

Human ticklishness is a widespread, culturally shared, and bodily organised sensory experience

Corresponding Author: Mr Ziliang Xiong

Version 0:

Decision Letter:

3rd February 2026

Dear Mr Xiong,

Thank you once again for your manuscript, entitled "Human ticklishness is a universal, cross-cultural, and somatotopically organized sensory experience," and for your patience during the peer review process.

Your manuscript has now been evaluated by 3 reviewers, whose comments are included at the end of this letter. Although the reviewers find your work to be of interest, they also raise some important concerns. We are interested in the possibility of publishing your study in *Nature Human Behaviour*, but would like to consider your response to these concerns in the form of a revised manuscript before we make a decision on publication.

In particular, Reviewers #1 and #3 remark that the negative social touch theory is not very strongly supported. We encourage you to be clear in your writing that this is only one possible explanation consistent with the data, and that the answer is not definitive. Reviewers #1 and #3 also comment on the lack of exploration of potential sex or gender differences. We suggest that you perform these analyses, or explain why this is not possible.

Finally, your revised manuscript must comply fully with our editorial policies and formatting requirements. Failure to do so will result in your manuscript being returned to you, which will delay its consideration. To assist you in this process, I have attached a checklist that lists all of our requirements. If you have any questions about any of our policies or formatting, please don't hesitate to contact me.

In sum, we invite you to revise your manuscript taking into account all reviewer and editor comments. We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

We hope to receive your revised manuscript within two months. I would be grateful if you could contact us as soon as possible if you foresee difficulties with meeting this target resubmission date.

With your revision, please:

- Include a "Response to the editors and reviewers" document detailing, point-by-point, how you addressed each editor and referee comment. If no action was taken to address a point, you must provide a compelling argument. When formatting this document, please respond to each reviewer comment individually, including the full text of the reviewer comment verbatim followed by your response to the individual point. This response will be used by the editors to evaluate your revision and sent back to the reviewers along with the revised manuscript.

- Highlight all changes made to your manuscript or provide us with a version that tracks changes.

- **EXTENDED DATA FIGURES**

When re-submitting your manuscript, please ensure that any supplementary figures and tables that are crucial to the manuscript's conclusions are converted into Extended Data figures and tables to increase visibility of these data. Extended Data figures and tables are online-only (present in the online PDF and full-text HTML versions of the paper), peer-reviewed display items that provide essential background to the article but are not included in the main article due to space constraints. A maximum of ten Extended Data display items (figures and tables) is permitted.

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Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work. Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

Sincerely,

[REDACTED]

Nature Human Behaviour

Reviewer expertise:

Reviewer #1: Cognitive neuroscience, social cognition, touch

Reviewer #2: Body representation, somatosensory perception, pain

Reviewer #3: Affective touch, pain, body representation

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

In the present study, the authors conducted a systematic investigation of ticklishness across cultures and somatotopic patterns using questionnaires and high-resolution body maps. Specifically, they compared levels of ticklishness across three cultures and examined whether body-dependent patterns could be explained by five hypotheses: the physiological theory, skin thickness theory, social touch exposure theory, vulnerability theory, and hedonic theory. They found that ticklishness exhibited culturally invariant patterns of tickling experiences. Furthermore, their body-part-dependent analyses demonstrated that, while the social touch exposure theory explained the data to some extent, a combination of all theories better predicted the somatotopic patterns of ticklishness. They argued that, in contrast to anatomy-related hypotheses, ticklishness is strongest in rarely touched regions, supporting Darwin's hypothesis.

This is an interesting and well-written study. As the authors suggest, there are few psychological or physiological studies on ticklishness, and we know little about its underlying mechanisms in contrast to those of discriminative touch. Ticklishness is often explained by physiological hypotheses (e.g., Cole et al., 2006; Varlamov et al., 2022). Along with Kiltani (2025), this study makes an important contribution to framing ticklishness in terms of existing theoretical hypotheses. I believe this paper is suitable for publication in this journal, provided that the authors address the concerns raised below.

Major concerns

1. Hypotheses regarding cultural differences

The Abstract appears to emphasize the contribution of Darwin's hypothesis (i.e., the social touch exposure theory), while the overall pattern of ticklishness is reported to be culturally invariant. However, the extent of social touch exposure is likely influenced by cultural norms, such as Hall's distinction between contact and non-contact cultures, which has been supported by previous studies. In this context, it is unclear whether the reported cross-cultural consistency is fully compatible with the social touch exposure hypothesis. Specifically, this hypothesis might predict that individuals in cultures with higher levels of social touch would experience greater ticklishness than those in less tactile cultures. Although the authors mention some cultural differences in ticklishness (line 134), such patterns may also be reflected in the somatotopic maps. The authors should either discuss this possibility in more detail or more clearly justify their interpretation.

2. Sex differences

It would be interesting to know whether the authors observed any sex differences. Previous studies have shown sex differences of social touch (e.g., Russo et al., 2019). If the authors' predictions are correct, male participants might therefore be expected to report higher levels of ticklishness than female participants. This possibility could be directly examined using the authors' existing dataset.

3. Physiological theory (Figure 4)

It is interesting to observe the relationship between inverse social touch and ticklishness. However, both may be driven by tactile sensitivity. In other words, certain body parts (e.g., the armpit) may be perceived as ticklish because they are physiologically more sensitive to tactile stimulation, which in turn could lead to less frequent social touch in these regions. Given that touch sensitivity is grounded in physiological mechanisms, it is unclear why tactile sensitivity (or tactility) is not explicitly considered under the physiological theory (Figure 4A). Because social touch exposure is contrasted with physiology and anatomy, this conceptual distinction should be further clarified. More generally, the authors do not sufficiently explain how these theories are not mutually exclusive. Please expand the logic on page 13 (line 409) to better articulate how these theoretical accounts can coexist.

4. Skin thickness theory and vulnerability theory

It is unclear why the authors did not collect subjective data on perceived skin thickness and vulnerability. While arterial diameter

may be related to physical vulnerability, this represents only one parameter of more complex physiological mechanisms. It is also important to consider participants' subjective sense of vulnerability and skin thickness. For example, the armpit contains relatively little superficial muscle bulk compared to neighboring regions, as it mainly serves as a fat-filled passageway between surrounding muscles. This anatomical feature could increase tactile sensitivity and the subjective experience of vulnerability. These issues should be discussed more explicitly.

5. Differences in gargalesis and knesmesis

The authors collected somatotopic maps for gargalesis but not for knesmesis. However, previous studies on ticklishness have often focused on knesmesis (e.g., Blakemore et al., 2000). Because knesmesis is also considered a form of ticklish sensation, it is unclear why the authors did not collect data on knesmesis and directly compare the two types (e.g., by contrasting gargalesis with knesmesis). This issue should be discussed.

6. Conclusion

The Conclusion (line 530) appears to emphasize the biological and evolutionary nature of ticklishness, whereas the Abstract highlights the social touch exposure theory. If ticklishness is primarily of biological origin, it is unclear why it cannot be sufficiently explained by physiological or anatomical factors alone. This apparent inconsistency should be clarified. This issue may stem from a lack of clarity regarding the predictions of the social touch exposure hypothesis (i.e., whether it predicts culturally variant or invariant patterns).

Minor comments

(1) Title

The title could be revised. It is unclear why the authors included the term "cross-cultural," given that they argue for cultural universalism. Moreover, as the data were collected from only three countries, "cross-cultural similarity (or regularities)" may be more appropriate than "universalism."

(2) Lines 411–415

I could not fully understand the procedure described here. The rationale for using PCA should be explained more clearly.

(3) Figures

(a) Some figures are difficult to read. In Figures 1A and 1B, as well as Figure 1D, it is unclear what the values 0 and 40 represent. In Figure 4, the yellow fonts are difficult to see.

(b) The number of data points in Figure 4 is unclear. It would be helpful to add maps for each body part. For example, the boundaries of body parts for each theory are not clearly defined. In addition, it is unclear why each theory includes a different number of variables. Should the same set of body parts be used to directly compare the hypotheses?

Reviewer #2 (Remarks to the Author):

This paper, "Human ticklishness is a universal, cross-cultural, and somatotopically organized sensory experience", by Xiong and Kiltner, reports a large, cross-cultural study of ticklishness. The authors combine a structured questionnaire, free-responses, and a body-colouring task in a large sample of participants from China, Greece, and the Netherlands. The authors report striking cross-cultural similarities in attitudes towards tickling and the spatial topography of self-reported ticklishness. They also use their data to test several longstanding theories of ticklishness, finding no simple answer, but a strong contribution from social touch.

This is a well-executed and very interesting study addressing an important and longstanding issue. Despite the ubiquity and familiarity of ticklishness, comparatively little psychological and neuroscientific research has investigated this topic. As such, this study makes a very significant contribution to the field and I strongly support publication. I do, however, have a few concerns and suggestions about the present version of the paper. I hope the authors find these helpful in revising this paper and in continuing with this interesting and valuable line of research.

My biggest concern relates to the use of the term 'somatotopy' (and its derivatives 'somatotopic' and 'somatotopically'). In neurophysiology, the word somatotopy has a precise technical meaning to indicate the property of neural representations of the body in which adjacent bits of the body are represented by adjacent neurons. Moreover, somatotopy in this sense is analogous to properties of other sensory systems with similar map-like structure, such as retinotopy in the visual system, in which adjacent bits of the retina are represented by adjacent neurons, and tonotopy in the auditory system, in which adjacent frequencies are represented by adjacent neurons.

In the present paper, in contrast, 'somatotopy' appears to be used in a vague and inconsistent way, that is not consistent with how it is typically used in the field. For example, in the first paragraph of the paper, the authors give a seeming definition of somatotopy: "why certain parts of the body are more sensitive to being tickled than others (somatotopy)". I find that definition of somatotopy to be insipid and not at all consistent with how the term is used in the field generally. When in the title of the paper the authors claim that ticklishness is "somatotopically organized", does that just mean that people report that some body parts (e.g., the soles of the feet, the armpits) are more ticklish than other body parts? It would have been astonishing if that wasn't true, so I have trouble accepting that as a main finding of the present study.

Similarly, on page 7, the authors write about the coloring maps that "the resulting t-scored maps revealed a highly somatotopic representation of ticklishness". I can't follow what that means, and I don't understand what pattern of results would have provided evidence against somatotopic representation in the sense that the authors mean here.

Other points:

1. Pg 7: regarding the t-tests on maps from the coloring test, I wasn't clear on the logic of using one-sample t-tests to compare mean scores to 0. As I understood the task, participants color in the body based on which regions of the body feel ticklish. They can click

multiple times to make the color more intense. So it seems that no coloring is a score of 0 and different intensities are positive scores. But the t-tests test the null hypothesis that scores are symmetrically distributed around 0 (i.e., that negative scores are as likely as positive scores). But it seems like negative scores can't exist at all. Could you please clarify this?

2. Pg 7: When using the Dice-Sorensen overlap coefficients, I agree that the scores appear to indicate high similarity. But is there some null distribution that these could be compared against? It seems important to understand how large a value might plausibly be expected to happen by chance.

3. Pg 2: Why is Aristotle cited in a footnote, rather than as a standard citation?

Reviewer #3 (Remarks to the Author):

This paper uses a relatively novel method to compare evidence for several longstanding theories of ticklishness within a large, multicultural dataset of self-reported touch body maps. The authors demonstrate a compelling association between ticklishness and body areas that are infrequently socially touched, with additional predictive value from areas with reduced tactile innervation density or reduced hedonic rating. The conceptual approach is innovative and the methodology and statistics are highly rigorous. The paper is strongly written. I am enthusiastic about the approach and findings, with some reservations and caveats:

1. While the three cultures are a strength, two of the cultures are European. Similarly, the age range of 18-30 limits generalizability to a variety of ages and generations. This could be included as a limitation and/or direction for replication and follow-up. Relatedly, the strong claim of cultural universality is not well supported. Three cultures is hardly enough to justify statements like "the universal cross-cultural nature of tickling" (line 461); "the phenomenology of ticklishness... are culturally invariant" (line 456); etc. It would also be important to show the sample population's basic demographic information, including education level, and to argue that nationality-based cultural differences are truly meaningful given contemporary international cultural similarities among 18-30-year-old internet users with university or high school-level educations. I recommend softening the universality and cross-cultural claims throughout and include a discussion of these and other important limitations, including those derived from data collected in online survey form in exchange for a monetary incentive.

2. I do not see any testing of sex or gender differences. Were these conducted? Can the authors examine exploratory effects of sex on tickle behavior or percepts? This could provide potential insight into the nature of tickling behavior.

3. Some participants reported tickling as an unpleasant experience. I am concerned that this rating was collected for tickling experiences in general, rather than probing variability in tickling experiences, such as the percent of tickling experiences that were positive versus negative, or the social context of the tickling. As a somewhat intimate form of touch, tickling is prone to abuse. Similar ratings might be expected for affective touch or genital touch, with many unpleasant ratings potentially reflecting instances of unwanted touch and many pleasant ratings reflecting wanted touch. Averaging across tickling experiences in general risks losing a rich variability of purposes, contexts, and effects of tickling behavior. At minimum, this concern should be discussed as a limitation of the current study and a direction for future follow-up. The exploratory analysis of sex effects might also hint at trends related to abuse.

4. Relatedly, I am concerned that the paper omits any discussion about intent or consent. Tickling that is con-consensual or that continues while the ticklee protests is not infrequently used as a form of control and even abuse that is sometimes more socially accepted than other forms of sexual abuse. Highly ticklish individuals can experience a loss of bodily control including inability to speak, difficulty breathing, or loss of bladder control. It is possible that tickling behavior is inherently an exploration of power and control over others' bodies in ways that can be either harmless (even functional) or harmful. It would be informative to consider how frequently such experiences occur in tickling behavior and what motivation or effects the tickler reports in their various experiences of tickling. This is distinct from the occurrence of tickling in the context of kink that is briefly referenced in the paper (although there may be overlap). Indeed, it is revealing that common responses to tickling reported in the current paper include resist and escape, and that tickling is typically directed to same-age or younger peers. However, I appreciate that the focus of the paper is on the reason for the spatial mapping of ticklishness, rather than its functional purpose. Please make sure this is clearly distinguished in the paper.

5. What were the inclusion and exclusion criteria for the study? If individuals with chronic pain were included, was pain explored as a variable influencing tickle experience?

6. The results provide support for the negative social touch theory, but statistically this is only a partial explanation. The authors conclude that ticklishness is driven by areas that almost never receive touch. However, this explanation is not fully satisfying. Children do not typically receive touch on their genitals, yet these areas are not described as ticklish or tickled. Similarly, the bottom of the foot is depicted as much more ticklish than the top, but no difference in touch frequency is apparent. Might this reflect differences in areas rarely exposed to the air (due to shirts and shoes)?

7. Is there any association between reported frequency of childhood tickling, and being less ticklish as an adult? In other words, if ticklishness relates to areas with less touch exposure, is this modifiable through behavior, or do the data suggest this is wired at least from childhood? Anecdotally it seems that ticklish children remain ticklish adults.

8. With thanks to my trainee trained in Anthropology: If the authors take their data to support the Darwinian theory that areas of the body less frequently touched by others tend to be more ticklish, then some variability in the somatotopy of social touch practices would be needed, along with correlated variation in ticklishness somatotopy, to claim that this data empirically supports or proves the Darwinian theory. I recommend including a discussion of this and a corresponding softening of the relevant claims.

9. With thanks to my trainee trained in Anthropology: Notably, Darwin also describes how he tickled the sole of his seven-day-old infant, who jerked it away with curled toes, something he took to mean that "such movements, as well as laughter from being tickled, are manifestly reflex actions." Also: "[Yet in the case] of laughter from being tickled, the mind must be in a pleasurable condition; a young child, if tickled by a strange man, would scream from fear." And: "From the fact that a child can hardly tickle itself, or in a much less degree than when tickled by another person, it seems that the precise point to be touched must not be known; so with the mind, something unexpected—a novel or incongruous idea which breaks through an habitual train of thought—appears to be a strong element in the ludicrous." Darwin's thoughts clearly go beyond just social exposure and towards a rather more complex understanding of the phenomenon which even includes a discussion of surprise. While the authors' claim that "ticklishness emerges as culturally invariant because it relates not with where people receive touch on their body, which can vary across societies, but with where they almost never receive touch," makes logical sense, Darwin himself talks about the soles of the feet and the buttocks as important exceptions. Given the limited number of ticklish body areas, these exceptions are especially salient and should be evaluated alongside the evidence presented when making claims about the social touch exposure theory. A nuanced discussion of these points as well as a more generous reading of Darwin would likely benefit the reader.

10. The Discussion suggests that tickling is highly conserved due to its functional importance. It does appear highly conserved, but the functional importance remains unclear. Do the authors have a theory about this? Either way, please clarify that this remains unclear and is an interesting direction for future research.

11. Supplement page 5 question 4- I find it a leading question to state that tickling in a professional context is inadvertent. This is likely, but it could also be intentional, for example if a photographer tickled a child to get them to smile. I suggest acknowledging this somewhere in the paper.

12. Page 8 line 246: Please clarify the statement that "all p-values = 1/1,001"? Is this the threshold or should it say $< 1/1,001$?

13. I suggest introducing the terms gargalesis and knismesis earlier on and defining them, as these are not common knowledge.

14. Extended Data Fig. 3.: is there a way to display the values for each region, or a heat map?

Reviewer #3 (Remarks on code availability):

The code is available. I do not have time/expertise to trial it.

Version 1:

Decision Letter:

Our ref: NATHUMBEHAV-25126187A

28th May 2026

Dear Dr Xiong,

Thank you for submitting your revised manuscript "Human ticklishness is a widespread, culturally shared, and bodily organised sensory experience" (NATHUMBEHAV-25126187A). It has now been seen by the original referees and their comments are below. As you can see, the reviewers find that the paper has improved in revision. We will therefore be happy in principle to publish it in Nature Human Behaviour, pending minor revisions to satisfy the referees' final requests and to comply with our editorial and formatting guidelines.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements within two weeks. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Please do not hesitate to contact me if you have any questions.

Sincerely,



Nature Human Behaviour

Reviewer #1 (Remarks to the Author):

To the authors,

I would like to thank the authors for addressing my previous concerns. I have a few additional minor comments:

(1) Figure 1k–p. While the percentages for each culture in childhood are clear, it is harder to interpret cultural similarities and differences in adulthood. It is currently unclear how to read the ratios across cultures in adulthood. Could the authors consider presenting these data in a way that facilitates comparison across cultures?

(2) Figure 2c (right). In the 4-fold cross-individual validation scheme, the training set is described as “60% and 20%.” However, it is unclear why the training data are split in this way. Could the authors clarify how the data were partitioned?

(3) Page 15. The authors downsampled non-ticklishness maps to match the number of ticklishness maps. Could the authors clarify whether this downsampling procedure was performed only once or repeated across multiple random samples (e.g., similar to the permutation procedure used for Dice–Sørensen coefficients)? If it was performed only once, it would be helpful to comment on the robustness of the results with respect to this random sampling.

(4) lines 659–671. In this part, the authors conduct a cross-validation analysis at the individual level using a stratified group cross-validation scheme. However, this procedure evaluates cross-participant generalization (i.e., generalization to unseen individuals), not cross-cultural generalization.

Given that they state “to test whether cultural similarities generalise to the individual level”, I think the current analysis does not fully match this phrasing. To directly test whether cultural similarities generalise across individuals, the authors would need to: (1) train a PLS regression model on a subset of individuals within one culture, (2) test the model’s performance both on unseen individuals from the same culture and on individuals from the other cultures, and (3) repeat this procedure for each of the three cultures.

Unless the authors perform such an analysis, I would recommend that they modify the phrase “To test whether cultural similarities generalise to the individual level” (line 659), and the corresponding Results text, to reflect that this analysis assesses cross-participant generalization within the pooled multi-cultural sample, rather than cross-cultural generalization per se. For instance, “whether the topography of ticklishness generalises across individuals in a multi-cultural sample” may be an alternative phrasing.

Reviewer #2 (Remarks to the Author):

The authors have satisfactorily addressed the points I raised in my previous review. I support publication.

Reviewer #3 (Remarks to the Author):

Thank you, the authors have fully addressed my concerns.

-Laura Case

Version 2:

Decision Letter:

Dear Mr Xiong,

We are pleased to inform you that your Article "Human ticklishness is a widespread, culturally shared, and bodily organised sensory experience", has now been accepted for publication in Nature Human Behaviour.

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To all reviewers:

We thank the reviewers for their constructive and thought-provoking comments. In addition to our point-by-point responses below, we report here two revisions made to the manuscript regarding the test of Darwin's theory:

In the previous version of the manuscript, we operationalise Darwin's theory regarding the spatial pattern of ticklishness (i.e., "*the parts of the body that are most easily tickled are those that are not commonly touched*") by inverting the maps of social touch, effectively creating maps where others touch us less frequently.

After extensive discussion within and outside our lab, partially prompted by a comment of Reviewer 3, in the present version of the manuscript, we expand his theory to include both touch applied to the body by others (social touch maps) and self-generated touch (self-touch maps). Our motivation was that Darwin's text does not explicitly target touch by others and that the text could also be interpreted as including self-touch. In order not to limit the interpretation of Darwin's text (and thus, our analysis) to social touch alone, we now adopt a more holistic approach to the sources of touch (self and others).

We thus conducted a new analysis using the *touch exposure* maps (i.e., combining social touch and self-touch maps to a composite map, and normalising and inverting it), and we report that these *inverse touch exposure* maps significantly predict the ticklishness topography and explain more variance than the previous approach focusing only on inverse social touch ($R^2 = 0.34$ vs. $R^2 = 0.19$). We believe that these new results provide a stronger and more complete test of Darwin's proposal. Identical to our previous version, as expected, inverse social touch remains a significant predictor when used separately (after applying multiple comparison corrections, now in Extended Data Fig. 5). However, inverse self-touch is also a significant predictor on its own (Extended Data Fig. 5).

Our conclusions remain unchanged: areas that are least frequently touched are reported as more ticklish. We clarify that this is the strongest result among single-theory tests, but still only a partial explanation of ticklishness topography. We have updated the manuscript and Extended Data to reflect these analyses.

The second revision refers to Figure 4e, which has now been updated to reflect the effect of inverse touch exposure (rather than only inverse social touch). We also note that the previous version did not correctly include all 35 body areas, although the analysis reported in the text was correct.

Reviewer #1:

This is an interesting and well-written study. As the authors suggest, there are few psychological or physiological studies on ticklishness, and we know little about its underlying mechanisms in contrast to those of discriminative touch. Ticklishness is often explained by physiological hypotheses (e.g., Cole et al., 2006; Varlamov et al., 2022). Along with Kiltani (2025), this study makes an important contribution to framing ticklishness in terms of existing theoretical hypotheses.

REPLY: We thank the reviewer for their positive evaluation, and we agree that the mechanisms of ticklishness remain poorly understood. Much of the prior work has focused on the light, feather-like form of tickle (often termed as knismesis or “light tickle”), whereas our study targets the intense, laughter-inducing form (gargalesis or “heavy tickle”). To avoid ambiguity, we have revised the text in the Introduction to make our focus on gargalesis more explicit (lines 28–29), and we refer to the previous studies by Cole and Varlamov on knismesis (line 29). We have also added text in our Discussion to discuss that knismesis may have a different topography (lines 439–442).

1. Hypotheses regarding cultural differences

The Abstract appears to emphasize the contribution of Darwin’s hypothesis (i.e., the social touch exposure theory), while the overall pattern of ticklishness is reported to be culturally invariant. However, the extent of social touch exposure is likely influenced by cultural norms, such as Hall’s distinction between contact and non-contact cultures, which has been supported by previous studies. In this context, it is unclear whether the reported cross-cultural consistency is fully compatible with the social touch exposure hypothesis. Specifically, this hypothesis might predict that individuals in cultures with higher levels of social touch would experience greater ticklishness than those in less tactile cultures. Although the authors mention some cultural differences in ticklishness (line 134), such patterns may also be reflected in the somatotopic maps. The authors should either discuss this possibility in more detail or more clearly justify their interpretation.

REPLY: We thank the reviewer for raising this comment.

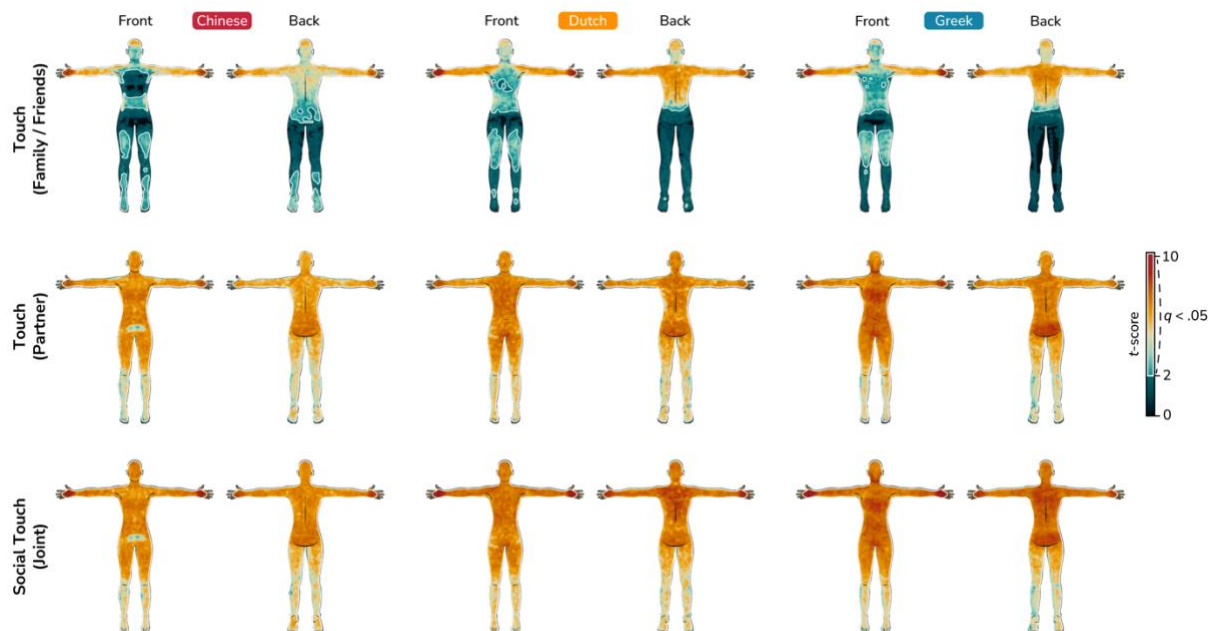
The reviewer is correct. Although Darwin’s theory is the one most strongly supported by our data (both in the univariate and multivariate analyses), we might have given the impression that it can fully explain ticklishness, and we apologise for this. Darwin’s predictor of inverse touch (now including both social and self-touch) explains a significant proportion of the variance in ticklish body areas (adjusted $R^2 = 0.47$). However, PC1—combining contributions from inverse touch, tactile innervation density, and pleasure—provided a better fit (adjusted $R^2 = 0.57$). Therefore, our interpretation is not that a single predictor or theory prevails, but rather that ticklishness is best accounted for by a broader socio–psycho–physiological interplay. We have revised the Abstract (lines 20–23) and amended the manuscript in several places to clarify that Darwin’s theory provides only a partial explanation (e.g., lines 16–19, lines 49–50).

As mentioned above, we have expanded Darwin’s theory to include touch exposure from both others and oneself. This combined measure of touch exposure provides the best predictor of

ticklishness topography when each theory is tested separately. When the different sources of touch exposure are examined independently (social, self), each significantly explains part of the ticklishness topography. Thus, the reviewer's question about cultural differences in relation to inverse social touch and ticklishness remains valid and relevant, regardless of the new operationalisation of Darwin's theory. We address the comment below.

We agree with the reviewer that at first glance, it may seem inconsistent that ticklishness is related to social touch exposure, while social touch varies across cultures and ticklishness does not. However, these patterns can be reconciled once we consider that our correlation captures the shared spatial structure of how social touch and ticklishness relate across the body regions, rather than the between-culture differences in overall levels.

First, prompted by the reviewer's comment, we have now examined cultural differences in our social touch maps and observed cultural differences—in strong alignment with the earlier literature the reviewer mentions. Specifically, our social touch maps replicate previously documented patterns of higher social touch prevalence in contact cultures (e.g., Southern European or Latino cultures) than non-contact cultures (e.g., Northern European or Asian cultures)¹⁻³. As shown in the figure below, we observe significantly lower levels of social touch in Chinese participants compared with Dutch and Greek participants. For example, we observe a lower number of significant pixels reflecting touch by family and friends among Chinese participants compared to Dutch and Greek participants. Additionally, we also observe a visible intensity difference in, for example, private parts, regarding partner touch or joint social touch when comparing Chinese and Dutch/Greek participants.



We reasoned that if cultural differences are more prominent in social touch than ticklishness, then the topography of ticklishness would generalise better across cultures than the topography of social touch. Thus, we directly tested whether PLS better predicted ticklishness patterns at the pixel level across cultures compared to social touch patterns. We trained and tested two models—one distinguishing ticklishness versus non-ticklishness, and the other distinguishing social touch versus non-social touch—against the same reference class: maps that were neither

labelled as ticklishness nor social touch (i.e., pain, tactility, pleasure, and self-touch). We then compared the difference in their AUROC scores to null distributions generated through permutation testing. The results showed that the social touch model performed significantly worse than the ticklishness model ($\Delta\text{AUROC} = -0.05$, $p = 0.021$, 95% CI: $[-0.091, -0.008]$), suggesting that ticklishness generalises better across cultures than social touch. We interpret this finding as additional evidence that ticklishness might be better described by shared biological and sensory mechanisms between cultures than by culturally specific norms.

Second, the important point that needs to be stressed regarding the relationship between inverse social touch and ticklishness is that cultural differences in social touch do not necessarily predict cultural differences in ticklishness; yet a relationship between the two can still be observed. When testing the different theories, we used the ticklishness topography that generalises across individuals derived from PLS models (Fig. 2e), which contains the information that transcends cultural differences. When testing Darwin's theory in particular, we tested for a relationship within this shared topography across cultures. This analysis asks whether regions that receive more social touch are also more ticklish; it does not test for between-culture differences. For example, if Culture A is more tactile than Culture B overall, but the relative pattern across body regions remains the same (for example, hands and face are touched more frequently than the back in both cultures), the linear relationship with ticklishness can be the same in both cultures. Therefore, cultures can differ in overall social touch levels while sharing the same ticklishness topography.

We have now conducted an additional analysis to better illustrate this point and directly address the reviewer's question. We first trained new PLS models across individuals within each culture to generate culture-specific PLS coefficient maps for ticklishness. These models demonstrated strong cross-validation performance, with AUROCs ranging from 0.79 to 0.92 (p -values = $1/1,001$). Next, we extracted the PLS coefficients corresponding to the 35 areas outlined in the body masks, following the same approach detailed in the manuscript. We then examined the relationship between ticklishness and inverse social touch across these 35 areas, including culture as a predictor (both main effect and interaction with inverse social touch). We compared two models: one that included culture as a predictor (and its interaction with inverse social touch) and another that excluded it—identically to the method we used to evaluate cultural effects on survey items. Both the BIC and Bayes factor provided strong evidence favouring the model without culture as a predictor ($\Delta\text{BIC} = 13.69$, $BF_{\text{No culture}} = 8.30$), suggesting that culture does not play a significant role in the relationship between inverse social touch and ticklishness. The same pattern of results was obtained when using the inverse touch (inverse social and self-touch combined): $\Delta\text{BIC} = 8.89$, $BF_{\text{No culture}} = 2.94$.

To summarise, we replicate previous literature on cultural effects in social touch, and we show that cultural differences in social touch do not necessarily impose cultural differences in the ticklishness topography, as the relationship between the two concerns the body regions.

2. Sex differences

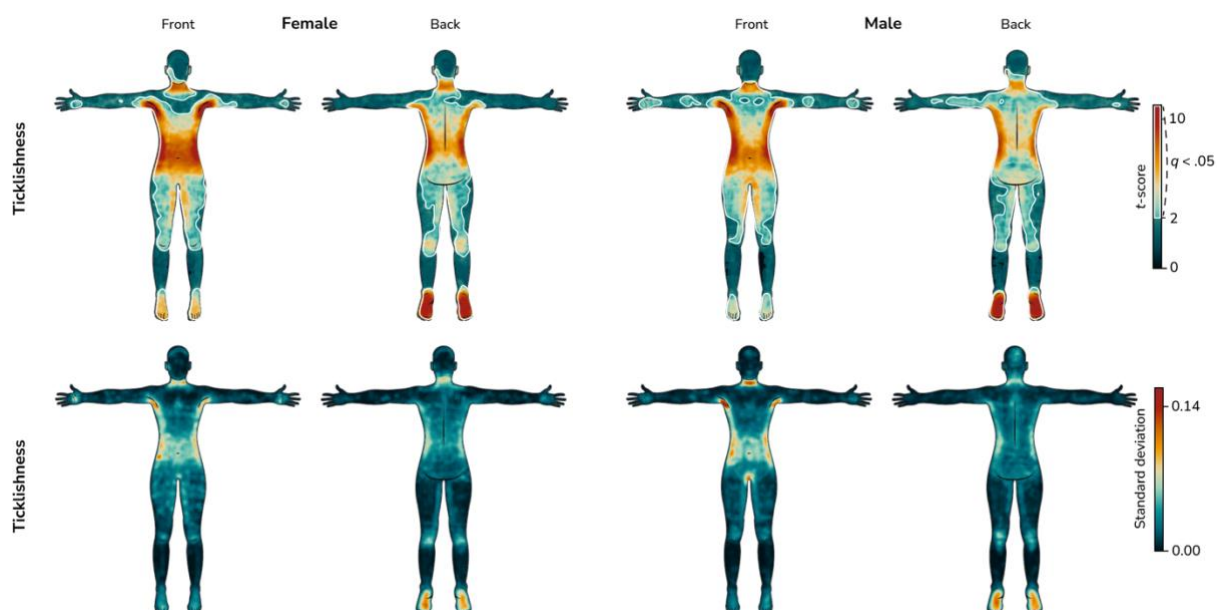
It would be interesting to know whether the authors observed any sex differences. Previous studies have shown sex differences of social touch (e.g., Russo et al., 2019). If the authors' predictions are correct, male participants might therefore be expected to report higher levels of ticklishness than female participants. This possibility could be directly examined using the authors' existing dataset.

REPLY: We thank the reviewer for raising this point. We understand that the reviewer refers to the meta-analysis by Russo et al. (2020) on “*Affective touch: A meta-analysis on sex differences*”, which showed that women rated affective touch as more pleasant than men.

We have followed the reviewer's suggestion, and we have now conducted exploratory analyses of sex effects. We followed the same culture-based model comparison approach used in the manuscript, but here aggregated participants across all three cultures to maximise power. Three participants who selected “*prefer not to say*” regarding their sex were excluded, resulting in a final sample of $N = 445$.

Overall, we did not find meaningful sex effects in self-reported ticklishness, frequency of tickling experiences, or affective values associated with tickling behaviours, either as a ticklee or tickler, neither in childhood nor in adulthood, with the model excluding sex as a predictor being supported for all survey items (ΔBIC range: [1.87, 29.04]).

With respect to the ticklishness maps, we computed the t -scored maps separately for female and male participants (collapsed across cultures). As shown below, the spatial patterns for ticklishness, along with their variability, are very similar between sexes: the neck, torso, armpits, and soles of feet are among the most commonly reported areas of the body that are ticklish. As shown below, the spatial patterns for ticklishness (*top*), along with their variability (*bottom*), are very similar between sexes: the abdomen, armpits, and soles of feet are among the most commonly reported areas of the body that are ticklish.



To explore whether the ticklishness topography is consistent across sexes or unique to each, we trained PLS models on ticklishness versus non-ticklishness maps separately using data from male and female participants (identically to our approach regarding cultures). When these

models were tested on participants of the opposite sex, they demonstrated strong generalizability, suggesting that the ticklishness topography generalizes between males and females (tested on males: AUROC = 0.85, $p = 1/1,001$, 95% CI: [0.31, 0.40]; tested on females: AUROC = 0.86, $p = 1/1,001$, 95% CI: [0.32, 0.40]).

We have now added text in our Results (lines 163–166, 224–226) to present these new analyses, and we also mention that these analyses are exploratory.

3. Physiological theory (Figure 4)

It is interesting to observe the relationship between inverse social touch and ticklishness. However, both may be driven by tactile sensitivity. In other words, certain body parts (e.g., the armpit) may be perceived as ticklish because they are physiologically more sensitive to tactile stimulation, which in turn could lead to less frequent social touch in these regions. Given that touch sensitivity is grounded in physiological mechanisms, it is unclear why tactile sensitivity (or tactility) is not explicitly considered under the physiological theory (Figure 4A). Because social touch exposure is contrasted with physiology and anatomy, this conceptual distinction should be further clarified. More generally, the authors do not sufficiently explain how these theories are not mutually exclusive. Please expand the logic on page 13 (line 409) to better articulate how these theoretical accounts can coexist.

REPLY: We thank the reviewer for raising these questions regarding the relationships among tactile sensitivity, inverse (social) touch, and ticklishness.

First, we agree with the reviewer that we should more explicitly explain why these theories are not mutually exclusive. We have now added text to clarify that different theories can jointly shape ticklishness (lines 341–344).

Second, we would like to mention that the reviewer's proposed explanation (i.e., highly sensitive areas to touch are more ticklish, and thus receive less touch) is not supported by our data. In our PCA, tactile innervation density loaded negatively on PC1 (loading = -0.92). Similarly, in the updated PCA, which incorporates inverse touch combining both social and self-touch, the loading remained negative (loading = -0.88). These indicate that body areas reported as more ticklish tended to have *lower* A β afferent innervation density (i.e., lower tactile innervation as a proxy for discriminative touch sensitivity), rather than higher. This shouldn't be surprising though, as our hands, which are densely innervated, are not a particularly ticklish area of our body. This pattern also applies to the reviewer's example: although the armpit is indeed reported as less touched and more ticklish than, for example, the face, it is not a body region characterised by particularly high A β afferent density.

Third, the reviewer is correct in that we did not explain in detail how each theory was operationalised. For the *physiological* theory, we used data on A β afferent innervation density⁴, which we considered the most direct test of the link between skin physiology and ticklishness. When designing our analyses, we chose not to use prior psychophysical measurements (e.g., ref.⁵) because these are limited to a few body locations, nor our own tactility maps, as participants had previously completed multiple ticklishness survey items, which could bias reports of touch sensitivity toward tickle sensitivity. We have now added text in our Methods to explain in detail how each theory was operationalised (lines 711–727).

4. Skin thickness theory and vulnerability theory

It is unclear why the authors did not collect subjective data on perceived skin thickness and vulnerability. While arterial diameter may be related to physical vulnerability, this represents only one parameter of more complex physiological mechanisms. It is also important to consider participants' subjective sense of vulnerability and skin thickness. For example, the armpit contains relatively little superficial muscle bulk compared to neighboring regions, as it mainly serves as a fat-filled passageway between surrounding muscles. This anatomical feature could increase tactile sensitivity and the subjective experience of vulnerability. These issues should be discussed more explicitly.

REPLY: We apologise again for not being clear enough in the previous version of our manuscript regarding how each theory was operationalised.

For the *vulnerability* theory, we used external data of arterial diameter rather than self-reported vulnerability, as the latter would likely introduce variability in how participants interpret vulnerability and could easily be confounded with perceived pain. For example, participants might rate areas such as their fingers as highly “vulnerable” because they are sensitive to pain. However, this perception of vulnerability may not necessarily align with the actual severity of injuries to the fingers, which was framed for physical vulnerability in the theory. Specifically, vulnerability was described in terms of the potential consequences of an injury in certain body regions, e.g., “...in any one of the regions specified above, a deadly wound would be inflicted.” (ref. ⁶, p. 415). In this context, vascular features offer a close anatomical proxy for bodily regions where injury could plausibly lead to severe outcomes.

For the *skin thickness* theory, we used anatomical maps of skin thickness rather than subjective estimates, which would depend on participants' knowledge of anatomy and could introduce confusion. For example, participants might incorrectly assume that areas like the palms have thin skin because they feel sensitive, whereas these regions are not among the thinnest in the body.

We have now added text in our Methods about this point (lines 717–724).

5. Differences in gargalesis and knesmesis

The authors collected somatotopic maps for gargalesis but not for knesmesis. However, previous studies on ticklishness have often focused on knesmesis (e.g., Blakemore et al., 2000). Because knesmesis is also considered a form of ticklish sensation, it is unclear why the authors did not collect data on knesmesis and directly compare the two types (e.g., by contrasting gargalesis with knesmesis). This issue should be discussed.

REPLY: We thank the reviewer for this comment. As also noted by the reviewer, the present study focuses on intense, laughter-inducing tickling (gargalesis), which is the less studied form of tickling, compared to the light, feather-like sensations (knesmesis) that have been addressed in multiple studies. We agree that directly comparing knesmesis and gargalesis would provide valuable insights and help to dissociate the two. Indeed, in a recent review of the literature on

ticklishness, we noted that these two types of tickle sensations are often mixed and emphasised the need to experimentally distinguish between them⁷. We view the present study as a first step toward systematically characterising gargalesis, thereby informing future work specifically aimed at distinguishing between the two. We have added text in the Introduction (lines 28–29) and Discussion (lines 440–442) to clarify this distinction, mention the specific focus of the present study, and prompt related future research.

6. Conclusion

The Conclusion (line 530) appears to emphasize the biological and evolutionary nature of ticklishness, whereas the Abstract highlights the social touch exposure theory. If ticklishness is primarily of biological origin, it is unclear why it cannot be sufficiently explained by physiological or anatomical factors alone. This apparent inconsistency should be clarified. This issue may stem from a lack of clarity regarding the predictions of the social touch exposure hypothesis (i.e., whether it predicts culturally variant or invariant patterns).

REPLY: We thank the reviewer for this comment.

First, we did not intend to suggest that the touch exposure theory is the sole explanation of ticklishness. In the present study, we evaluated candidate theories both in isolation and in combination. While inverse touch showed a reliable association with the ticklishness map, our multivariate results (PCA) indicate that ticklishness is better captured by a combination reflecting multiple contributors: inverse touch, pleasure, and tactile innervation density. Accordingly, the inverse touch–ticklishness relationship is only part of the conclusion. Interestingly, our new analysis considering touch exposure both by others and oneself also speaks in favour of touch exposure regardless of the source as a significant predictor of the ticklishness topography. We have revised the Abstract (lines 22–23) to more accurately convey the multi-factor contribution and to align it with the Discussion (lines 422–423).

Second, we would also like to stress that in the present study we only tested whether innervation density and arterial diameter can explain the ticklishness topography, aiming to reflect the physiological and anatomical dimensions. These two features should not be viewed as an exhaustive investigation of the role of physiology and/or anatomy on ticklishness. For example, one cannot exclude that other anatomical or physiological features (e.g., differences in brain anatomy or in skin biomechanics) are relevant. Moreover, we think that biological or evolutionary traits should not be restricted to anatomical and physiological characteristics (such as the properties of skin or peripheral nerves), but can include behaviours that promote the organism's survival or reproduction. For example, caregiving behaviours in parents can be considered biological or evolutionary traits because they increase offspring survival. Based on similarities in tickling behaviours we observe between humans and other great apes, as well as the fact that tickling behaviours and topography generalise across cultures, we argue that ticklishness may reflect a biological or evolutionary trait. We have now rephrased our text in the Discussion to exclusively refer to the similarities with other great apes, and we explicitly acknowledge that we do not currently know the functional relevance of tickling (lines 461–463).

Finally, it is important to note that the touch exposure theory does not make any culture-specific predictions; as stated in our reply to point #1, cultures might differ in social touch but not in ticklishness if the spatial structure within the body remains the same.

Minor comments

(1) Title

The title could be revised. It is unclear why the authors included the term “cross-cultural,” given that they argue for cultural universalism. Moreover, as the data were collected from only three countries, “cross-cultural similarity (or regularities)” may be more appropriate than “universalism.”

REPLY: We agree with the reviewer. We misused the term “cross-cultural” when we intended to refer to effects across cultures. We also used the term “universal” to describe the high prevalence of tickling behaviours.

We have now revised the manuscript and instead refer to a “widespread” sensory experience that “shares/generalises across cultures.” We have also revised the title and replaced “cross-cultural” throughout the manuscript. All changes are highlighted in yellow.

(2) Lines 411–415

I could not fully understand the procedure described here. The rationale for using PCA should be explained more clearly.

REPLY: Our intention in using PCA was to test whether ticklishness topography is better accounted for by (a) single-theory predictors considered one at a time vs. (b) a reduced set of latent components that summarise the shared structure across predictors from the five theories.

This PCA analysis was therefore meant to complement our single-predictor regression approach: whereas the regressions quantify how much variance each predictor dataset explains in isolation, PCA addresses the fact that several theory-derived datasets may be correlated with one another (i.e., multicollinearity) and may jointly reflect broader underlying constructs. PCA is an established dimensionality reduction technique that transforms the original, collinear predictors into orthogonal principal components, which can then be used to predict ticklishness without statistical instability due to multicollinearity.

To address the reviewer’s concern, we have revised the Results to more explicitly explain our motivation for using PCA (lines 341–344).

(3) Figures

(a) Some figures are difficult to read. In Figures 1A and 1B, as well as Figure 1D, it is unclear what the values 0 and 40 represent. In Figure 4, the yellow fonts are difficult to see.

REPLY: We apologise for our figures not being sufficiently clear.

For Figures 1a and 1b, each square corresponds to one participant who reported having been tickled (or tickling others) at least once in their lifetime. For Figure 1d, the values correspond to counts of the most frequently used words participants provided to describe their tickling experiences. To make these panels easier to interpret, we added visual elements and legend texts directly in the figures.

We also agree that the yellow/light-coloured font in Figure 4 was difficult to read. We have adjusted the labelling style to improve contrast.

(b) The number of data points in Figure 4 is unclear. It would be helpful to add maps for each body part. For example, the boundaries of body parts for each theory are not clearly defined. In addition, it is unclear why each theory includes a different number of variables. Should the same set of body parts be used to directly compare the hypotheses?

REPLY: We thank the reviewer for his/her questions about the masking procedure and the comparability of analyses across theories.

First, we agree that the number of data points contributing to each scatterplot in Figure 4 was not sufficiently clear. In the revised figure, we now explicitly report the number of body areas for each panel. Additionally, the information regarding body mask boundaries is provided as an Extended Data figure (Extended Data Fig. 3).

Second, we need to emphasise that each theory necessarily includes a different number of body areas because the datasets used as predictors included a different number of body areas. For example, the external dataset on arterial diameter included 15 body areas; consequently, our test was bounded to these 15 areas. Similarly, the dataset used for skin thickness included 23 body areas, and thus, our assessment was restricted to these 23 areas. Overall, for the single-theory tests, we used all available body areas for each theory to best capture the variance in that dataset and to maximise sensitivity.

For the PCA, however, the comparison requires a set of body areas matched across all theories (and datasets). Accordingly, we restricted the PCA to the common body regions available across all theory-based datasets (i.e., 11 body areas), so that the resulting components are computed from the same set of body areas.

Reviewer #2:

This is a well-executed and very interesting study addressing an important and longstanding issue. Despite the ubiquity and familiarity of ticklishness, comparatively little psychological and neuroscientific research has investigated this topic. As such, this study makes a very significant contribution to the field and I strongly support publication.

REPLY: We thank the reviewer for his/her positive assessment.

My biggest concern relates to the use of the term ‘somatotopy’ (and its derivatives ‘somatotopic’ and ‘somatotopically’). In neurophysiology, the word somatotopy has a precise technical meaning to indicate the property of neural representations of the body in which adjacent bits of the body are represented by adjacent neurons. Moreover, somatotopy in this sense is analogous to properties of other sensory systems with similar map-like structure, such as retinotopy in the visual system, in which adjacent bits of the retina are represented by adjacent neurons, and tonotopy in the auditory system, in which adjacent frequencies are represented by adjacent neurons.

In the present paper, in contrast, ‘somatotopy’ appears to be used in a vague and inconsistent way, that is not consistent with how it is typically used in the field. For example, in the first paragraph of the paper, the authors give a seeming definition of somatotopy: “why certain parts of the body are more sensitive to being tickled than others (somatotopy)”. I find that definition of somatotopy to be insipid and not at all consistent with how the term is used in the field generally. When in the title of the paper the authors claim that ticklishness is “somatotopically organized”, does that just mean that people report that some body parts (e.g., the soles of the feet, the armpits) are more ticklish than other body parts? It would have been astonishing if that wasn’t true, so I have trouble accepting that as a main finding of the present study.

Similarly, on page 7, the authors write about the coloring maps that “the resulting t-scored maps revealed a highly somatotopic representation of ticklishness”. I can’t follow what that means, and I don’t understand what pattern of results would have provided evidence against somatotopic representation in the sense that the authors mean here.

REPLY: We thank the reviewer for raising this concern regarding our use of the term “somatotopy.” We agree with the reviewer that in neurophysiology, “somatotopy” has a specific technical meaning indicative of neuronal representations. Our use of the term was not intended to imply such a claim, and we acknowledge that our wording could be interpreted as inconsistent with standard usage in the field. Accordingly, we have replaced “somatotopy” and its derivatives throughout the manuscript, including the title, with “bodily organised” and “topography” to refer to the spatial pattern (highlighted in yellow).

As for the question regarding the meaning of *t*-scored maps, our intention was to describe the spatial activation pattern of the reported ticklishness across body regions as revealed by the thresholded, group-level *t*-scored maps.

Other points:

1. Pg 7: regarding the t -tests on maps from the coloring test, I wasn't clear on the logic of using one-sample t -tests to compare mean scores to 0. As I understood the task, participants color in the body based on which regions of the body feel ticklish. They can click multiple times to make the color more intense. So it seems that no coloring is a score of 0 and different intensities are positive scores. But the t -tests test the null hypothesis that scores are symmetrically distributed around 0 (i.e., that negative scores are as likely as positive scores). But it seems like negative scores can't exist at all. Could you please clarify this?

REPLY: The reviewer is correct. Given our task design, pixel intensities are bounded at 0 (i.e., negative values cannot occur). A one-sample t -test, however, does not assume that the raw values are symmetrically distributed around 0, nor does it require the existence of negative observations. Instead, it tests whether the population mean differs from a reference value (here, 0), under the assumption that the sampling distribution of the mean is approximately normal. Raw data can be bounded and a one-sample t -test against 0 can still be valid, particularly when means are computed from large sample sizes. By the Central Limit Theorem, the sampling distribution of the mean approaches normality as the sample size increases, even when the underlying data are non-normal and bounded. In our case, the per-culture sample sizes are relatively large (Chinese: $N = 149$; Dutch: $N = 150$; Greek: $N = 149$), so the sampling distribution of the mean is expected to be close to normal even if individual pixel intensities are zero-inflated and non-normal.

Additionally, we would like to emphasise that the inferred p -values from these one-sample t -tests are used primarily as a conventional way to visualise and summarise the group-level bodily topographies rather than as a central inferential result. Here, 0 is a meaningful reference point because it corresponds to “no colouring.” The t -scored maps therefore quantify, at each pixel, whether participants' mean colouring intensity is reliably greater than 0, and they provide a standardised effect index (i.e., t -score; mean relative to variability across participants) that is commonly used as a group-level descriptive metric and has been previously used for reporting group-level social touch topography¹. While we summarised thresholded t -scored maps using FDR-corrected p -values (q), our main results—including PLS, similarity matrix analyses (and the follow-up hierarchical clustering analysis), and theory testing—are based on analyses using either the raw intensity values or group-level t -scores rather than relying on q -values from one-sample t -tests.

2. Pg 7: When using the Dice-Sorensen overlap coefficients, I agree that the scores appear to indicate high similarity. But is there some null distribution that these could be compared against? It seems important to understand how large a value might plausibly be expected to happen by chance.

REPLY: We thank the reviewer for this helpful suggestion. To address the concern, we conducted a permutation test for each pairwise cross-cultural comparison. We first computed the observed Dice coefficient between the two culture-level ticklishness maps (i.e., by family/friends, and partner). We then generated a null distribution by randomly permuting the spatial locations of

pixels in one culture's map while leaving the other culture's map unchanged (1,000 permutations). One-sided p -values were computed as the proportion of permuted Dice coefficients greater than or equal to the observed coefficient, similar to our approach of permutation testing for evaluating PLS model performance.

Across all pairwise comparisons, the observed Dice coefficients were significantly larger than any value in the corresponding null distributions (all p -values = 1/1,001). Specifically, for ticklishness elicited by family/friends: Chinese vs. Dutch, $\beta_{\text{Dice}} = 0.76$, 95% CI: [0.52, 0.53]; Chinese vs Greek, $\beta_{\text{Dice}} = 0.83$, 95% CI: [0.61, 0.61]; Dutch vs Greek, $\beta_{\text{Dice}} = 0.86$, 95% CI: [0.59, 0.60]. And for ticklishness elicited by partner: Chinese vs. Dutch, $\beta_{\text{Dice}} = 0.81$, 95% CI: [0.38, 0.39]; Chinese vs Greek, $\beta_{\text{Dice}} = 0.73$, 95% CI: [0.38, 0.39]; Dutch vs Greek, $\beta_{\text{Dice}} = 0.76$, 95% CI: [0.39, 0.40].

We have added the permutation testing procedure for Dice coefficients to the Methods and the corresponding results to the Results section (lines 197–199, lines 618–625). Additionally, we added the code for this analysis to the code repository.

3. Pg 2: Why is Aristotle cited in a footnote, rather than as a standard citation?

REPLY: We have now removed the footnote and replaced it with a citation: Lennox, J. G. *Aristotle: On the Parts of Animals I-IV*. (Oxford University Press, Oxford, New York, 2001).

Reviewer #3:

The conceptual approach is innovative and the methodology and statistics are highly rigorous. The paper is strongly written. I am enthusiastic about the approach and findings

REPLY: We thank the reviewer for their positive feedback.

1. While the three cultures are a strength, two of the cultures are European. Similarly, the age range of 18-30 limits generalizability to a variety of ages and generations. This could be included as a limitation and/or direction for replication and follow-up. Relatedly, the strong claim of cultural universality is not well supported. Three cultures is hardly enough to justify statements like “the universal cross-cultural nature of tickling” (line 461); “the phenomenology of ticklishness... are culturally invariant” (line 456); etc. It would also be important to show the sample population’s basic demographic information, including education level, and to argue that nationality-based cultural differences are truly meaningful given contemporary international cultural similarities among 18-30-year-old internet users with university or high school-level educations. I recommend softening the universality and cross-cultural claims throughout and include a discussion of these and other important limitations, including those derived from data collected in online survey form in exchange for a monetary incentive.

REPLY: We thank the reviewer for raising these points.

We agree with the reviewer that strong statements such as “universal” and “culturally invariant” may not be satisfactorily supported by our data from three cultural groups, particularly given that two of the groups are European. Accordingly, we have softened the language throughout the manuscript (all highlighted in yellow). Specifically, we replaced terms such as “universal” and “invariant” with more appropriate wording (e.g., “widespread”, “similar,” and “consistent across the three cultural groups”).

Regarding the participants’ demographics, we report their age and biological sex in line 52. Further, we reported ethnicity and nationality in the Extended Data Fig. 1a-b. We did not collect educational background in this study. We agree with the reviewer that contemporary globalised online environments may reduce nationality-based cultural differences. However, we would also like to clarify that our grouping approach was not strictly nationality-based. As explained in our Methods (lines 475–476), participants were prescreened by primary language use (Chinese, Dutch, or Greek) and completed the study in their primary language. We chose the primary language as our criterion because it is more directly related to daily communication and cultural context, and can target cultural differences better than a pure nationality-based screening. Primary language is deeply tied to the social groups and media platforms that individuals engage with, making it a more relevant factor than nationality per se. Related to this point, we have now amended the legend of Figure 1 to refer to our language-defined groups by replacing “red for China, orange for the Netherlands, and blue for Greece” with “red for Chinese-speaking, orange for Dutch-speaking, and blue for Greek-speaking participants” (lines 805–806).

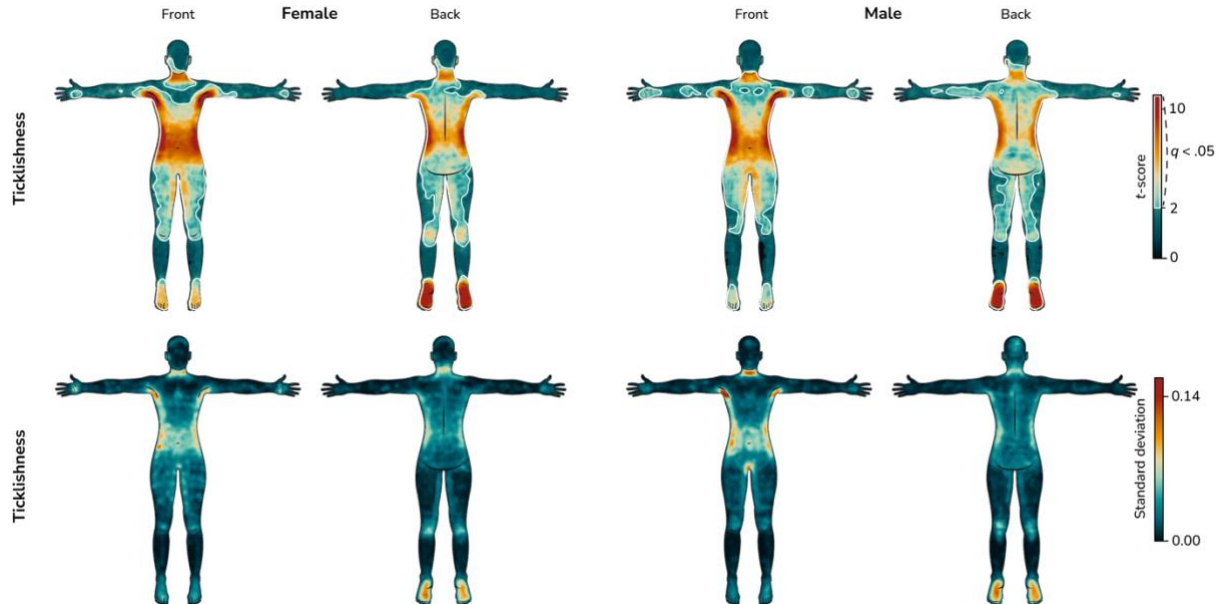
We have now expanded the Discussion to explicitly acknowledge key limitations, including the restricted number of cultures sampled, the relatively young participant population, and the

reliance on data collected via online surveys with monetary incentives. We also highlight the need for future research using more diverse samples and alternative data collection methods, including developmental approaches (lines 442–448).

2. I do not see any testing of sex or gender differences. Were these conducted? Can the authors examine exploratory effects of sex on tickle behavior or percepts? This could provide potential insight into the nature of tickling behavior.

REPLY: We thank the reviewer for the suggestion. We have now performed exploratory analyses of sex effects. We followed the same culture-based model comparison approach used in the manuscript, but here aggregated participants across all three cultures to maximise power. Three participants who selected “*prefer not to say*” regarding their sex were excluded, resulting in a final sample of $N = 445$.

Overall, we did not find meaningful sex effects in self-reported ticklishness, frequency of tickling experiences, or affective values associated with tickling behaviours, either as a ticklee or tickler, neither in childhood nor in adulthood, with the model excluding sex as a predictor being supported for all survey items (ΔBIC range: [1.87, 29.04]). With respect to the ticklishness maps, we computed the t -scored maps separately for female and male participants (collapsed across cultures). As shown below, the spatial patterns for ticklishness, along with their variability, are very similar between sexes: the neck, torso, armpits, and soles of feet are among the most commonly reported areas of the body that are ticklish.



To explore whether the ticklishness topography is consistent across sexes or unique to each, we trained PLS models on ticklishness versus non-ticklishness maps separately using data from male and female participants (identically to our approach regarding cultures). When these models were tested on participants of the opposite sex, they demonstrated strong generalizability, suggesting that the ticklishness topography generalizes between males and females (tested on males: AUROC = 0.85, $p = 1/1,001$, 95% CI: [0.31, 0.40]; tested on females: AUROC = 0.86, $p = 1/1,001$, 95% CI: [0.32, 0.40]).

We have now added text in our Results (lines 163–166, 224–226) to present these new analyses, and we also mention that these analyses are exploratory, given that our study was not designed to study sex effects.

3. Some participants reported tickling as an unpleasant experience. I am concerned that this rating was collected for tickling experiences in general, rather than probing variability in tickling experiences, such as the percent of tickling experiences that were positive versus negative, or the social context of the tickling. As a somewhat intimate form of touch, tickling is prone to abuse. Similar ratings might be expected for affective touch or genital touch, with many unpleasant ratings potentially reflecting instances of unwanted touch and many pleasant ratings reflecting wanted touch. Averaging across tickling experiences in general risks losing a rich variability of purposes, contexts, and effects of tickling behavior. At minimum, this concern should be discussed as a limitation of the current study and a direction for future follow-up. The exploratory analysis of sex effects might also hint at trends related to abuse.

REPLY: We thank the reviewer for this comment.

We strongly agree with the reviewer. This is exactly the reason why we included *both* pleasantness and unpleasantness items to capture participants' affective evaluations of being tickled and tickling others. We did not assume that individual experiences are purely positive or negative; nor did we assume that, when evaluating past experiences, people would not have mixed feelings. Such mixed responses may reflect the fact that tickling can be both positive (e.g., wanted touch) and negative (e.g., unwanted touch). In addition, we assessed the perceived social functions of tickling from a third-person perspective, carefully including both positive and negative aspects (Fig. 1q) to further probe individual differences in participants' evaluations.

The reviewer is correct that our study did not distinguish between wanted and unwanted tickling. We have now added text addressing this point in the Discussion (lines 453–456).

4. Relatedly, I am concerned that the paper omits any discussion about intent or consent. Tickling that is con-consensual or that continues while the ticklee protests is not infrequently used as a form of control and even abuse that is sometimes more socially accepted than other forms of sexual abuse. Highly ticklish individuals can experience a loss of bodily control including inability to speak, difficulty breathing, or loss of bladder control. It is possible that tickling behavior is inherently an exploration of power and control over others' bodies in ways that can be either harmless (even functional) or harmful. It would be informative to consider how frequently such experiences occur in tickling behavior and what motivation or effects the tickler reports in their various experiences of tickling. This is distinct from the occurrence of tickling in the context of kink that is briefly referenced in the paper (although there may be overlap). Indeed, it is revealing that common responses to tickling reported in the current paper include resist and escape, and that tickling is typically directed to same-age or younger peers. However, I appreciate that the focus of the paper is on the reason for the spatial mapping of ticklishness, rather than its functional purpose. Please make sure this is clearly distinguished in the paper.

REPLY: We agree with the reviewer regarding the importance of intent and consent in tickling interactions and acknowledge that our study did not address these factors. We have added text in the Discussion to highlight this as an important direction for future work (lines 453–456).

5. What were the inclusion and exclusion criteria for the study? If individuals with chronic pain were included, was pain explored as a variable influencing tickle experience?

REPLY: We thank the reviewer for this point. We did not specifically exclude participants with chronic pain; however, volunteers were eligible to participate in the study only if they had no current or past neurological and/or psychiatric conditions. Participants were also required to be between 18 and 30 years of age and to have Chinese, Dutch, or Greek as their primary language. We have now added these criteria to the Methods section in the revised manuscript (lines 469–471). Regarding exclusion, this was applied after data collection; specifically, we excluded participants who showed inattentive performance in the body-colouring task (doodling). This resulted in the exclusion of two participants (one Chinese and one Greek-speaking participant), as reported in lines 476–478.

Regarding the relationship between ticklishness and pain, we included survey items probing whether participants experienced being tickled (as ticklees) or tickling others (as ticklers) as painful, separately for childhood and adulthood. The majority of participants reported that tickling experiences were not painful (ticklees: 86.7% in childhood, 85.4% in adulthood; ticklers: 96.3% in childhood, 95.6% in adulthood) (Fig. 1o–p). We also included a body-colouring task in which participants indicated regions sensitive to pain, excluding visceral and muscle pain. We found that the spatial distribution of pain sensitivity was largely distinct from that of ticklishness, although there was some overlap in specific regions (e.g., the abdomen and the soles of the feet). Nevertheless, we believe that a proper investigation of the relationship between pain and ticklishness would warrant a dedicated, likely laboratory-based, systematic study.

6. The results provide support for the negative social touch theory, but statistically this is only a partial explanation. The authors conclude that ticklishness is driven by areas that almost never receive touch. However, this explanation is not fully satisfying. Children do not typically receive touch on their genitals, yet these areas are not described as ticklish or tickled. Similarly, the bottom of the foot is depicted as much more ticklish than the top, but no difference in touch frequency is apparent. Might this reflect differences in areas rarely exposed to the air (due to shirts and shoes)?

REPLY: The reviewer is correct. Although Darwin's theory is the one most strongly supported by our data (both in the univariate and multivariate analyses), we might have given the impression that it can fully explain ticklishness, and we apologise for this. Darwin's predictor of inverse touch (now including both social and self-touch) explains a significant proportion of the variance in ticklish body areas (adjusted $R^2 = 0.47$). However, PC1—combining contributions from inverse touch, tactile innervation density, and pleasure—provided a better fit (adjusted $R^2 = 0.57$). Therefore, our interpretation is not that a single predictor or theory prevails, but rather that ticklishness is best accounted for by a broader socio–psycho–physiological interplay. We have

revised the Abstract (lines 20–23) and amended the manuscript in several places to clarify that Darwin's theory provides only a partial explanation (highlighted in yellow).

Regarding the reviewer's point about children, we reiterate that Darwin's account provides only a partial explanation. When considering this theory more closely, we can propose three possible alternatives. First, if the genitals are rarely touched in children due to strong social constraints surrounding this body region, this would also limit tickling behaviours targeting that area and, consequently, reports of ticklishness. Second, infants and toddlers do receive touch in these areas during caregiving routines (e.g., diaper changes or toileting assistance), and for infants in particular, such contact is relatively frequent. In relation to this, we have now expanded the theoretical framework to include self-generated touch, meaning that tactile experience is not limited to externally applied stimulation. Third, our results are based on adult participants, and the relationship between ticklishness and inverse touch exposure may develop over the course of the lifespan.

Regarding the reviewer's point about the foot sole being more ticklish than the foot dorsum, it is important to emphasise that we quantified touch exposure specifically from the hands of others and oneself, but not from objects. This is reported in Extended Data Table 2, and we have now also added text in the Methods section (line 571). Although the reviewer's point is valid and interesting, we cannot assess it with the existing data. However, we speculate that it might also have to do with the type of stimulation a body part usually receives (see also our Discussion in lines 450–451).

7. Is there any association between reported frequency of childhood tickling, and being less ticklish as an adult? In other words, if ticklishness relates to areas with less touch exposure, is this modifiable through behavior, or do the data suggest this is wired at least from childhood? Anecdotally it seems that ticklish children remain ticklish adults.

REPLY: We thank the reviewer for raising this question. To address this, we used the participants' self-reported frequency of being tickled in childhood and in adulthood to predict their overall ticklishness ratings. We found no evidence for an association between frequency in childhood and overall ticklishness ($\beta = 0.08$, $SE = 0.14$, odds-ratio = 1.09, $p = .551$; 95% CI: [0.83, 1.43]). In contrast, frequency in adulthood was significantly related to higher overall ticklishness ($\beta = 0.49$, $SE = 0.11$, odds-ratio = 1.63, $p < .001$; 95% CI: [1.30, 2.03]).

Nevertheless, we believe this relationship should be interpreted with caution for two reasons. First, all participants were adults and therefore assessed their childhood experiences retrospectively. We think that changes in ticklishness across the lifespan require a dedicated investigation. Second, we did not ask participants to rate how ticklish they were during childhood; instead, we assessed their current ticklishness (in adulthood), along with the reported frequency of tickling behaviours in both childhood and adulthood. However, the frequency of tickling behaviour may not necessarily reflect an individual's tickle sensitivity: a very ticklish person may be more frequently targeted by others, but the relationship could also operate in the opposite direction.

We share the anecdotal observation that ticklish children remain ticklish adults, but we have also been anecdotally told by some individuals that they were so ticklish in childhood that they learned to suppress their responses to cope with interactions (e.g., with siblings), which itself represents an interesting avenue for future research.

We have added a point to the Discussion regarding the need for future investigation regarding the developmental dimension of ticklishness (lines 446–448).

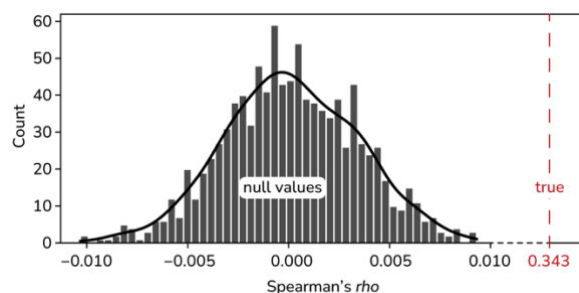
8. With thanks to my trainee trained in Anthropology: If the authors take their data to support the Darwinian theory that areas of the body less frequently touched by others tend to be more ticklish, then some variability in the somatotopy of social touch practices would be needed, along with correlated variation in ticklishness somatotopy, to claim that this data empirically supports or proves the Darwinian theory. I recommend including a discussion of this and a corresponding softening of the relevant claims.

REPLY: We thank the reviewer (and the trainee) for this comment.

To illustrate individual variability in inverse social touch and ticklishness, we have computed standard deviation maps across all participants for inverse social touch and ticklishness. As shown in the figure below, there are individual differences in both maps, with the ticklishness variability being overall lower compared to that of inverse social touch.



To examine whether the variabilities are shared between inverse social touch and ticklishness, we computed Spearman's correlation between the two standard deviation maps and assessed significance using permutation testing. Specifically, we computed the correlation 1,000 times while randomly shuffling the pixel locations of the ticklishness map to generate a null distribution. We observed a positive, significant correlation relative to the null ($\rho = 0.34$, $p = 1/1,001$, 95% CI: [0.34, 0.35]).



A similar result was observed for ticklishness and inverse touch exposure (i.e., expanded operationalisation of Darwin's theory): $\rho = 0.29$, $p = 1/1,001$, 95% CI: [0.28, 0.30].

We agree with the reviewer, and we have now softened our claims throughout the manuscript (Abstract and Discussion), explicitly mentioning that Darwin's theory is a partial explanation of the ticklishness topography.

9. With thanks to my trainee trained in Anthropology: Notably, Darwin also describes how he tickled the sole of his seven-day-old infant, who jerked it away with curled toes, something he took to mean that "such movements, as well as laughter from being tickled, are manifestly reflex actions." Also: "[Yet in the case] of laughter from being tickled, the mind must be in a pleasurable condition; a young child, if tickled by a strange man, would scream from fear." And: "From the fact that a child can hardly tickle itself, or in a much less degree than when tickled by another person, it seems that the precise point to be touched must not be known; so with the mind, something unexpected—a novel or incongruous idea which breaks through an habitual train of thought—appears to be a strong element in the ludicrous." Darwin's thoughts clearly go beyond just social exposure and towards a rather more complex understanding of the phenomenon which even includes a discussion of surprise. While the authors' claim that "ticklishness emerges as culturally invariant because it relates not with where people receive touch on their body, which can vary across societies, but with where they almost never receive touch," makes logical sense, Darwin himself talks about the soles of the feet and the buttocks as important exceptions. Given the limited number of ticklish body areas, these exceptions are especially salient and should be evaluated alongside the evidence presented when making claims about the social touch exposure theory. A nuanced discussion of these points as well as a more generous reading of Darwin would likely benefit the reader.

REPLY: We thank the reviewer and their trainee for highlighting additional hypotheses raised by Darwin and for encouraging us to broaden our discussion accordingly. We are aware of Darwin's additional remarks, and we agree with the reviewer that our account should not appear reductionist with respect to his views. In the present manuscript, we focused on his claims regarding topography. However, in our research group, we currently run experiments in which we aim to address the roles of surprise, stimulation type, and emotional state (unpublished data).

As mentioned above, we have now revisited our interpretation of Darwin's theory to account for exposure to touch both by others and by oneself. We believe this provides a more holistic view of Darwin's account of touch exposure, rather than focusing exclusively on social touch.

We have also added text to the Discussion to explicitly note that Darwin referred to factors such as surprise, state of mind, and stimulation type as influencing the experience of ticklishness, which are not addressed in the present study (lines 450–452).

10. The Discussion suggests that tickling is highly conserved due to its functional importance. It does appear highly conserved, but the functional importance remains unclear. Do the authors

have a theory about this? Either way, please clarify that this remains unclear and is an interesting direction for future research.

REPLY: At present, we do not have a solid theory about what function ticklishness serves. Our approach is first to characterise the phenomenology and topography of ticklishness (the present study) as well as its triggers and responses (unpublished; in lab-based experiments) in order to address the follow-up question about its function. Our intention in the Discussion was to raise the possibility that ticklishness has a function based on the observation that the behaviours are observed across hominids.

We have revised the relevant text to make it clear that the function is not currently known (lines 462–463).

11. Supplement page 5 question 4- I find it a leading question to state that tickling in a professional context is inadvertent. This is likely, but it could also be intentional, for example if a photographer tickled a child to get them to smile. I suggest acknowledging this somewhere in the paper.

REPLY: The reason we described an example of a professional context to the participants was to provide options they might not have considered. We included the term “inadvertently” to avoid conflating professional and personal relationships. We agree with the reviewer that tickling in a professional context may, in some cases, be intentional, which was not considered in our study. We have therefore added a brief acknowledgement of this in the caption of Figure 1 (line 814).

12. Page 8 line 246: Please clarify the statement that “all p -values = $1/1,001$ ”? Is this the threshold or should it say $< 1/1,001$?

REPLY: We thank the reviewer for the question. In our permutation tests, the notation “all p -values = $1/1,001$ ” reports the exact p -values after applying a standard pseudocount correction to avoid zero p -values, rather than a significance threshold. Specifically, we ran 1,000 permutations and counted how often the permuted (null) statistic was as extreme as the observed statistic; we then added 1 to both this count and to the total number of permutations. When none of the permuted statistics were as extreme as the observed one, this yields the smallest non-zero p -value possible under this correction, namely $1/1,001$. We report the detailed calculation and formulas in the Methods (lines 624, 656).

13. I suggest introducing the terms gargalesis and knismesis earlier on and defining them, as these are not common knowledge.

REPLY: We have now added text in the Introduction and Discussion to emphasise that our study focused on laughter-inducing tickling (often termed gargalesis), rather than feather-like tickling (often termed knismesis) (lines 28–29, 439–442).

14. Extended Data Fig. 3.: is there a way to display the values for each region, or a heat map?

REPLY: Extended Data Fig. 3 is a methodological illustration showing how we constructed the parcellated body masks for each theory, ensuring that they matched the body regions available in the external datasets used for theory testing. Accordingly, the figure displays the masks (i.e., the specific pixels or areas included in each parcellation). We have added in the figure caption a description to more explicitly state the representation of the figure (lines 28–29).

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Response to the reviewers

Reviewer #1:

(1) Figure 1k–p. While the percentages for each culture in childhood are clear, it is harder to interpret cultural similarities and differences in adulthood. It is currently unclear how to read the ratios across cultures in adulthood. Could the authors consider presenting these data in a way that facilitates comparison across cultures?

REPLY: We thank the reviewer for this helpful suggestion. We have modified all the panels to present the culture-wise responses for childhood and adulthood in separate plots. Because the response patterns are broadly consistent across life stages, this revised visualisation facilitates more direct comparisons across cultures.

(2) Figure 2c (right). In the 4-fold cross-individual validation scheme, the training set is described as “60% and 20%.” However, it is unclear why the training data are split in this way. Could the authors clarify how the data were partitioned?

REPLY: We apologise for the confusion caused by our previous schematic, and we have updated Fig. 2c and the legend text to clarify the illustration (lines 851–852). In this analysis, we used five-fold cross-validation: in each iteration, 20% of the body-colouring map data were held out as the test set (one fold), and the remaining 80% were used as the training set (the other four folds). Thus, the data were not partitioned into 60% and 20%; the “60% + 20%” labelling in the previous figure was intended to illustrate the iterative procedure between the training and test sets. We have updated the labelling to clearly reflect the correct 80% training and 20% test split.

(3) Page 15. The authors downsampled non-ticklishness maps to match the number of ticklishness maps. Could the authors clarify whether this downsampling procedure was performed only once or repeated across multiple random samples (e.g., similar to the permutation procedure used for Dice–Sørensen coefficients)? If it was performed only once, it would be helpful to comment on the robustness of the results with respect to this random sampling.

REPLY: We thank the reviewer for this important question. In our pipelines, downsampling was performed once per training iteration (i.e., once for each training set used to fit the model), rather than repeatedly within the same fold over multiple random draws. Specifically, in the cross-cultural validation, the PLS model was trained iteratively on three training sets (corresponding to the three training cultures across iterations), and thus the downsampling was applied three times in total. In the five-fold cross-individual validation, the model was trained on five training sets (one per fold), and thus the downsampling was applied five times in total.

Although we did not additionally repeat the downsampling multiple times within each fold, we believe our main findings are robust for two reasons. First, the model performance is consistent across validation folds (Fig. 2d–e), which suggests that the results are not driven by a single random sample of the non-ticklishness maps. Second, our multi-class modelling analysis (Fig. 3l), where each map type was treated as a separate class and therefore no downsampling was required, demonstrated that the models reliably distinguish ticklishness bodily patterns from other map patterns.

We have revised the text in the Methods to clarify how often downsampling was applied in the analysis pipeline (line 644).

(4) lines 659–671. In this part, the authors conduct a cross-validation analysis at the individual level using a stratified group cross-validation scheme. However, this procedure evaluates cross-participant generalization (i.e., generalization to unseen individuals), not cross-cultural generalization. Given that they state “to test whether cultural similarities generalise to the individual level”, I think the current analysis does not fully match this phrasing. To directly test whether cultural similarities generalise across individuals, the authors would need to: (1) train a PLS regression model on a subset of individuals within one culture, (2) test the model’s performance both on unseen individuals from the same culture and on individuals from the other cultures, and (3) repeat this procedure for each of the three cultures. Unless the authors perform such an analysis, I would recommend that they modify the phrase “To test whether cultural similarities generalise to the individual level” (line 659), and the corresponding Results text, to reflect that this analysis assesses cross-participant generalization within the pooled multi-cultural sample, rather than cross-cultural generalization per se. For instance, “whether the topography of ticklishness generalises across individuals in a multi-cultural sample” may be an alternative phrasing.

REPLY: We thank the reviewer for raising this important point. We agree that our original phrasing was misleading. We have revised the relevant text to align with what the analysis actually tests (lines 218–219 and 659–661). The revised wording now emphasises that the cross-individual validation procedure assesses whether the ticklishness topography generalises across individuals, without grouping them based on cultural backgrounds.

We also agree with the reviewer that a direct culture-to-culture individual-level test would require the train/test pipeline outlined in the suggestion. We did not add this additional analysis because our manuscript already includes an explicit cross-cultural generalisation test with consistently high performance. Therefore, we believe that the proposed analysis would be unlikely to provide additional insights beyond those already captured by the existing results.