Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Note

Anisotropy in tactile time perception

Souta Hidaka [a,b,*], Luigi Tamè [c], Antonio Zafarana [c] and Matthew R. Longo [b]

[a] *Department of Psychology, Rikkyo University, 1-2-26, Kitano, Niiza-shi, Saitama, Japan*
[b] *Department of Psychological Sciences, Birkbeck, University of London, United Kingdom*
[c] *School of Psychology, University of Kent, Canterbury, United Kingdom*

ARTICLE INFO

Article history:
Received 25 August 2019
Reviewed 16 October 2019
Revised 26 January 2020
Accepted 1 March 2020
Action editor Rob McIntosh
Published online 3 April 2020

Keywords:
Touch
Anisotropy
Hand
Spatial–temporal perception
Body distortions

ABSTRACT

Spatial distortions in touch have been investigated since the 19th century. For example, two touches applied to the hand dorsum feel farther apart when aligned with the mediolateral axis (i.e., across the hand) than when aligned with the proximodistal axis (along the hand). Stimulations to our sensory receptors are usually dynamic, where spatial and temporal inputs closely interact to establish our percept. For example, physically bigger tactile stimuli are judged to last longer than smaller stimuli. Given such links between space and time in touch, we investigated whether there is a tactile anisotropy in temporal perception analogous to the anisotropy described above. In this case, the perceived duration between the onset of two touches should be larger when they are aligned with the mediolateral than with the proximodistal axis of the hand dorsum. To test this hypothesis, we asked participants to judge which of two tactile temporal sequences, having the same spatial separation along and across the dorsum, felt longer. A clear anisotropy of the temporal perception was observed: temporal intervals across the hand were perceived as longer than those along the hand. Consistent with the spatial anisotropy, the temporal anisotropy did not appear on the palm side of the hand, indicating that the temporal anisotropy was based on perceptual processes rather than top-down modulations such as attentional or decisional/response biases. Contrary to our predictions, however, we found no correlation between the magnitudes of the temporal and spatial anisotropies. Our results demonstrated a novel type of temporal illusion in touch, which is strikingly similar in nature to the previously reported spatial anisotropy. Thus, qualitatively similar distorted somatosensory representations appear to underlie both temporal and spatial processing of touch.

* *Corresponding author*. Department of Psychology, Rikkyo University, 1-2-26, Kitano, Niiza-shi, Saitama, 352-8558 Japan.
E-mail address: hidaka@rikkyo.ac.jp (S. Hidaka).

https://doi.org/10.1016/j.cortex.2020.03.011

1. Introduction

Our perception depends on the operating properties of our sensory receptors, and it is often intrinsically distorted due to particular characteristics of sensory receptors. Spatial distortions in touch have been demonstrated since the 19th century for across body parts (Anema, Wolswijk, Ruis, & Dijkerman, 2008; de Vignemont, Majid, Jola, & Haggard, 2009; Goudge, 1919; Green, 1982; Longo & Sadibolova, 2013; Marks et al., 1982; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004; Weber, 1996) and even within a single body part (Fiori & Longo, 2018; Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014; Longo, Ghosh, & Yahya, 2015; Longo & Haggard, 2011; Stone, Keizer, & Dijkerman, 2018).The perceived distance on the hairy skin surface of a hand (dorsum side), for example, is approximately 40% bigger when the stimuli are aligned with the medio-lateral axis (*across* hand axis) compared to the proximo-distal axis (*along* hand axis) (Longo & Haggard, 2011) (Fig. 1A). This effect is much smaller (or absent entirely) on the glabrous skin of the palm of the hand (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015; Longo & Haggard, 2011). These perceptual distortions on hand surface can be explained by the differences in tactile acuity across the medio-lateral and proximo-distal axes (Cody, Garside, Lloyd, & Poliakoff, 2008; Schlereth, Magerl, & Treede, 2001, Weber, 1996/1834) and the anisotropy of the shape of the tactile receptive fields in the primary somatosensory cortex (SI) (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961; Powell & Mountcastle, 1959) on hairy skin surface. A recent functional magnetic resonance (fMRI) study has shown that the most likely origin of such distortions at neural level are the primary sensorimotor cortices (Tamè, Tucciarelli, Sadibolova, Sereno, & Longo, 2019).

Our interactions with objects in the external world are usually dynamic and extended across time, where spatial and temporal information are combined to establish a coherent tactile percept (Burtt, 1917; Shore, Gray, Spry, & Spence, 2005; Yamamoto & Kitazawa, 2001). For instance, bigger tactile stimuli are judged to last longer than smaller stimuli (Cholewiak, 1999; Goldreich, 2007; Suto, 1952). Given a tight link between space and time in touch (Goldreich, 2007), there would exist an anisotropy in temporal perception corresponding to perceptual anisotropy in space, such as the one described above (Longo & Haggard, 2011), even when tactile spatial distance is kept constant. However, while tactile perceptual distortions in space have been extensively studied, it remains unknown whether there are analogous tactile illusions of time.

Here, we demonstrate an anisotropy in tactile time perception. We sequentially presented two tactile temporal sequences to the dorsum of the participant's left hand, and asked them to judge which interval was longer (Fig. 1B). One sequence consisted of two touches oriented along the length of the hand and the other across the width of the hand. The actual distance between these two axes was consistent (3.5 cm). Nevertheless, we report a significant bias for temporal intervals oriented across the hand to be perceived as longer than those oriented along the hand, an anisotropy in tactile time perception. Remarkably, this temporal illusion closely mirrors the well-established spatial anisotropy to overestimate the distance between touches oriented with hand width (Longo & Haggard, 2011). Indeed, in a second experiment we show that the anisotropy in tactile time perception, like spatial illusions, is reduced on the glabrous skin of the palm. Contrary to our predictions, however, the third experiment failed to provide any evidence for a correlation in the magnitudes of the temporal and spatial anisotropies across participants. Our results provide the first demonstration of a novel type of temporal illusion in touch and reveal striking phenomenological correspondence between spatial and temporal tactile anisotropies, although underlying somatosensory processing can be independent between them.

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants and apparatus*

Seventy two healthy participants took part in the study, 15 in Experiment 1 (10 females; mean age: 29.9 years, SD: 8.9 years, mean handedness score according to the Edinburgh Inventory (Oldfield, 1971): $M = 86.38$, all right-handed, range: 57.89–100), 15 in Experiment 2 (11 females; mean age: 25.8 years, SD: 5.3 years, mean handedness score: $M = 81.88$, all right-handed, range: 41.18–100), and 42 in Experiment 3 (30 females; mean age: 26.98 years, SD: 7.97 years, mean handedness score: $M = 94.5$, all right-handed, range: 67–100). For Experiments 1 and 2, we determined the sample size based on the previous study reporting the spatial anisotropy (Longo & Haggard, 2011). For Experiment 3, the sample size was determined as around 30 with targeting a moderately positive relationship of $r = .50$, 90% power, and one-tailed alpha of .05. All participants reported no abnormalities in tactile perception and were naïve to the purpose of the experiments. They were paid or given course credits for their participation. One participant was excluded from analyses in each experiment, because they claimed not to be able to clearly feel the tactile stimuli. One participant was also excluded in Experiment 1 due to problems in tactile stimulators. These participants were replaced by new recruited participants. In Experiment 3, five and three participants were excluded from analyses for temporal and spatial tasks due to poor convergence of QUEST sequence (Watson & Pelli, 1983) and poor fitting results ($R^2 < .50$), respectively. One participant's data in Experiment 2 and two participants' data in the temporal task of Experiment 3 were regarded as outlier based on the Smirnov–Grubbs test ($P < .05$) and excluded from subsequent analyses. All procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London. The study was conducted in accordance with the principles of the Declaration of Helsinki. Written Informed consent was obtained from each participant before conducting the

CORTEX 128 (2020) 124–131

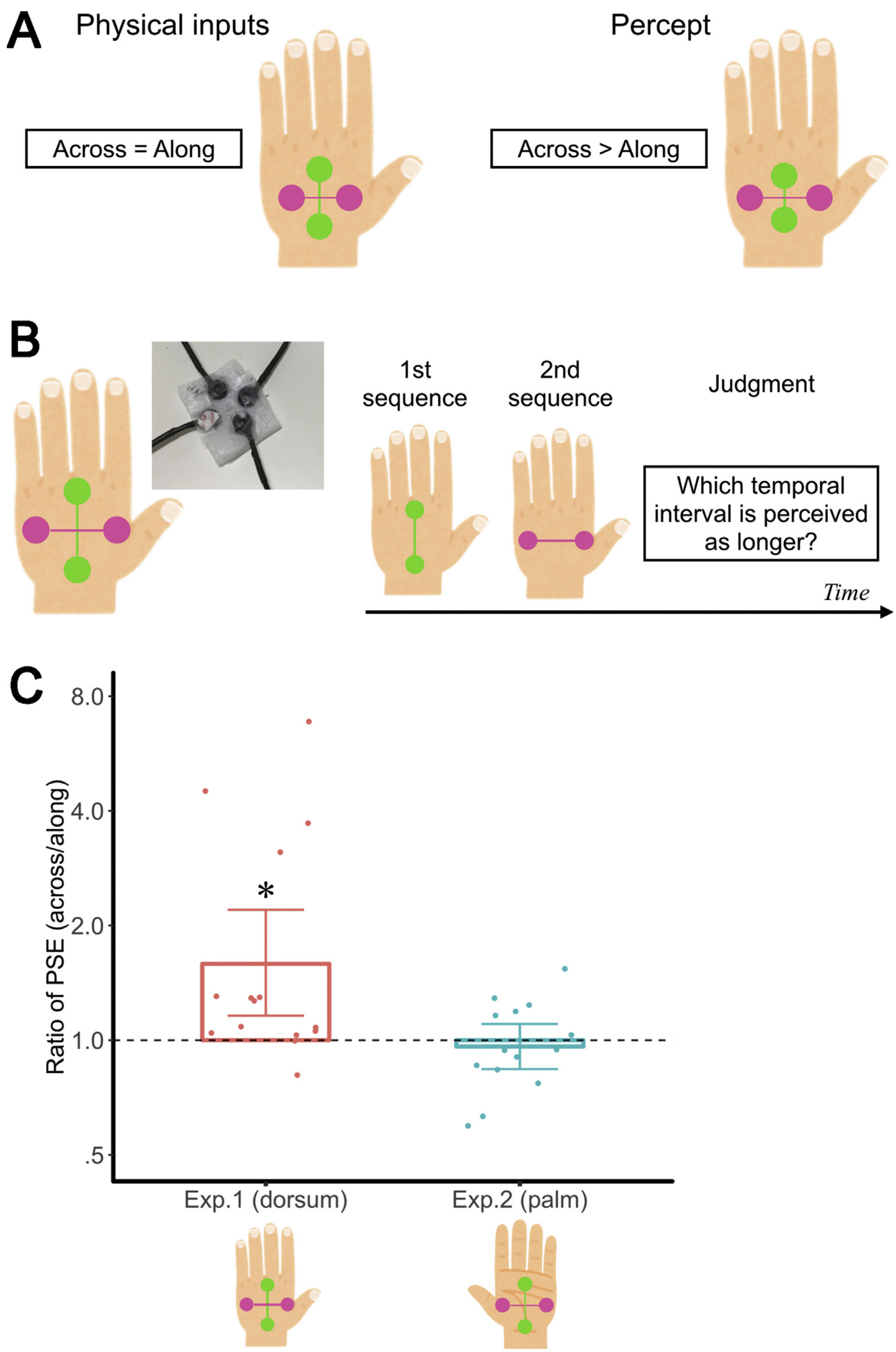

Fig. 1 – (A) Schematic illustration of the anisotropy in tactile distance perception across hand axes on the hand. (B) Schematic illustrations of the experimental setups. Two tactile temporal sequence, one is along and the other is across hand axes, were sequentially presented by two tactile stimulators on the participant's left hand. The distance between these two axes was consistent (3.5 cm). Participants judged whether the first or the second duration felt longer. We estimated each participant's point of subjective equality (PSE) of tactile temporal perception: In one sequence, the ISI for along hand axis was fixed at 300 ms and that for across hand axis varied according to participant's response (along-standard sequence). The other sequence, the ISI for across hand axis was fixed (across-standard sequence). Experiments 1 and 2 tested the dorsum and palm side of the hand, respectively. (C) Mean ratio of the PSEs across the along- and across-hand axes estimate by the bootstrap method (10^4 iterations) in each experiment ($N = 15$ and 14 for Experiments 1 and 2, respectively). Each dot represents a single participant's data. Error bars denote bootstrapped 95% CI. An asterisk denotes a significant difference from a ratio of 1 ($P < .05$).

experiments. No part of the study procedures was preregistered prior to the research being conducted.

Each tactile stimulus consisted of three square-wave pulses with 25 ms (ms) on-phases (single pulse) and two interleaved 10 ms off-phases, resulting in a 95 ms vibration for tactile temporal perception in Experiments 1–3. The stimuli were delivered through 15 mm diameter solenoid tappers with a flat tip (Heijo Research Electronics, Kent, UK) at suprathreshold intensity presented with the maximum indented height (4 mm). The stimulators with an amplifier were connected with a PC (Dell Precision T3500) and controlled by a custom MATLAB (MathWorks, Natick, MA) script with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A numeric keypad was used to record participants' responses. We also used headphones (Sennheiser HD 439 Audio Headphones) and a portable audio player (iPod shuffle, Apple, CA) to present white noise bursts in order to prevent the participants from hearing artificial noises of the tactile stimulators. The matrix of the tactile stimulators (top, right, bottom, and left on the hand surface) was rotated for each participant in order to control possible effects of tactile stimulators on a specific simulation cite. For tactile spatial perception (Experiment 3), stimulus was a pair of pointed wooden rods mounted on foamboard (Longo & Haggard, 2011) separated by 2, 3, or 4 cm. The tip of the rods was rounded off to form a blunt point (approximately 1 mm width). The participants were blindfolded with an eye mask throughout the experiments.

2.2. Stimuli and procedures

Experiments 1 and 2 tested tactile temporal perception on the dorsum and the palm of the participant's left hand, respectively. Four tactile stimulators, embedded in a foam cushion, were placed on the participant's left hand. Two stimulators were placed along hand axis and the other two were across hand axis (Fig. 1B). The distance between each pair of the stimulators was 3.5 cm forming a perfect square. The center of the simulators was consistent with that of each participant's hand, which was defined as the midpoint between the knuckle (Experiment 1) or the base (Experiment 2) of the middle finger and the center of the base of the hand. Each tactile stimulation was 30 Hz and presented for 95 ms consisting of three times 25 ms duration and 10 ms inter-pulse intervals. In each axis, two tactile stimulations were sequentially presented with a certain inter stimulus interval (ISI) with 1000 ms blank period between them. In order to estimate each participant's PSE, we used QUEST method and run two interleaving QUEST sequences in each session. In one sequence, the ISI for along hand axis was fixed at 300 ms and that for across hand axis (i.e., tested axis) varied according to participant's response (along-standard sequence). The ISI for across hand axis was fixed in the other sequence (across-standard sequence). The initial ISI of the tested axis in each sequence was set as either 590 ms (descending series) or 10 ms (ascending series). Each sequence consisted of 30 trials so that 60 trials were completed in each session. The session was repeated four times (240 trials in total). After the presentation of two temporal interval across the hand axes in each sequence, the participant reported which sequence was perceived as having longer temporal interval by pressing one of two buttons (1 or 3 key) on the numeric keypad without time pressure. This two-interval forced choice response mode, orthogonal to the tested dimension (i.e., judging directly which of the along or across hand axes was perceived as longer), reduced the possible involvement of response or decisional biases (Longo & Haggard, 2011). The order of which along- or across-standard sequence was presented as ascending or descending series was introduced with ABBA design (e.g., the along-standard sequence was presented as descending, ascending, ascending and descending series in order) and counterbalanced among participants. The presentation order of two sequences was randomized in each session. The presentation order of each tactile stimulator in each hand axis (e.g., for the along-standard sequence, whether the upper or bottom stimulation was presented first) was also randomized among the trials.

Experiment 3 tested both tactile temporal and spatial perception on the dorsum of the participant's left hand. The stimuli and procedures of the temporal task were identical with those in Experiments 1 and 2. The participants completed the along- and across-sequences two times so that 120 trials were used in total. The stimuli and procedures of the spatial task were very similar with those used in the previous study (Longo & Haggard, 2011). On each trial, two-points stimuli were presented twice, once oriented across the width of the hand and once oriented along the length of the hand, approximately at the center of the hand. Stimuli were delivered manually by the experimenter for around 1 s. Participants were asked to report verbally, and without time pressure, whether the first or the second stimulus was perceived as having larger spatial distance (two-alternative forced choice task). There were five pairs of stimuli, according to the size of the along and across stimuli (across/along): 2/4 cm, 3/4 cm, 3/3 cm, 3/2 cm, and 4/2 cm. In each session, each pair was applied 12 times. Two sessions were completed so that 120 trials were introduced in total. The order of which along- or across-hand axis was presented first was randomized in each session. The temporal and spatial tasks were presented in an ABBA design and counterbalanced among participants.

2.3. Data analysis

For the temporal task in Experiments 1–2 and Experiment 3, we averaged four and two estimated PSEs in each QUEST sequence for each participant, respectively. We then calculated a ratio for the PSEs by the following formula in order to estimate the magnitude of the temporal perceptual anisotropy: PSE across-standard/PSE along-standard. The data of Experiments 1 and 3 violated the assumption of normality (Shapiro–Wilk test, $P < .05$). Thus, we used the bootstrap method and bootstrap *t*-test (10^4 iterations) for statistical comparisons (Efron & Tibshirani, 1993) for all the experiments. All statistical tests and averaging were performed on base 10 log-transformed values which were converted back to ratios to report means. We used R software (R Core Team, 2019) with the outliers (Komsta, 2011), simpleboot (Peng, 2019), boot (Cathy & Ripley, 2019), and ggplot2 (Wickham, 2016) packages. For the spatial task in Experiment 3, the proportion of trials in which the stimulus was presented across the hand and was judged as larger was analyzed as a function of the ratio of the length of the along and across stimuli. The data were plotted logarithmically to produce a symmetrical distribution. We fitted cumulative Gaussian functions to each participant's data with Bayesian inference and estimated each participant's PSE with psignifit (Schütt, Harmeling, Macke, & Wichmann, 2016). The estimated PSE values were converted such that positive values indicates larger perceptual biases toward the across hand axis. We also calculated a correlation between the PSEs of the temporal and spatial tasks in Experiment 3. The statistical tests were performed using JASP (JASP Team, 2019). The data has been made publicly available via the Open Science Framework and can be accessed at https://osf.io/ydum8/. No part of the study analyses was pre-registered prior to the research being conducted.

3. Results

3.1. *Experiment 1*

In Experiment 1, we stimulated the hairy skin of the hand dorsum, on which there is a large perceptual anisotropy in the spatial domain (Longo & Haggard, 2011) (Fig. 1A). Corresponding with the spatial anisotropy, we observed that temporal intervals feel longer across the width of the hand. The mean PSE for the across-standard sequence was longer than the along-standard sequence (Supplementary Figure S1A) while the spatial distance between the stimuli was the same. We calculated the ratio for the PSEs by the following formula in order to estimate the magnitude of the temporal perceptual anisotropy: PSE across-standard/PSE along-standard. A bootstrap *t*-test (Efron & Tibshirani, 1993) (the threshold *t* value is 2.73) confirmed that the ratio (base 10 logarithm) was significantly different from 1 (Mean = 1.59 (.20), bootstrap 95% CI = [2.25 (.35) 1.19 (.07)], $P = .04$) (Fig. 1C).

3.2. *Experiment 2*

In Experiment 2, we tested the palm of participant's left hand. As we know from previous reports, the anisotropy of spatial distance perception across hand axes is much smaller or absent on the glabrous skin of the palm (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015; Longo & Haggard, 2011). Therefore, we predicted that PSEs were comparable between the along- and cross-standard sequences. The results were consistent with our prediction (Supplementary Figure S1B, Fig. 1C). The bootstrap *t*-test (the threshold *t* value is −1.15) found that the ratio (base 10 logarithm) of the PSEs for the along- and across-standard sequences was not significantly different from 1 (Mean = .92 (−.08), bootstrap 95%CI = [1.06 (.02) .59 (−.23)], $P = .36$). The absence of the anisotropy on the palm of the hand indicates that the anisotropy could not be simply explained by top-down modulations like attentional effects (e.g., attentional temporal dilation effect, Tse, Intriligator, Rivest, & Cavanagh, 2004) and/or response/decisional biases like the sequence across the width of the hand should have longer temporal interval. We further noted that the perceptual temporal anisotropy observed in Experiment 1 would be mainly due to the overestimation of the temporal interval across hand axis because the estimated PSEs in the across-standard condition were different between the experiments but those in the along-standard conditions were comparable and close to the physical interval (300 ms) (Supplementary Figure S1AB, see also the results of Experiment 3 in Supplementary Figure S1C).

3.3. *Experiment 3*

The results of Experiments 1 and 2 showed that the phenomenological characteristics of the tactile temporal anisotropy is highly correspondent with those of the spatial anisotropy: the percepts are stretched toward the across hand axis and the anisotropies appear only on the surface of the dorsum of the hand. These aspects strongly suggest shared underlying mechanisms of these perceptual distortions. To investigate this possibility, we measured the magnitudes of the temporal and spatial anisotropies and investigated whether they are positively correlated across the participants (Fig. 2, Supplementary Figure S1CD). For the temporal task ($N = 35$), the bootstrap *t*-test (the threshold *t* value is 2.10) revealed that the ratio (base 10 logarithm) of the PSEs for the along- and across-standard sequences was significantly different from 1 (Mean = 1.16 (.06), bootstrap 95%CI = [1.33 (.12) 1.01 (.01)], $P = .04$). For the spatial task ($N = 39$), one sample *t*-test showed that the PSE for the ratio (base 10 logarithm) was significantly different from 1 (Mean = 1.37 (.14), $t(38) = 8.48$, $P < .001$). These results clearly replicate the temporal and spatial anisotropies (Fig. 2A) we found in the previous experiment and in our previous study. However, the magnitudes of these anisotropies were not positively correlated: Pearson one-tailed correlation test showed no significant correlation ($N = 32$, $r = .03$, $P = .44$) (Fig. 2B). A Bayes factor analysis also showed that the correlation was more likely to have occurred under the null hypothesis than the alternative hypothesis ($BF_{01} = 4.04$ with a one-tailed Bayesian correlation analysis). These results suggest that tactile temporal and spatial anisotropies are likely to be mediated by different somatosensory processing.

4. Discussions

Our results provide the first demonstration of a novel type of temporal illusion in touch: we clearly demonstrated the presence of anisotropy in tactile time perception on the hand dorsum while stimuli have the same physical distance. The modulation of temporal perception has been reported based on differences in physical distance (Cholewiak, 1999; Goldreich, 2007; Suto, 1952) or even a perceived “phenomenal” distance between different body parts (two arms) (Suto, 1952). The current study stimulated a single body part (the hand surface), and the advantage of presenting tactile stimuli on the same body part is to control differences in perceived strength of tactile inputs (Weinstein, 1968), which affects temporal perception (e.g., Xuan, Zhang, He, & Chen, 2007).

Our findings also reveal the striking correspondences between spatial (Longo & Haggard, 2011) and temporal tactile

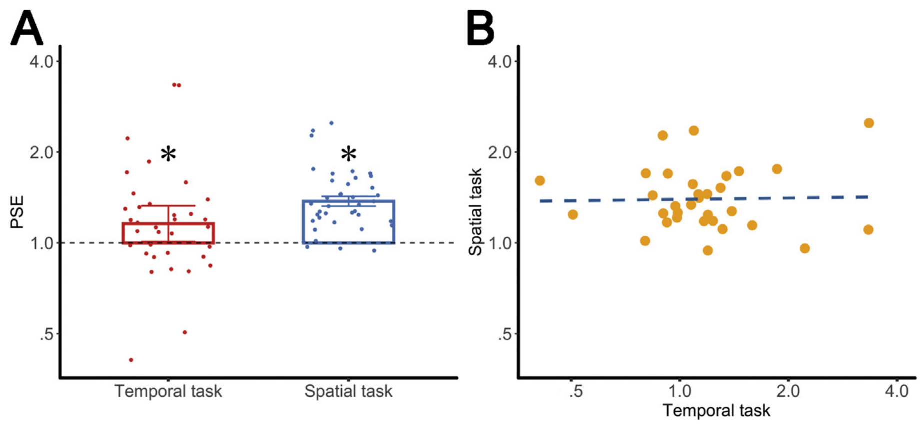

Fig. 2 – (A) Mean ratio of the point of subjective equality (PSE) for the temporal (N = 35) and spatial (N = 39) tasks. The positive PSE values indicates the perceptual bias toward the across-hand axis. Each dot represents a single participant's data. Error bars denote bootstrapped 95% CI and the standard error of the mean for the temporal and spatial tasks, respectively. Asterisks denote a significant difference from a ratio of 1 (P < .05). (B) Scatter plot of the PSEs for the temporal and spatial tasks (N = 32). A dotted line indicates a linearly regressed line.

anisotropies in terms of the results that the tactile temporal sequence presented across hand axis was perceived longer than that along hand axis (Experiments 1 and 3) and that the anisotropy was not observed on the palm side of the hand (Experiment 2). The perceptual anisotropy in space on the hand dorsum can be explained by the "pixel model" (Longo, 2017; Longo & Haggard, 2011). This model assumes that each input from touch is distributed in a 2-dimensional map of the skin surface as if they were pixels. Distances can be calculated by counting the number of pixels separating two stimulated locations on the skin surface. This idea successfully explains the differences in distance perception based on the sensitivities of skin surface (Cody et al., 2008; Schlereth et al., 2001, p. 1996). Further, the model proposes that each pixel is represented as an equally-sized, isotropic form (e.g., circle) at the perceptual level, even though actual receptive fields have different sizes and anisotropic, oval shapes (Alloway et al., 1989; Brooks et al., 1961; Powell & Mountcastle, 1959). This assumption is also able to predict the perceptual distortion toward the medio-lateral axis for representing hand surface. Also, the modulations of temporal perception by distance information can be explained by a Bayesian framework. In daily life, under a constant velocity a moving object takes longer time to travel bigger distance. Our brain is continuously exposed to and learns these relationships (a prior). Then, if we encounter the situation where two temporal sequences are presented with a fixed interval but different distances, the brain automatically applies the prior information to this situation and consequently induces illusory longer temporal perception to the sequence with bigger distance. With an assumption that the brain may presume a constant low velocity of objects on the skin surface, this Bayesian model well explains the biases in temporal perception based on distance information (Goldreich, 2007). The phenomenological correspondences between spatial and temporal anisotropies indicate that this Bayesian perceptual assumption is based on the somatosensory "pixel" space model on the hand surface (Longo, 2017; Longo & Haggard, 2011) rather than actual, physical space.

However, the results of Experiment 3 found no positive correlation between the magnitudes of the spatial and temporal tactile anisotropies across the participants. We may assume the underlying mechanism of the temporal anisotropy in two ways. One is that the temporal anisotropy is established based on the spatial anisotropy thorough a perceptual learning process, but they occur independently after the learning is consolidated: when tactile stimulations are applied to the hand surface, the anisotropy of distance is perceived, then this information is automatically applied to temporal perception each time. This transfer process can be learned many times and consolidated simply because spatial and temporal information usually coexist, then the spatial and temporal anisotropic perceptions appear spontaneously and independently in each in response to the presentation of touches. An alternative interpretation is that the temporal anisotropy occurs based on a somatosensory processing completely independent from the processing related to the spatial anisotropy. The Bayesian model (Goldreich, 2007) predicts that tactile spatial acuity can solely modulate temporal perception. Specifically, the model suggests that the stronger modulations of tactile temporal perception may occur with higher spatial acuity (less spatial uncertainty of tactile inputs). This indicates that the tactile temporal anisotropy could be explained from the finer spatial acuity on the across hand axis compared to the along hand axis due to the anisotropic shape of the tactile receptive fields on the hand dorsum (Alloway et al., 1989; Brooks et al., 1961; Powell & Mountcastle, 1959). Since the anisotropy of spatial acuity can solely predict the tactile temporal anisotropy across the hand axes even in the case where the physical and perceptual distances are equivalent, the magnitudes of the temporal and spatial anisotropies are not necessarily positively correlated across the participants.

These possibilities can be tested in the future, for example, by focusing on spatial and temporal characteristics in brain responses for the spatial and temporal perceptual anisotropies. Also, the Bayesian model (Goldreich, 2007) suggests that the magnitudes of the modulations of tactile temporal perception from tactile spatial information may depend on spatial acuity of body surface. The spatial anisotropies between the mediolateral and proximodistal axes have been reported body parts other than hand (Longo & Haggard, 2011) such as forehead, forearm and foot (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015; Stone et al., 2018). If the magnitudes of temporal anisotropy are consistent among different body parts having different spatial acuity, this would suggest that the temporal anisotropy is not fully independent from tactile spatial distance information. The Bayesian model also provides the prediction that the modulation of temporal perception by distance information may diminish when the temporal interval is sufficiently large. Future studies should test whether the temporal anisotropy across the hand axes disappear or not by using ISI longer (e.g., 1 s) than that used in this study (300 ms). In either way, the striking phenomenological correspondence between spatial and temporal tactile perceptual anisotropies indicate that very similar intrinsic, distorted somatosensory representations exist in both the spatial and temporal domains.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices.

Credit statement

Souta Hidaka: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization; Luigi Tamè Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - review & editing. Antonio Zafarana: Methodology, Software, Investigation, Writing - review & editing. Matthew R. Longo: Conceptualization, Validation, Resources, Writing - review & editing, Funding acquisition.

Acknowledgements

This research was supported by a Grant-in-Aid for Scientific Research (C) (No. 17K00214) from Japan Society for the Promotion of Science to SH and a grant from the European Research Council (ERC-2013-StG-336050) under the FP7 to MRL.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2020.03.011.

REFERENCES

Alloway, K. D., Rosenthal, P., & Burton, H. (1989). Quantitative measurements of receptive field changes during antagonism of GABAergic transmission in primary somatosensory cortex of cats. *Experimental Brain Research, 78*(3), 514–532. https://doi.org/10.1007/BF00230239.

Anema, H. A., Wolswijk, V. W. J., Ruis, C., & Dijkerman, H. C. (2008). Grasping Weber's illusion: The effect of receptor density differences on grasping and matching. *Cognitive Neuropsychology, 25*(7–8), 951–967. https://doi.org/10.1080/02643290802041323.

Brainard, D. H. (1997). The psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436. https://doi.org/10.1163/156856897X00357.

Brooks, V. B., Rudomin, P., & Slayman, C. L. (1961). Peripheral receptive fields of neurons in the cat's cerebral cortex. *Journal of Neurophysiology, 24*(3), 302–325. https://doi.org/10.1152/jn.1961.24.3.302.

Burtt, H. E. (1917). Tactual illusions of movement. *Journal of Experimental Psychology, 2*(5), 371–385. https://doi.org/10.1037/h0074614.

Cathy, A., & Ripley, B. (2019). Boot: Bootstrap R (S-Plus) functions. *R Package Version, 1.3-24*.

Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception, 28*(7), 851–875. https://doi.org/10.1068/p2873.

Cody, F. W. J., Garside, R. A. D., Lloyd, D., & Poliakoff, E. (2008). Tactile spatial acuity varies with site and axis in the human upper limb. *Neuroscience Letters, 433*(2), 103–108. https://doi.org/10.1016/j.neulet.2007.12.054.

de Vignemont, F., Majid, A., Jola, C., & Haggard, P. (2009). Segmenting the body into parts: Evidence from biases in tactile perception. *The Quarterly Journal of Experimental Psychology, 62*(3), 500–512. https://doi.org/10.1080/17470210802000802.

Efron, B., & Tibshirani, R. J. (1993). *An introduction to the Bootstrap*. New York: Chapman and Hall.

Fiori, F., & Longo, M. R. (2018). Tactile distance illusions reflect a coherent stretch of tactile space. *Proceedings of the National Academy of Sciences, 115*(6), 1238–1243. https://doi.org/10.1073/pnas.1715123115.

Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. *Plos One, 2*(3), e333. https://doi.org/10.1371/journal.pone.0000333.

Goudge, M. E. (1919). A qualitative and quantitative study of Weber's Illusion. *The American Journal of Psychology, 29*(1), 81–119. https://doi.org/10.2307/1414107.

Green, B. G. (1982). The perception of distance and location for dual tactile pressures. *Perception & Psychophysics, 31*(4), 315–323. https://doi.org/10.3758/BF03202654.

JASP Team. (2019). *JASP*. Version 0.9.2.

Komsta, L. (2011). Outliers: Tests for outliers. R Package Version 0.14 .

Le Cornu Knight, F., Longo, M. R., & Bremner, A. J. (2014). Categorical perception of tactile distance. *Cognition, 131*(2), 254–262. https://doi.org/10.1016/j.cognition.2014.01.005.

Longo, M. R. (2017). Distorted body representations in healthy cognition. *The Quarterly Journal of Experimental Psychology, 70*(3), 378–388. https://doi.org/10.1080/17470218.2016.1143956.

Longo, M. R., Ghosh, A., & Yahya, T. (2015). Bilateral symmetry of distortions of tactile size perception. *Perception, 44*(11), 1251–1262. https://doi.org/10.1177/0301006615594949.

Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance, 37*(3), 720–726. https://doi.org/10.1037/a0021921.

Longo, M. R., & Sadibolova, R. (2013). Seeing the body distorts tactile size perception. *Cognition, 126*(3), 475–481. https://doi.org/10.1016/j.cognition.2012.11.013.

Marks, L. E., Girvin, J. P., Quest, D. O., Antunes, J. L., Ning, P., O'Keefe, M. D., et al. (1982). Electrocutaneous stimulation II. The estimation of distance between two points. *Perception & Psychophysics, 32*(6), 529–536. https://doi.org/10.3758/BF03204206.

Miller, L. E., Longo, M. R., & Saygin, A. P. (2016). Mental body representations retain homuncular shape distortions: Evidence from Weber's illusion. *Consciousness and Cognition, 40*, 17–25. https://doi.org/10.1016/j.concog.2015.12.008.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442. https://doi.org/10.1163/156856897X00366.

Peng, R. D. (2019). Simpleboot: Simple bootstrap routines. *R Package Version, 1.1-7*.

Powell, T. P., & Mountcastle, V. B. (1959). Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey: A correlation of findings obtained in a single unit analysis with cytoarchitecture. *Bulletin of the Johns Hopkins Hospital, 105*, 133–162.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/.

Schlereth, T., Magerl, W., & Treede, R. D. (2001). Spatial discrimination thresholds for pain and touch in human hairy skin. *Pain, 92*(1–2), 187–194. https://doi.org/10.1016/S0304-3959(00)00484-X.

Schütt, H. H., Harmeling, S., Macke, J. H., & Wichmann, F. A. (2016). Painfree and accurate Bayesian estimation of psychometric functions for (potentially) overdispersed data. *Vision Research, 122*, 105–123. https://doi.org/10.1016/j.visres.2016.02.002.

Shore, D. I., Gray, K., Spry, E., & Spence, C. (2005). Spatial modulation of tactile temporal-order judgments. *Perception, 34*(10), 1251–1262. https://doi.org/10.1068/p3313.

Stone, K. D., Keizer, A., & Dijkerman, H. C. (2018). The influence of vision, touch, and proprioception on body representation of the lower limbs. *Acta Psychologica, 185*, 22–32. https://doi.org/10.1016/j.actpsy.2018.01.007.

Suto, Y. (1952). The effect of space on time estimation (S-effect) in tactual space. I. Japanese Journal of Psychology, 22, 45–57.

Tamè, L., Tucciarelli, R., Sadibolova, R., Sereno, M. I., & Longo, M. R. (2019). *Reconstructing neural representations of tactile space*. BioRxiv. https://doi.org/10.1101/679241.

Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience, 7*(3), 219–220. https://doi.org/10.1038/nn1199.

Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception and Psychophysics, 66*, 1171–1189. https://doi.org/10.3758/BF03196844.

Watson, A. B., & Pelli, D. G. (1983). Quest: A bayesian adaptive psychometric method. *Perception & Psychophysics, 33*(2), 113–120. https://doi.org/10.3758/BF03202828.

Weber, E. H. (1996). De subtilitate tactus. In H. E. Ross, & D. J. Murray (Eds.), *E. H. Weber on the tactile senses* (2nd ed.). London: Academic Press (Original work published 1834).

Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In D. R. Kenshalo (Ed.), *The skin senses* (pp. 195–222). Springfield, IL: Charles C. Thomas.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.

Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision, 7*(10). https://doi.org/10.1167/7.10.2.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience, 4*(7), 759–765. https://doi.org/10.1038/89559.