The skin crawls, the stomach turns

Ectoparasites and pathogens elicit distinct defensive responses in humans

Tom R. Kupfer[1,2*], Daniel M.T.Fessler[3,4,5], Bozhi Wu[3], Tiffany Hwang[3,6], Adam Maxwell Sparks[3,4], Sonia Alas[3], Theodore Samore[3,4], Vedika Lal[2], Tanvi Sakhamuru[3], and Colin Holbrook[7]

[1] Department of Psychology, Nottingham Trent University

[2] Department of Social and Organizational Psychology, Vrije Universiteit Amsterdam

[3] Department of Anthropology, University of California, Los Angeles

[4] UCLA Center for Behavior, Evolution, & Culture

[5] UCLA Bedari Kindness Institute

[6] Center for Data Sciences, Brigham and Women's Hospital, Harvard Medical School

[7] Department of Cognitive and Information Sciences, University of California, Merced

*Corresponding author:

Tom R. Kupfer
Department of Psychology,
Nottingham Trent University
thomas.kupfer@ntu.ac.uk
07830018099

ACCEPTED FOR PUBLICATION

IN

PROCEEDINGS OF THE ROYAL SOCIETY B: BIOLOGICAL SCIENCES

Abstract

Disgust has long been viewed as a primary motivator of defensive responses to threats posed by both microscopic pathogens and macroscopic ectoparasites. Although disgust can defend effectively against pathogens encountered through ingestion or incidental contact, it offers limited protection against ectoparasites, which actively pursue a host and attach to its surface. Humans might therefore possess a distinct ectoparasite defense system—including cutaneous sensory mechanisms and grooming behaviors—functionally suited to guard the body's surface. In two U.S. studies and one in China, participants (N = 1079) viewed a range of ectoparasite- and pathogen-relevant video stimuli and reported their feelings, physiological sensations, and behavioral motivations. Participants reported more surface-guarding responses towards ectoparasite cues than towards pathogen cues, and more ingestion/contamination-reduction responses towards pathogen cues than towards ectoparasite cues. Like other species, humans appear to possess evolved psychobehavioral ectoparasite defense mechanisms that are distinct from pathogen defense mechanisms.

Keywords: ectoparasites, pathogens, disgust, grooming, behavioral immune system

Disgust is widely regarded as an evolved mechanism that shapes behavior to defend against pathogens and parasites (1-3). Disgust's features, including nausea, an urge to vomit, contamination cognitions, and withdrawal, are well suited to protect against microbes encountered through ingestion or incidental contact (3-7). However, these responses offer little protection against macroscopic ectoparasites, such as fleas, ticks, or lice, which actively pursue a host and attach to its body surface. Ectoparasites exert selective pressure on hosts, hence we can expect selection to have crafted ectoparasite defenses tailored to this threat. Here, we report results of the first studies to test the hypothesis that humans possess different psychological and behavioral responses for defending against pathogens and ectoparasites.

Animal research indicates that ectoparasites pose an important fitness threat that has selected for discrete adaptations (8). For example, ectoparasites decrease reproductive success in barn swallows (9), while experimental removal of ectoparasites increases it in Cape ground squirrels (10). In addition to direct costs inflicted by feeding, ectoparasites are often vectors for infectious diseases (11). Behavioral adaptations to defend against ectoparasites include specialized grooming movements, such as scratching, picking, muscle twitching, and tail swishing (8) that are demonstrably effective at controlling ectoparasite loads (12,13).

Many animals have two forms of grooming. *Programmed grooming*, involving endogenously generated periodic movements that occur even in the absence of peripheral stimulation by ectoparasites, is thought to be important in removing larval- and nymphal-stage ectoparasites (14). *Stimulus-response grooming* is rapid, localized grooming in reaction to cutaneous sensations, such as itch, that cue the location of ectoparasites (15). Itching is primarily caused by histamine released following ectoparasite bites (8), while tickling sensations may indicate ectoparasites landing or walking on the body's surface (16).

Ectoparasites exert selective pressure on humans by feeding on blood and skin, and by transmitting diseases such as typhus and plague (11,17). Continuities between animal and human ectoparasite defense systems can therefore be expected, potentially extending to the distinction between programmed and stimulus–response grooming (17). Akin to programmed grooming, people spontaneously inspect their skin, and periodically groom the skin and hair with movements such as picking and rubbing (18,19). We hypothesise that, paralleling stimulus-response grooming, people react to ectoparasite stimuli with increased urges to scratch and groom, and with increased itch and tickle sensations.

Blake and colleagues (20) theorized that a class of stimuli, separate from ingestible pathogens, may elicit a "skin focused response", including skin crawling and scratching, that functions to defend against "skin transmitted pathogens". Skin-transmitted pathogens were conceptualized broadly, including "macroparasites, parasite vectors, and infectious lesions… disease transmission or venom injection via contact with a parasite vector, venomous insect, arachnid, or reptile". Blake et al. hypothesize that both ectoparasites and skin-related pathogen stimuli elicit a surface-guarding response. In contrast, we predict that cues indicating a risk of pathogen transfer through skin contact will elicit prototypical oral-gastric and contamination responses. Only ectoparasite cues, or generalizations of them, should elicit the surface-guarding response, including itching sensations and scratching behaviors, that is functionally suited to defend against ectoparasites. Thus, the current research is the first to test whether humans have responses to defend specifically against ectoparasites, in line with behavior documented in nonhuman species (8, 14).

Several studies report people being *disgusted* by ectoparasites and other arthropods (21-23), potentially supporting the view that disgust functions to defend against both pathogens and ectoparasites. However, because the folk-emotion word "disgust" refers to multiple distinct affective responses (5,24-26), participants' endorsement of this descriptor cannot be taken as showing that they are experiencing the pathogen-avoidance emotion, *disgust*, including sensations such as nausea. Distinct responses addressed by the same folk-emotion term can be disambiguated using fine-grained items corresponding to more precise affective feelings and sensations (27-30). Pathogen disgust can be distinguished from other responses by gauging participants' endorsement of items measuring oral-gastric sensations, such as nausea and the urge to gag (2,31), and contamination cognitions and feelings (24,32).

Research overview

The aim of this research was to determine whether humans show distinct defensive responses in reaction to cues of the presence of ectoparasites versus cues of the presence of pathogens. To test this hypothesis, three studies were conducted; two in the U.S. and one in China. Participants watched videos depicting ectoparasites, such as fleas, and videos depicting pathogen cues, such as feces (see Supplemental materials for links to stimuli). They then responded to questions measuring physical sensations and behaviors corresponding, respectively, to pathogen defense (e.g., nausea), and ectoparasite defense (e.g., itching). In Studies 1 and 3, participants also reported the number of times they scratched themselves during each video, and indicated how "disgusted" and "grossed out" they were during each video[1]. In Study 1, online U.S. participants viewed five[2] ectoparasite videos and six pathogen videos. One of the ectoparasite videos depicted a spider to test whether disgust reported towards spiders is associated more with the surface-guarding response characteristic of

[1] Because Study 2 was presented to participants bundled with an unrelated study, to reduce its length, fewer measures were included.

[2] Studies 1 and 2 included an additional video depicting a lice infestation. However, as we were subsequently unable to obtain permission to use this video from the person depicted, these data were removed due to ethical concerns. Excluding these data did not substantively alter findings. See Supplemental materials for full details.

ectoparasite defense (17, 20), or the oral-gastric response characteristic of pathogen defense (40). In Study 2, undergraduates at a U.S. university viewed two ectoparasite videos and three of the pathogen videos. Cultural models of emotion influence how people understand and report their inner states (27). Moreover, for a wide variety of stimuli, meanings and affective connotations are importantly colored by cultural meaning systems (27). Accordingly, claims of species-typical psycho-behavioral mechanisms should be tested cross-culturally. As a first step in such testing, in Study 3, passers-by were recruited in Shanghai, China to watch one ectoparasite video and one pathogen video. All studies were approved by the UCLA Office of the Human Research Protection Program. All hypotheses and methods, but not the analysis plan, were pre-registered and archived at https://osf.io/xmsv4/?view_only=c54b354e029f4c849ef2834f4fa48509, along with data. See online supplemental material for study materials.

Study 1: U.S. MTurk Sample

Methods

Participants

Four hundred U.S. participants were recruited via Amazon's Mechanical Turk (filtered for workers with a 95% approval rating with at least 100 HITs approved) for a 20-minute survey about "bodily reactions to videos" in exchange for US $2.00 (see online supplemental material for power analyses and sample size justification). After excluding individuals who failed to complete large portions of the survey, failed an attention check, or completed the survey in less than 7.3 minutes (the minimum time needed to view the videos and answer the questions as rapidly as possible) or more than 40 minutes, the final sample consisted of 395 individuals (M_{age} = 33.48, SD_{age} = 9.32; 138 female).

Stimuli

Video stimuli were created by conducting Internet searches using terms such as "disgusting", "gross", "skin-crawling", "rotten meat" and "fleas". Six videos that clearly and continuously depicted a pathogen cue (rotten meat, ear wax, cellulitis, an infected arm lesion, dirty toilets, and warts), and five videos that clearly and continuously depicted ectoparasites, or generalisations of them (fleas, bed bugs, ticks, mosquitos, and spiders), were each edited to be 90 seconds long and embedded into an online survey. To maximize participant attention throughout the study, each participant viewed only two randomly selected videos from each category.

Measures

Granular items were created to measure the feelings, sensations, and behaviors postulated to be associated, respectively with pathogen defense responses and ectoparasite defense responses. Pathogen defense items were derived from existing research (e.g., 5,7,28) outlining the prototypical disgust response, including both its oral-gastric and contamination components. Oral-gastric items were "I felt nauseous", "I felt like I could vomit", "I felt like I would gag or retch", "I felt a physical sensation in my stomach", "I felt a physical sensation in my throat", and "I felt an urge to cover my mouth or nose with my hands". Contamination items were "I had a feeling of contamination", "I felt unclean", and "I felt an urge to wash". Items intended to measure the skin-surface sensations hypothesized to function to defend the body's surface against ectoparasites (17) were: "I felt my skin crawl", "I felt ticklish", "I felt goosebumps", "I felt shivers", "I felt a physical sensation in my skin", "I felt an urge to shake myself", "I felt an urge to pick at my skin", "I felt an urge to scratch myself", and "I felt itchy”. Participants reported how strongly they experienced each physical feeling or sensation while watching the video, using a seven-point scale, ranging from “not at all” to “very strongly”. Participants also responded to single-item measures of “disgusted” and “grossed-out” using the same 7-point scale. Additionally, participants reported how many times they scratched themselves on a sliding scale from 0 to 10.

Procedure

After viewing each video, participants completed an attention check, then responded to the above measures.

Analytical strategy

Analyses employed SPSS 25.0. First, factor analysis was used to determine whether items measuring ectoparasite defense and pathogen defense responses formed the expected factor structure[3]. Repeated-measures general linear modelling was used to test whether pathogen and ectoparasite stimuli differed in the oral-gastric and skin-surface responses they elicited. Regression analyses were conducted to determine the extent to which single-item “disgust” and “grossed-out”, and self-reported scratching, were predicted by oral-gastric versus skin-surface responses.

Results

Factor analysis

To test whether surface-guarding and ingestion/contamination reduction constituted distinct responses, a factor analysis was conducted using maximum likelihood extraction and promax rotation. Visual inspection of the scree plot revealed a clear point of inflection after the third factor, suggesting that two factors be retained. These had eigenvalues of 12.06 and 1.84, and explained 67.01% and 10.23% of the variance, respectively. Items in each factor

[3] See supplemental materials for a note on the normality of the data

corresponded conceptually to the expected surface-guarding and ingestion/contamination reduction responses (Table 1). For each factor, the five items with the highest factor loadings were averaged to produce composite measures. We label these *skin-surface*, and, because the five highest loading ingestion/contamination reduction items were all ingestion related, *oral-gastric*, respectively. Pooling across all videos and participants, oral-gastric and skin-surface factors were correlated $r(1449) = .62$.

Table 1. Factor loadings corresponding to each response type in each study

	Study 1 (MTurk)	Factor		Study 2 (California students)	Factor		Study 3 (China)	Factor	
		1	2		1	2		1	2
Skin-surface responses	itchy	**0.99**	-0.12	scratch	**0.93**	-0.16	itchy	**0.93**	-0.03
	scratch	**0.98**	-0.10	skin-sensation	**0.93**	0.01	scratch	**0.92**	-0.01
	pick	**0.89**	0.01	pick	**0.83**	-0.03	pick	**0.85**	-0.00
	skin-sensation	**0.84**	-0.01	crawl	**0.81**	0.14	ticklish	**0.76**	-0.01
	ticklish	**0.84**	-0.02	ticklish	**0.77**	0.02	skin-sensation	**0.70**	0.20
	goosebumps	0.68	0.20	shake	0.70	0.18	shake	0.61	0.29
	shiver	0.63	0.26	shiver	0.66	0.23	goosebumps	0.34	0.52
	crawl	0.69	0.16	goosebumps	0.66	0.15	shiver	0.23	0.63
	shake	0.76	0.13						
Oral-gastric responses	nauseous	-0.09	**0.98**	vomit	-0.15	**1.06**	vomit	-0.08	**0.99**
	vomit	-0.10	**0.98**	nauseous	-0.07	**0.99**	stomach	-0.02	**0.87**
	stomach	-0.02	**0.86**	stomach	0.13	**0.82**	gag	0.06	**0.86**
	cover	0.08	**0.78**	throat	0.10	**0.77**	nauseous	0.02	**0.81**
	gag	-0.11	**1.00**	cover	0.21	**0.65**	throat	0.01	**0.81**
	contamination	0.25	0.63	contamination	0.40	0.48	cover	0.219	0.653
	wash	0.36	0.56	wash	0.57	0.26	contamination	0.27	0.59
	unclean	0.27	0.62				unclean	0.19	0.56
	throat	0.14	0.75				wash	0.55	0.34

Responses to ectoparasite and pathogen stimuli

To test whether ectoparasite and pathogen stimuli elicited distinct defensive responses**,** a repeated-measures ANOVA was conducted with content of stimulus type (pathogen; ectoparasite) and response (oral-gastric; skin-surface) as within-subjects variables. There was an interaction between stimulus type and response, $F(1, 394) = 220.29$, $p < .001$,

$\eta^2 = .36$. Simple effects analyses showed that pathogen videos elicited a higher oral-gastric response than skin-surface response, $F(1, 394) = 209.35$, $p < .001$, $\eta^2 = .35$, whereas ectoparasite videos elicited a higher skin-surface response than oral-gastric response, $F(1, 394) = 60.78$, $p < .001$, $\eta^2 = .13$ (Figure 1). Supplementary Figure S1 shows oral-gastric and skin-surface responses for each pathogen and ectoparasite video separately.

Given previous evidence of sex differences in disgust sensitivity (7), we explored the effect of participant sex on responses to each stimulus type by entering this as a between-subjects variable, which revealed a significant interaction between sex, stimulus type, and response, $F(2, 392) = 5.31$, $p < .001$, $\eta^2 = .03$; women showed stronger responses to both pathogen and ectoparasite stimuli (see Supplemental Table S2 for mean responses by sex).

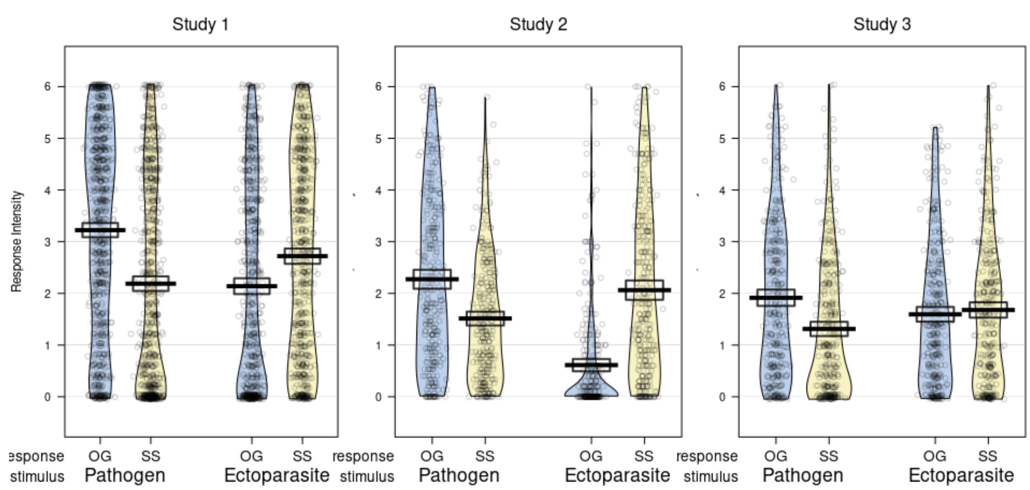

Figure 1. Participants' oral-gastric (OG) and skin-surface (SS) responses when viewing pathogen and ectoparasite video stimuli, in Studies 1, 2 and 3. Response intensity ranges from 0, "not at all" to 6, "very strongly". Raw data are jittered. Beans represent smoothed density of raw data. Boxes and lines represent 95% Confidence Intervals and means, respectively.

Predicting disgust

To investigate our suggestion that the “disgust” reported towards ectoparasites and arthropods (e.g., 22) may reflect participants’ use of the same folk-emotion term to refer to a response that differs from the prototypical disgust response towards pathogen cues, we regressed the skin-surface and oral-gastric composite measures on single-item disgust reported towards pathogen and ectoparasite cues. Disgust reported towards pathogen stimuli was positively associated with the oral-gastric response, $\beta = .81$, $t(392) = 15.54$, $p < .001$, but negatively associated with the skin-surface response, $\beta = -.23$, $t(392) = -4.49$, $p < .001$. Disgust reported towards ectoparasite stimuli was positively associated with both oral-gastric, $\beta = .44$, $t(392) = 8.06$, $p < .001$, and skin-surface responses, $\beta = .33$, $t(392) = 6.06$, $p < .001$.

Previous studies have suggested that “grossed out” more cleanly and specifically measures pathogen disgust (25). We therefore conducted another regression analysis predicting how grossed-out participants reported being by pathogen and ectoparasite stimuli. The pattern was similar. Oral-gastric responses were positively associated, $\beta = .85$, $t(392) = 16.74$, $p < .001$, and skin-surface responses negatively associated, $\beta = -.26$, $t(392) = -5.21$, $p < .001$, with how grossed out participants reported being towards pathogen stimuli. Both oral-gastric, $\beta = .45$, $t(392) = 8.63$, $p < .001$, and skin-surface, $\beta = .33$, $t(392) = 6.31$, $p < .001$, responses were associated with how grossed out participants reported feeling towards ectoparasite stimuli.

Scratching behavior

To test whether more scratching was elicited by ectoparasite stimuli than pathogen cue stimuli, a repeated-measures ANOVA was conducted with video content as the within-subjects variable. Participants reported scratching themselves more while watching ectoparasite videos ($M = 2.6$, $SD = 2.86$) than while watching pathogen videos ($M = 2.06$, $SD = 2.78$), $F(1, 390) = 37.02$, $p < .001$, $\eta^2 = .09$. Scratching during pathogen videos was positively associated with the skin-surface response, $\beta = .78$, $t(389) = 15.52$, $p < .001$, and negatively associated with the oral-gastric response, $\beta = -.11$, $t(389) = -2.23$, $p < .001$. Scratching during ectoparasite videos was positively associated with the skin-surface response $\beta = .53$, $t(392) = 9.87$, $p < .001$, and with the oral-gastric response, $\beta = .25$, $t(392) = 4.60$, $p < .001$.

Study 2: Californian Student Sample

Methods

Participants

Undergraduates ($N = 333$) were recruited at a large public university in California in fulfillment of a course requirement. After excluding participants who skipped some portions of the videos; were unable to watch the full videos due to technical difficulties; whose responses were not recorded; or who failed to complete the survey, the final sample consisted of 318 individuals (241 women, $M_{age} = 19.39$, $SD_{age} = 1.61$).

Materials

Participants viewed three pathogen-cue videos (rotten meat, dirty toilets, and an infected lesion) and two ectoparasite videos (mosquitos and ticks) employed in Study 1. After each video, participants responded to the same self-report measures used in Study 1, except that the items “gag”, “unclean”, “itchy”, “disgusted”, “grossed-out” and scratch frequency were not measured.

Procedure

Participants watched the six videos and responded to the measures in a laboratory; a research assistant noted any distractions or other concerns. As part of a related study not reported here, participants were also randomly assigned to view videos of animals either scratching or not scratching themselves; participants were video-recorded throughout, and were aware of this.

Results

Factor analysis

To test whether surface-guarding and ingestion/contamination reduction constituted distinct responses, a factor analysis with maximum likelihood extraction and promax rotation was conducted. Inspection of the scree plot revealed a clear inflection point after factor 3, suggesting that two factors be retained. These two factors had eigenvalues of 10.17 and 1.34, and explained 67.81% and 8.99% of the variance, respectively; the items in each corresponded conceptually to surface-guarding and ingestion reduction responses (see Table 1). For each factor, the five items with the highest factor loadings were again averaged to give composite oral-gastric and skin-surface measures, respectively. The two measures were correlated, $r(318) = .71$, $p < .001$.

Responses to ectoparasite and pathogen videos

To test whether ectoparasite and pathogen stimuli elicited distinct defensive responses**,** a repeated-measures ANOVA was conducted with response (oral-gastric; skin-surface) and stimulus type (pathogen; ectoparasite) as within-subjects factors. There was an interaction between stimulus type and response, $F(1, 317) = 431.79$, $p < .001$, $\eta^2 = .58$. Simple effects analyses showed that pathogen videos elicited a higher oral-gastric response than skin-surface response, $F(1, 317) = 105.54$, $p < .001$, $\eta^2 = .25$, whereas ectoparasite videos elicited a higher skin-surface response than oral-gastric response, $F(1, 317) = 344.61$, $p < .001$, $\eta^2 = .52$. Figure S2 shows mean responses towards each pathogen and ectoparasite video. Adding participant sex as a between-subjects variable revealed a significant three-way interaction, $F(1, 314) = 5.73$, $p < .001$, $\eta^2 = .05$; women showed stronger responses to both pathogen and ectoparasite stimuli (see Supplemental Table S2 for details).

Study 3: Shanghai Public Sample

Methods

Participants

Participants ($N = 394$) were recruited in public areas in Shanghai, China for a study about the relationship between feelings, visual perception, and memory in return for 30 RMB (~U.S. $4.25). Thirty-three participants were excluded for having rushed through the survey, or as having been distracted while participating, leaving 361 individuals (178 women) in the final sample ($M_{age} = 31.85$, $SD_{age} = 12.36$).

Materials and procedure

Participants viewed stimuli and answered questions on a tablet computer in a quiet public location. One pathogen-cue video (infected lesion) and one ectoparasite video (fleas) from Study 1 were presented in random order, followed by the self-report items. Items used in Study 1 were independently translated into Mandarin (see Supplement) by two bilingual native speakers, with any differences reconciled through discussion with other native speakers. Lacking an equivalent Mandarin phrase, the item "I felt my skin crawl" was excluded. A research assistant noted any concerns regarding participant attention.

Results

Factor analysis

To test whether surface-guarding and ingestion/contamination reduction constituted distinct responses, factor analysis was again conducted. Visual inspection of the scree plot reflected a clear inflection point after factor 3, suggesting that two factors be retained. The two factors had eigenvalues of 11.63 and 1.08, and explained 68.44% and 6.36% of the variance, respectively. The items in each factor again corresponded to surface-guarding and ingestion reduction responses (see Table 1). For each factor, the five items with the highest factor loadings were averaged to give composite oral-gastric and skin-surface measures, respectively. These measures were correlated $r(361) = .76$, $p < .001$.

Responses to pathogen and ectoparasite cues

To test whether ectoparasite and pathogen stimuli elicited distinct defensive responses**,** a repeated-measures ANOVA was conducted with stimulus type (pathogen; ectoparasite) and response (oral-gastric; skin-surface) as within-subjects factors. There was an interaction between stimulus and response, $F(1, 353) = 99.81$, $p < .001$, $\eta^2 = .22$. Simple effects analyses showed that a stronger oral-gastric response was elicited by the pathogen video than by the ectoparasite video, $F(1, 353) = 21.29$, $p < .001$, $\eta^2 = .06$, whereas a stronger skin-surface response was elicited by the ectoparasite video than by the pathogen video, $F(1, 353) = 36.12$, $p < .001$, $\eta^2 = .09$ (Figure 1). Participant sex did not interact with stimulus type, $F(2, 345) = 0.40$, $p = .67$, $\eta^2 = .00$, or response, $F(2, 345) = 1.26$, $p = .29$, $\eta^2 = .01$.

Predicting disgust

To test whether single-item "disgust" and "grossed out" were predicted by skin-surface responses in addition to oral-gastric responses, we regressed the skin-surface and oral-gastric composite measures on single-item disgust reported towards pathogen and ectoparasite stimuli. Towards the pathogen video, the oral-gastric response predicted disgust (*ěxīn,* 恶心), $\beta = 0.83$, $t(356) = 20.31$, $p < .001$, and grossed-out (*yànwù,* 厌恶), $\beta = .72$, $t(356) = 14.68$, $p < .001$, whereas the skin-surface response did not, $\beta = -.002$, $t(356) = -.05$, $p = .96$, and $\beta = .02$, $t(356) = .46$, $p = .65$, respectively. Towards the ectoparasite video, the oral-gastric response predicted disgust, $\beta = .76$, $t(352) = 16.15$, $p < .001$, and grossed out, $\beta =$

.63, $t(353) = 10.9$, $p < .001$, but the skin-surface response ($\beta = 0.06$, $t(352) = 1.3$, $p = 0.2$ and $\beta = .07$, $t(353) = 1.19$, $p = .23$) did not.

Scratching behavior

To test whether more scratching was elicited by ectoparasite stimuli than pathogen cue stimuli, a repeated-measures ANOVA was conducted with self-reported scratching behavior and stimulus type (pathogen versus ectoparasite) as within-subjects factors. The ectoparasite video ($M = 1.01$, $SD = 1.68$) elicited more scratching behavior than the pathogen video ($M = 0.88$, $SD = 1.57$), $F(1, 349) = 3.94$, $p = .05$, $\eta^2 = .01$. Scratching behavior elicited by the ectoparasite video was positively associated with the skin-surface response, $\beta = .52$, $t(351) = 7.09$, $p < .001$, but not with the oral-gastric response, $\beta = .05$, $t(351) = 0.83$, $p = .41$. Scratching behavior elicited by the pathogen video was positively associated with the skin-surface response, $\beta = .73$, $t(352) = 13.24$, $p < .001$, and negatively associated with the oral-gastric response, $\beta = -.13$, $t(352) = - 2.27$, $p = .02$.

Discussion

Overlooking both the differing task demands of defending against dissimilar threats and evidence that animals possess distinct behavioral defenses against ectoparasites, previous accounts nominate disgust as a key motivator of human defensive responses to pathogens and ectoparasites. Across three studies we found that humans respond differently towards cues of pathogens versus cues of ectoparasites. Pathogen cues elicited more prototypical disgust responses, such as nausea and the urge to vomit, which are functionally consistent with avoidance of ingestible sources of pathogens. Ectoparasites elicited more surface-guarding responses, such as itching and scratching, which are functionally consistent with defense against ectoparasites that actively seek to attach to the body's surface. Pathogen cues present on human skin, including warts and an infected lesion, elicited more of an ingestion-reduction response than a surface-guarding response, indicating that the latter is elicited by ectoparasites specifically, rather than by skin-transmitted pathogens in general (cf., 20). These findings are consistent with the hypothesis that humans possess an ectoparasite defense system distinct from the pathogen avoidance system.

Previous studies report that, like pathogen cues, ectoparasite cues elicit disgust (21-23). Indeed, our participants also reported being “disgusted” and “grossed out” by ectoparasite cues. However, granular measures showed that participants’ responses involved more cutaneous sensations and action tendencies than prototypical oral-gastric disgust sensations and action tendencies. Additionally, regression analyses supported the notion that the categorical terms “disgust” and “grossed out” are used imprecisely by participants: the degree to which participants experienced both skin-surface sensations and oral-gastric sensations predicted how disgusted and grossed-out they reported being by ectoparasite cues. Interestingly, this was not the case in Study 3, raising the possibility that Mandarin speakers may use *ěxīn* (恶心), the folk-emotion equivalent of the English “disgust,” with greater precision than English speakers’ use of “disgust”.

Despite clear differences between the two classes of responses, our findings also reveal overlap, suggesting incomplete dissociation between ectoparasite defense and pathogen defense mechanisms. Participants reported experiencing some oral-gastric sensations towards ectoparasite cues. And oral-gastric sensations, in addition to skin-surface sensations, predicted the overall level of “disgust” participants reported towards ectoparasite cues. Either or both of two explanations may obtain. First, consistent with processes of neural reuse in the evolution of psychological adaptations, particularly when there are overlapping task domains (e.g., attending to the body-environment interface), defense mechanisms plausibly share some elementary architecture, resulting in overlap in patterns of responding (33). Second, even if two mechanisms are quite distinct, they may nevertheless be co-activated by some stimuli. One limitation of our design is that exclusively visual stimuli were employed. Together with olfaction, vision is a powerful pathway for canonical disgust elicitation (34). In contrast, ectoparasites are often detected via skin sensations when an ectoparasite lands on a host (16), with vision plausibly being a secondary mode of detection. It is therefore possible that our choice of stimulus modality may have reduced dissociation in response patterns; employing other modalities might increase the distinction between responses towards ectoparasite and pathogen cues (e.g., 35). Consonant with this possibility, Stevenson and colleagues (36) have argued that oral-gastric disgust is frequently anticipatory, occurring to prevent contact with a stimulus. In contrast, ectoparasite defense responses may be more strongly activated after contact has occurred.

Contrary to expectations, granular items measuring contamination sensations, and contamination-removing urges, did not cleanly load with the items intended to measure ingestion-reducing sensations. Video stimuli may not adequately activate contamination sensations, given that these are predominantly elicited by physical contact with a stimulus (37). Future research could use tactile as well as visual stimuli to better test whether contamination sensations are elicited more strongly by pathogen cues than by ectoparasites cues. Similarly, measures of behavior in addition to reported qualia might more effectively distinguish between responses.

Like other categorical emotion words (27,29), “disgust” is imprecise and polysemous (25,31), and may subsume multiple functionally distinct responses; these can be distinguished using fine-grained items that more precisely measure sensations and action tendencies. As illustrated here, this approach can distinguish distinct reactions previously conflated under a single emotion term, and may prove valuable for resolving other debates, such as whether moral disgust involves the full disgust response, or is primarily metaphorical (6).

Considerable research has posited a "behavioral immune system" in humans, largely because of links with important health and social outcomes, including intergroup attitudes and political sentiments (38). Much of this research has focused on individual variation in pathogen disgust sensitivity (39). Our findings raise the question of whether variation in ectoparasite defense sensitivity also contributes to these outcomes. Studies have also identified links between disgust and psychopathologies (2,40). Some of these conditions, including skin-picking disorders (41), delusional infestation (42), and trypophobia (43), involve skin sensations and grooming behaviors, and may be more closely related to pathologies of ectoparasite defense than to pathologies of pathogen avoidance (17). Of similar translational importance, even as COVID-19 has focused researchers ever more intently on pathogen avoidance, vector-borne diseases continue to expand. Understanding the psychology of ectoparasite defense may importantly enhance campaigns to combat illnesses which kill or debilitate millions every year.

Acknowledgments: Research supported by an European Union grant to TRK (MSCA-IF-2017-800096-EmoPun) and a UCLA Gold Shield Award to DF. We thank FessLab and the Inner Heart Psychology Club for assistance.

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Supplemental Materials

Contents

1. Hyperlinks to video stimuli

The ectoparasite videos:

Fleas https://www.youtube.com/watch?v=3DvSKOdtmVg

A tick https://www.youtube.com/watch?v=j0YFF0yZYtc

A spider https://www.youtube.com/watch?v=6lwuItwsyP4

Mosquitos https://www.youtube.com/watch?v=Sg-b3VQ5098

Bed bugs https://www.youtube.com/watch?v=SQbLYOh5hA0

*

The pathogen-cue videos:

Rotting meat https://www.youtube.com/watch?v=ZCklZ5egXHA

Ear Wax https://youtu.be/Ceygsj2_T04

Cellulitis https://www.youtube.com/watch?v=K7vATqCSHM8

Infected arm lesion https://www.youtube.com/watch?v=WqhfxXya3Xg

Dirty festival toilets https://www.youtube.com/watch?v=6fwmDEdIIEo

Wart https://www.youtube.com/watch?v=ur-Tyimz65Q

* **Note**. This study included an additional video clip of ectoparasites. Searching publicly-available materials on YouTube.com, we identified a video depicting a girl suffering a severe infestation of head lice. We edited the video down to a short clip in which only the scalp is visible, being careful to excise any features of the video, including sound, that could reveal the identity of the individual depicted. The UCLA Office of the Human Research Protection Program approved use of the edited clip. Following the conclusion of the project it was brought to our attention that, in the unedited video, the individual suffering the lice infestation – who is a minor – states that she does not want the recording to be posted online. We therefore sought permission from the individual and her parents to utilize the edited version of the video. Unfortunately, we were unable to reach these individuals and obtain permissions. For ethical reasons, we have therefore omitted the video clip from the archived materials and omitted the data obtained using this clip from both the archived dataset and the results reported in this paper.

Removing these data from the analyses does not substantively alter the results: In Study 1, the mean oral-gastric response to ectoparasite stimuli was 2.18 (SD = 1.84) including the lice video, compared to 2.12 (SD = 1.89) excluding the lice video, and the mean skin-surface response was 2.75 (SD = 1.81) including the lice video, compared to 2.71 (SD = 1.87) excluding the lice video. In Study 2, the mean oral gastric response to ectoparasite stimuli was 0.73 (SD = 1.12) including the lice video, compared to 0.61 (SD = 1.07) excluding the lice video, and the mean skin-surface response to ectoparasite stimuli was 2.25 (SD = 1.69) including the lice video, compared to 2.06 (SD = 1.69) excluding the lice video. These minor differences did not change the outcome of any of the tests of statistical significance.

2. Power analysis

Given that this was the first research to compare oral-gastric and skin-surface responses towards pathogen and ectoparasite cues, there was uncertainty about the expected effect size, and we sought to power the studies sufficiently to detect small effects. For 95% power to detect a small effect size (f = 0.1) using repeated measures ANOVA and a correlation of).5 between dependent measures, G*Power recommended a total sample size of 327. For Study 1 we chose to exceed this recommendation and recruited 400 participants (as detailed in the study preregistration), in part to allow for exclusions based on pre-registered criteria. Sample sizes for Studies 2 and 3 were partially determined by our ability to recruit participants (volunteers for a lab study in Study 2 and volunteer passers-by in Shanghai, China for Study 3) but we still recruited enough participants (333 in Study 2 and 394 in Study 3) to detect small effect sizes.

3. Note on the normality of the data

The data were distributed across all scores on the 7-point scales; however, there was some departure from normality, mostly due to left skewness, especially measures of oral-gastric responses towards ectoparasite cues, and skin-surface responses towards pathogen cues (as expected according to our hypothesis). However, the departure from normality was moderate and our sample sizes were large, and ANOVA (without transformation of data) is robust to moderate departures from normality, especially with large sample sizes such as the ones we used (Blanca et al., 2017; Schmider et al., 2010).

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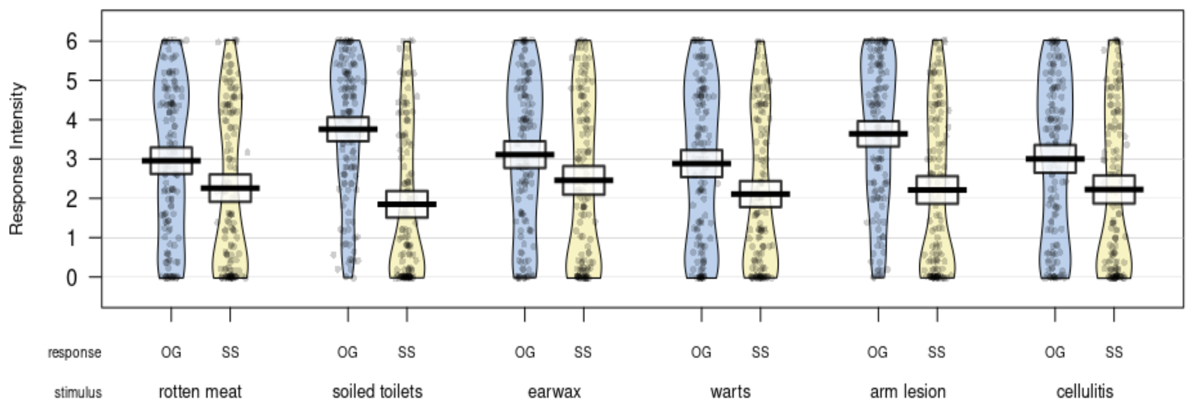
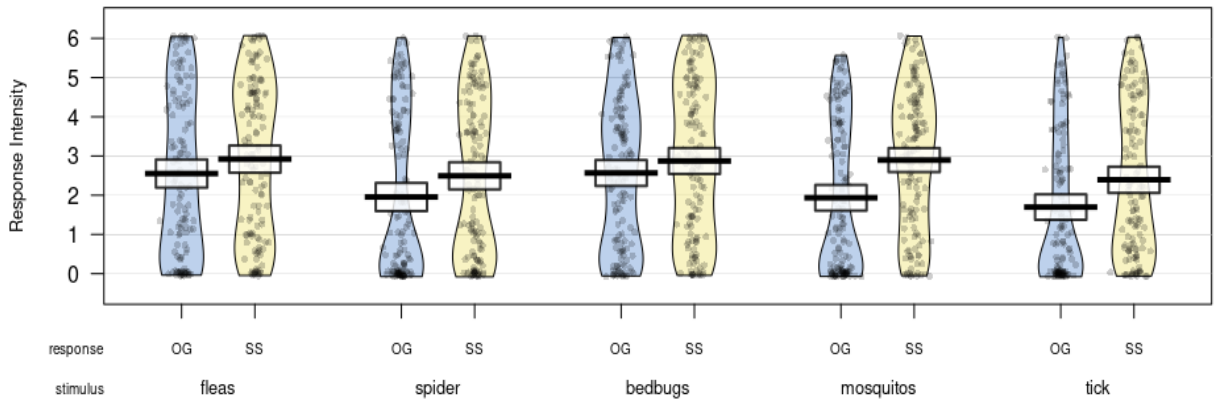
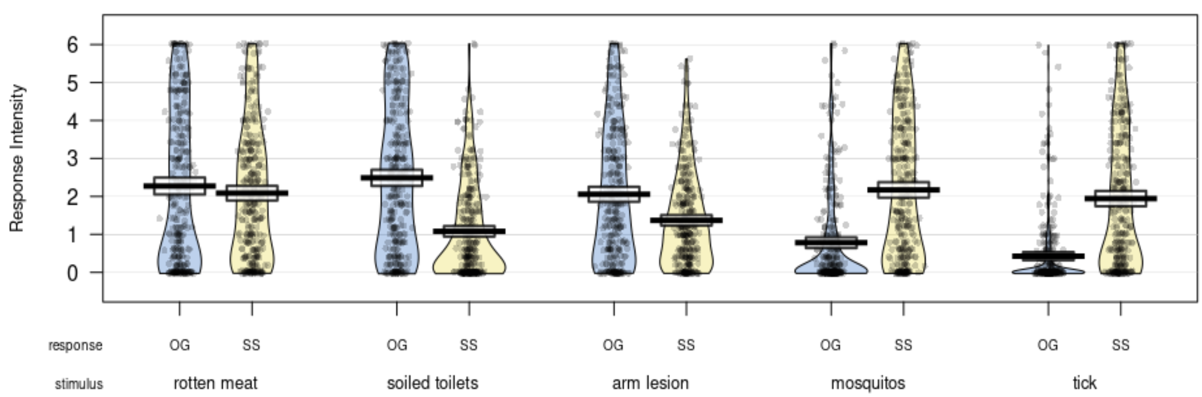


3. *Figure S1*. Mean responses to each pathogen video in Study 1 (U.S. MTurk sample). Response types are Ingestion/contamination reduction (IC) or Surface-guarding (SG).



3. *Figure S2*. Mean responses to each ectoparasite video in Study 1 (U.S. MTurk sample). Response types are Ingestion/contamination reduction (IC) or Surface-guarding (SG).



4. *Figure S3*. Mean responses to each pathogen and ectoparasite video in Study 2 (Californian student sample). Response types are Ingestion/contamination reduction (IC) or Surface-guarding (SG).

5. Table S1. Mean (and standard deviation) disgust and grossed-out ratings in Study 1 (MTurk) and Study 3 (China)

		Study 1	**Study 3**
Disgust	Pathogen videos	4.33 (1.57)	2.77 (1.9)
	Ectoparasite videos	3.21 (1.82)	2.49 (1.87)
Grossed-Out	Pathogen videos	4.32 (1.52)	2.74 (1.9)
	Ectoparasite videos	3.01 (1.83)	2.68 (1.81)

6. Table S2. Mean (and standard deviation) oral-gastric and skin-surface responses by participant sex

			Study 1 (MTurk)	**Study 2 (UCLA)**	**Study 3 (China)**
Oral-gastric	Male	Pathogen videos	3.12 (1.82)	1.65 (1.53)	2.13 (1.55)
	Female		3.42 (1.87)	2.47 (1.66)	1.67 (1.44)
Oral-gastric	Male	Ectoparasite videos	2.08 (1.87)	0.46 (0.84)	1.76 (1.51)
	Female		2.21 (1.94)	0.66 (1.14)	1.42 (1.19)
Skin-surface	Male	Pathogen videos	2.27 (1.96)	1.34 (1.25)	1.54 (1.49)
	Female		2.03 (1.84)	1.57 (1.20)	1.12 (1.15)
Skin-surface	Male	Ectoparasite videos	2.60 (1.84)	1.67 (1.54)	1.84 (1.57)
	Female		2.93 (1.92)	2.18 (1.72)	1.51 (1.27)

7. Survey Items used in Study 1

Please rate how much you agree that each of the following statements describes how you felt while watching the video:

	0 (Not at all) (0)	1 (Very Little) (1)	2 (a little) (2)	3 (somewhat) (3)	4 (moderately) (4)	5 (Strongly) (5)	6 (Very strongly) (6)
I felt a physical sensation in my stomach	○	○	○	○	○	○	○
I felt a physical sensation in my throat	○	○	○	○	○	○	○
I felt ticklish	○	○	○	○	○	○	○
I felt like I could vomit	○	○	○	○	○	○	○
I had a feeling of contamination	○	○	○	○	○	○	○
I felt an urge to pick at my skin	○	○	○	○	○	○	○
I felt an urge to cover my mouth or nose	○	○	○	○	○	○	○
I felt a physical sensation in my skin	○	○	○	○	○	○	○
I felt my skin crawl	○	○	○	○	○	○	○

ECTOPARASITE DEFENSE

After having watched the video, rate how much you agree with the following statements:

	0 (Not at all)	1 (Very Little)	2 (a little)	3 (somewhat)	4 (moderately)	5 (Strongly)	6 (Very strongly)
I felt nauseas	○	○	○	○	○	○	○
I felt goosebumps	○	○	○	○	○	○	○
I felt shivers	○	○	○	○	○	○	○
I felt an urge to shake myself	○	○	○	○	○	○	○
I felt an urge to wash	○	○	○	○	○	○	○
I felt an urge to scratch myself	○	○	○	○	○	○	○
I felt itchy	○	○	○	○	○	○	○
I felt like I would gag or retch	○	○	○	○	○	○	○
I felt unclean	○	○	○	○	○	○	○

ECTOPARASITE DEFENSE

How strongly did you experience the following feelings while watching the video:

	0 (Not at all) (0)	1 (Very little) (1)	2 (A Little) (2)	3 (Somewhat) (3)	4 (Moderately) (4)	5 (Strongly) (5)	6 (Very Strongly) (6)
Disgusted	○	○	○	○	○	○	○
Grossed out	○	○	○	○	○	○	○

About how many times did you scratch yourself?

	0	1	2	3	4	5	6	7	8	9	10

Survey Items used in Study 3 (Mandarin)

Q76 如果您同意参与本次研究，请选择“我同意”。您仍然可以在任何时候选择退出。

- 我同意
- 我不愿意参与

Q112 请完整观看下一页中的视频。在观看过程中，请仔细关注您的身体感受/感知。稍后，我们将会就这些身体感受/感知向您进行提问。在观看视频90秒后，页面将会自动跳转到答题页。

Q1 我们想了解您在观看该短片时的身体感受/感知。请您对以下感受的强烈程度进行评价。

ECTOPARASITE DEFENSE

【0-完全没有，1-几乎没有，2-轻微，3-有一些，4-中度，5-强烈，6-非常强烈】

- 我感觉我的胃部有生理反应。
- 我感觉我的喉咙有生理反应。
- 我感到痒（类似被挠胳肢窝的痒）。
- 我感觉快要呕吐了。
- 我有种被污染的感觉。
- 我有种想要抠/捏皮肤的冲动。
- 我有种想要捂住口鼻的冲动。
- 我感觉我的皮肤有生理反应。
- 我感到恶心。
- 我感觉我起了鸡皮疙瘩。
- 我感到哆嗦。
- 我有种想要抖动自己的冲动。
- 我有种想要清洗自己的冲动。
- 我有种想要抓挠自己的冲动。
- 我感到痒（皮肤瘙痒）。
- 我感觉我想干呕。
- 我感到不干净。

Q86 在观看视频时，您对以下感受的体验有多强烈？

- 恶心
- 厌恶

Q87 **您大**约抓挠了自己几次？

Q220 **您的年**龄是？

Q83 **以下哪个**选项最好地描述了您？

- **男性**
- **女性**
- **其他/不愿作答**

Q248 **晴天的**时候，天空是什么颜色的？

- 红色
- 绿色
- 蓝色

Q249 **您**对待此次研究有多认真？（请如实回答，您的回答将不会影响到您的报酬）

- **非常**认真
- **一般**
- **完全不**认真

Q78 **非常感**谢您参与本次研究。本次研究的目的是测量人们对于多种恶心刺激的反应，以理解**"病原体**恶心"**（感染、**粪便、腐烂的食物）和**"外寄生虫**恶心"**（虱子、蚊子、跳蚤）的区**别。我们希望通过研究人们对于这些刺激的不同反应来揭示其不同的演化起源。同时，我们也希望研究的结果能帮助我们进一步理解其他的演化学谜题，例如痒意。如果您有更多的问题，或是对研究结果感兴趣，请联系主要研究人员丹尼尔·费斯勒（Daniel M.T. Fessler）**博士。**邮箱：dfessler@anthro.ucla.edu.