Title
The skin crawls, the stomach turns: ectoparasites and pathogens elicit distinct defensive responses in humans

Journal
Proceedings of the Royal Society B, 288(1955)

ISSN
0962-8452

Authors
Kupfer, Tom R
Fessler, Daniel MT
Wu, Bozhi
et al.

Publication Date
2021-07-28

DOI
10.1098/rspb.2021.0376

PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Kupfer TR *et al*. 2021 The skin crawls, the stomach turns: ectoparasites and pathogens elicit distinct defensive responses in humans. *Proc. R. Soc. B* **288**: 20210376.
https://doi.org/10.1098/rspb.2021.0376

Received: 14 February 2021
Accepted: 7 July 2021

Subject Category:
Behaviour

Subject Areas:
behaviour, evolution

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

Author for correspondence:
Tom R. Kupfer
e-mail: thomas.kupfer@ntu.ac.uk

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5525614.

THE ROYAL SOCIETY
PUBLISHING

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[3,4,7], Sonia Alas[3], Theodore Samore[3,4], Vedika Lal[2], Tanvi P. Sakhamuru[3,8] and Colin Holbrook[9]

[1]Department of Psychology, Nottingham Trent University, Nottingham NG1 4FQ, UK
[2]Department of Social and Organizational Psychology, Vrije Universiteit, 1081 HV Amsterdam, The Netherlands
[3]Department of Anthropology, University of California, Los Angeles, Los Angeles, CA 90095, USA
[4]UCLA Center for Behavior, Evolution and Culture, Los Angeles, CA 90095-1553, USA
[5]UCLA Bedari Kindness Institute, Los Angeles, CA 90095, USA
[6]Center for Data Sciences, Brigham and Women's Hospital, Harvard Medical School, Boston, MA 02115, USA
[7]Department of Psychology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada
[8]University of California, Davis School of Law
[9]Department of Cognitive and Information Sciences, University of California, Merced, Merced, CA 95343, USA

TRK, 0000-0003-1147-6082; DMTF, 0000-0002-7795-7500; AMS, 0000-0001-9916-2074

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 defence system—including cutaneous sensory mechanisms and grooming behaviours—functionally suited to guard the body's surface. In two US 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 behavioural motivations. Participants reported more surface-guarding responses towards ectoparasite stimuli than towards pathogen stimuli, and more ingestion/contamination-reduction responses towards pathogen stimuli than towards ectoparasite stimuli. Like other species, humans appear to possess evolved psychobehavioural ectoparasite defence mechanisms that are distinct from pathogen defence mechanisms.

1. Introduction

Disgust is widely regarded as an evolved mechanism that shapes behaviour 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 defences tailored to this threat. Here, we report results of the first studies to test the hypothesis that humans possess different psychological and behavioural 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]. Behavioural 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 defence 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 hypothesize 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 *et al.* [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. By 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 behaviours, 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 behaviour documented in non-human 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].

(a) 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 US and one in China. Participants watched videos depicting ectoparasites, such as fleas, and videos depicting pathogen cues, such as faeces (see electronic supplementary material for links to stimuli). They then responded to questions measuring physical sensations and behaviours corresponding, respectively, to pathogen defence (e.g. nausea) and ectoparasite defence (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 US 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 ectoparasite defence [17,20], or the oral-gastric response characteristic of pathogen defence [33]. In Study 2, undergraduates at a US university viewed two ectoparasite videos and three 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 coloured by cultural meaning systems [27]. Accordingly, claims of species-typical psychobehavioural 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/, along with data. See electronic supplementary material for study materials.

2. Study 1: US MTurk sample

(a) Methods

(i) Participants

Four hundred US participants were recruited via Amazon's Mechanical Turk (filtered for workers with a 95% approval rating with at least 100 tasks approved) for a 20 min survey about 'bodily reactions to videos' in exchange for US \$2.00 (see electronic supplementary 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 min (the minimum time needed to view the videos and answer the questions as rapidly as possible) or more than 40 min, the final sample consisted of 395 individuals ($M_{\text{age}} = 33.48$, $\text{s.d.}_{\text{age}} = 9.32$; 138 females).

(ii) 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 generalizations of them (fleas, bed bugs, ticks, mosquitoes, and spiders), were each edited to be 90 s 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.

(iii) Measures

Granular items were created to measure the feelings, sensations, and behaviours postulated to be associated, respectively, with pathogen defence responses and ectoparasite defence responses. Pathogen defence 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 seven-point scale. Additionally, participants reported how many times they scratched themselves on a sliding scale from 0 to 10.

(iv) Procedure

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

(v) Analytical strategy

Analyses employed SPSS 25.0. First, factor analysis was used to determine whether items measuring ectoparasite defence and pathogen defence 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.

(b) Results

(i) 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 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, $r_{1449} = 0.62$.

(ii) 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, $F_{1,394} = 220.29$, $p < 0.001$, $\eta^2 = 0.36$. Simple effects analyses showed that pathogen videos elicited a higher oral-gastric response than skin-surface response, $F_{1,394} = 209.35$, $p < 0.001$, $\eta^2 = 0.35$, whereas ectoparasite videos elicited a higher skin-surface response than oral-gastric response, $F_{1,394} = 60.78$, $p < 0.001$, $\eta^2 = 0.13$ (figure 1). Electronic supplementary material, figure 1 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, $F_{2,392} = 5.31$, $p < 0.001$, $\eta^2 = 0.03$; women showed stronger responses to both pathogen and ectoparasite stimuli (see electronic supplementary material, table S2 for mean responses by sex).

(iii) 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, $\beta = 0.81$, $t_{392} = 15.54$, $p < 0.001$, but negatively associated with the skin-surface response, $\beta = -0.23$, $t_{392} = -4.49$, $p < 0.001$. Disgust reported towards ectoparasite stimuli was positively associated with both oral-gastric, $\beta = 0.44$, $t_{392} = 8.06$, $p < 0.001$, and skin-surface responses, $\beta = 0.33$, $t_{392} = 6.06$, $p < 0.001$.

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, $\beta = 0.85$, $t_{392} = 16.74$, $p < 0.001$, and skin-surface responses negatively associated, $\beta = -0.26$, $t_{392} = -5.21$, $p < 0.001$, with how grossed-out participants reported being towards pathogen stimuli. Both oral-gastric, $\beta = 0.45$, $t_{392} = 8.63$, $p < 0.001$, and skin-surface, $\beta = 0.33$, $t_{392} = 6.31$, $p < 0.001$, responses were associated with how grossed-out participants reported feeling towards ectoparasite stimuli.

(iv) Scratching behaviour

To test whether more scratching was elicited by ectoparasite stimuli than pathogen stimuli, a repeated-measures ANOVA was conducted with video content as the within-subjects variable. Participants reported scratching themselves more while watching ectoparasite videos ($M = 2.6$, s.d. $= 2.86$) than while watching pathogen videos ($M = 2.06$, s.d. $= 2.78$),

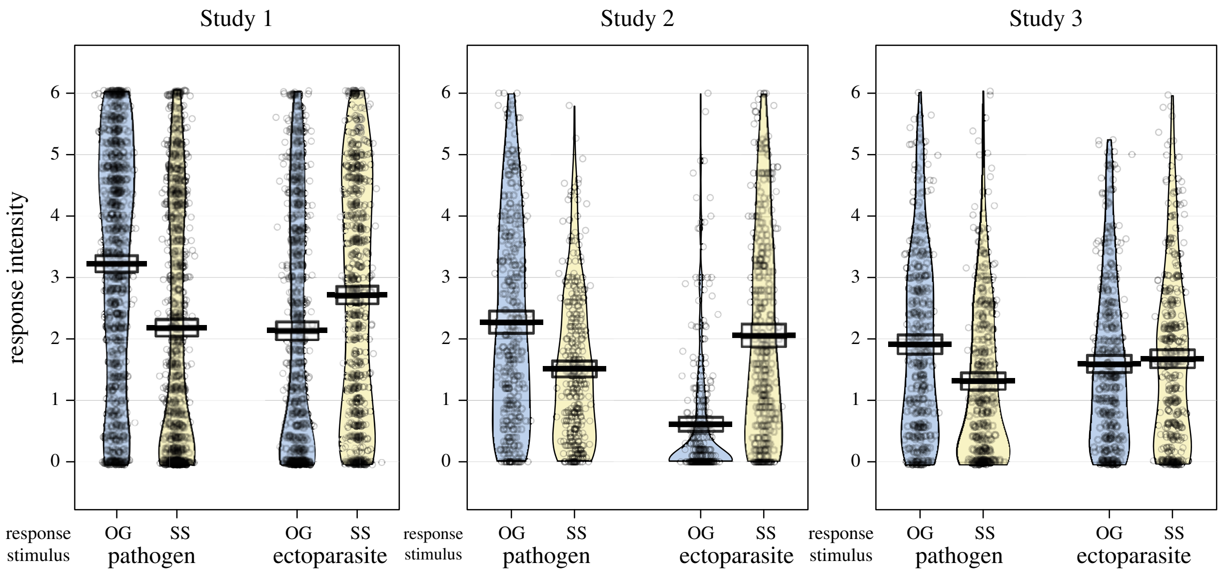

Figure 1. Participants' oral-gastric (OG) and skin-surface (SS) responses when viewing pathogen and ectoparasite video stimuli in Studies 1, 2, and 3. Response intensity ranges from 0, 'not at all' to 6, 'very strongly'. Raw data are jittered. Beans represent smoothed density of raw data. Boxes and lines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

Table 1. Factor loadings corresponding to each response type in each study. Loadings of the items used to make composite measures appear in bold.

	Study 1 (MTurk)			Study 2 (Californian students)			Study 3 (China)		
		Factor			Factor			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
	shake	0.76	0.13	shake	0.70	0.18	shake	0.61	0.29
	crawl	0.69	0.16	shiver	0.66	0.23	goosebumps	0.34	0.52
	goosebumps	0.68	0.20	goosebumps	0.66	0.15	shiver	0.23	0.63
	shiver	0.63	0.26						
oral-gastric responses	gag	−0.11	**1.00**	vomit	−0.15	**1.06**	vomit	−0.08	**0.99**
	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**
	throat	0.14	0.75	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
	unclean	0.27	0.62	wash	0.57	0.26	contamination	0.27	0.59
	wash	0.36	0.56				unclean	0.19	0.56
							wash	0.55	0.34

$F_{1,390} = 37.02$, $p < 0.001$, $\eta^2 = 0.09$. Scratching during pathogen videos was positively associated with the skin-surface response, $\beta = 0.78$, $t_{389} = 15.52$, $p < 0.001$, and negatively associated with the oral-gastric response, $\beta = -0.11$, $t_{389} = -2.23$, $p < 0.001$. Scratching during ectoparasite videos was positively associated with the skin-surface response $\beta = 0.53$, $t_{392} = 9.87$, $p < 0.001$, and with the oral-gastric response, $\beta = 0.25$, $t_{392} = 4.60$, $p < 0.001$.

3. Study 2: Californian student sample

(a) Methods

(i) Participants

Undergraduates ($N = 333$) were recruited at a large public university in California in fulfilment 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, $M_{\text{age}} = 19.39$, $\text{s.d.}_{\text{age}} = 1.61$).

(ii) Materials

Participants viewed three pathogen-cue videos (rotten meat, dirty toilets, and an infected lesion) and two ectoparasite videos[2] (mosquitoes 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.

(iii) Procedure

Participants watched the five 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.

(b) Results

(i) 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 (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, $r_{318} = 0.71$, $p < 0.001$.

(ii) Responses to pathogen and ectoparasite videos

To test whether pathogen and ectoparasite 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, $F_{1,317} = 431.79$, $p < 0.001$, $\eta^2 = 0.58$. Simple effects analyses showed that pathogen videos elicited a higher oral-gastric response than skin-surface response, $F_{1,317} = 105.54$, $p < 0.001$, $\eta^2 = 0.25$, whereas ectoparasite videos elicited a higher skin-surface response than oral-gastric response, $F_{1,317} = 344.61$, $p < 0.001$, $\eta^2 = 0.52$. Electronic supplementary material, 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, $F_{1,314} = 5.73$, $p < 0.001$, $\eta^2 = 0.05$; women showed stronger responses to both pathogen and ectoparasite stimuli (see electronic supplementary material, table S2 for details).

4. Study 3: Shanghai public sample

(a) Methods

(i) 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 Yuan (approx. \$4.60). 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 ($M_{\text{age}} = 31.85$, $\text{s.d.}_{\text{age}} = 12.36$).

(ii) 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 electronic supplementary material) 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.

(b) Results

(i) 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 (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, $r_{361} = 0.76$, $p < 0.001$.

(ii) Responses to pathogen and ectoparasite cues

To test whether pathogen and ectoparasite 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, $F_{1,353} = 99.81$, $p < 0.001$, $\eta^2 = 0.22$. Simple effects analyses showed that a stronger oral-gastric response was elicited by the pathogen video than by the ectoparasite video, $F_{1,353} = 21.29$, $p < 0.001$, $\eta^2 = 0.06$, whereas a stronger skin-surface response was elicited by the ectoparasite video than by the pathogen video, $F_{1,353} = 36.12$, $p < 0.001$, $\eta^2 = 0.09$ (figure 1). Participant sex did not interact with stimulus type, $F_{2,345} = 0.40$, $p = 0.67$, $\eta^2 = 0.00$, or response, $F_{2,345} = 1.26$, $p = 0.29$, $\eta^2 = 0.01$.

(iii) 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), $\beta = 0.83$, $t_{356} = 20.31$, $p < 0.001$, and grossed-out (*yànwù*, 厌恶), $\beta = 0.72$, $t_{356} = 14.68$, $p < 0.001$, whereas the skin-surface response did not, $\beta = -0.002$, $t_{356} = -0.05$, $p = 0.96$, and $\beta = 0.02$, $t_{356} = 0.46$, $p = 0.65$, respectively. Towards the ectoparasite video, the oral-gastric response predicted disgust, $\beta = 0.76$, $t_{352} = 16.15$, $p < 0.001$, and grossed-out, $\beta = 0.63$, $t_{353} = 10.9$, $p < 0.001$, but the skin-surface response ($\beta = 0.06$, $t_{352} = 1.3$, $p = 0.2$ and $\beta = 0.07$, $t_{353} = 1.19$, $p = 0.23$) did not.

(iv) Scratching behaviour

To test whether more scratching was elicited by ectoparasite stimuli than pathogen stimuli, a repeated-measures ANOVA was conducted with self-reported scratching behaviour and stimulus type (pathogen versus ectoparasite) as within-subjects factors. The ectoparasite video ($M = 1.01$, s.d. = 1.68) elicited more scratching behaviour than the pathogen video ($M = 0.88$, s.d. = 1.57), $F_{1,349} = 3.94$, $p = 0.05$, $\eta^2 = 0.01$. Scratching behaviour elicited by the ectoparasite video was positively associated with the skin-surface response, $\beta = 0.52$, $t_{351} = 7.09$, $p < 0.001$, but not with the oral-gastric response, $\beta = 0.05$, $t_{351} = 0.83$, $p = 0.41$. Scratching behaviour elicited by the pathogen video was positively associated with the skin-surface response, $\beta = 0.73$, $t_{352} = 13.24$, $p < 0.001$, and negatively associated with the oral-gastric response, $\beta = -0.13$, $t_{352} = -2.27$, $p = 0.02$.

5. Discussion

Overlooking both the differing task demands of defending against dissimilar threats and evidence that animals possess distinct behavioural defences 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 the avoidance of ingestible sources of pathogens. Ectoparasites elicited more surface-guarding responses, such as itching and scratching, which are functionally consistent with defence 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 defence 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 towards ectoparasite cues 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 defence and pathogen defence 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 apply. 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), defence mechanisms plausibly share some elementary architecture, resulting in overlap in patterns of responding [34]. 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 [35]. By 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. [36]). Consonant with this possibility, Stevenson *et al.* [37] have argued that oral-gastric disgust is frequently anticipatory, occurring to prevent contact with a stimulus. By contrast, ectoparasite defence 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 [38]. 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 ectoparasite cues. Similarly, measures of behaviour 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 focused on the 'behavioural immune system' in humans, largely because of links with important health and social outcomes, including intergroup attitudes and political sentiments [39]. Much of this research has focused on individual variation in pathogen disgust sensitivity [40]. Our findings raise the question of whether variation in ectoparasite defence sensitivity also contributes to these outcomes. Studies have also identified links between disgust and psychopathologies [2,33]. Some of these conditions, including skin-picking disorders [41], delusional infestation [42], and trypophobia [43], involve skin sensations and grooming behaviours, and may be more closely related to pathologies of ectoparasite defence 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 defence may importantly enhance campaigns to combat illnesses which kill or debilitate millions every year.

Ethics. All studies were approved by the UCLA Office of the Human Research Protection Program.

Data accessibility. Pre-registration documents, data, and code are archived at https://osf.io/xmsv4/. For study materials, see the electronic supplementary material.

Authors' contributions. T.R.K.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing-original draft, writing-review, and editing; B.W.: investigation, methodology, project administration; T.H.: investigation, methodology, project administration; S.A.: investigation, methodology, project administration; T.S.: investigation, methodology, project administration, writing-review, and editing; V.L.: formal analysis, project administration, writing-review, and editing; T.P.S.: investigation, methodology, project administration; D.M.T.F.: conceptualization, funding acquisition, investigation, methodology, project administration, writing-original draft, writing-review, and editing; A.M.S.: formal analysis, investigation, methodology, project administration, visualization; C.H.: investigation, methodology, project administration, writing-review, and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This research is supported by a European Union grant to T.R.K. (MSCA-IF-2017-800096-EmoPun) and a UCLA Gold Shield Award to D.M.T.F.

Acknowledgements. We thank FessLab and the Inner Heart Psychology Club for assistance.

Endnotes

[1] Because Study 2 was presented to participants bundled with another 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 the electronic supplementary material for full details.

[3] See the electronic supplementary material for a note on the normality of the data.

References

1. Curtis V, Biran A. 2001 Dirt, disgust, and disease: is hygiene in our genes? *Perspect. Biol. Med.* **44**, 17–31. (doi:10.1353/pbm.2001.0001)
2. Davey GC. 2011 Disgust: the disease-avoidance emotion and its dysfunctions. *Phil. Trans. R. Soc. B* **366**, 3453–3465. (doi:10.1098/rstb.2011.0039)
3. Oaten M, Stevenson RJ, Case TI. 2009 Disgust as a disease-avoidance mechanism. *Psychol. Bull.* **135**, 303. (doi:10.1037/a0014823)
4. Curtis V, Aunger R, Rabie T. 2004 Evidence that disgust evolved to protect from risk of disease. *Proc. R. Soc. B* **271**, 131–133. (doi:10.1098/rsbl.2003.0144)
5. Royzman EB, Leeman RF, Sabini J. 2008 'You make me sick': moral dyspepsia as a reaction to third-party sibling incest. *Motiv. Emot.* **32**, 100–108. (doi:10.1007/s11031-008-9089-x)
6. Rozin P, Haidt J, McCauley CR. 2008 Disgust. In *Handbook of emotions* (eds M Lewis, JM Haviland-Jones, LF. Barrett), pp. 757–776, 3rd edn. New York, NY: Guilford.
7. Tybur JM, Lieberman D, Kurzban R, DeScioli P. 2013 Disgust: evolved function and structure. *Psychol. Rev.* **120**, 65. (doi:10.1037/a0030778)
8. Hart BL. 1990 Behavioral adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* **14**, 273–294. (doi:10.1016/S0149-7634(05)80038-7)
9. Moller AP. 1990 Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* **71**, 2345–2357. (doi:10.2307/1938645)
10. Hillegass MA, Waterman JM, Roth JD. 2010 Parasite removal increases reproductive success in a social African ground squirrel. *Behav. Ecol.* **21**, 696–700. (doi:10.1093/beheco/arq041)
11. Lounibos LP. 2002 Invasions by insect vectors of human disease. *Annu. Rev. Entomol.* **47**, 233–266. (doi:10.1146/annurev.ento.47.091201.145206)
12. Akinyi MY, Tung J, Jeneby M, Patel NB, Altmann J, Alberts SC. 2013 Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Anim. Behav.* **85**, 559–568. (doi:10.1016/j.anbehav.2012.12.012)
13. Eckstein RA, Hart BL. 2000 Grooming and control of fleas in cats. *Appl. Anim. Behav. Sci.* **68**, 141–150. (doi:10.1016/S0168-1591(00)00095-2)
14. Mooring MS, Hart BL, Fitzpatrick TA, Reisig DD, Nishihira TT, Fraser IC, Benjamin JE. 2006 Grooming in desert bighorn sheep (*Ovis canadensis mexicana*) and the ghost of parasites past. *Behav. Ecol.* **17**, 364–371. (doi:10.1093/beheco/arj039)
15. Hawlena H, Bashary D, Abramsky Z, Khokhlova IS, Krasnov BR. 2008 Programmed versus stimulus-driven antiparasitic grooming in a desert rodent. *Behav. Ecol.* **19**, 929–935. (doi:10.1093/beheco/arn046)
16. Robinson L. 1907 The science of ticklishness. *N. Am. Rev.* **185**, 410–419.
17. Kupfer TR, Fessler DM. 2018 Ectoparasite defence in humans: relationships to pathogen avoidance and clinical implications. *Phil. Trans. R. Soc. B* **373**, 20170207. (doi:10.1098/rstb.2017.0207)
18. Hayes SL, Storch EA, Berlanga L. 2009 Skin picking behaviors: an examination of the prevalence and severity in a community sample. *J. Anxiety Disord.* **23**, 314–319. (doi:10.1016/j.janxdis.2009.01.008)
19. Kwok YLA, Gralton J, McLaws ML. 2015 Face touching: a frequent habit that has implications for hand hygiene. *Am. J. Infect. Control* **43**, 112–114. (doi:10.1016/j.ajic.2014.10.015)
20. Blake KR, Yih J, Zhao K, Sung B, Harmon-Jones C. 2016 Skin-transmitted pathogens and the heebie jeebies: evidence for a subclass of disgust stimuli that evoke a qualitatively unique emotional response. *Cogn. Emot.* **31**, 1153–1168. (doi:10.1080/02699931.2016.1202199)
21. Gerdes AB, Uhl G, Alpers GW. 2009 Spiders are special: fear and disgust evoked by pictures of arthropods. *Evol. Hum. Behav.* **30**, 66–73. (doi:10.1016/j.evolhumbehav.2008.08.005)
22. Lorenz AR, Libarkin JC, Ording GJ. 2014 Disgust in response to some arthropods aligns with disgust provoked by pathogens. *Global Ecol. Conserv.* **2**, 248–254. (doi:10.1016/j.gecco.2014.09.012)
23. Prokop P, Fančovičová J. 2010 The association between disgust, danger and fear of macroparasites and human behaviour. *Acta Ethol.* **13**, 57–62. (doi:10.1007/s10211-010-0075-4)
24. Kupfer TR. 2018 Why are injuries disgusting? Comparing pathogen avoidance and empathy accounts. *Emotion* **18**, 959. (doi:10.1037/emo0000395)
25. Nabi RL. 2002 The theoretical versus the lay meaning of disgust: implications for emotion research. *Cogn. Emot.* **16**, 695–703. (doi:10.1080/02699930143000437)
26. Shenhav A, Mendes WB. 2014 Aiming for the stomach and hitting the heart: dissociable triggers and sources for disgust reactions. *Emotion* **14**, 301–309. (doi:10.1037/a0034644)
27. Fiske AP. 2019 The lexical fallacy in emotion research: mistaking vernacular words for psychological entities. *Psychol. Rev.* **127**, 95–113. (doi:10.1037/rev0000174)
28. Roseman IJ, Wiest C, Swartz TS. 1994 Phenomenology, behaviors, and goals differentiate discrete emotions. *J. Pers. Soc. Psychol.* **67**, 206. (doi:10.1037/0022-3514.67.2.206)
29. Scarantino A. 2012 How to define emotions scientifically. *Emot. Rev.* **4**, 358–368. (doi:10.1177/1754073912445810)

30. Scherer KR. 2005 What are emotions? And how can they be measured? *Soc. Sci. Inform.* **44**, 695–729. (doi:10.1177/0539018405058216)
31. Royzman EB, Sabini J. 2001 Something it takes to be an emotion: the interesting case of disgust. *J. Theory Soc. Behav.* **31**, 29–59. (doi:10.1111/1468-5914.00145)
32. Rozin P, Haidt J, Fincher K. 2009 From oral to moral. *Science* **323**, 1179–1180. (doi:10.1126/science.1170492)
33. Olatunji BO, Armstrong T, Elwood L. 2017 Is disgust proneness associated with anxiety and related disorders? A qualitative review and meta-analysis of group comparison and correlational studies. *Perspect. Psychol. Sci.* **12**, 613–648. (doi:10.1177/1745691616688879)
34. Holbrook C. 2016 Branches of a twisting tree: domain-specific threat psychologies derive from shared mechanisms. *Curr. Opin. Psychol.* **7**, 81–86. (doi:10.1016/j.copsyc.2015.08.006)
35. Croy I, Laqua K, Süß F, Joraschky P, Ziemssen T, Hummel T. 2013 The sensory channel of presentation alters subjective ratings and autonomic responses toward disgusting stimuli—blood pressure, heart rate and skin conductance in response to visual, auditory, haptic and olfactory presented disgusting stimuli. *Front. Hum. Neurosci.* **7**, 510. (doi:10.3389/fnhum.2013.00510)
36. Hunt DF, Cannell G, Davenhill NA, Horsford SA, Fleischman DS, Park JH. 2017 Making your skin crawl: the role of tactile sensitivity in disease avoidance. *Biol. Psychol.* **127**, 40–45. (doi:10.1016/j.biopsycho.2017.04.017)
37. Stevenson RJ, Case TI, Oaten MJ, Stafford L, Saluja S. 2019 A proximal perspective on disgust. *Emot. Rev.* **11**, 209–225. (doi:10.1177/1754073919853355)
38. Oum RE, Lieberman D, Aylward A. 2011 A feel for disgust: tactile cues to pathogen presence. *Cogn. Emot.* **25**, 717–725. (doi:10.1080/02699931.2010.496997)
39. Schaller M, Murray DR, Bangerter A. 2015 Implications of the behavioural immune system for social behaviour and human health in the modern world. *Phil. Trans. R. Soc. B* **370**, 20140105. (doi:10.1098/rstb.2014.0105)
40. Terrizzi Jr JA, Shook NJ, McDaniel MA. 2013 The behavioral immune system and social conservatism: a meta-analysis. *Evol. Hum. Behav.* **34**, 99–108. (doi:10.1016/j.evolhumbehav.2012.10.003)
41. Gieler U *et al.* 2013 Self-inflicted lesions in dermatology: terminology and classification—a position paper from the European Society for Dermatology and Psychiatry (ESDaP). *Acta Derm. Venereol.* **93**, 4–12. (doi:10.2340/00015555-1506)
42. Freudenmann RW, Lepping P. 2009 Delusional infestation. *Clin. Microbiol. Rev.* **22**, 690–732. (doi:10.1128/CMR.00018-09)
43. Kupfer TR, Le AT. 2018 Disgusting clusters: trypophobia as an overgeneralised disease avoidance response. *Cogn. Emot.* **32**, 729–741. (doi:10.1080/02699931.2017.1345721)