The Animal Origins of Disgust: Reports of Basic Disgust in Nonhuman Great Apes.

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Abstract

Intrinsic to an evolved disease avoidance account of disgust is Darwin's assumption of continuity between the emotional lives of humans and animals. However, beyond the case of avoiding stimuli that taste bad, there has been little exploration of the existence of basic disgust elicitors in animals. Moreover, one influential perspective holds that disgust is unique to humans--a preadaptation of distaste that expands through culture to include a wide range of elicitors (e.g., Rozin, 2015). The present study represents a broad-scope investigation into disgust-like responses that might be present in nonhuman great ape species. A survey of aversions, contamination reactions, and signs of disgust in nonhuman great apes (principally chimpanzees) was collected from 74 great ape researchers, fieldworkers, and keepers. Overall, the results suggest that nonhuman great apes share with humans an aversion to a restricted range of core pathogen sources, which extends beyond distaste to resemble human disgust. However, in nonhuman great apes, this aversion is muted. Candidates for this difference between humans and other great apes are considered, including frequent exposure to basic disgust elicitors in nonhuman great apes and increased dependence on meat-eating in hominin ancestry. We suggest that differences in disgust–like behavior between humans and nonhuman great apes reflect the specific ecological standpoint of the animal and that rather than being unique to humans, disgust is a continuation of the armoury of disease avoidance behavior ubiquitous in animals.

Keywords: Pathogen, Primate, Disease avoidance, Evolution, Aversions

Public significance statement: A systematic survey of great ape experts suggests that nonhuman great apes have an aversion to a restricted range of core pathogen sources that they share with humans. This extends beyond distaste to resemble a muted form of disgust. Long thought to be unique to humans, disgust is likely a continuation of the armoury of disease avoidance behavior ubiquitous in animals.

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In their influential account of disgust, Rozin et al. (1993, 2008; see also Rozin, 2015) proposed that disgust has its evolutionary origin as an aversion to distasteful food. However, this aversion to bad tastes was co-opted in humans to form disgust to a wide range of elicitors. Importantly, they argue that even repulsion to the most potent, or core, disgust elicitors (e.g., feces, rotting meat) concerns the nature and origin of the food, not the taste, and is thus acquired through culture. As such, disgust and the contamination response are thought to be acquired and unique to humans (Rozin, 2015).

Consistent with Darwin's (1872/1965) assumption of continuity, however, recent approaches hold that human disgust is a continuation of disease avoidant behavior that is ubiquitous in animals (e.g., Curtis & Biran, 2001; Oaten, Stevenson, & Case, 2009). These accounts focus on disgust as a behavioral strategy that reduces the likelihood of contact with potentially harmful pathogens. Since the function of disgust is to drive pathogen avoidance, these accounts focus on universal disease risk cues (e.g., body waste products and envelope violations, spoiled foods, certain animals, death, certain sexual acts, and unhygienic people; see Curtis, de Barra, & Aunger, 2011) to the exclusion of more abstract forms such as moral disgust, which might or might not represent a discrete form of disgust (e.g., Case, Oaten, & Stevenson 2012; Oaten et al., 2018). In contrast, while Rozin et al. (1993, 2008) hold that the evolutionary origin of disgust is distaste, they depart from disease avoidance approaches in that they maintain that the expansion of disgust from distaste to a wide range of elicitors is driven by cultural evolution, not directly as disease avoidance (see also Rottman, 2014, for a recent cultural account of disgust).

If disgust is acquired entirely through enculturation there should not be any evidence of disgust—beyond rejection of distasteful food—in nonhuman animals. However, disease avoidance behavior has been extensively documented in animals (e.g., Hart, 1990; Hart & Hart, 2018). For example, ungulates such as sheep, cattle and horses avoid grazing near fresh feces, and many animals avoid eliminating near their nesting or sleeping areas (Hart, 1990). Furthermore, many species, including primates, engage in time-consuming grooming and preening, which reduces parasite load. Other actions that reduce disease risk include: fly-repelling, such as tail switching and muscle twitching; using bactericidal substances in saliva to clean wounds; avoiding cannibalism of dead and possibly diseased conspecifics; and eating plants with medicinal properties (Hart & Hart, 2018). These disease avoidance actions by animals might signal the antecedents of disgust in humans. Alternatively, instinctual disease avoidance routines that are widespread in species such as ungulates or rodents might not be driven or accompanied by experienced or imagined revulsion—disgust.

If a specific emotion resembling human disgust exists in nonhuman animals, a fruitful place to search for it might be in the closest living relatives of humans: other great ape species. Great apes and their ancestral species (Hominidae) have faced similar selective pressures from infectious diseases. It is, therefore, plausible that the last common ancestor of Hominidae evolved behavioral disease avoidance mechanisms. If disgust is part of this system, it is expected to be present, in some form, in nonhuman great apes.

Observations of Disgust-like Behavior in Chimpanzees

Although disease avoidance behavior has been extensively documented in animals, investigations of the presence of specifically disgust-like reactions in nonhuman great ape species have been infrequent. Early accounts of chimpanzee behavior rarely mentioned disgust, and where contact with disgust-relevant stimuli was noted these accounts suggested an absence or highly attenuated form of disgust. For example, in his classic study of nine captive chimpanzees over a six-year period at the Tenerife anthropoid station, Köhler (1925/1957) provided details of chimpanzees drinking and licking foul wastewater from a reservoir, smearing themselves with excrement, and engaging in coprophagy. However, he also observed that if chimpanzees stepped in excrement, they frequently used twigs, rags or paper to remove the feces, rather than removing it with their bare hands.

Another early work on chimpanzee behavior by Ladygina-Kohts (1935/2002) described her observations of a juvenile chimpanzee (Joni) that she reared at home. Again, disgust was rarely mentioned, but in one exception Joni was described as having a fear of raw meat and was observed wiping off the point of contact with the meat with his hand, as if to remove the smell. Moreover, when presented with a dead bird, Joni was described as grimacing with disgust and then pushing the bird aside. Ladygina-Kohts also included photographs of Joni's facial expressions, with one of these described as capturing the expression of disgust.

Behavior relevant to disgust was mentioned in the early longitudinal field studies of wild chimpanzees and bonobos. Whereas coprophagy was rare, on the few occasions that it was observed chimpanzees typically picked out food material from the feces (Wrangham, 1977; Goodall, 1986, p546; Nishida et al., 1999; McGrew et al., 1988). Other contact with body fluids included licking wounds (Nishida et al., 1999), menstrual blood (Kano, 1998), and picking and eating nasal discharge (Nishida et al., 1999).

That coprophagy exists in chimpanzees at all might suggest that they do not share a level of disgust sensitivity that approximates human disgust. However, Goodall (1986a, p.545) states that the chimpanzees "…seem to have an almost instinctive horror of being soiled with excrement and have only very rarely been seen to touch feces (their own or another's) with their bare hands." Other behavior reported also suggest disgust sensitivity, for example, the use of leaves to wipe themselves, and others, when they became soiled. Leaves are used by male and female chimpanzees and bonobos to wipe semen from themselves after mating (Goodall, 1986; Ingmanson, 1996; Nishida, 1999; O'Hara & Lee, 2006; Whiten et al. 1999). On one occasion a male chimpanzee at Gombe was observed using leaf napkins to clean feces from a female prior to mating and "[m]others usually clean themselves at once if they are accidentally dirtied by the excrement of their infant." (Goodall, 1986, p. 546). Chimpanzees with diarrhea are also occasionally observed to wipe their own rumps with leaf napkins; wiping of other body products (e.g., urine, blood) and other matter (e.g., mud, sticky fruit juices) was also observed, but less often than for feces (Goodall, 1986; Nishida, 1999; Whiten et al. 1999). These observations provided initial grounds to suspect that chimpanzees might experience disgust, at least towards feces.

Experimental Investigations of Disgust-like Behavior in Primates.

Several recent systematic investigations have provided some further evidence to suggest that Japanese macaques, chimpanzees, and bonobos might demonstrate disgust-like responses. In one study, free-ranging Japanese macaques were less likely to eat a grain of wheat that was placed on fresh macaque feces, or imitation plastic feces, than when the wheat was placed on a plastic control substrate (Sarabian & MacIntosh, 2015). Furthermore, reluctance to consume grain placed on feces and imitation feces was associated with lower parasite (geohelminth) infection, which is consistent with a parasite avoidance account. However, this study also revealed that feces were only a mild deterrent. Whereas grain placed on the plastic control substrate was always consumed, grain placed on fresh feces was still eaten by over a third of the macaques, and over one half ate the grain atop the imitation feces. Moreover, when a highly preferred peanut was used instead of wheat grain, it was always consumed, regardless of whether it had been in contact with feces or not. As the authors suggest, it is unclear whether the reluctance to eat the feces-contacted wheat in these sweet potato-washing Japanese macaques is driven by a disgust-like aversion to feces (or to the appearance of feces) or a general proclivity to avoid or wash food that is potentially contaminated with gritty sand and soil.

In another series of studies, the effects of visual, olfactory, and tactile disgust cues were investigated in captive chimpanzees (Sarabian, Ngoubangoye, & MacIntosh, 2017). Neither presenting a banana atop imitation feces nor in association with fecal, blood or semen odours, reliably inhibited banana consumption. However, chimpanzees were less likely to eat a concealed banana placed atop a wet, smooth substrate—dough—than a banana placed atop a dry, hard substrate—rope. The dough approximated the consistency of feces, so inhibition of banana consumption in this circumstance may serve to avoid contaminated food. However, as the authors note, contact with this novel substrate (vs. the familiar feel of rope) might have elicited surprise, rather than disgust.

Lastly, a series of experiments was conducted on captive bonobos to investigate the effects of visual and olfactory disgust cues on feeding (Sarabian, Belais, & MacIntosh, 2018). In line with a behavioral strategy that serves to reduce the risk of ingesting potentially hazardous foods, bonobos were expected to demonstrate a conservative approach to novel foods (neophobia). Unexpectedly, however, the bonobos demonstrated a preference for novel fruit over familiar fruit. In a second study using a three-choice task, Sarabian et al. (2018) obtained evidence of contamination avoidance. The bonobos had a clear preference for an uncontaminated apple over feces-contaminated or soil-contaminated apple. However, there were no reliable differences between avoidance of the feces-contaminated apple and the soil-contaminated apple.

This research on bonobos also provided some evidence of contamination sensitivity. Using a chain of contagion method, Experiment 3 examined the gradient of avoidance of banana slices that were placed successively adjacent to fresh feces. Whereas only a third of the bonobos fed on a banana placed atop fresh feces, this proportion increased the farther pieces of banana were placed away from the feces, with the last banana in the chain (15cm away from the feces) being consumed by three-quarters of individuals. Although this suggests that the bonobos responded to the risk of contamination, avoidance might have been driven by a preference for bananas farther away from the source of the fecal odor, rather than reduced likelihood of prior contact with the contaminant. Interestingly, the results of a further study (Sarabian, Belais, & MacIntosh, 2018; Expt. 4), where visual cues of a fecal contaminant were removed, found no difference between consumption of a previously contaminated banana and a control banana. This suggests that, unlike adult human disgust, contamination cues may need to be present (e.g., visual, olfactory) for the food to be avoided.

A final study in the series (Sarabian, Belais, & MacIntosh, 2018; Expt. 5) found that odors emanating from contaminants (feces, rotten meat, and spoiled fruit) that were applied to an enclosure door, inhibited contact with the door and reduced attempts to secure an out-of-reach apple through the enclosure door. Thus, olfactory cues that signal contamination led to avoidance in contrast to control odors (water, detergent), which is consistent with the presence of a system that motivates avoidance of potential sources of infectious disease. The authors also note that, unlike the reliable sex differences found for human disgust sensitivity (Sparks et al., 2018), they did not find that female bonobos were any more avoidant of contamination risk than the males across their studies. However, there was some evidence to suggest that juvenile bonobos were less contamination-risk averse than adults, which is consistent with developmental research on human disgust (e.g., Stevenson et al., 2010).

In sum, the recent systematic investigations of disgust-like avoidance in primates conducted by Sarabian and her colleagues have provided some evidence consistent with the existence of a rudimentary form of disgust in great apes. Overall, their findings suggest that food contaminated with feces or dirt is avoided, but a substantial proportion of individuals will still consume such contaminated food. Findings varied with species: food with visual cues of a contaminant unaccompanied by odor (imitation feces) was avoided by Japanese macaques, but not by chimpanzees; fecal odors and rotten food odors inhibit attempts to secure uncontaminated fruit in bonobos, but not in chimpanzees, whereas tactile cues of contamination apparently render a food less desirable to chimpanzees.

The Present Study

One aspect of these initial studies, which have used rigorous experimental procedures to investigate the effects various disgust-related contaminants in different primate species, is that their scope has been necessarily narrow. In addition, the findings have been somewhat inconsistent across experiments, perhaps reflecting species or environmental and individual differences. Accordingly, many questions remain about whether other disgust-like disease avoidance behavior might be observed in nonhuman great apes (e.g., avoiding sick conspecifics); whether or not there are differences in disgust-like behavior between species of nonhuman great apes; and whether or not captive, compared to wild, nonhuman great apes differ in disgust-like behavior.

To gain a broader picture of the possibility that disgust might exist in nonhuman great apes, we surveyed great ape experts using an instrument comprising ratings and open-ended questions to investigate observations of distaste, aversions and contamination-type reactions in great apes. This approach permitted exploration of the presence of disgust-like behavior among all well-studied species of nonhuman great apes, both captive and wild, and across multiple domains of disgust. Further, qualitative accounts from expert respondents, drawn from their experiences with multiple target animals over many years, potentially captures a wide range of disgust-like behavior across a wide variety of situations. Thus, this survey approach to investigating the presence of disgust-like behavior in nonhuman great apes was intended to be generative and to complement the recent experimental work, in providing direction for subsequent focussed investigations. Consistent with a disease avoidance account of disgust, we expected that disgust-like avoidance of potential sources of pathogens would be observed in nonhuman great apes. This bias was expected for taste, smell, contaminated objects, sick conspecifics, tool sharing, body fluids and feces. However, we were also interested in identifying any exceptions and instances that appeared to undermine the existence of disgust in great apes (e.g., coprophagy, consuming rotten carrion).

Method

Overview

An anonymous online survey of disgust in nonhuman great apes was distributed through research networks to potential respondents. Our intention in making the survey anonymous was to encourage respondents to freely report any observations relevant to disgust, however unconventional these might be. Open to researchers, fieldworkers, and keepers who had observed chimpanzees, bonobos, gorillas, or orang-utans in the wild or in captivity, the survey asked respondents to nominate a target great-ape species that they had the most experience observing and to then complete the survey questions in relation to that target group. The survey comprised both rating scales and qualitative responses concerning respondents' recall of instances of aversions and avoidance behavior in relation to taste, smell, contaminated objects (including neutralizing actions), sick conspecifics, tool sharing, body fluids and feces, and instances of coprophagy. Respondents also completed a self-report measure of their own level of pathogen disgust and a measure of the target ape group's aversion to a variety of human pathogen disgust elicitors. The survey and the study protocol was approved by the university research ethics committee.

Participants

Ninety-three respondents commenced the survey, with 19 failing to complete more than the demographic items and the initial aversion questions. The final sample comprised 74 researchers, fieldworkers, and keepers (25 men, 46 women; 3 did not report gender) who all self-identified as having experience observing great apes. The mean age was 41.06 years (*SD* = 13.07 years; 2 did not report age). The respondents were highly educated: 65% were PhD qualified, 27% held Masters degrees, and 8% held undergraduate degrees. Most respondents also reported holding academic or senior research positions, with 34% listing their position as Professor/ Associate Professor, Senior Researcher, Senior Lecturer, Lecturer, or non-specified faculty; 23% as Post-doctoral researcher; 26% as PhD students; 13% as other researcher; and 4% as Keeper. Thirty-five percent of the sample identified as American (USA), 20% British, 12% German, 8% French, 5% Canadian, 4% Dutch, and Spanish, Japanese, Israeli, Swiss, Polish, South Korean each comprised less than 4% of the sample. Overall, the survey sample was likely to be a reasonable reflection of the pool of potential participants with the unique experience to qualify for inclusion in this study: There are approximately 1,200 members of the International Primatological Society and great ape specialists comprise only a subset of this membership.

Time observing great apes. When combined, respondents' sum total years of observing great apes was over 670 years. Average time observing great apes was high but variable, ranging from 3.5 months to 45 years with a median of 4 years (*M* = 9.17 years, *SD* = 10.64 years). Only

11% of the sample reported having one year or less experience observing great apes. As might be expected, there was a strong positive correlation between respondents' age and years observing great apes, r (72) = .59, $p < .001$, which corroborates this self-report data.

Locations of stations/facilities/zoos. Overall, participants listed working at facilities and stations in 20 countries, with some working in more than one country. The locations of most facilities and stations listed by participants were in African countries (58.8%): Uganda (26%), Democratic Republic of the Congo (9.6%), Côte d'Ivoire (5.8%), Rwanda (4.8%), Tanzania (4.8%), and Republic of the Congo, Senegal, Guinea, Nigeria, Kenya, and Gabon (each less than 2% of the locations listed). Many also listed facilities and zoos in the USA (21.2%), Germany (6.7%), Netherlands (2.9%), UK (2.9%), Indonesia (2.9%) and Spain, France, Belgium, and Japan (each less than 2% of the locations listed).

Target group of apes. Respondents nominated a great ape group that they had spent the most time observing and were instructed to answer all the subsequent survey questions in relation to their 'target' ape group. Since most of our respondents reported working in stations in Africa, it was not surprising that over half of the sample selected a target ape group that they had observed in the wild, with only 42.8% selecting apes that they had observed in a sanctuary or in captivity as their target group. Consistent with the self-reported captivity status of the target apes, the wild target apes were rated (1= *humans never or rarely provide food/care* to 3 = *humans are responsible for providing care/food on a daily basis*) as being less dependent on humans for food (M = 1.05, SD = .22) and care (M = 1.07, SD = .26) than were those target apes observed in a sanctuary or captivity (food M = 3.0, SD = 0; care M = 2.84, SD = .37), food dependence t(41) = 58.70; care dependence t(53.25) = 23.13, both $ps < .001$. As can be seen in Table 1, most respondents selected chimpanzees as their target ape. However, all well-studied great ape species were represented.

<<<INSERT TABLE 1 HERE>>>

There was large variation in estimates of the number of apes in each target group, which ranged from seven gorillas (*Gorilla sp.*) in a sanctuary or captivity to 400 common chimpanzees (*Pan troglodytes*) in captivity. Across all target apes, the median estimated group size was 45 (*M* = 55.1, *SD* = 57.78) and did not differ significantly by the reported captivity status of the target apes. It is likely that group size estimates reflected experience with multiple target groups over many years.

Overall, the sample was characterised by respondents who had many years of experience observing groups of apes, representing all well-studied species, both in the wild and in captivity. Thus, if disgust-like behavior is exhibited by great apes, the respondents would likely have noticed it.

Survey

The cover page to the anonymous online survey invited respondents to participate in a study investigating whether great apes experience the basic emotion of disgust. The survey took respondents a median of 28.2 minutes to complete. After demographic questions concerning respondent characteristics (e.g., age and great ape observation experience), and characteristics of the respondents' nominated target ape group, the survey was divided into questions assessing domains of ape aversions, a measure of respondents' level of pathogen disgust, and a Great Ape Aversion Scale.

Domains of great ape aversions. The main part of the survey comprised ratings and open-ended questions assessing seven domains of aversions observed in the nominated target ape group: (1) taste, (2) smell, (3) contamination, (4) social contamination, (5) tool sharing, (6) contact with body products, and (7) coprophagy. These domains were informed by instruments commonly used to assess human disgust (e.g., Haidt, Rozin & McCauley, 1994; Tybur, Lieberman, & Griskevicius, 2009), but were designed specifically to represent the variety of possible aversions that great apes might experience. Apart from omitting higher order domains of disgust concerning socio-moral exemplars or sex, the domains we selected departed from measures of human disgust in several important ways. First, although items concerning taste are not usually included in measures of disgust, we included taste to serve as a point of comparison to the remaining domains. Specifically, we expected base rates for observing taste aversions to be higher than for the other domains because taste aversions in great apes are well established (Steiner et al., 2001) and unlike taste, other sensory modalities (sight, smell, and touch) might involve less obvious passive avoidance of an elicitor. Second, since insects and rodents are regularly consumed by some species of great apes, we omitted the domain of disgusting animals from the great ape survey. Third, we included tool sharing because the mouth is central to forming and using tools in great apes and sharing saliva soaked tools might potentially be aversive in apes. Finally, we included coprophagy, because, although it rarely reported in humans (Josephs et al. 2016), it occurs with some frequency in great apes (e.g., Bertolani, 2011; Krief et al., 2004). Each of these seven domains was presented randomly and comprised a parallel set of ratings and open-ended questions. As an example, the questions included for the domain of "contact with body products" are presented in Table 2.

<<<INSERT TABLE 2 HERE>>>

Pathogen disgust and Ape Aversions Scale. In addition to questions assessing the seven specific domains of aversion, respondents reported their level of pathogen disgust (7-item subscale; Tybur, Lieberman, & Griskevicius, 2009), and completed a 14-item Ape Aversions Scale, devised specifically for this study. Like common self-report measures of human disgust (e.g., Haidt, Rozin, & McCauley, 1994; Tybur, Lieberman, & Griskevicius, 2009), the Ape Aversions Scale comprised a list of situations involving potential disgust elicitors. Respondents rated their confidence (0 = *not at all confident that this would be aversive*; 6 = *highly confident that this would be aversive*) that mature individuals from their nominated target ape group would find each of the situations aversive (see Table 3 for Ape Aversions Scale). The position of the Ape Aversions Scale in the survey was counterbalanced with the items assessing the seven domains of aversions.

<<<INSERT TABLE 3 HERE>>>

In order to reduce the 14 items comprising the Ape Aversions Scale to a smaller subset of summary variables, the ratings were subjected to a principal components analysis with varimax rotation (see Table 3 for the rotated component matrix for the Ape Aversions Scale). The Kaiser–Meyer–Olkin index was .76 and Bartlett's test of sphericity was significant, χ^2 (91, N = 73) = 609, p < .001, suggesting that these data were appropriate for this analysis. Four components had eigenvalues greater than 1. The first component, which we labelled *wounds,* accounted for 39.4% of the variance and comprised four items concerning the sight of open or infected wounds. The second component accounted for 15.6% of the variance and comprised five items concerning sight, smell, or contact with death and decay. We labelled this component *death & decay*, although one of these five items concerned contact with objects that a sick conspecific has touched, which only implies a link to death and decay through contamination. The third component accounted for 11.6% of the variance and comprised three items concerning contact with feces and urine, which we labelled *contact with body products*. The fourth component accounted for 7.4% of the variance and comprised two items concerning the presence of body products without physical contact. We labelled this component, *sight & smell of body products.*

As *contact with body products* was the only component that was normally distributed, non-parametric correlations performed on the four components comprising the Ape Aversions Scale (see Table 4 for intercorrelations) revealed that all components were significantly intercorrelated. Further, when combined, the 14-item Ape Aversions Scale produced a highly reliable scale (Cronbach's α = .87), but was not normally distributed, w = .96 (70), p = .056. For the subsequent analyses, we use both the total Ape Aversions Scale and the four components.

<<<INSERT TABLE 4 HERE>>>

Results

14-item Ape Aversions Scale

Approach to analysis. Distributions departed significantly from normal for the 14-item Ape Aversions Scale (as mention above) and Time Observing Apes, $w = .76$ (70), $p < .001$. For analyses involving these variables, non-parametric procedures were used. Bonferroni adjustments are reported for all multiple comparisons.

Time observing and Ape Aversions Scale. It might be expected that the more time that a respondent reports observing great apes, the more chance they will have of witnessing instances of disgust. However, time observing great apes was not significantly correlated with the Ape Aversions Scale, r_s (73) = .016, $p = .90$. Thus extended time observing apes was not associated with an increased tendency to report instances of disgust-like behavior in apes.

Respondents' disgust sensitivity and Ape Aversions Scale. To investigate whether those who were high in disgust sensitivity were more likely to report noticing aversions and disgust-like behavior in great apes than those low in disgust sensitivity, the 7-item Pathogen disgust subscale of the Three Domains of Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009; Cronbach's $\alpha = .77$ in this sample) was completed by the respondents (5 did not complete the scale). Compared to the undergraduate sample reported in Tybur et al. (Study 4, 2009; $M = 3.87$, $SD = 1.19$), the survey respondents reported less pathogen disgust sensitivity ($M = 3.22$, $SD = 1.05$), $t(68) = 5.11$, $p < .001$. Consistent with the robust sex differences for disgust sensitivity observed in the disgust literature (Sparks et al., 2018) men were less disgust sensitive ($M = 2.73$, $SD = 1.01$) than women ($M = 3.53$, $SD = .99$) in our sample of respondents, $t(64) = 3.12$, $p = .003$. The relationship between respondents' disgust sensitivity and the Ape Aversion Scale was only marginally significant, r_s (69) = .27, $p = .053$. Overall, our respondents were low in disgust sensitivity, but they confirmed the sex difference in disgust that is typically observed. At best, there was only a weak relationship between respondents' disgust sensitivity and their ratings of the existence of disgust-like behavior in great apes on the Ape Aversions Scale.

Captive vs. wild apes. Apes in the wild have greater freedom to avoid high pathogen risk areas, such as roosting sites, than those in captivity and might, therefore, encounter less exposure to basic disgust elicitors than might captive apes. As prolonged exposure to disgust elicitors has been shown to attenuate disgust in humans (e.g., Rozin, 2008), the greater day-to-day exposure to basic elicitors such as feces and urine might be expected to reduce aversions to basic disgust elicitors in captive, compared with wild, apes. However, Mann-Whitney tests revealed that there were no significant differences between wild apes and captive apes in the Ape Aversions Scale and subscales (see Table 5 for means and ranges for wild vs. captive apes). Further, the tendency for the respondents to report aversions to the various stimuli were low, with positively skewed distributions.

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Chimpanzees. Since most of the nominated target apes were chimpanzees, we re-ran the above analyses on chimpanzees (excluding bonobos). Although this reduced the target apes to 23 reports concerning captive and 30 reports concerning wild chimpanzees, it provided a more homogenous subset of great apes. Consistent with the findings for the full sample, time observing apes was not associated with the Ape Aversions Scale. Respondents' pathogen disgust sensitivity was also not significantly correlated with the Ape Aversions Scale, nor were there differences between ratings of wild and captive target chimpanzees on the Ape Aversions Scale.

Gorillas, orang-utans, and bonobos. Using only the ratings of the 21 reports concerning target apes that were not *Pan troglodytes*, the same pattern of non-significant correlations that occurred for chimpanzees was obtained. Comparing chimpanzees to the remaining great apes, chimpanzees tended to be rated higher on the Ape Aversions Scale (*Mdn* = 1.77, range = 3.93) than the other great apes (*Mdn* = 1.14; range = 2.93), and this difference approached significance, $U = 370.5$, $p = .064$, $r = .25$. There were no reliable differences on the Ape Aversion Scale when chimpanzees and bonobos were combined and compared to the remaining great apes ($p > .1$). However, this comparison only left 11 reports concerning observations of gorillas and orangutans.

In sum, respondents' pathogen disgust sensitivity and the amount of time they had spent observing great apes had little discernible relationship with their tendency to endorse target ape aversions to various disgust elicitors. This finding suggests that these factors were not confounds. Further, our expectation that Ape Aversions Scale ratings would be affected by the captivity status of the target apes was unfounded. Finally, the same pattern of findings emerged for both chimpanzees and other great apes when they were analysed separately, and when these two groups of apes were compared to each other, the difference was only marginally significant. Overall, the generally low ratings for ape aversions suggests that if nonhuman great apes share aversions to basic disgust elicitors with humans, it is likely to be an attenuated form of disgust. In the next section, we provide an in-depth analysis of each specific domain of aversion.

Domains of Aversion

Since there were no indications of reliable differences between wild and captive apes or between the different species of apes on the Ape Aversions Scale, we conducted the analyses of the domains of aversions on the combined sample of nominated target apes. However, given the overrepresentation of chimpanzees as nominated target apes by our respondents, the findings are likely to predominantly reflect aversions in chimpanzees. Nonetheless, the inclusion of all well-studied species of nominated target apes permitted insights into disgust-like behavior gained from an analysis of the open-ended responses about the other species of great apes.

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From Table 6, the percentage of respondents who noticed aversions in the target apes confirmed that expelling potentially bad tasting food items (1. TASTE) was the most noticed aversion; with wiping off body products (6. BODY PRODUCTS) and attempts to neutralize contaminated, but desirable foods (3b. CONTAMINATION NEUTRALISE) all being observed by around half or more of the respondents. Withdrawing from putrid odors (2. SMELL) and avoiding contaminated objects (3a. CONTAMINATION AVOID) were also observed in over a third of respondents. However, unexpectedly, avoiding sick or injured conspecifics (4a. SOCIAL CONTAMINATION AVOID), and attempts to neutralize objects that had been in contact with sick or injured conspecifics (4b. SOCIAL CONTAMINATION NEUTRALISE) were reported only by 10% or less of the respondents. Further, although most respondents had observed tool use, avoiding tools that had been in a conspecific's mouth (5. TOOLS) was almost never observed. The results also suggest that most of the respondents could recall target apes ingesting their own feces (7a. COPROPHAGY SELF), whereas far fewer reported seeing apes ingest a conspecific's feces (7b. COPROPHAGY OTHER). Finally, it is also clear from Table 6 that, regardless of the percentage of respondents that observed each aversion, none of the aversions occurred universally, nor were they performed frequently.

Analysis of Open Responses to Domains of Aversions

For each domain, open responses were categorised by two independent coders, and differences were resolved through discussion. Interrater agreement is provided in each section describing the categories with the strength of agreement ranging from moderate to almost perfect, according to Landis and Koch's (1977) criteria. Respondents often provided more than one instance of a category, and where a respondent mentioned behavior (e.g., spitting out unripe fruit) in another domain (e.g., CONTAMINATION AVOID), the behavior was added to the total of the appropriate domain (e.g., TASTE in this example). Thus, the open response category totals for each domain did not match exactly the self-report ratings for each domain in Table 6.

Taste. The domain of taste served as a point of comparison to the other domains of aversion. As noted above, although most respondents had observed target apes expelling potentially bad tasting food items and this was also the most reported disgust-like behavior, it was not particularly frequent. It is likely that this reflects effective avoidance of unpalatable food items—potentially bad tasting food that is avoided cannot be observed being expelled. We also note the following comment in the open responses on taste: "…they have little experience with potentially disgusting foods because they won't try them if they aren't familiar" (common chimpanzees in captivity). This observation suggests conservative food preferences would reduce the likelihood that novel foods would be tasted and expelled.

<<<INSERT TABLE 7a HERE>>>

Instances of expelling bad tasting substances. Forty-nine respondents reported a total of 63 instances describing expelled substances, which were represented by six categories (see Table 7a for open responses to taste in great apes). The largest category was *Rejection not otherwise described*, which tended to contain responses that might have been included in other taste categories if further details about the behavior were provided. For example, one respondent described the following: “The chimps in the Tai forest regularly taste fruit (e.g. Irvingia spp.) and reject it after tasting” (western chimpanzees in the wild). As there was no information provided about whether the food was spoiled or novel, it could not be coded into a more specific category. From the responses forming the other categories, it is clear that great apes expel bad tasting, inappropriate, and novel foods. In addition, in the category of *Disgust-like,* there were reports of apes expelling stimuli that would resemble basic disgust elicitors in humans. For example, “…during meat-eating apparent disinterest in the carcass following discovery of an anal gland” (western chimpanzees in the wild). Another example from this category was “An adult female acquired an egg from a bird’s nest. She once put it in the mouth but expelled it on the palm. Then she stared [at] it. At last, she dropped it. Later I checked the opened egg, which was still pulsing” (bonobos in the wild).

Other behavior accompanying bad tasting substances. A subset of the above respondents (*n* = 23) who reported taste aversions in apes, provided comments on expressions or behavior, apart from expelling food, that might have indicated that the target apes did not like the taste of a food. These were coded into five categories (see Table 7b for taste in great apes—other behavior). The majority of these involved actively rejecting or discarding the food. Facial expressions were also occasionally observed accompanying bad tasting, inappropriate, or novel foods.

<<<INSERT TABLE 7b HERE>>>

Summary of open responses for the domain of taste. Overall, the reports suggest that many of our respondents had observed great apes rejecting potentially bad tasting, inappropriate, and novel foods. Further, they sometimes also reject items that resemble basic disgust elicitors in humans. In addition to expelling these foods from the mouth, great apes also drop and avoid disliked food. Expressions such as tongue protrusions and grimacing sometimes accompany bad tasting food. Finally, additional comments from the respondents on taste suggested that there are considerable individual differences in taste preferences within target apes, with some tolerating extremely bitter foods, while others were finicky. There was also a comment that "…preferences are more noticeable in high ranking individuals—adult females—lower ranking individuals often end up with the rejects" (bonobos in the wild). This suggests that lower ranked individuals might often have to tolerate less desired food out of necessity.

Smell. Compared to aversive tastes, fewer respondents reported noticing target apes withdrawing after sniffing strong smelling objects (see Table 6). However, as mentioned above for tastes, effective avoidance reduces the chance that such behavior will be observed.

Instances of withdrawing after sniffing a putrid odor. Twenty-one respondents provided a total of 24 instances describing target apes withdrawing after sniffing strong odors. These were represented by five categories (see Table 8a for open responses to smell in great apes). The majority of these instances described target apes withdrawing after sniffing decaying carrion or after smelling feces.

<<<INSERT TABLE 8a HERE>>>

Other behavior accompanying bad smelling objects. Other behavior that accompanied withdrawal from bad smells was provided by 18 respondents. Twenty-two instances were represented by five categories (see Table 8b for other behavior accompanying bad smells). The largest category was avoiding after sniffing, but vocalisations and nose wrinkles were also observed after sniffing.

<<<INSERT TABLE 8b HERE>>>

Summary of open responses for the domain of smell. Although the open responses to the domain of smell described reactions to offensive stimuli (e.g., rotting carcasses) that resemble human disgust reactions to putrid odours, some respondents contributed additional comments that were contradictory, suggesting an indifference to pungent odors. Examples of such responses included:

> Some infants and juveniles seemed to be very interested in a dead duiker. They even carefully touched (poked) it. Other adult individuals rested close to the dead duiker, it seemed they were not disturbed by the smell. (mountain gorillas in the wild)

> …we saw cannibalism of a dead infant (possible stillborn) after the mother had carried it for a while and it smelled REALLY rotten. There didn't appear to be any aversion to eating this rotten meat. (bonobos in the wild)

Finally, there were several comments concerning the importance of smell and frequency of sniffing in apes. For example, "Apes smell things all the time. Smell is important for apes. They especially smell food items and also vaginal odours" (eastern chimpanzees in the wild). Overall, there was some evidence that great apes avoid putrid odours, but the several counterexamples of observed indifference to the putrid odor of rotting carcasses suggest that unlike human disgust, bad smells are not so aversive to great apes.

Contamination. An object or food can be rendered aversive when it has been in contact with a contaminant, which is a distinctive feature of human disgust (Haidt et al, 1994). The open-ended questions on contamination concerned observations where a liked object or food was avoided after it had been in contact with a disliked object (e.g., feces). Further questions probed for attempts to neutralise (e.g., washing or wiping) contaminated desirable foods or objects. Parallel questions were included to capture any instances of social contamination (see next section).

Instances of avoiding desirable food/objects that have been in contact with undesirable food/object (Contamination Avoid). Over half of the respondents provided a total of 48 comments about contamination. Of the six categories, desirable food that had been in contact with sand, mud or feces were the most frequent instances of contamination (see Table 9a for open responses to Contamination Avoid). Common to these instances was the noted or implied presence of sensory (visual or smell) cues of contamination: mud or feces was visible on the food or sniffing the food might have revealed the smell of feces or urine. It is unclear whether a contaminated desirable food would have been avoided if visual or olfactory signs of the contaminant on the food were not present. We also note there were some reports of apes eating food that had been in contact with feces, which points to the presence of individual variation in contamination sensitivity. For example,

> I accidentally threw some food into the cage and it fell on some other's feces. Any chimp took the food from it. They were 3 apes: all adult, middle rank, two males and one female. (western chimpanzees in captivity)

> If a grape rolls into a pile of feces, MOST individuals will not eat it and look at you/ask for another one, which we give them. It is possible that if we didn't give another one to replace the dirty one that there would be more individuals that would eat it from a feces pile but most don't with the current system. (common chimpanzees in captivity)

It is also possible that less concern about desirable, but contaminated, foods might be driven by hunger or by limited access to desired foods due to low social status.

<<<INSERT TABLE 9a HERE>>>

Other behavior accompanying contaminated food/objects. Other responses to contamination were provided by only 11 respondents, who reported a total of 15 comments represented by three categories (Inter-rater agreement was moderate, $\kappa = .59$, $p < .001$). Most comments (53.3%) concerned turning away, rejecting, discarding, dropping, or flicking away contaminated foods. For example, “Throwing the food down after picking it up and examining it. Not wanting to touch it or "flicking" it away from their body. Shoving the food or object under the mesh” (common chimpanzees in captivity). The other two categories of comments concerned the presence of the nose wrinkle in response to contaminated foods (20%) and other behavior such as sniffing and inspecting (26.7%).

Attempts to neutralize contaminated desirable food/objects (Contamination Neutralize). An additional question in this section probed for any attempts by great apes to neutralize contaminated desirable foods/objects. Forty respondents provided a total of 52 comments represented by four categories (see Table 9b for open responses to attempts to neutralize contaminated food/objects). Washing and rubbing off dirt or mud from food was clearly apparent. However, few of the comments concerned washing or cleaning feces from food/objects. One exception was the following observation: “I have seen adults, mostly females, remove feces from plastic tokens by wiping it on the caging, before returning the tokens to me” (common chimpanzees in captivity). It is possible that foods that have been in contact with feces might retain the strong feces odor despite washing or cleaning and are thus simply avoided.

<<<INSERT TABLE 9b HERE>>>

Additional comments that respondents made about contamination included the instances below, suggesting that bodily contact with feces is aversive and that there are attempts to *clean* the feces off.

> The other blatant instances of disgust come when a chimp is in an argument/fight with another conspecific and gets another conspecific’s feces on their hair. They will wipe off their hair briskly ("in disgust") trying to get the feces off. (common chimpanzees in captivity)

> I have also observed bonobos wiping or cleaning their feet and hands when stepping in mud or faeces. It is unclear to me whether they do this out of 'disgust' or because it simply feels foreign and/or uncomfortable. (bonobos in captivity).

Whereas most respondents had noticed cleaning or washing, there were several inconsistent comments. Specifically, one respondent suggested that they had “…never seen signs of contamination avoidance" (eastern chimpanzees in the wild). Another commented that "All the captive chimps ate food that contacted faeces (western chimpanzees in captivity). Finally, there was a suggestion that "washing/soaking could be to enhance taste." (eastern chimpanzees in the wild).

Social contamination. Only nine respondents provided a total of 10 comments regarding avoidance of sick or injured conspecifics (Social Contamination Avoid), which were coded into 2 categories (Inter-rater agreement was substantial, $\kappa = .70$, $p = .003$). These comments concerned avoidance of individuals who displayed visual signs of illness (80%). For example, "Some individuals, especially immatures in most cases, show behavior like threatening toward sick individuals" (bonobos in the wild). The other category concerned and avoidance of low-status individuals who had been in a fight (20%). For example,

> A young silverback got badly injured by the dominant silverback. All other group members avoided him after the fight and the following day. When he got better, some females and their infants stayed closer to him again. (mountain gorillas in the wild)

However, other observations suggested that aversion to sick conspecifics might not be present. For example,

> It's not clear whether it is that other individuals avoid a sick individual or whether the sick individual removes themselves from the group (maybe falls behind or is too tired to be in the stressful centre of a feeding group). (bonobos in the wild)

> When one is injured or sick, young males (juveniles) often provoke them since they are not very active to react to them. The young might use that chance to outrank the sick individual. That might be related to the fact that when a male bonobo got sick or injured they were missing for several days or even months. (bonobos in the wild)

Social contamination expressive and neutralizing behavior. As there were too few open responses describing expressive behavior toward sick conspecifics and neutralizing behavior, we did not code these into categories. However, the several expressive actions reported were aggressive reactions to sick conspecifics. For example, “Threats expressed via gestures and vocalizations, aggressive behaviors” (Central African chimpanzees in the wild); and “They became aggressive and slapped and stamped on a young female” (common chimpanzees in captivity). The few neutralizing actions concerned wiping or cleaning a body part that had been in contact with an injured conspecific’s wound. For example, “On occasion when an individual is bleeding and some of their blood comes in contact with another individual, I have seen this individual then wipe this off with a leaf” (eastern chimpanzees in the wild).

Additional comments on social contamination. Twenty-three respondents provided a total of 34 additional comments about social contamination in great apes, the most for this domain. These comments were coded into five categories, which were all inconsistent with the existence of aversions to sick conspecifics (see Table 10 for additional comments regarding social contamination in great apes). Rather than evidence of social contamination, the observations suggest that sick conspecifics are approached and groomed and that the products of illness (e.g., mucus and blood) were often contacted. Together, these comments strongly suggest that social contamination is not a feature of great ape aversion.

<<<INSERT TABLE 10 HERE>>>

Summary of open responses for the domains of contamination and social contamination. The open responses for the domain of contamination suggest that great apes avoid food that has obvious signs of contact with feces, mud or sand. Moreover, there were many reports of attempts to neutralise (e.g., wipe, wash) contaminated food. However, there was a difference between contamination with mud or sand and contamination with feces: attempts to wipe or wash food was rarely observed when feces were the contaminant, which suggests that washing or wiping food that had been in contact with feces is ineffective at removing fecal odours. Interestingly, the observation that chimpanzees in conflict wiped a conspecific's feces off their hair suggests that when avoidance is not an available option, attempts to neutralise feces contamination might occur.

Although there was evidence suggesting that great apes will avoid food that is contaminated, it remains unclear whether food briefly contacted with a contaminant, but not bearing any sensory signs of the contaminant would be avoided. In terms of social contamination, the few open responses suggested that aggressive displays toward sick conspecifics might reflect the sick individual's inability to defend their social status. However, it was clear from the many responses in the additional comments section that great apes do not tend to avoid sick conspecifics or the products of their illness; on the contrary, many of the comments described approach, interest, and increased contact with sick conspecifics.

Tool sharing. The majority of respondents (85%) reported that target apes used tools such as sticks (to probe or fish for termites, and raking objects closer), leaves (carrying water and swabbing/cleaning), and rocks (e.g., for hammering open nutshells). However, consistent with the low endorsement (2%) in Table 6, there were only six comments about avoiding tools used by conspecifics, which precluded coding of the responses. Four of these comments concerned target apes tending not to reuse wet tools such as leaf sponges or leaf napkins. For example, "To me, they make their own leaf sponges rather than picking up from the ground old ones and reusing" (eastern chimpanzees in the wild). One participant reported that they had not seen termite probes reused, except by infants, and the other comment concerned lack of interest in reuse of a non-feeding tool. There were no comments provided in response to the question about other behavior accompanying tool sharing.

Additional comments on tool sharing. Twenty-six respondents provided a total of 26 additional comments on tool sharing which were coded into four categories. These responses tended to suggest that aversion to tool sharing is unusual in great apes (see Table 11 for additional comments regarding tool sharing in great apes).

<<<INSERT TABLE 11 HERE>>>

Summary of open responses for the domain of tool sharing. Together, these comments suggest that aversion to tool sharing is not apparent in great apes. Although there were many comments confirming that tool sharing is common, several comments suggest that sharing of wet tools such as leaf sponges might be less common. However, it remains unclear whether this is due to an aversion to the saliva-soaked leaf sponge or whether such tools are prone to damage after single use.

Contact with body products. The responses to the questions about instances where apes wiped or cleaned themselves of a conspecific's body products (e.g., feces, urine, or semen) using leaves or other materials are directly relevant to the existence of disgust-like aversions in apes. Over half of the respondents provided a total of 60 comments about wiping off a conspecific's body products, which were coded into five categories. Of these categories, cleaning-off feces from a foot or body part was the most common instance (see Table 12a for wiping off body products). Leaves and other materials were also used to wipe off urine. While semen was sometimes wiped-off using leaves or objects, this body product might not be aversive in the same way as feces and urine. Sex of the target apes were reported for 27 of these instances. Male target apes were equally likely to be observed displaying this behavior as females. As an illustration of this domain, the electronic supplementary material presents a video clip of an adult female chimpanzee of the Waibira community in the Budongo Forest Reserve, Uganda using leaves to remove her infant's feces from her body.

<<<INSERT TABLE 12a HERE>>>

Other behavior accompanying contact with body products. Other than wiping off body products, behavior accompanying contact with feces, urine, or semen was reported by 35 respondents. A total of 50 comments were coded into four categories (see Table 12b for other behavior accompanying contact with body products). Consistent with the reports obtained for wiping off body products, most comments concerned avoidance of contact with feces and urine.

This avoidance of feces was even observed to occur at the cost of missed copulation opportunities as is described in the following comments.

<<<INSERT TABLE 12b HERE>>>

> Males sometimes avoid copulating with females when their swelling is covered with fresh diarrhoea. (western chimpanzees in the wild)
>
> I have also seen a female have faeces all over her back. She repeatedly and vigorously rubbed her back against trees and wiped her back with leaves. She was in full oestrus at the time, and several males solicited her and approached her for copulation. Upon seeing the faeces on her back, ALL males recoiled and quickly moved away. (eastern chimpanzees in the wild)

Several respondents also provided comments to suggest that semen was not aversive or was not avoided like feces and urine. For example,

> There is a big difference between feces and urine on the one side and semen on the other side. Individuals are never averse to semen, males touch their penis after ejaculation and lick the fingers, females touch their genitals and eat the sperm plugs, infants touch penises as well and lick their fingers. (western chimpanzees in the wild)
>
> They avoid it/move away from urine/faeces when it occurs near them. They also brush it off themselves if it occurs on their fur. Bonobos in this population don't seem to have any problem with semen—the chests of males are often covered in dried semen as a result of ejaculating while mounting other males. Semen on males is much more common than seeing it leftover on females. Females tend to shake or pull it out if it is left over after copulation. (bonobos in captivity)

Contact with conspecifics' body products vs. contact with own body products. Here we were interested in investigating whether individuals demonstrated greater aversion to a conspecific's body products than their own (the source effect for disgust; see Case et al., 2006; Stevenson & Repacholi, 2005). Of the open responses to this question, only eight respondents identified differences—too few to impose a coding scheme. Three of these implied a greater aversion to contact with a conspecific's (vs. own) feces. For example,

> Some animals will feces smear but only ever with their own feces. I have seen chimps throw feces (at humans or conspecifics) that is not their own but never smear it. (common chimpanzees in captivity)

Two others noted that coprophagy is most likely to involve the ape's own feces, not that of a conspecific. The remainder described greater aversion to a conspecific's urine and unfamiliar stimuli than their own body products. The vast majority of the respondents (n = 27), however, commented that they could not be sure of the source of the body product. Although there was little in the open responses on this item that could be taken as evidence for a source effect, the open responses suggest that the respondents were cautious in interpreting ambiguous behavior as consistent with evidence of disgust in apes.

Additional comments on contact with body products. Many of the additional comments concerned the low frequency of contact with body products and the difficulty in knowing if feces that were stepped in belonged to the target apes or a conspecific. However, some suggested that contact with body products was not aversive. For example, "Mountain gorillas will sleep on their own dung" (mountain gorillas in the wild); "Chimps throw faeces. Seems like they either appreciate the effect it has on each other (and on humans) when they do it…" (Chimpanzees in captivity). Others mentioned the prevalence of coprophagy, which we examine specifically in the next section. There were several observations suggesting that while adults go to lengths to avoid or wipe off urine or feces, juveniles are indifferent to them. Finally, one respondent observed bonobos with a preference for conspecifics' mucus:

> My study group members sometimes suffer from flu-like disease. When they have flu, their faces are full of nose mucus. However, some healthy individuals in the same group, they like to eat mucus of others. (bonobos in the wild)

Summary of open responses for the domain of contact with body products. Overall, the open responses suggest that great apes often avoid or attempt to wipe off contact with feces and urine from a conspecific. Semen was less aversive than feces and urine. There were, however, reports of indifference to contact with feces and other body products, but this seemed to have been more common in juveniles. Nonetheless, the frequent reports of coprophagy seem inconsistent with the comments that contact with feces is avoided. We address this in the next section.

Coprophagy. The responses were clear that coprophagy was more likely to involve ingestion of the target ape's own feces than for ingestion of a conspecific's feces (see Table 6), and this difference was significant, $\chi^2(1) = 14.21, p < .001$. Open responses on the characteristics of the individuals that ingested their own feces (Coprophagy Self) were provided by 44 participants, and 19 participants provided comments on target apes that ingested a conspecific's feces (Coprophagy Other). The comments were coded into six categories. As can be seen in Table 13, coprophagy was observed in healthy adult males and females, but was more common in females. Reflecting the responses in Table 6, ingesting own feces was reported more often than ingesting a conspecific's feces, except for juveniles, who were observed ingesting their mothers' seed-filled feces. Respondents also commented that the target apes were picking through feces for undigested nutrients such as seeds or meat. For example,

> Both male and female, adult and immature. Especially when the seeds of particular fruits are inside. We do not observe the coprophagy often. You can see them a few times/100-hour observation. They look for the seeds inside the feces. (bonobos in the wild)

Another similar comment was:

> I would like to clarify that I have seen healthy chimpanzees (both mature and immature) picking out seeds from their or other chimps' feces (also from elephant dung). I define this

> as a separate behavior from consuming the feces matrix, which I have not seen in the wild, but I frequently see in captive chimpanzees. (eastern chimpanzees in the wild).

The social transmission of coprophagy was also commented on by several respondents. For example,

> We have about a 2-3% rate of coprophagy in our colony. If an adult female performs coprophagy, it is often passed down (socially-learned) to their infant when they are quite young. (chimpanzees in captivity)

A final comment again suggests an absence of aversion to ingesting the apes' own feces.

> Healthy adult female who would, interestingly, only ingest her feces when she was menstruating. She would also lick her menstrual blood off of her hand (which she used to wipe her vagina for the purpose of getting the blood). The coprophagy was not incidental to eating the blood, she would also defecate into her hand and eat the fresh feces during this time (menstruation). (common chimpanzee in captivity)

Summary of open responses for the domain of coprophagy. While coprophagy is apparent in healthy target apes, there is a clear source effect, so that ingestion of the target ape's own feces is more common than ingestion of a conspecific's feces. Furthermore, coprophagy is often pursued in the service of gaining access to once digested and softened nutrients.

Final comments from respondents about disgust in great apes. After completing the comments and rating of each of the domains, respondents had an opportunity to leave additional comments about disgust in great apes and about the survey in general. Many of the comments repeated responses made to specific domains. However, several observations were notable. One described chimpanzees forgoing high valued food to first wipe feces from their feet. This is consistent with the observations reported in the above section on *Contact with body products* where two respondents described avoidance of feces even at the cost of missed copulation opportunities in wild chimpanzees.

> They are very keen to remove feces from their body if they accidentally step in it or are defecated on. They will do this even in a context where waiting until a little bit later would seem beneficial. For example, if grapes are being passed out and an individual approaches the keeper and accidentally steps in feces they would often take the time to stop, usually smell it or look at it, and wipe it off on the caging, floor, etc. before proceeding and hence, at least theoretically, 'miss out' on getting some of their favorite food item. (common chimpanzees in captivity)

Another comment suggests that the type of wiping that occurs in response to contact with feces is distinct from wiping away other body fluids. “I base this on the haste that chimpanzees display when they are wiping away feces from their body. I have not seen them act this way with other bodily fluids, such as semen” (eastern chimpanzees in the wild).

Other comments also suggested that individual differences in disgust-like behavior might be important.

> There appears to be a lot of individual variation. I have worked with >200 chimpanzees and some seem very fastidious while others do not. Also, it should be noted that I only work with captive animals so it is less likely that they come into contact with many of the stimuli mentioned in this survey. However, all of the chimpanzee groups I have worked with have killed local wildlife (rabbits, skunks etc.) and often play with or wear the dead animal carcasses - they do not seem disgusted by them. They do, however, seem to be more commonly disgusted by feces, especially when they step in it or it touches enrichment devices or food. (common chimpanzees in captivity)

Another similar comment was:

> You may find considerable inter-individual variation in apes in the reactions of interest. An adult female P.t. in our population is, compared to other individuals, notably "fastidious" in not stepping in feces, mud, etc. and "tidy" in pushing out paper trash, nut shells, and fruit

> peels from her cage; in her case, this seems to be a generalized trait or temperament feature. (eastern Chimpanzees in captivity)

Finally, one comment suggests disgust in apes is highly attenuated:

> Disgust seems too strong a word. They seem rather indifferent to disgusting things, although they might avoid them rather nonchalantly. (common chimpanzees in captivity)

Another comment provided a graphic example of approach behavior towards basic disgust elicitors that would be repulsive to humans.

> … I have observed captive chimps avoid urine/feces, but I have also seen them be attracted to it (urophagy/coprophagy, throwing feces). Other instances that clearly produce disgust in human observers do not seem to have the same effect in chimps: once an older female was badly attacked, resulting in a large chunk of her sexual swelling to be pulled off. Other chimps in the group begged the possessor as if it were a healthy piece of meat! Nearly all humans were queasy after watching this interaction. (common chimpanzees in captivity)

Discussion

The aim of this research was to investigate the existence, in nonhuman great apes, of behavior resembling human disgust given to a range of potential sources of pathogens. The results of the survey of fieldworkers, researchers, and keepers, confirm that great apes expel bad tasting foods, withdraw from pungent odours, avoid or neutralize (wash or wipe) preferred foods when they have been contaminated, and avoid or neutralize contact with conspecifics’ body products. While these actions are consistent with a disease avoidance account of disgust (e.g., Oaten, Stevenson, & Case, 2009), our data suggest that disgust-like behavior in great apes occurs to only a restricted range of the stimuli that represent human disgust elicitors. Specifically, there was a noteworthy absence of disgust-like behavior to sick conspecifics and to sharing saliva-soaked objects/tools. Moreover, compared with human reactions to basic disgust elicitors, the reactions of great apes were often attenuated, and there were many reports of counterexamples—where great apes were indifferent to contact with putrid stimuli. Thus, while the survey responses are consistent with the existence of disgust-like responses in great apes, our closest relatives appear to be far less sensitive to basic disgust elicitors than are we.

Evidence of Disgust-like Behavior in Great Apes

There were many reports that great apes avoided eating feces-contaminated food and that they attempt to remove fecal matter on contact with it (e.g., after stepping in it). This was even observed to occur at the cost of forgoing a highly valued food or mating opportunity. Feces are a known pathogen vector for numerous viral, bacterial, and helminth infections (Curtis & Biran, 2001; Curtis & de Barra, 2018), and avoidance of feces is common in many animal species (e.g., Hart, 1990). As such, avoidance of feces and attempts to brush-off direct contact with feces is consistent with the disease avoidance account of disgust. Reports that great apes tend to avoid contact with feces and food contaminated with feces also converges with field observations (e.g., Goodall, 1986a) and recent experimental studies of food contaminated with feces, showing aversion in bonobos (Sarabian, Belais, & MacIntosh, 2018) and neutralising (processing) behavior in Japanese Macaques (Sarabian & MacIntosh, 2015).

As a basic disgust elicitor in humans, we would expect feces and the accompanying odor to present a more potent disgust elicitor than soil in great apes. However, Sarabian, Belais, and MacIntosh (2018) did not find any reliable differences between consumption of food contaminated with soil and food contaminated with feces in bonobos. In our survey, food that was contaminated with soil or mud was often avoided or brushed off, but some of the observations suggest that feces might be more aversive than soil or mud. Specifically, wiping or rubbing food was frequently observed when it was contaminated with mud or dirt. However, wiping was rarely observed when feces was the contaminant—rather, the food was avoided altogether. This difference suggests that feces might be more disgusting than mud or soil. Moreover, wiping off feces might be ineffective at removing fecal odor from food contaminated with feces. Interestingly, the observations that during a fight chimpanzees wiped a conspecific’s feces off their hair, or wiping after apparently unintended contact (for example, stepping in feces), suggests that when avoidance is not an available option, attempts to neutralise feces contamination might occur. Another observation that suggests feces are more aversive than soil is that vigorous brushing/shaking was observed on direct contact with feces, which was not apparent on contact with mud. These reports suggest that great apes might react differently to feces compared with soil, but further research is needed to confirm this. It is possible that avoidance of feces-contaminated food represents a disgust-like aversion, but that brushing food that is contaminated with soil simply serves the purpose of removing grit that might be uncomfortable when chewing.

Muted Expression of Disgust-like Behavior in Great Apes

Although rotten carrion was often avoided, several counterexamples, involving consumption of rotten carcasses, suggest that disgust-like aversion to rotten meat is sometimes absent or highly attenuated in great apes. Further, the instance of cannibalism of a rotting dead infant bonobo (see section on Summary of open responses for the domain of smell), described by one respondent, is difficult to explain from a disease-avoidance account of disgust because it violates the generally strict avoidance of cannibalism that protects the animal from exposure to potentially lethal infectious disease that might have resulted in the death of the conspecific (Hart & Hart, 2018). This instance of cannibalism and the instance describing captive chimpanzees begging for a piece of an injured female’s torn-off swelling (see section on Final comments from respondents about disgust in great apes), suggest that, although cannibalism is rare (e.g., Brand et al., 2014), it might not be as aversive as it is to humans.

Whereas avoiding and wiping off a conspecific’s urine was reported by the respondents, it was reported less frequently than avoiding and wiping off feces and might represent an aversion to being wet rather than to urine specifically. Body products such as blood, semen, and mucous were typically met with indifference and even approach. As urine, semen, mucous (including sharing saliva-soaked tools), and blood are disease vectors and basic disgust elicitors in humans (Curtis & Biran, 2001; Haidt et al., 1994; Tybur et al., 2009), the attenuated disgust-like behavior in great apes in response to these body products is another notable departure from human disgust.

Similarly, the avoidance of social contamination (e.g., avoidance of sick conspecifics) was rare in great apes. Rather, reactions tended to comprise approach (e.g., grooming the sick conspecific), indifference, and sometimes aggression. Occasional aggressive reactions to sick individuals might have reflected opportunistic attempts to outrank an individual who was less able to defend itself due to its illness. Moreover, the products of a conspecific's illness (e.g., mucus and blood) were often contacted with interest or indifference. Whereas avoiding those who appear sick is a key feature of human disease avoidance (Kurzban & Leary, 2001; Ryan et al., 2012), the reports obtained in this survey suggest that avoiding social contamination is not a typical feature of great ape behavior (cf. Goodall, 1986b).

Perhaps one of the more difficult findings to reconcile with the presence of disgust-like responses in great apes is the observation of coprophagy. Coprophagy was the most frequently observed domain in the survey—just slightly higher than apes expelling bad tasting food from the mouth. This apparent paradox for the existence of disgust-like responses in great apes might be understood within the context of the ecological adaptiveness of coprophagy. Specifically, coprophagy often involves selective picking of seeds from apes' own feces, which is likely to render the seed husk softer to ingest (Bertolani, & Pruetz, 2011; Krief, Jamart, & Hladik, 2004). As such, the reingestion of seeds and other difficult to ingest foods, such as meat, can provide fundamental nutrients. This hypothesis is further supported by an apparent source effect (Case et al., 2006; Stevenson et al., 2005) for coprophagy, whereby consumption of the ape's own feces was observed more often than consumption of a conspecific's feces, except in juveniles who were observed consuming their mother's feces. We speculate that the pathogen threat posed to the ape by consuming its own feces would be less than that posed by consuming a conspecific's feces. This is also likely to extend to the juvenile who consumes its mother's feces. Further, the mother's fecal matter might be an important source of gut bacteria for the young (Mueller et al., 2015). As such, coprophagy in great apes affords a nutritious supplement and is accompanied by potentially little pathogen threat. Although there are likely nutritional benefits of coprophagy, this behavior—

ingestion of a basic disgust elicitor—might also contribute to a more general tolerance that nonhuman great apes appear to have to a wide range of disgust elicitors.

Expressions, Sex, and Age

Facial expressions or vocalization in response to disgust elicitors in great apes were infrequently reported. The nose wrinkle is a distinct feature of the prototypical facial expression of disgust in humans and has been observed in chimpanzees in response to bitter tastants (Steiner et al., 2001). The presence of a distinct 'distaste' expression (e.g., the nose wrinkle, tongue protrusion) in response to the sight (as opposed to taste and smell) of disgust elicitors would go a long way to establishing that avoidance of a potential disgust elicitor might be disgust-driven, rather than due to other states such as fear, irritation, or novelty. However, nose wrinkles or tongue protrusions were not common in our survey, even in response to bad tasting foods. The infrequency of reported facial expressions to disgust elicitors might reflect successful avoidance, or that the respondents had difficulty noticing spontaneous, subtle and rapid expressions from a distance. We also note that in a study coding several hundred facial displays from spontaneous photographs and videos of over 100 chimpanzees, Parr et al. (2007) observed the nose wrinkle (AU9) in only three displays.

One reliable finding to emerge from the disgust literature is that women report being more disgust sensitive than men (e.g., Haidt et al., 1994; Tybur et al., 2009). High stakes competition for women in a polygynous mating system has favoured the selection of greater risk-taking traits in males, which is also argued to account for greater acceptance of disease-risk and lower disgust sensitivity in men compared with women (see Sparks et al., 2018 for a review). Sex differences in disgust were apparent in our respondents' self-reported disgust sensitivity, but where they made mention of the sex of the target ape, they reported that there were no sex differences in the relevant disgust-like behavior. Whereas this suggests that the respondents were not influenced by their preconceived notions of sex differences, it is unexpected in light of the disease avoidance account of disgust and obtained sex differences in the tendency to consume feces-contaminated food in

Japanese macaques (Sarabian & MacIntosh, 2015). These null findings for sex are, however, consistent with an absence of sex differences in experimental investigations of aversions in captive bonobos (Sarbian et al., 2018) and chimpanzees (Sarabian et al., 2017). It is possible that any sex differences might be obscured by factors that attenuate disgust overall in great apes (e.g., high exposure to disgust elicitors and diet). We consider such factors in the next section.

One finding to emerge from the great ape survey that is broadly consistent with developmental differences in human disgust (e.g., Rozin, 2015; Stevenson et al, 2010) is that juveniles tended to show less avoidance of disgust elicitors that did adults. This was particularly notable for ingestion of a conspecific's feces, where most of the reports concerned juveniles. With experience, juveniles might learn what should be avoided because it tastes bad. Although children as young as 3-4 years old tend to be less disgust sensitive than older children and adults, they still demonstrate some avoidance of basic elicitors and contaminated items (Siegal & Share, 1990). This occurs even without explicit knowledge of contamination and conservation (Stevenson et al., 2010). Thus, it would be useful to identify if there are specific stimuli that repel juvenile great apes, as there are for human children.

Why is Disgust-like Behavior Muted in Great Apes?

The wide-ranging disgust elicitors in humans, compared with the restricted range of core elicitors in nonhuman great apes, likely reflects the greater capacity for humans to rapidly learn what stimuli to avoid and the ability to explicitly imagine contamination. However, even without such cognitively sophisticated capacities, great apes were reported to show evidence of disgust-like behavior to core elicitors. This finding stands in contrast to the view that, apart from distaste, disgust is primarily the result of culture and is unique to humans (e.g., Rozin 2015).

Nonetheless, there were also many counterexamples where some individuals were indifferent or showed interest in elicitors that were commonly avoided. These counterexamples suggest the presence of individual differences in disgust-like reactions among great apes. Individual variation was specifically noted by several respondents, who described some chimpanzees as being more fastidious and tidy than others (see section on Final comments from respondents about disgust in great apes). Thus, as for human disgust sensitivity (Haidt et al., 1994; Olutunji et al. 2007; Rozin, 1999; Tybur et al., 2009), there likely exists individual variation in tolerance of disgust elicitors in great apes.

Furthermore, when recalling instances of target ape behavior in this survey, unusual but surprising instances, such as consumption of rotten meat or begging for a piece of an injured conspecific's sexual swelling, are likely to be salient and more easily recalled than mundane avoidance of feces and other elicitors. As such, it is possible that these surprising instances might comprise rare exceptions that are overreported in the survey. However, despite this likely bias, respondents frequently recalled more instances of disgust-like behavior than counterexamples: such as withdrawing from putrid odours, avoidance of contaminated preferred foods, and avoiding contact with conspecifics' body products.

The base-rate for disgust-like behavior in great apes is also expected to be low, in comparison to humans, because they experience less hygienic conditions. Frequent bathing, use of soap and deodorants, and prohibitions regarding excretions, which has occurred in high-income countries since the 19th century (Miller, 1997; Rozin, 2015; Soo & Stevenson, 2007), has reduced our exposure to disgust elicitors and likely expanded the range of stimuli that have the potential to elicit disgust. In contrast, the conditions that great apes experience, in captivity or in the wild, frequently exposes them to disgust elicitors (including coprophagy as a nutritional supplement), which should lead to habituation (Rozin, 2008). As such, great apes might be expected to possess an attenuated form of disgust compared to modern humans. Humans living in less hygiene-obsessed conditions, might be expected to exhibit attenuated disgust and a reduced range of elicitors, and hence provide a more realistic baseline for comparison. Nonetheless, with the exception of variations in culturally sanctioned uncontaminated foods (e.g., parmesan cheese, cured meat etc.), consumption of basic disgust elicitors (such as feces or carrion) by humans is exceedingly rare.

Finally, we argue that attenuated disgust-like behavior and a restricted range of elicitors in great apes might stem from a fundamental difference in diet between humans and other great apes (see also Kelly, 2011). Specifically, meat makes up a far greater quantity of the human diet than that of nonhuman great apes, with butchery likely to have emerged in ancestral humans over 2 million years ago (Domínguez-Rodrigo et al., 2005). Overall, hunting and meat-eating have played a central role in the evolution of human cognition and social behaviour (Stibbard-Hawkes, Attenborough, & Marlowe, 2018). Carnivory is a strategy that addresses the high energy requirements for dietary protein to sustain both large body size and the large human brain (Milton, 1999; Milton, 2003; Ragir et al., 2000). This reliance on meat in *Homo* ancestors, however, was accompanied by a far greater risk of gastrointestinal illness posed by consuming dead meat that is rapidly contaminated by bacteria (Ragir et al., 2000). Although cooking meat has been one recent technological development that might have reduced this risk (Ragir et al., 2000), cross-contamination from hands and utensils is likely to have negated the decontaminating benefits of cooking (Fessler & Navarrete, 2003). Thus, greater disgust sensitivity in humans may have evolved alongside preference for meat, providing a solution to the omnivore’s dilemma (Rozin & Fallon, 1987). In short, an emotion-driven behavioral system that motivates avoidance of contaminated meat is adaptive in an omnivorous species that has not evolved specialised immunologic defences or low gastric pH to eliminate pathogens, as occurs in some dedicated scavenger species such as vultures (Blumstein et al., 2017; see also Fessler & Navarrete, 2003). Overall, then, attenuated disgust-like behavior in nonhuman great apes might reflect their low dependence on meat.

This explanation for greater disgust sensitivity in humans compared with nonhuman great apes, based on meat consumption, is consistent with observations that chimpanzees tend to feed on bacteria-free meat that they had freshly killed, while they tend to ignore opportunities for scavenging meat, even when fresh (Brand et al., 2014; Watts, 2008). This highly conservative strategy for meat-eating precludes the necessity of a sensitive disgust system to detect contaminated meat before it is ingested. Further, it is consistent with reported instances of indifference to the putrid odor of rotting carcasses in the section of the survey on odor—meat that is not freshly killed is rarely consumed, so a disgust system that is highly sensitive to repelling the animal from consuming rancid meat is less necessary than it is in hominins whose diet might have included scavenged meat (e.g., Watts, 2008; c.f. Domínguez-Rodrigo, & Pickering, 2003) or meat that was otherwise contaminated with bacteria.

Other converging evidence suggesting that meat-eating played a central role in the evolution of a highly sensitive disgust system in humans includes the high frequency of meat-aversions and proscriptions concerning meat, despite meat being a high-value staple (e.g., Fessler, 2001; Fessler & Navarrete, 2003). Whereas selective pressure posed by meat-borne bacteria might have played a primary role in shaping disgust sensitivity in ancestral humans, several other factors are also likely to have contributed. Important among these is the selective pressure of infectious disease that accompanied contact with hunter-gatherer trade networks and increases in population size (Fessler, Clark, & Clint, 2015).

Strengths and Limitations

This research was the first broad assessment of the existence of disgust-like behavior in nonhuman great apes. The merit of this survey approach is that it permitted insights into a wide range of disgust-like behavior from a sample of highly qualified observers, who had extensive experience covering all well-studied great ape species, both captive and in the wild, over many years. Further, there are several indicators that speak to the validity of the survey responses. First, the respondents accurately identified taste aversions as the most frequent disgust-like behavior in great apes. We expected this because taste aversions in great apes are well established (Steiner et al., 2001) and expelling food is less ambiguous than the passive avoidance that might follow sensory information involving smell, sight, or touch. Second, it was clear from the low ratings on the Ape Aversion Scale and the open responses that the highly trained respondents, practised in objective scientific observation, were reluctant to over-interpret target ape behavior as disgust-like.

Moreover, the respondents often provided cautions and caveats qualifying their responses. Lastly, (although we acknowledge that the sample was small) the tendency to report disgust-like behavior in great apes was only weakly associated with the respondents' level of disgust sensitivity. Therefore, we are confident that the findings from this survey method provide an accurate account of the respondents' observations of disgust-like behavior in great apes. However, there are several potential limitations to this study.

One potential limitation is that, although we used an anonymous survey to encourage respondents to freely report any observations relevant to disgust, we could not verify our respondents' expertise. Although we have no way of determining the accuracy of the respondents' reports, false reporting on expertise might be expected to be minimal because the survey was distributed through primate research networks to those who were appropriately qualified.

Another potential limitation of the study is that our sample of primate experts was not large for this methodological approach, with very few experts reporting on some of the species (e.g., orang-utans). However, we were targeting a specialized population, and at any given facility (e.g., chimpanzee station, zoo, etc.) there are likely only a few people with the experience to be eligible to meet the inclusion criteria for our survey. Thus, it would be difficult to obtain a much larger sample. Furthermore, since the focal data for this study were recalled instances of great ape behavior, the value of the obtained sample was in the combined years of observational experience—which was extensive, and more than adequate to address the question of whether disgust-like behavior can be observed in great apes. Nonetheless, the chances of being in the right place at the right time to incidentally observe relatively infrequent disgust behavior are limited. Moreover, disgust elicitors are usually easily avoided, so the opportunity to observe an animal confronting a disgust elicitor is low. These challenges are compounded by the fact that none of the expert observers was specifically looking to document instances of disgust at the time of observing the target apes.

Future Research

The findings of this survey study point to several potential directions for future research on disgust-like behavior in great apes. One direction is to investigate differences in preference for food contaminated with feces compared with food contaminated with dirt. There was an indication in this survey that feces contamination might be more aversive than soil or mud contamination. However, this has yet to be demonstrated experimentally in nonhuman great apes. Further, the findings of this survey could not address whether food that was in contact with a contaminant (e.g., feces), but no longer showed visual or olfactory signs of the contact would be avoided. This would be an unusual occurrence for great apes and would need to be experimentally manipulated. Such invisible contamination is a reliable feature of human disgust (Haidt et al, 1994) and even occurs in young children (e.g., Siegal & Share, 1990; Stevenson et al., 2010). The only experimental investigation of this in nonhuman great apes suggests that once visual cues of contamination are removed, bonobos do not avoid contaminated food (Sarabian et al., 2018). Demonstrating avoidance of invisible contaminants in the various species of great apes would provide further insight into the existence of a core cognitive feature of disgust in apes. Further, identifying expressive signs such as the nose wrinkle or tongue protrusion in response to the sight of a disgust elicitor (e.g., feces-contaminated food) would suggest that the aversion is likely disgust-driven, rather than due to other states.

Future investigations might also seek to establish whether chimpanzees are more disgust sensitive than great apes that feed almost exclusively on vegetation and insects (gorillas or orang-utans). In our comparison of chimpanzees and the remaining great apes on the Ape Aversions Scale, we found only a marginally significant trend for chimpanzees to show greater disgust-like behavior. However, our sample was small. Evidence of such a difference would be consistent with the proposal that meat-eating in great apes is associated with increased disgust, which reduces the risk of consuming contaminated carrion. Finally, the results of the great ape survey suggest that future investigations of sex differences in disgust-like behavior and of disgust-like behavior towards sick individuals might not be as apparent as they are for human disgust.

Conclusion

The methods used in this study of great ape experts covers broad ground in assessing evidence of the existence of disgust-like behavior in nonhuman great apes. The findings contrast with the view that the emotion of disgust is uniquely human and predominantly a product of culture (e.g., Rozin, 2015). In addition to expelling bad tasting foods and withdrawing from putrid odors, great apes were reported to avoid or neutralize food when it had been contaminated, and avoid or neutralize contact with body products. However, the survey findings were clear that the range of stimuli that were avoided by great apes was restricted, and disgust-like behavior was muted. Greater disgust sensitivity in humans, compared with other great apes, might have resulted from our hominin ancestors' greater reliance on carnivory, and the consequent risk of gastrointestinal illness associated with consuming contaminated carrion. In addition, the frequency of coprophagy as a nutritional supplement in nonhuman great apes might have contributed to the tolerance that great apes appear to have to a wide range of disgust elicitors. This suggests that differences in disgust–like behavior between great apes is best understood from the ecological standpoint of the animal. Overall, these findings are consistent with the continuity of an evolved behavioral disease-avoidance mechanism—disgust—in our closest relatives.

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Table 1.

Frequencies for each target ape by captivity status (N = 74)

Reported target apes	Sanctuary/Captive n	Wild n
Chimpanzee (unspecified)	20	-
Western chimpanzee *(Pan troglodytes verus*)	2	9
Central African Chimpanzee (*Pan troglodytes troglodytes*)	-	1
Eastern Chimpanzee (*Pan troglodytes schweinfurthii*)	1	20
Bonobo (*Pan paniscus*)	5	5
Gorilla (unspecified)	2	-
Western lowland gorilla (*Gorilla gorilla gorilla*)	1	-
Mountain gorilla (*Gorilla beringei beringei*)	-	6
Northwest Bornean orangutan (*Pongo pygmaeus pygmaeus*)	1	-
Central Bornean orangutan (*Pongo pygmaeus wurmbii*)	-	1
Total	32	42

Table 2.

Items comprising the domain of contact with body products.

Item	Response option
Have you noticed any of the individuals from the target group using leaves or other objects to clean themselves of a conspecific's feces, urine or semen (e.g., after stepping in it)?	Yes / No
I have seen this in:	a. only one individual b. several individuals c. the majority of individuals
How often do they use objects to wipe off a conspecific's feces, urine or semen?	1= almost never; 5 = almost always
Please briefly describe some instances where individuals from the target group used leaves or other objects to clean themselves of a conspecific's feces, urine or semen, and, where known, provide the sex, age and relationship of the individuals (i.e., infant/juvenile/adult; male/female; parent/offspring/siblings/unrelated)	Open response
Apart from using an object to clean themselves, have you noticed any other behavior or expressions that made you think that individuals from the target group did not like coming into contact with a conspecific's feces, urine or semen?	Yes / No
Please describe these other behavior or expressions that made you think that individuals from the target group did not like coming into contact a conspecific's feces, urine or semen.	Open response
Please rate the extent to which each of the following occurs when an individual from the target group comes into contact with a conspecific's feces, urine or semen.	(1= never noticed; 5 = usually occurs) nose wrinkle upper lip raise tongue protrusion vomit vocalisations
Is the response to stepping in a conspecific's feces, urine or semen different to when they come in contact with their own feces, urine or semen?	Yes / No/ I don't know
Please describe how it is different.	Open response
Please make any additional comments about contact with body products in apes here.	Open response

Skip logic was used if "No" was selected

Table 3.

Rotated Component Matrix for the Ape Aversions Scale.

Item	Comp. 1 (wounds)	Comp. 2 (death & decay)	Comp. 3 (contact with body products)	Comp. 4 (sight & smell of body products)
The sight of the ape's own infected wound	**.878**	.136	-.053	.002
The sight of the ape's own bleeding open wound	**.862**	.065	.184	.164
The sight of a conspecific's infected wound	**.837**	.265	.142	.084
The sight of a conspecific's bleeding open wound	**.786**	.244	.273	.171
The sight or smell fresh carrion	-.011	**.794**	.107	.374
The sight or smell of rotten meat	.149	**.731**	.175	.421
Touching objects that a sick conspecific has touched	.188	**.709**	-.066	.095
Touching a dead conspecific	.380	**.684**	.159	-.304
The sight of a dead conspecific	.466	**.657**	.223	-.373
Stepping in a conspecific's feces	-.042	.046	**.862**	.181
Being urinated on by a conspecific	.209	.062	**.843**	.188
Urinating on self	.222	.118	**.709**	.121
The sight or smell of a conspecific defecating	.142	.062	.252	**.726**
The sight or smell of a conspecific's urine or feces near where the individual is eating	.182	.281	.391	**.694**
Cronbach's α	.904	.808	.800	.744

Note: An additional item concerning stepping in mud was omitted from the scale because it did not involve a basic disgust elicitor and it had the lowest item-total correlation of all the scale items (*r* = .23).

Table 4.

Ape Aversions Scale Component correlations (Spearman's rho; N = 73).

	Wounds	Death & decay	Contact with body products	Sight & smell of body products
Wounds	-	.640**	.324*	.452*
Death & decay		-	.329*	.381*
Contact with body products			-	.474**
Sight & smell of body products				-

Note. ** $p < 0.001$; * $p < 0.05$

Table 5.

Mean and Range for Ape Aversions for Wild and Captive Apes

	Mean (Range)	
	Wild	Captive
Ape Aversions Scale (total)	1.81 (3.71)	1.79 (3.71)
Wounds	1.15 (4.00)	1.36 (5.50)
Death & decay	1.87 (5.00)	1.68 (3.8)
Contact with body products	3.06 (6.00)	3.01 (6.00)
Sight & smell of body products	1.12 (3.50)	1.07 (4.50)

Note. All captive vs. wild comparisons were non-significant.

Table 6.

Responses to Domains of Aversions (N=74)

Domain	Noticed (yes %)	No. of individuals this was observed in (Mdn)	Frequency of behavior (Mdn)
1. TASTE: Eject bad tasting food	62%	several	rarely
2. SMELL: Withdraw after smelling putrid odor	30%	several	sometimes
3a. CONTAMINATION AVOID: Avoid liked object contacted by a disliked object	39%	several	sometimes
3b. CONTAMINATION NEUTRALISE: Wash or wipe a contaminated desirable food/object	46%	-	-
4a. SOCIAL CONTAMINATION AVOID: Avoid sick/injured appearing conspecifics	11%	several	sometimes
4b. SOCIAL CONTAMINATION NEUTRALIZE: Wash or wipe body part or object that was in contact with sick/injured conspecific	8%	-	-
5. TOOLS: Avoid undamaged tools from conspecific's mouth	2%	several	sometimes
6. BODY PRODUCTS: Wipe off conspecific's body products	50%	several	sometimes
7a. COPROPHAGY SELF: Ingest own feces	64%	several	sometimes
7b. COPROPHAGY OTHER: Ingest conspecific's feces	26%	several	rarely

Note: Tool use was reported in 85% of target ape groups. Dashes "-" denote that a question was not presented for a specific domain.

Table 7a.

Open Responses to Taste in Great Apes (n = 49)

Categories of aversive tastes	% of total (63) instances	Examples
1. Distaste	27.0	bitter, sour, medicine (vet prescribed), chilli, unripe fruit, tannin
2. Inappropriate foods	4.8	bark, skins of fruit
3. Disgust-like	7.9	live foetus in egg, anal gland, spoiled food
4. Neophobia (new foods)	17.5	novel vegetables, tomato, hard-boiled egg, avocado
5. Finicky rejection	11.1	*"…they keep pellets and grapes but throw out apples"* (common chimpanzees in captivity).
6. Rejection not otherwise described	31.7	*"...put food on lip top, look at, tasted and pushed back out of enclosure with mouth"* (common chimpanzees in captivity); passively dropping fruit out of mouth; sampling and resampling the same food.

Inter-rater agreement ($\kappa = .96$, $p < .001$) was almost perfect (Landis & Koch, 1977).

Table 7b.

Open Responses to Taste in Great Apes—Other Behavior (n = 23)

Categories of other behavior	% of total (30) instances	Examples
1. Sniffing	6.7	"S*niffing intensively at food*" (common chimpanzees in captivity)
2. Facial expressions	26.6	tongue protrusions, closed eyes, and grimacing "*…closed eyes, bared teeth, pulled up lips, pulling away from the source, sometimes scratching"* (Central Bornean orangutans in the wild).
3. Avoiding	16.7	"*Simple refusal to take the food. Turning away when it's offered*" (common chimpanzees in captivity).
4. Rejecting, discarding, dropping	33.3	*"Throwing food away"* (western chimpanzees in captivity).
5. Other	16.7	vocalisation, mother removing food *"It is more the absence of the typical vocalizations - bonobos vocalize at different levels based, presumably, on food preference - the vocs sound like yum-yum noises and are used most in very ripe fruit trees"* (bonobos in the wild).

Inter-rater agreement ($\kappa = .91$, $p < .001$) was almost perfect.

Table 8a.

*Open Responses to Smell in Great Apes (n =*21*)*

Categories of aversive smells	% of total (24) instances	Examples
1. Rotting plant matter (food/non-food)	4.2	*"…in one instance several individuals poked at and then jumped back from a rotten pumpkin"* (western lowland gorillas in captivity).
2. Feces or urine (as well as on food)	29.2	"*In a few instances, I observed individuals put the faeces to their faces and quickly pull back their upper lip and quickly put down or throw the faeces away from them. Additionally, they would wipe their hand on the wall/floor directly after. However, the majority of these cases were toward a conspecific's faeces and not their own*" (bonobos in captivity).
3. Rotting or fresh carcass (food/ non-food)	37.4	*"Individuals of all age sex classes do this when sniffing on dead animals in advanced state of decomposition"* (western chimpanzees in the wild).
4. Novel or unusual smells	4.2	"*Chimps will sniff at unfamiliar objects, including food and faeces. When there is an unpleasant smell, they pull away in the way we would. I've never seen extreme disgust though - no gagging behavior, for example*" (common chimpanzees in captivity).
5. Sniffing withdrawal not otherwise described	25.0	sniffing ground, small trees, non-specified strong odors

Inter-rater agreement ($\kappa = .89$, $p < .001$) was almost perfect.

Table 8b.

*Other Behavior Accompanying Bad Smells (n =*18*)*

	Categories of aversive smells	% of total (22) instances	Examples
1.	Vocalisations	13.6	"*alarm barking*" (common chimpanzees in captivity).
2.	Facial expressions (e.g., wipe nose, nose wrinkle)	18.2	*"…a chimp may swipe a human, sniff their fingers and slightly wrinkly their nose"* (common chimpanzees in captivity).
3.	Avoiding (turning away) or rejection, discarding, dropping	45.5	*"Smelling fruits with strong odour and discarding them"* (eastern chimpanzees in the wild).
4.	No reaction	4.5	*"When bonobos found a snare that villagers set up, an adult male and a juvenile male sniffed them and went away. Other immatures also approached and showed interests the snare. The snare did not have a special smell or odor"* (bonobos in the wild).
5.	Other (e.g., probe with finger)	18.2	*"Poking carcass or putrid fruit with finger, then sniffing finger, not followed by further inspection of tasting object"* (eastern chimpanzees in the wild).

Inter-rater agreement ($\kappa = .75$, $p < .001$) was substantial.

Table 9a.

Open Responses to Contamination Avoid (n = 39)

Categories of contaminants	% of total (48) instances	Examples
1. Food contacted with feces/urine	29.2	*"both genders; all ages - avoided food that had come into contact with urine or feces"* (gorillas in captivity). *"I have seen several females and one male avoid eating food that had come into contact with faeces or urine. The same subjects did eat the same food when it had not been in contact with faeces or urine"* (common chimpanzees in captivity).
2. Food contacted with sand, mud etc	47.8	"*Food falls into dirt/mud, onto unclean floor; most will avoid picking up (adults, both sexes)"* (common chimpanzees in captivity).
3. Food contacted with rotten food	2.1	*"…when a liked fruit is dropped on to the ground and then lies with rotten fruits. Chimps will not eat such fruits"* (eastern chimpanzees in the wild).
4. Feces on conspecific	4.2	*"In addition to food, I've seen males avoid females in estrous who had fecal material on their swelling. While I can't say that avoidance was because of the feces, it appeared that way"* (eastern chimpanzees in the wild).
5. Food on the ground or lower branches	12.5	"*Generally when the individuals are up in a feeding tree, they tend to avoid the lower-hanging fruit that might have been urinated or defecated on"* (eastern chimpanzees in the wild).
6. Avoidance of contamination not otherwise described	4.2	*"They usually take the food item in hand, look at it, smell it and then put it back down"* (bonobos in captivity).

Inter-rater agreement ($\kappa = .78, p < .001$) was substantial.

Table 9b.

Open Responses to Attempts to Neutralize Contaminated Food/Objects (Contamination Neutralize) (n = 40*)*

Categories of neutralizing behavior	% of total (52) instances	Examples
1. Washing food with water	32.7	“Washing in water when food was dirty, mostly covered in dust or dirt” (western chimpanzees in captivity).
2. Wiping or rubbing food/object	50.0	*“Wiping and rubbing behavior on fruits or on their own bodies”* (Central African chimpanzees in the wild). *“Wiping muddy foods on other parts of the body, with the hand, or against a substrate (a climbing structure or the grass)” (common chimpanzees in captivity).*
3. Picking materials (e.g., sand) off food	7.7	*“Individuals regularly pick of debris (dirt/mud etc.) from food items with their lips and on rare occasions with their fingers before eating, however, the food items are usually far from clean when ingested”* (bonobos in captivity).
4. Other neutralising behavior	9.6	*“leaves, water, grass, hay used to wipe feces/dirt off of food”* (western lowland gorillas in captivity)

Inter-rater agreement ($\kappa = .79$, $p < .001$) was substantial.

Table 10.

Additional Comments Regarding Social Contamination in Great Apes (n = 23)

Categories of inconsistent observation	% of total (34) instances	Examples
1. Approach and interest in sick or injured individuals	29.4	*"I believe that the chimpanzees are actually more social & responsive with sick individuals from my experience and they tend to approach and give positive attention to those individuals. Almost seems to be them showing "concern" for their group-mates"* (common chimpanzees in captivity). *"…in most case, individuals are very interested in other's injuries and unusual health situations. For example, when a subadult female had a miscarriage and was visibly in pain, she received a lot of attention, and one other adult female actually pulled out the undeveloped foetus/placenta from her vulva and ate it directly"* (bonobos in captivity).
2. Grooming or additional contact with sick or injured	23.5	*"On the contrary, a sick or injured individual usually gets groomed quite intensely"* (western chimpanzees in the wild).
3. Carrying a dead infant	5.9	*"Actually mountain gorillas seem quite curious about injuries in others, and even when a dead baby carried around."* (mountain gorillas in the wild).
4. Contact with sickness related stimuli (e.g., mucus, wound, blood)	20.6	*"When individuals have an open wound, they themselves groom and lick the wounds, but also others may groom and lick"* (Central Borneo orang-utan in the wild) *"Actually, sometimes adults pick a sick individual's nose as well, but very rarely. Adults will sometimes pick their own runny nose and then lick their hands"* (bonobos in the wild).
5. Other contradictory behavior	20.6	*"One had a clear skin condition. I was actively looking out for avoidance. Nothing!"* (common chimpanzees in captivity). *"Have several injured or disfigured (some severely) individuals. See no difference in association/mating that is different from age/rank effects."* (bonobos in the wild)

Inter-rater agreement ($\kappa = .89$, $p < .001$) was almost perfect.

Table 11.

Additional Comments Regarding Tool Sharing in Great Apes (n = 26)

Categories of inconsistent observation	% of total (26) instances	Examples
1. Tool use is very rare	26.9	*"They may not "need" to use tools as there's plenty of food available all year in their environment."* (Central African chimpanzees in the wild).
2. Tool sharing is common	38.5	*"I observed many instances of sponges reuse"* (eastern chimpanzees in the wild).
3. Apes do not share if the tool is too damaged to be functional	7.7	*"I think the only case in which a chimp would not reuse another individual's tool is if the first user had rendered the tool useless-- e.g. chewed the end of a stick until it was too frayed to insert into a hole for honey dipping"* (common chimpanzees in captivity).
4. Other contradictory behavior	26.9	*"Might re-use sponges but not napkins (as other leaves are available)"* (eastern chimpanzees in the wild).

Inter-rater agreement ($\kappa = .89$, $p < .001$) was almost perfect.

Table 12a.

Wiping off Body Products (n = 41)

Categories of body products	% of total (60) instances	Examples
1. Shake off or wipe feces from own foot or body using leaves or objects	56.7	*"I saw an adult male step in feces and then pick up a stick to wipe it off his foot. Usually, though, I see the chimps vigorously shaking a body part until the offending waste is shaken off"* (common chimpanzees in captivity).
2. Wipe urine from own body using leaves or objects	11.7	*"Almost every time an individual either stepped in feces or especially if they were defecated or urinated on (all individuals were unrelated), they would use material such as a blanket, bark, or paper towels (often 'requesting' them, via gestures, from keepers). All individuals were observed to do this with the exception of the infants who did begin to do this when they were older and classed as juveniles."* (common chimpanzees in captivity).
3. Wipe semen from own body using leaves or objects	13.3	*"Also after mating, I have observed males often wiping semen off of their penises with leaves…"* (eastern chimpanzees in the wild)
4. Wipe feces from conspecific using leaves or objects	3.3	*"When a female's swelling is covered in faeces, a male will sometimes wipe it with a leaf before copulating"* (western chimpanzees in the wild).
5. Not otherwise specified	15.0	*"Females will also use their hand to wipe away menses blood from their swelling"* (Chimpanzees in captivity).

Inter-rater agreement ($\kappa = .92$, $p < .001$) was almost perfect.

Table 12b.

Other Behavior Accompanying Contact With Body Products (n = 35)

Categories of behavior	% of total (50) instances	Examples
1. Avoiding feces	40.0	*"…when traveling on the ground, they do not tread on feces (intentionally?), as ground collected feces are never squashed even if among footprints, etc."* (bonobos in the wild).
2. Avoiding urine	32.0	*"I once saw a male chimpanzee quickly move to avoid the urine stream of a small juvenile sitting above him in the tree. He later hit the juvenile."* (eastern chimpanzees in the wild) *"Adult male and female gorillas appeared to be annoyed after being accidentally urinated upon by others, usually infants or youngsters."* (mountain gorillas in the wild)
3. Facial expressions	6.0	*"Eye squint, dodge/avoid, surprise/fast wiping (like if human had bug on arm)"* (common chimpanzees in captivity)
4. Other avoiding	22.0	*"If an individual wishes to station themselves in an area where there is urine or faeces, they will often pull nesting materials over to sit on, providing a barrier."* (common chimpanzees in captivity)

Inter-rater agreement (κ = .87, $p < .001$) was almost perfect.

Table 13.

Coprophagy

Categories	Ingesting own feces: % of total (104) instances	Ingesting a conspecific's feces: % of total (37) instances
1. Adult females	36.6	27.0
2. Adult males	27.9	13.5
3. Juveniles	20.2	37.9
4. Picking out nutrients (seeds/meat)	9.6	13.5
5. Social transmission	3.8	5.4
6. Other comments	1.9	2.7

Inter-rater agreement for own coprophagy ($\kappa = .96$, $p < .001$) and for other coprophagy ($\kappa = .89$, $p < .001$) was almost perfect.