at the beginning of the paper, and framing them in terms of disgust in particular, we can answer as follows:

1) Fitness value: If disgust evolved to prevent the ingestion of pathogens, its contributions to fitness are not expected to be equivalent across the lifespan. Rather, disgust should be especially beneficial to survival during the immediate post-weaning period, between the ages of 3 and 5.
2) Flexibility: According to the Oral Origins hypothesis, a universal set of "core elicitors" should be evolutionarily prepared for dealing with pathogenic vectors that recur across all typical environments, and flexible learning should be largely unnecessary in most cases.
3) Theory evaluation: Disgust does not appear to develop by the point in childhood when humans are most susceptible to the dangers of ingesting pathogens. Additionally, evidence suggests that disgust evolved such that many of its elicitors are primarily shaped through social learning, rather than being biologically prepared. Thus, a comprehensive assessment of the existing developmental evidence makes the Oral Origins hypothesis less credible as a freestanding explanation for the existence of disgust.

Overall, the current evidence does not convincingly indicate that children have developed the emotion of disgust before the age of 5. Although it is true that children under this age sometimes avoid potentially disgusting substances, there are currently few empirical reasons to believe that they are experiencing an adult-like emotion of disgust when doing so. Because the content of disgust elicitors may be dependent on learning cultural information about what is locally considered disgusting, and because young children may be delayed in their acquisition of this information due to an inability to adequately recognize the "disgust face," it is unlikely that disgust plays a major role in driving young children to avoid ingesting pathogens. Instead, the selection of what and

what not to eat may rely more heavily on listening to trusted adults and imitating their food choices, which does not require disgust (Lumeng, Cardinal, Jankowski, Kaciroti, and Gelman, 2008; Shutts et al., 2013; Shutts, Kinzler, McKee, and Spelke, 2009). Other early-emerging computational mechanisms may also contribute to the avoidance of certain categories of potentially harmful substances (e.g., Wertz and Wynn, 2014), and again these likely arise independently of disgust. If future research confirms that disgust does not develop until middle childhood, this will suggest that humans do not benefit from the disgust reaction at a time when the Oral Origins hypothesis predicts that it would produce the greatest survival advantage.

Perhaps the late emergence of disgust is due to a lack of necessary cognitive abilities or to evolutionary design constraints that prevent an early, unsocialized emergence of the emotion and the ability to recognize it in others. In addition, one might contend that much of the disease transmission that causes diarrhea and related diseases is waterborne or airborne, and therefore might be practically unavoidable or lack cues needed for the disgust response – but this argument would also constrain the scope of the fitness-enhancing value of disgust under the Oral Origins hypothesis. Alternatively, it could be argued that disgust is unnecessary in young children because parents' own disgust responses are sufficient to keep their children away from pathogens (e.g., Curtis and Biran, 2001; Tybur et al., 2013). However, even though young children in small-scale societies are often carried around and fed exclusively by caregivers, they are also often given opportunities to experiment with their environments (especially after weaning), and therefore children still have the potential to occasionally put infectious substances into their mouths. Finally, one might reason that ingesting a wide range of substances during early childhood would presumably strengthen the immune system of surviving children, and therefore an initial lack of disgust could actually be adaptive (e.g., Herz, 2012). This fitness benefit would not likely outweigh the potential costs of overzealous pathogen consumption, however. The fact that diarrhea is the second largest child killer worldwide suggests that there would have been major selection pressures for the emergence of disgust in early childhood *if* disgust is indeed a mechanism that is primarily geared toward preventing the ingestion of contaminated substances, and presuming that diarrhea was also a major cause of child mortality in the environments of evolutionary adaptedness. In sum, the Oral Origins hypothesis cannot sufficiently account for the available developmental data.

Other Evolutionary Accounts of Disgust

Inconsistencies between the Oral Origins hypothesis and the current developmental evidence suggest that other possible evolutionary explanations of disgust should be carefully considered. For example, one alternative hypothesis is that disgust arose as an adaptation for regulating social interactions rather than oral ingestion. In particular, disgust could serve as a mechanism for behaviorally avoiding pathogen transmission from people who exhibit disease-related cues (Park, Faulkner, and Schaller, 2003; Schaller, 2011; Schaller and Park, 2011). This hypothesis identifies an obvious selection pressure that would have led to this uniquely human adaptation: Because parasite risk greatly increases with social group size and density (Côté and Poulin, 1995), prehistoric humans'

unprecedented move to living in close proximity with each other would have placed them at a higher risk of acquiring harmful microorganisms from other people. Research has consistently demonstrated that disgust can be elicited in adults by presenting them with images of people displaying signs of illness or morphological abnormalities, or by presenting them with scenarios of people engaging in deviant social behaviors such as incest, cheating, or blasphemy (e.g., Ryan, Oaten, Stevenson, and Case, 2012; also see Chapman and Anderson, 2013; Haidt et al., 1997; Rottman and Young, 2014). Furthermore, individual differences in disgust sensitivity are predictive of negative attitudes toward outgroup members and people who behave in ways that are considered to be non-normative (Hodson and Costello, 2007; Inbar, Pizarro, Knobe, and Bloom, 2009; Navarrete and Fessler, 2006; Terrizzi, Shook, and Ventis, 2010). Other functional hypotheses about the evolution of disgust are possible as well, and developmental evidence will provide an important empirical tool for assessing their plausibility.

Conclusions and Future Directions

Current evidence suggesting a late developmental emergence of disgust is problematic for the Oral Origins hypothesis. Of course, further research on developmental trajectories and acquisition patterns is necessary before confident claims can be made about this account, as the developmental evidence is currently sparse and future investigations could potentially uncover an earlier emergence of disgust, thereby overturning my present evaluation. However, if such additional empirical studies cannot yield supportive developmental evidence, this will significantly diminish the plausibility that the Oral Origins hypothesis can fully account for the existence of disgust.

In conclusion, a thorough consideration of the relevant developmental evidence can benefit evolutionary psychologists investigating the legitimacy of various functional claims. Although the present paper has specifically looked at disgust as a case study, the approach used here can substantially contribute to the evaluation of adaptationist hypotheses about a wide variety of other traits, ranging from the psychological (e.g., religious belief) to the morphological (e.g., bipedalism). Scholars evaluating competing hypotheses about the functional origins of a trait may find this method especially beneficial. Overall, this approach can serve as valuable way to combine evolutionary and developmental perspectives.

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