

BIROn - Birkbeck Institutional Research Online

Hidaka, S. and Tucciarelli, Raffaele and Azañón, Elena and Longo, Matthew (2022) Tilt adaptation aftereffects reveal fundamental perceptual characteristics of tactile orientation processing on the hand. *Journal of Experimental Psychology: Human Perception and Performance* 48 (12), pp. 1427-1438. ISSN 0096-1523.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/48785/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>
contact lib-eprints@bbk.ac.uk.

or alternatively

Tilt adaptation aftereffects reveal fundamental perceptual characteristics of tactile orientation processing on the hand

Souta Hidaka^{1,2*}, Raffaele Tucciarelli², Elena Azañón³⁻⁵, and Matthew R. Longo²

1. Department of Psychology, Rikkyo University, 1-2-26, Kitano, Niiza-shi, Saitama, Japan.

2. Department of Psychological Sciences, Birkbeck, University of London, United Kingdom

3. Department of Neurology, Otto-von-Guericke University Magdeburg, 39129 Magdeburg, Germany

4. Department of Behavioral Neurology, Leibniz Institute for Neurobiology, 39118 Magdeburg, Germany

5. Center for Behavioral Brain Sciences, 39106 Magdeburg, Germany

*Corresponding author

Contact information

Souta Hidaka: hidaka@rikkyo.ac.jp

Raffaele Tucciarelli: rtucciarelli@gmail.com

Elena Azañón: eazanyon@gmail.com

Matthew R. Longo: matrrlongo@gmail.com

Word count (excluding title, references, author affiliations, acknowledgments, figures and figure legends, abstract, and public significance statements): 6398 words

Abstract

Orientation information contributes substantially to our tactile perception such as feeling an object's shape on the skin. For vision, a perceptual adaptation aftereffect (tilt aftereffect; TAE), which is well explained by neural orientation selectivity, has been used to reveal fundamental perceptual properties of orientation processing. Neural orientation selectivity has been reported in somatosensory cortices. However, little research has investigated the perceptual characteristics of the tactile TAE. The aim of the current study was to provide the first demonstration of a tactile TAE on the hand and investigate the perceptual nature of tactile TAE on the hand surface. We used a two-point stimulation with minimal input for orientation. We found clear TAEs on the hand surface: Adaptation induced shifts in subjective vertical sensation toward the orientation opposite to the adapted one. Further, adaptation aftereffects were purely based on orientation processing given that the effects transferred between different lengths across adaptor and test stimuli and type of stimuli. Finally, adaptation aftereffects were anchored to the hand: tactile TAE occurred independently of hand rotation and transferred from palm to dorsum sides of the hand, while the effects did not transfer between hands. Our findings demonstrate the existence of hand-centered perceptual processing for basic tactile orientation information.

Keywords: touch, tactile orientation, tilt aftereffects, somatosensory processing, hand

Public significance statements

Perceptual adaptation aftereffects have been used to reveal underlying perceptual properties for specific stimulus dimensions. In vision, the tilt aftereffect (TAE) has contributed to uncover perceptual characteristics such as interocular integration for orientation information, which substantially contributes to perceive object's shape. However, perceptual characteristics of tactile TAE remain unclear. Here, we provide the first demonstration of tactile TAE on the hand surface. Further, we demonstrate that the tactile TAE transfer between different hand's surfaces, but not across the hands. The aftereffects also occurred regardless of hand rotation. Our findings demonstrate the existence of hand-centered perceptual processing for basic tactile orientation information.

The orientation of edges and contours is a critical source of information for object perception in both vision (Oliva & Torralba, 2007) and touch (Hsiao et al., 2002). In the visual system, the orientation-selectivity of neurons in the primary visual cortex has been extensively studied since the seminal work of Hubel and Wiesel (1962), and appears to reflect one of the key computational steps of early cortical visual processing (Marr, 1982). Analogous orientation selectivity has also been found in the somatosensory cortex (Bensmaia, Denchev, et al., 2008; Fitzgerald et al., 2006; Hsiao et al., 2002; Thakur et al., 2006), suggesting important commonalities in the organization of these sensory systems.

In vision, one of the main tools used by perceptual psychophysicists to study orientation processing has been adaptation aftereffects, such as the so-called tilt aftereffect (TAE) (Gibson & Radner, 1937). Adaptation aftereffects have been extensively investigated because the revealing window they provide into underlying perceptual mechanisms (Solomon & Kohn, 2014). In the TAE, prolonged observation of a line or contour at one orientation (e.g., tilted 10° clockwise (CW) from vertical) induces a perceptual aftereffect in which stimuli are perceived as vertical when tilted in the direction opposite to adaptation (e.g., counterclockwise (CCW) from vertical). This contrastive perceptual aspect of the TAE is well explained by suppression of neural activity selective to the adapted orientation and changes in neural population coding of orientation tuned responses (Clifford, 2014; Jin et al., 2005; Solomon & Kohn, 2014). The TAE has provided a revealing link between psychophysical studies of visual perception and its underlying neurophysiology (Clifford, 2014; Coltheart, 1971; Magnussen & Kurtenbach, 1980b; see Thompson & Burr, 2009 for other forms of adaptation aftereffects that do not entail contrastive effects but modulations of perceptual sensitivity without perceptual bias).

Contrastive adaptation aftereffects have also been reported in touch for location (Li et al., 2017), distance (Calzolari et al., 2017), curvature (van der Horst et al., 2008), and size (Kappers & Bergmann Tiest, 2013; Maravita, 1997; Uznadze, 1966) as well as the other forms of the effects for frequency of vibration (Tommerdahl et al., 2005), vibrotactile pressure (Delemos & Hollins, 1996), and location (Tannan et al., 2006). However, despite an extensive neurophysiological literature showing that orientation-selectivity is a key mechanism used by the somatosensory system, just as by the visual system, there is scarce evidence that TAEs can be induced in touch. To our knowledge, only one unpublished dissertation has reported tactile TAEs on the fingertips (Silver, 1969). The perceptual characteristics of tactile TAEs, however, remain unknown.

Adaptation aftereffects like TAE are not mere by-products of sensory systems, but rather reflect ecologically-important functions of perceptual processes (Gibson, 1937; Thompson & Burr, 2009). Visual TAE studies have provided rich insight into perceptual mechanisms including the frames of reference used for orientation coding (Knapen et al., 2011; Mathôt & Theeuwes, 2013; Melcher, 2005, 2007; Nakashima & Sugita, 2017; Zimmermann et al., 2013), interocular integration of orientation information (Campbell & Maffei, 1971; May & Zhaoping, 2016; Movshon et al., 1972), and sequential processing stages involved in orientation coding (D. He et al., 2012; S. He & MacLeod, 2001; Saad & Silvanto, 2013). In touch, both behavioral (Bensmaia, Hsiao, et al., 2008; Silver, 1969) and neurophysiological (Bensmaia, Denchev, et al., 2008; Fitzgerald et al., 2006; Hsiao et al., 2002; Pruszynski & Johansson, 2014; Suresh et al., 2016; Thakur et al., 2006) studies have revealed underlying mechanisms for basic aspects of tactile orientation processes such as detection and discrimination. However, many perceptual aspects of tactile orientation coding

remain unclear. In the first place, fundamental aspects of tactile orientation processes such as the frame of reference (hand-centered or not) and contra-lateral (across hands) or inter-surface (palm and dorsum) transfer remain uninvestigated. Also, studies concerning tactile orientation processing have consistently used line stimuli such as indented bars or edges with or without movement. These stimuli may provide redundant information such as surface area and contours, in addition to orientation. To purely investigate tactile orientation processing, it is thus critical to use stimuli with minimal input, such as two-point tactile stimuli (Calzolari et al., 2017; Fiori & Longo, 2018; Longo & Haggard, 2011; Tong et al., 2013). Furthermore, previous studies of tactile orientation perception have just focused on the fingertips. While the finger is one of the most sensitive body areas (Vallbo & Johansson, 1984; Weinstein, 1968), somatosensory cortices cover the entire body (Penfield & Boldrey, 1937) and the same types of tactile afferent neurons are distributed both fingertips and hand surface (Vallbo & Johansson, 1984). It can be thus expected that the perceptual and neural processes for orientation are common over the entire hand surface, rather than limited to the fingertips.

Here, we demonstrate TAEs on the hand surface for the first time, and exploit these effects to investigate perceptual properties of tactile TAE. In eight experiments, tactile stimuli were applied passively to exclude an involvement of proprioceptive and kinesthetic information. As in the previous study regarding tactile distance adaptation aftereffects (Calzolari et al., 2017), we mainly applied stimulation to the hand dorsum instead of the palm. We could consider that there can be common or integrated perceptual representations between the hand surfaces (Longo, 2020; Longo & Haggard, 2012; Manser-Smith et al., 2018), whereas there exists a difference in basic tactile acuity (Mancini et al., 2014). We found that adaptation to a tilted orientation clearly induced TAEs on the hand surface in the

proximo-distal (Exps. 1-2) and medio-lateral (Exp.3) hand axes. Adaptation aftereffects were purely based on tactile orientation information because, in addition to using a two-point tactile stimulus with minimal information regarding orientation, the effects transferred between different lengths (3 cm and 4 cm; Exp. 4) and stimuli types (object line and two-points; Exp. 5) across adaptor and test stimuli. Whereas TAEs did not transfer between the left and right hands (Exp. 6), the aftereffects occurred regardless of hand rotation (Exp. 7) and transferred from the palmar to the dorsal side of the hand (Exp. 8). Our findings regarding tactile TAE indicate that perceptual processing for basic tactile orientation information is anchored to the hand.

Methods

This study was not preregistered.

Participants

Ninety-nine healthy volunteers participated in 8 experiments. According to a poor model fit criterion ($R^2 < 0.5$ in at least one condition), data from 4 participants (2 in Exp. 5 and 1 each in Exps. 6 and 7) were excluded from analyses. One participant was also excluded in Exp. 8 as an outlier based on the Smirnov-Grubbs test ($p < .05$). Fitting results to the remaining data were good with a mean (SD) across experiments of 0.86 (0.11). The remaining sample was as follows: Exp. 1 (mean (SD) = 27 (6.61) y; $n = 15$, 9 females), Exp. 2 (29.41 (15.42) y; $n = 12$, 7 females), Exp. 3 (24.33 (7.05) y; $n = 12$, 5 females), Exp. 4 (30.17 (8.62) y; $n = 12$, 5 females), Exp. 5 (33.10 (14.84) y; $n = 10$, 3 females), Exp. 6 (36.64 (13.48) y; $n = 11$, 5 females), Exp. 7 (26.18 (11.56) y; $n = 11$, 8 females), and Exp. 8 (28.82 (12.34) y; $n = 11$, 5 females). The sample size was determined in reference to the previous study regarding tactile distance adaptation

aftereffects (Calzolari et al., 2017). In their first and second experiments, the effects had effect sizes of Cohen's $d_z = 2.44$ and 1.59 in paired sample t-tests. A power analysis using G*Power 3.1 software (Faul et al., 2009) with this effect size, alpha of 0.05, and power of 0.8 indicated that 4-6 participants were needed. Thus, our sample size is appropriately powered to detect a comparably sized effect. All but 7 participants were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971), with a mean (SD) across experiments of 82.69 (18.19). 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, and gave written informed consent before initiating the experiments. The study was conducted in accordance with the principles of the Declaration of Helsinki and was approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London (Reference number: 171887; Title: Building body representations: an investigation of the formation and maintenance of body representations).

Stimuli and General Procedure.

Stimulus was a pair of pointed wooden rods mounted on foamboard and separated by 3 cm, similar to those used in previous studies (Calzolari et al., 2017; Le Cornu Knight et al., 2014; Longo & Haggard, 2011). The tip of each rod was rounded off. Stimuli were delivered passively and manually by the experimenter on the dorsum side of the participants' left hand to exclude an involvement of proprioceptive and kinesthetic information. The locations of tactile stimulation were marked with a water-based ballpoint pen on the hand dorsum using a plastic template. On each trial, participants were exposed to an adaptation phase and a test phase. To reduce the intrinsic variability of a manual stimulation, stimuli in the adaptation

phase was presented approximately every second (self-paced counting), impressing pressure on each touch as constantly as possible, avoiding wavering, and touching the skin simultaneously (Calzolari et al., 2017). If any error occurred in any given trial during test phase (e.g., non-simultaneous presentation of the two rods, or perceived changes in pressure across the two rods), the stimulation was applied again in the same trial. Participants were blindfolded and sat with their palm resting on the table in front of the experimenter, with the digits oriented toward the experimenter. They were asked to keep their hands still, and the position was monitored by the experimenter. The experiments were performed by a custom MATLAB (MathWorks, Natick, MA) script and Psychtoolbox-3 (Brainard, 1997; Pelli, 1997) with a laptop computer (MacBook Pro, Apple, CA).

Exp. 1: Aftereffects with different adaptation orientations and the method of limits.

Participants were exposed to an adaptation phase and a test phase on each trial with a two-point stimulus (**Fig. 1**). One stimulus point was always located at the center of the wrist as an origin of rotation, and the other points were located at an angle ranging from from 0 (vertical) to 60° in 20° steps at CW and CCW directions across the proximodistal axis of the hand (i.e., a line between the center of the wrist and the knuckle of the middle finger). The length of the stimuli (i.e., the distance between the origin and each angle point) was 3 cm. To prevent participants from feeling pain, the tips of each rod were covered by a rubber material (Blu Tack), 3 mm in width. In each trial, adaptation was applied at either 20°, 40°, or 60° (CW or CCW) for 10 seconds. Longer periods of adaptation (60 second approximately) were delivered on the first trial of each session to adapt the new condition and de-adapt from possible residual adaptation from the previous adaptation condition. These adaptation durations (60 seconds for the initial adaptation and 10 seconds top-ups on each trial) were chosen based on previous studies

(Calzolari et al., 2017; van der Horst et al., 2008). Adaptation was applied in either constant, i.e., with the stimulus staying on the hand for the entire adaptation period, or tapping fashion., i.e., with the stimulus moving up and down in 1 second intervals.

Following adaptation, the experimenter manually changed the angle of the stimulus gradually (approximately 2.5° steps per around 1 second) from a random location between 40° and 60° at CW or CCW side toward the other side via the vertical (0°) point. Participants were asked to report immediately when they felt the applied angle corresponded to their vertical sensation. Vertical was defined and clearly told to participants as the straight line between the center of the wrist and the knuckle of the middle finger. When participants indicated their response, the experimenter stopped the rotation of the stimulus. Then, the tip of a baton (34 cm length, 2 mm diameter) was placed at the location of the rotated rod (the other side of the origin), and a photograph was taken with a web camera (Logitech Webcam Pro 9000 HD suspended on a tripod at 49.5 cm above the participant's hand, 1600×1200 pixels) (Longo & Haggard, 2010).

At the beginning of the experiment, participants performed a baseline condition without adaptation (no-adaptation) because of the possibility of systematic biases in the subjective vertical perception, away from the actual physical vertical (0°). Then, two adaptation modes (i.e., constant and tapping) were introduced as a block design. In each adaptation session, one of the six adaptation conditions, consisting of two directions (i.e., CW and CCW) and three angles (i.e., 20° , 40° , and 60°), was sequentially introduced. In each condition, four trials were performed. Thus, the experiment consisted of 52 trials: 48 trials with two adaptation modes (constant and tapping), two directions (CW and CCW), three adaptation angles, and four repetitions plus four trials of the no-adaptation. The order of adaptation mode was

counterbalanced among participants. The order of the adaptation directions was also counterbalanced with ABBA design among participants. The order of three adaptation angles were randomized for each adaptation direction in each adaptation direction. The rotation of the stimulus during the test phase started from CW side in the half of the trials and from CCW side in the other half in a random manner.

Exp. 2: Aftereffects with the method of constant stimuli. Participants were exposed to a 40° tapping adaptation either at CW or CCW direction (**Fig. 3A, B**). Adaptation on each trial was applied for 10 seconds. Longer periods of adaptation (60 second approximately) were also delivered on the first trial and after a break introduced in the middle of the block. In each trial, after the adaptation, a test stimulus was presented for approximately 1 second at either 0° (vertical), 7.5°, 15°, 22.5° or 30° in a CW or CCW direction. We marked 22 dots on the hand dorsum, and draw lines (5 cm) between the corresponding dots through the center (i.e., the midpoint between the center of the wrist and the knuckle of the middle finger). A 3 cm tactile stimulus (i.e., consisting of 2 separate points) was presented in a random location along each line at every stimulation both in the adaptation and test phases so that the stimuli were never applied systematically to the exact same locations. Applying touches across different skin locations served to induce adaptation to the spatial relation between two tactile events and to avoid sensitization or pain from repeated stimulation of the same skin locations (Calzolari et al., 2017).

Participants made unspeeded judgments of whether the test stimulus was perceived as vertical or not. This response mode, orthogonal to the tested dimension (i.e., CW/CCW directions), reduces the likelihood that any biases observed are because of response bias, rather than perceptual bias (Calzolari et al., 2017).

The experiment consisted of 216 trials with two adaptation directions (CW and CCW), nine test angles and twelve repetitions. The experiment was divided into four blocks of 54 trials and the order of adaptation directions was counterbalanced across the participants with ABBA design. Each test angle was randomly repeated 6 times in each block.

Exp. 3: Aftereffects along the medio-lateral hand axis. Methods in Exp. 3 were identical to those in Exp. 2 except that the adaptation and test stimuli were presented along the medio-lateral hand axis. We drew the matrix orthogonal to the proximodistal axis of the hand (**Fig. 3C**). Participants were asked to judge whether the test stimulus was perceived as horizontal or not. Horizontal was defined and clearly told to participants as the straight line across the hand axis thorough the midpoint between the wrist and the knuckle of the middle finger.

Exp. 4: Aftereffects with different stimulus lengths. Methods in Exp. 4 were identical to those in Exp. 2 except that adaptation was performed with a 4 cm two-point tactile stimulus and the test was applied with a 3 cm two-point tactile stimulus (**Fig. 5A**).

Exp. 5: Aftereffects with different stimulus types. Methods in Exp. 5 were identical to those in Exp. 2 except that adaptation was applied with a line stimulus, which was made of a kitchen sponge and cut at 3 cm length and 5 mm width (**Fig. 5B**). The test was performed with the two-point 3 cm tactile stimulus.

Exp. 6: Bilateral transfer. Methods in Exp. 6 were similar to those in Exp. 2 except that adaptation was performed on the participant's right hand, and the test was presented on the left hand (**Fig. 6A**).

Exp. 7: Aftereffects with hand rotation. Methods in Exp. 7 were similar to those in Exp. 2, with the exception that, in the adaptation phase, the participant's left hand was rotated 90° to the right (digits toward to the midsagittal plane) (**Fig. 6B**). After the adaptation phase, and

before the delivery of the test stimuli, participants were asked to bring the hand back to the canonical position (0°). At the end of the trial, after the response was given, participants were asked to bring the hand back to the rotated position. The experiment consisted of 180 trials with two adaptation directions, nine test angles and ten repetitions.

Exp. 8: Aftereffects with palm-side adaptation. Methods in Exp. 8 were similar to those in Exp. 2, with the exception that adaptation was applied on the palm of the participant's hand (**Fig. 6C**). During adaptation, participants were asked to rest their left hand palm up. After the adaptation phase, and before the delivery of the test stimuli, participants were asked to flip their hand palm down. At the end of the trial, after the response was given, participants were asked to bring the hand back to the palm up position. The design and number of trials are identical to that of Exp. 7.

Analyses.

In Exp. 1, data coding of the photographs taken and analyses were conducted using a custom MATLAB script and Psychtoolbox. Mean x-y pixel coordinates were calculated for the origin of the rotation and for locations of the rotated rod which participant judged as consistent with the subjective vertical sensation in each condition. Distances of mean x-y pixel coordinates between the origin and locations of the rotated rod were then calculated. We calculated angles from distances as the point of subjective verticality (PSV) based on trigonometry. A three-way repeated measures analysis of variance (ANOVA) was performed.

For the rest of experiments, the proportion of trials in which the test stimulus delivered to the left hand was judged as vertical (horizontal in Exp. 3) was analyzed as a function of the test angles. We fitted the following Gaussian function to each adaptation orientation for each participant using nonlinear least squares method (Curve fitting toolbox, MATLAB):

$$f(x) = (p_{max} - p_{min}) \exp\left[\frac{-(x - m)^2}{2\sigma^2}\right] + p_{min}$$

Here, m , σ , p_{max} , and p_{min} denote the mean (PSE), standard deviation, and upper and lower asymptotes of the proportions, respectively.

The PSEs of each adaptation direction were compared using two-tailed, paired sample t -tests. We also performed a mixed-designed ANOVA for the comparisons of the data between Exps. 2 and 4-6. T -tests were also performed for the standard deviation and peak value ($p_{max} - p_{min}$) of the function, but no significant differences were found.

All statistical tests used two-tailed p values with a level of significance set at $\alpha = 0.05$ with JASP (version 0.9) (JASP Team, 2018). To quantify the magnitude of the effects we report, we provide partial η_p^2 values for F-tests and Cohen's d_z for paired t tests (Cohen, 1988).

The data have been made publicly available via the Open Science Framework and can be accessed at <https://osf.io/sbqm5/>.

Results

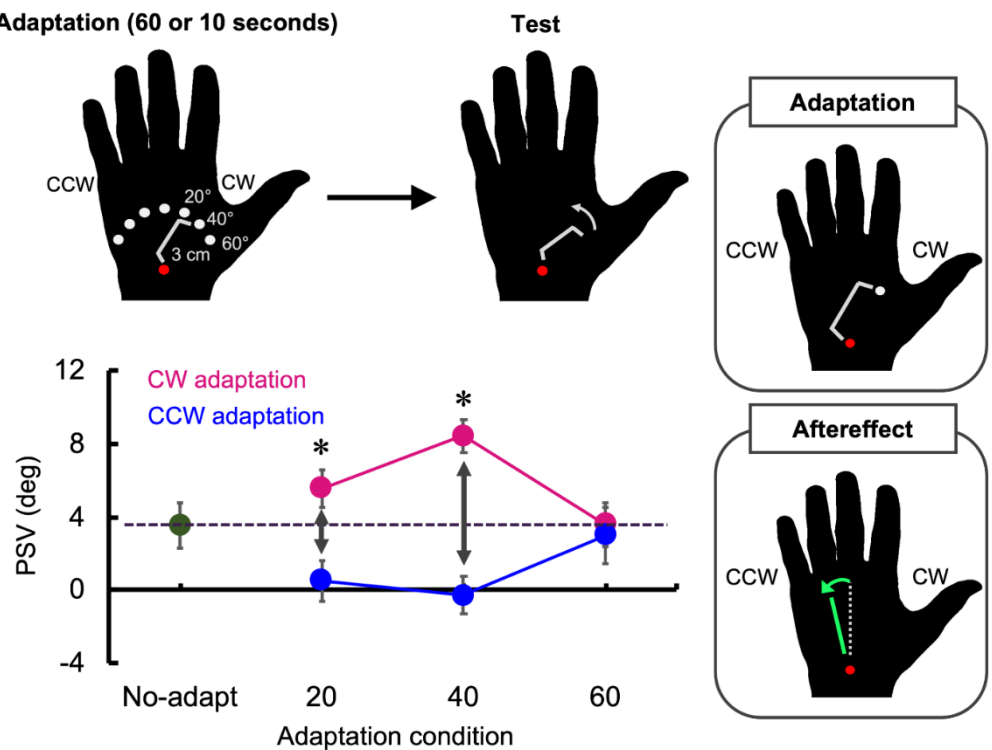
Tilt aftereffects on the hand dorsum (Exp. 1).

We first aimed to demonstrate the existence of a basic TAE on the hand dorsum. To our knowledge, there is just a single, unpublished, report of tactile TAEs at the fingertips from half a century ago (Silver, 1969). If a TAE occurs, PSVs should be shifted away from the adapted angle. Hence, an orientation tilted some degrees toward the adapted angle is consequently perceived as vertical. We found clear evidence for a tactile TAE on the hand dorsum between the adaptation directions (CW/CCW) using the method of limits, while subjective verticality also

deviated from the physical verticality (**Fig. 1**): PSVs shifted toward the adapted angle at 20° and 40° of adaptation, irrespective of the mode of adaptation condition (constant or tapping) (**Fig. 2**). A three-way repeated measures ANOVA with factors adaptation type (2: constant and

Figure 1

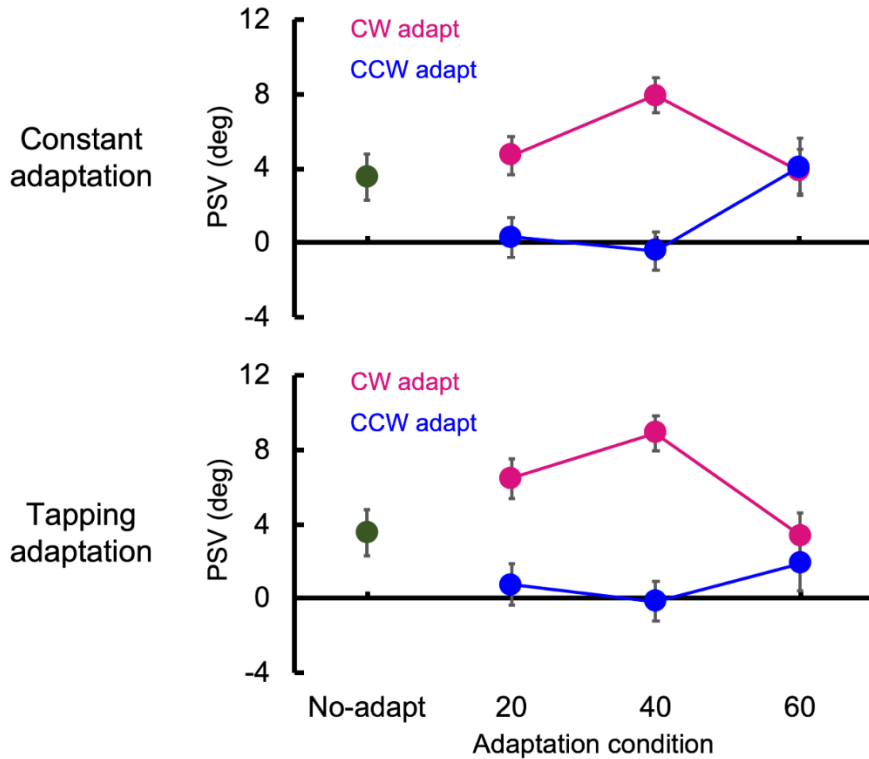
Procedure and results of Exp. 1



Note. Top panel shows schematic illustrations of the presentation of tactile stimuli in the adaptation and test phases. The adaptation was applied at 20, 40, or 60° CW or CCW. Right panels illustrate the tilt adaptation aftereffect. A physical stimulus with the vertical angle (a white dotted line) is perceived as tilted toward the angle opposite to the adapted one (a green line). The bottom panel shows the PSVs (N = 15) for each adaptation orientation against the adaptation conditions collapsed across the mode of adaptation (constant or tapping). Positive and negative values of the vertical axis correspond to CW and CCW test angles, respectively. Asterisks denote significant differences ($p < .05$). Error bars denote the SEM.

Figure 2

Results of Exp. 1 in each adaptation mode



Note. Each panel shows the constant and tapping adaptation modes. Error bars denote the SEM.

tapping), direction (2: CW and CCW), and angle (3: 20°, 40°, and 60°) showed a significant interaction between the direction of adaptation and the angle ($F(2, 28) = 36.39, p < .001, \eta_p^2 = 0.72$), as well as a main effect of adaptation direction ($F(1, 14) = 90.32, p < .001, \eta_p^2 = 0.87$). Simple main effects of adaptation direction were significant at 40° and 20° ($F(1, 42) = 99.27, 33.47, ps < .001$) but not at 60° ($F(1, 42) = 0.51, p = .49$).

Our findings demonstrate TAEs for the first time on the hand dorsum. In addition, TAEs occurred using two-point tactile stimulation containing minimal information regarding orientation

which had never been tested in the previous tactile TAE study at the fingers (Silver, 1969). Moreover, we found some important characteristics of the effect. First, adaptation to an angle of 40° is an optimal condition to introduce TAE irrespective of the type of the passive stimulation (constant and tapping). The existence of an optimal adapting orientation is reminiscent to the 10° rotation of a line stimulus in vision (Magnussen & Kurtenbach, 1980a). Second, the difference in the magnitude of the adaptation among the different adaptation angles indicates that the effects cannot be simply explained by attentional effects or response/decisional biases. Third, the adaptation effect did not transfer between proximo-distal (vertical) and medio-lateral (horizontal) hand axes given that no adaptation effect was observed at 60° of vertical (i.e., 30° from the horizontal) angle.

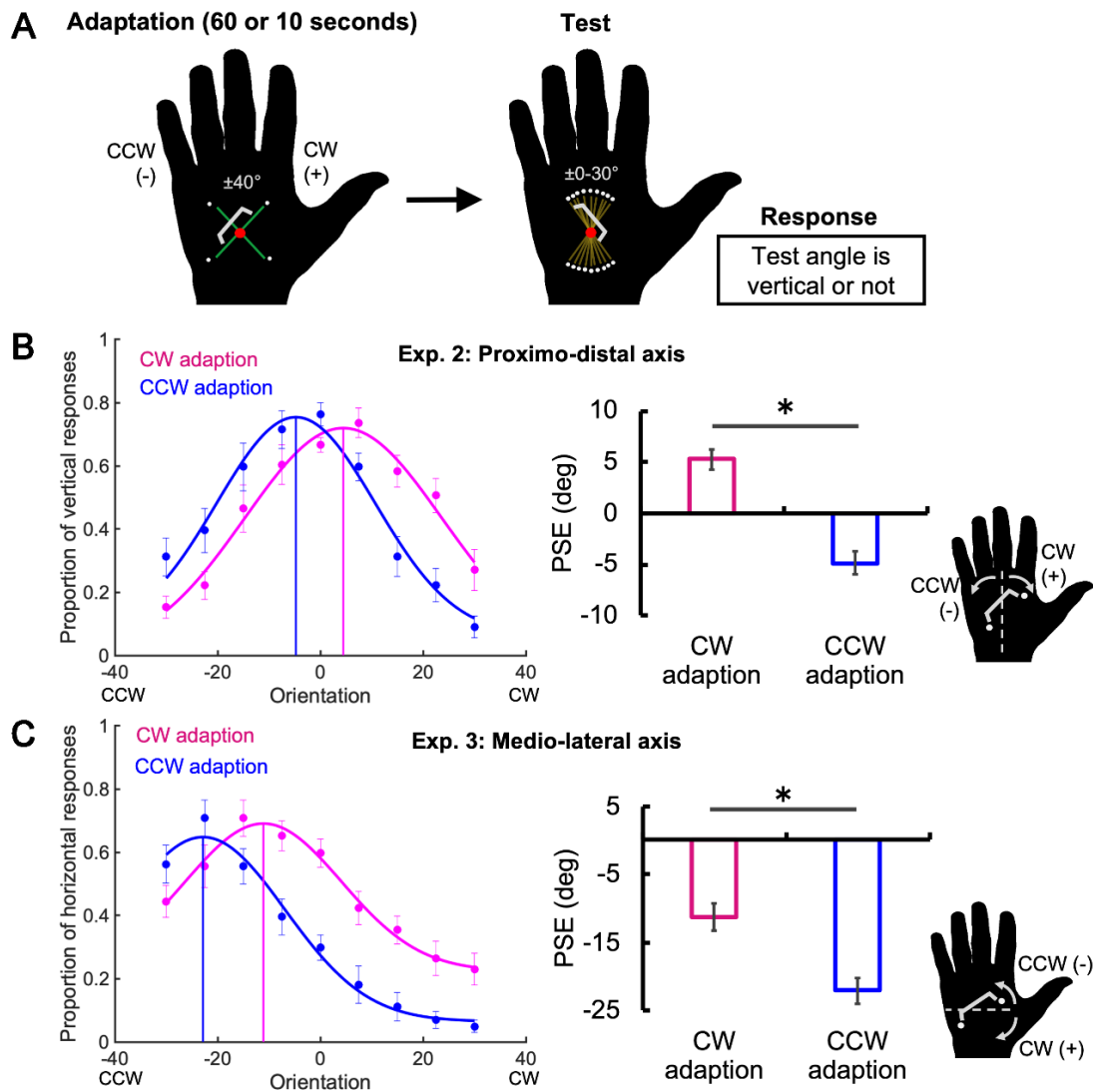
Tilt aftereffects in proximo-distal and medio-lateral hand axes (Exps. 2 and 3).

Exp.1 identified the optimal parameters for inducing TAEs on the hand using the method of limits. Exp.2 clearly replicated the TAE on the hand with a more precise psychophysical method (the methods of constant stimuli; **Fig. 3A, B, and Fig. 4**). After tapping adaptation, PSEs obtained from the psychometric functions shifted toward the adapted directions. A two-tailed pairwise *t*-test showed that PSEs were significantly different between adaptation directions ($t(11) = 7.03, p < .001, d_z = 2.03$).

Exp. 3 was performed to demonstrate the existence of the TAE in the horizontal (medio-lateral) hand axis. We found a clear TAE along the horizontal hand axis (**Fig. 3C and Fig. 4**). PSEs were significantly different between the two adaptation conditions along the medio-lateral hand axis ($t(11) = 6.90, p < .001, d_z = 1.99$). The data also showed a general bias where the horizontal perception shifted toward the CW direction, irrespective of the adaptation directions.

Figure 3

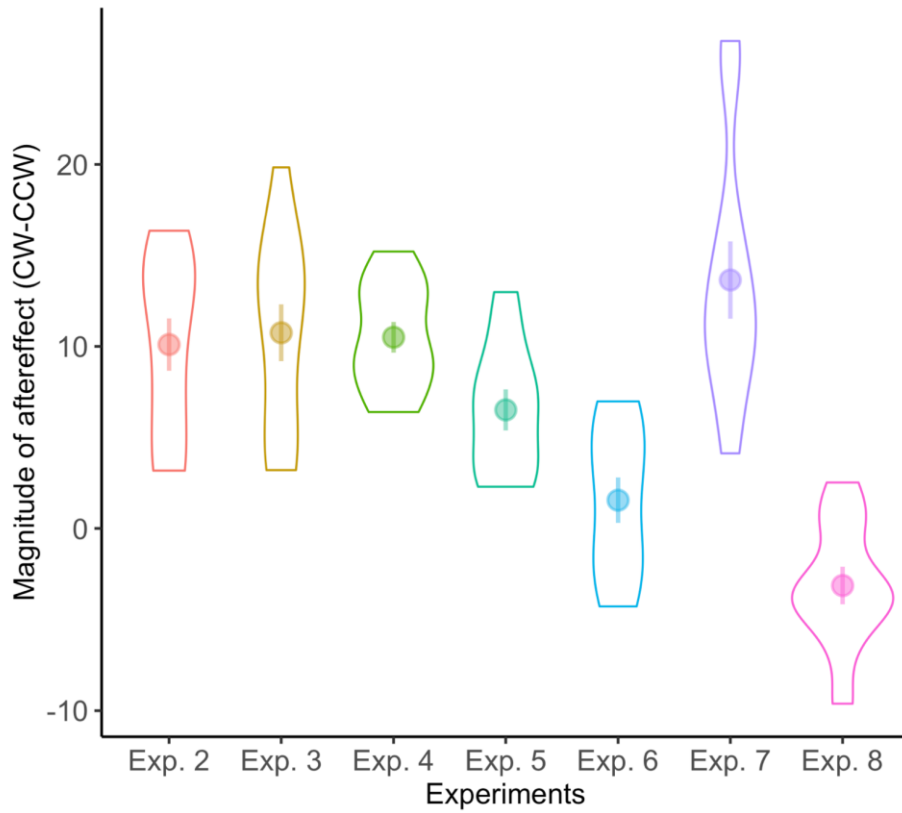
Procedure and results of Exps. 2 and 3



Note. (A) Schematic illustrations of the presentation of tactile stimuli in the adaptation and test phases. Tapping Adaptation was repeatedly presented at 40° orientation either in CW or CCW direction. After adaptation, a test stimulus was presented at one of the test angles. (B, C) Results of Exps. 2 and 3 (Ns = 12). Adaptation and test were held along the proximo-distal (vertical) and medio-lateral (horizontal) hand axes in Exps. 2 and 3, respectively. The left panels show the psychometric functions of subjective vertical/horizontal sensation against test angles. The vertical lines indicate the means (PSEs) for each adaptation orientation. The right panels show the mean PSEs. Asterisks denote significant difference ($p < .05$). Error bars denote the SEM.

Figure 4

Magnitude of the tilt aftereffect for Experiments 2-8.



Note. Magnitudes were calculated by subtracting the PSEs of CCW adaptation from those of CW adaptation. Each violin plot shows the distribution, and each dot shows the mean. Error bars denote the SEM.

While this may imply the existence of a basic bias for the perception of horizontality (c.f. Fiori & Longo, 2018), further investigations are beyond the scope of this study.

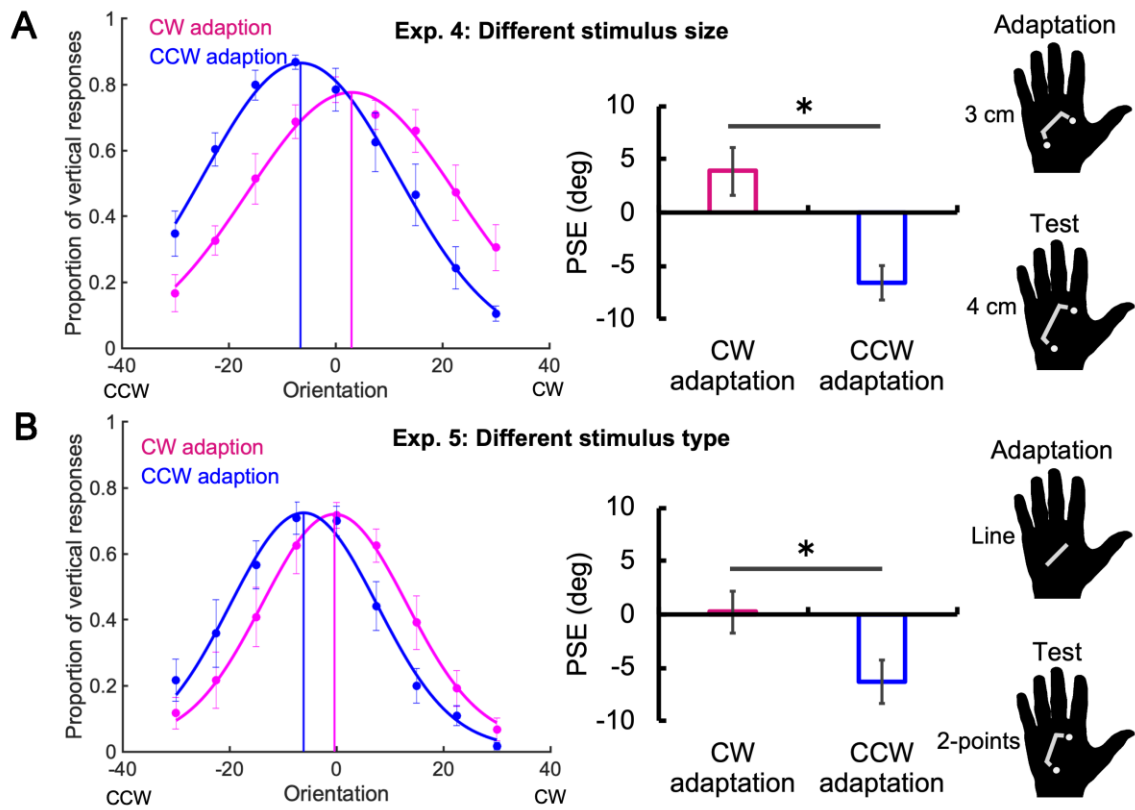
Transfer of tilt aftereffects across stimulus types (Exps. 4 and 5).

The preceding experiments presented the same 3 cm two-point tactile stimulus in both the adaptation and test phases. Tactile orientation discrimination thresholds (Bensmaia, Hsiao, et al., 2008) and orientation selectivity for neurons in tactile afferents (Pruszynski & Johansson, 2014; Suresh et al., 2016) and somatosensory cortices (Bensmaia, Denchev, et al., 2008) are known to be comparable among different stimulus properties such as moving and static stimuli or indented bars and edges. If TAEs transfer across adaptor and test stimuli of different dimensions, one could argue that TAEs are purely based on orientation processing.

In order to test this hypothesis, Exp.4 varied stimulus size by presenting a 3 cm two-point stimulus during the adaptation and a 4 cm two-point stimulus during the test (**Fig. 5A and Fig. 4**). We found clear TAEs across different lengths ($t(11) = 12.48, p < .001, d_z = 3.60$). In Exp. 5, we presented a 3 cm bar during the adaptation and the 3 cm two-point stimulus during the test (**Fig. 5B and Fig. 4**). Clear TAEs were observed across different stimuli types ($t(9) = 5.79, p < .001, d_z = 1.83$). We also confirmed that the magnitudes of the aftereffects were comparable between the situations where the adaptation and test stimuli were different (Exps. 4 and 5) and consistent (Exp. 2): A mixed-designed ANOVA with factors experiments (between participants factor, Exps.4 or 5 and Exp. 2) and adaptation direction (within participants factor) showed no significant main effects of experiments (Exp.4: $F(1, 22) = 0.59, p = .50, \eta_p^2 = 0.03$; Exp.5: $F(1,20) = 2.83, p = .11, \eta_p^2 = 0.12$) nor significant interactions (Exp.4: $F(1, 22) = 0.06, p = .81, \eta_p^2 = 0.00$; Exp.5: $F(1, 20) = 3.63, p = .07, \eta_p^2 = 0.15$), while there were significant main effects of adaptation direction (Exp.4: $F(1, 22) = 153.14, p < .001, \eta_p^2 = 0.87$; Exp.5: $F(1, 20) =$

Figure 5

Schematic illustrations of the presentation of tactile stimuli and results of Exps. 4 and 5



Note. (A) In Exp. 4 (N = 12), 3 cm and 4 cm two-point tactile stimuli were presented in the adaptation and test phases, respectively. (B) In Exp. 5 (N = 10), line and two-point tactile stimuli were presented in the adaptation and test phases, respectively. Asterisks denote significant difference ($p < .05$). Error bars denote the SEM.

77.99, $p < .001$, $\eta_p^2 = 0.80$). These results demonstrate that the TAEs on the hand transfer across different types of stimuli, indicating that the effects reflect orientation specific processing.

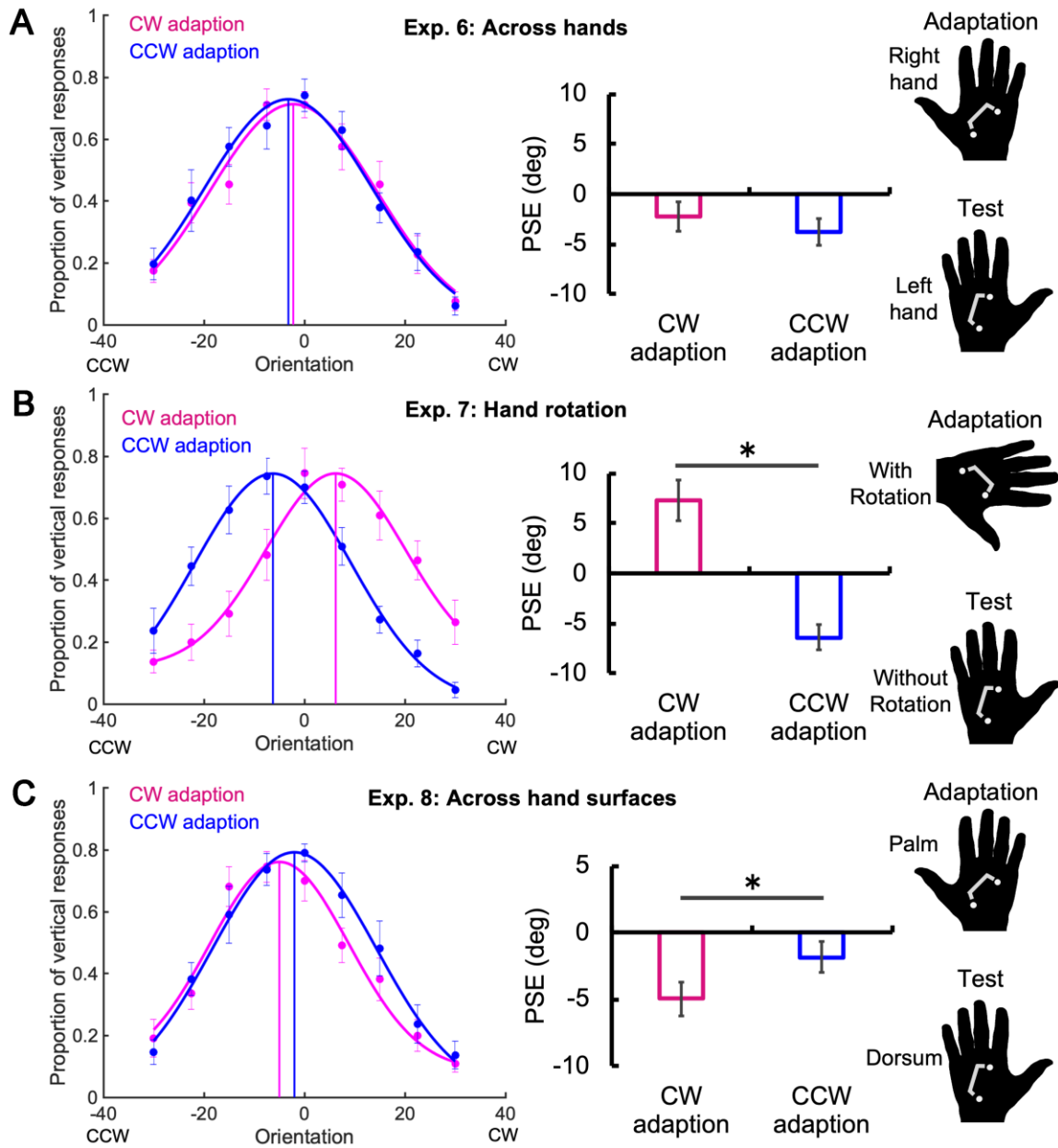
Hand-centered aspects of tilt aftereffects (Exps. 6-8).

Single-unit neurophysiological studies in monkeys have reported that neurons both in SI and SII show orientation selectivity (Bensmaia, Denchev, et al., 2008; Fitzgerald et al., 2006; Thakur et al., 2006). Neurons with receptive fields (RFs) covering homologous skin regions on both sides of the body have also been found in SII as well as SI (Iwamura, 2000). These findings posed a question of whether the TAE transfers contralaterally between the hands. To test this, in Exp. 6, adaptation was applied to the participants' right hand, and the test stimulus to their left hand (**Fig. 6A**).

We found that the TAE did not transfer across hands. PSEs were not significantly different between the adaptation directions ($t(10) = 1.24$, $p = .24$, $d_z = 0.38$) (**Fig. 6A and Fig. 4**). We also tested the lack of transfer of tactile TAE across the hands in Exp. 6 against the TAE observed in Exp. 2, where adaptation and test were performed within the same hand. A mixed-designed ANOVA showed a significant interaction ($F(1, 21) = 19.79$, $p < .001$, $\eta_p^2 = 0.49$) as well as main effects of experiment and adaptation direction ($F(1, 21) = 4.68, 36.84$, $p < .05, .001$, $\eta_p^2 = 0.18, 0.64$, respectively). These findings further support the lack of bilateral transfer of tactile TAE across the hands.

Figure 6

Schematic illustrations of the presentation of tactile stimuli and results of Exps. 6 to 8



Note. (A) In Exp. 6 (N = 11), adaptation and test stimuli were held on the right and left hands, respectively. (B) In Exp. 7 (N = 11), the hand was rotated 90° during the adaptation phase. (C) In Exp. 8 (N = 11), adaptation and test stimuli were held on the palm and dorsum sides of the left hand, respectively. Asterisks denote significant difference ($p < .05$). Error bars denote the SEM.

Exp. 7 investigated a hand centered aspect of the TAE. We can perceive tactile inputs either in a hand-centered reference frame (e.g., a touch is on my left hand surface) or in an external frame (e.g., a touch is on the left side, not the right side). Studies have shown that tactile inputs are rapidly transformed (by around 180 ms) from hand-centered to external space coordinates, taking posture into account (Azañón & Soto-Faraco, 2008a, 2008b). Therefore, orientation selectivity might be represented in an external frame of reference. To test this possibility, we asked participants to rotate their left hand at 90° to the right (digits toward to the midsagittal plane) during adaptation (**Fig. 6B**). Then, participants were asked to bring the hand back to the canonical, vertical position (0°) during the test phase. If orientation information is represented in an external space of reference, the orientation may be perceived as horizontal during the adaptation phase with the hand rotation but as vertical on the test phase without the hand rotation. Thus, based on the results of Exp.1, no TAE should occur. However, we observed a clear TAE after hand rotation ($t(10) = 6.42, p < .001, d_z = 1.94$) (**Fig. 6B and Fig. 4**). Furthermore, the magnitudes of the aftereffects between Exps. 2 (without hand rotation) and 7 (with hand rotation) were comparable: A mixed-designed ANOVA showed no significant main effects of experiments ($F(1, 21) = 0.03, p = .87, \eta_p^2 = 0.001$) nor significant interactions ($F(1, 21) = 1.97, p = .18, \eta_p^2 = 0.09$), while there were significant main effects of adaptation direction ($F(1, 21) = 88.31, p < .001, \eta_p^2 = 0.81$). This finding suggests that orientation information is represented in a hand-centered reference frame.

It remains unclear whether and how neural representations overlap between the dorsal and palmar skin surfaces in the human somatosensory cortices. Neurophysiological studies have shown that the dorsal and palmar hand surfaces are closely represented in primates' primary somatosensory cortex (SI) (Kaas et al., 1979; Merzenich et al., 1978, 1983, 1987; Pons

et al., 1987). Behavioral studies have demonstrated the existence of common or integrated perceptual representations between the hand surfaces (Longo, 2020; Longo & Haggard, 2012; Manser-Smith et al., 2018), while there exists a difference in basic tactile acuity (Mancini et al., 2014). Therefore, depending on the actual overlap of neural representations of hand surfaces in the human brain, the tactile TAE may transfer across these analogous skin surfaces. Exp. 8 tested transfer of TAE across the two hand surfaces. During adaptation, stimuli were presented on the palm by asking participants to rest their left hand palm up. Then, during the test phase, stimuli was presented on the dorsum, by asking participants to flip their hand palm down (**Fig. 6C**). We found a clear TAE on the dorsum after adaptation to the palm ($t(10) = -3.04$, $p = .01$, $d_z = -0.92$) (**Fig. 6C and Fig. 4**). Interestingly, adaptation on the palm did not produce the standard aftereffect on the dorsum, i.e., shifts toward the adapted direction. Instead, CCW adaptation on the palm produced CW-like adaptation aftereffects on the dorsum. The same was true for CW, which produced CCW-like adaptation aftereffects. These results showing the transfer of tactile TAE between the hand surfaces in a “see-through” manner further support the hand-centered view of tactile orientation processing.

Discussion

Our findings clearly demonstrate the existence of tactile TAEs on the hand surface. Passive adaptation to an orientation (especially at 40°) in the vertical (proximo-distal) or horizontal (medio-lateral) axes of the hand surface induced perceptual shifts of tactile orientation opposite to the adapted one. In consequence, the subjective vertical or horizontal perception of subsequent stimuli shifted toward the adapted orientation. Studies regarding vision have demonstrated that TAE is a key perceptual phenomenon related to neural

orientation selectivity in the brain (Clifford, 2014; Dragoi et al., 2001, 2002; Fang et al., 2005; Jin et al., 2005; Solomon & Kohn, 2014). Whereas neural orientation selectivity (Bensmaia, Denchev, et al., 2008; Fitzgerald et al., 2006; Hsiao et al., 2002; Pruszynski & Johansson, 2014; Suresh et al., 2016; Thakur et al., 2006) and the TAE (Silver, 1969) have been reported for tactile processing, these findings were limited to the finger pads. Our findings expand the understanding of tactile orientation processing regarding selectivity and perceptual aspects on the hand surface.

Here we demonstrated a tactile TAE with two-point stimuli, which contain the minimal information required to specify orientation. Single-unit physiological studies in monkeys and humans have shown that specific spatial firing patterns of the tactile afferent and cortical neurons contribute to encoding each orientation (Bensmaia, Denchev, et al., 2008; Pruszynski & Johansson, 2014; Suresh et al., 2016; Thakur et al., 2006). We can assume that simultaneous stimulations of “hot spots” in the receptive fields of these neurons can be enough to trigger reliable orientation tuning responses. In fact, reliable vertical-horizontal orientation discrimination has been demonstrated behaviorally with a two-point tactile stimulus on the hand (Tong et al., 2013). Furthermore, perceptual responses for distance on the hand surfaces are reported to change in response not only to a simple 90° orientation (Calzolari et al., 2017; Longo & Haggard, 2011) but also to a precise manipulation (rotation in 22.5° steps) (Fiori & Longo, 2018). Consistently, the data of the current study demonstrated clear psychometric functions with vertical/horizontal sensation against 20° steps of orientation. Of note, we observed that tactile TAE transferred between two-points stimuli and object line, which is reported to activate orientation selective neurons in somatosensory cortices (Bensmaia, Denchev, et al., 2008; Fitzgerald et al., 2006; Hsiao et al., 2002; Thakur et al., 2006), as well as the different length of

two points stimuli. These pieces of evidence strongly support the idea that our findings of tactile TAE with two-point stimuli, were purely based on orientation processing.

Tactile adaptation aftereffects have been reported for location (Li et al., 2017) and distance (Calzolari et al., 2017) on the hand. Our findings suggest, however, that TAEs are independent from these effects because transfer of aftereffects occurred across different lengths (3 and 4 cm) and stimulus types (line and two-point stimuli). In that regard, the TAEs reported here likely reflect purely orientation specific processing on the hand surface. This is in accordance with the fact that neural orientation selective responses are similar across different tactile stimulations (e.g., bars or edges, with or without stimulus' motion) (Bensmaia, Denchev, et al., 2008; Pruszynski & Johansson, 2014; Suresh et al., 2016).

We further demonstrate that TAEs occurred in a hand-centered manner. The adaptation aftereffects did not transfer between hands. This is reminiscent to the lack of transfer across hands for distance adaptation aftereffects (Calzolari et al., 2017). Similarly, curvature adaptation aftereffects do not transfer to the other hand (Vogels et al., 1997) or with minimal transfer (Van Der Horst et al., 2008) when stimuli are static and applied passively. In the current study, we did not observe inter-lateral transfer of the aftereffects by presenting orientation stimulation with random replacements and without movement. Furthermore, TAEs occurred independently of 90° rotation of the hand between adaptation and test phases. These findings indicate that orientation information is represented in a hand-centered reference frame, not in an external frame of reference.

The hand-centered aspect of tactile TAE was also supported by the finding that the adaptation aftereffects transferred from the palmar to dorsal sides of the hand in a “see-through” manner. Whereas RF structures and response characteristics are different between glabrous

and hairy skin surfaces (Longo & Haggard, 2011; Mancini et al., 2014; Mountcastle & Powell, 1959; Powell & Mountcastle, 1959), there exist common or integrated perceptual representations between the hand surfaces (Longo, 2020; Longo & Haggard, 2012; Manser-Smith et al., 2018). One plausible explanation is thus that orientation information is basically shared between the hand surfaces. This interpretation can be plausible given that tactile orientation perception is probably related to the perception of objects' properties like movement (i.e., motion direction) that occurs concurrently when haptically exploring an object. For example, when we pull our hand out of a pocket, the direction in which the fabric moves across the two sides of the hand is correlated in a 'see-through' way. Consistent with this idea, we observed the inter-surface transfer of tactile TAE in the situation where participants were asked to flip their hands upside down at a fixed spatial location. Notably, however, no inter-surface transfer was reported for distance aftereffects even with movements of turning the hand over (Calzolari et al., 2017). Our findings provide new insight into tactile orientation processing that, unlike other basic somatosensory features like distance, appears to arise from higher-level representations generalizing across the two skin surfaces of the hand.

Neural responses selective to visually presented orientation appear in the lateral geniculate nucleus (Vidyasagar & Urbas, 1982), and this information is projected onto the primary cortical areas (V1 and V2) (Hubel & Wiesel, 1962). The visual TAE has been explained by changes of neural responses in V1 neurons in terms of suppression of neural activity and changes in neural population coding (Clifford, 2014; Dragoi et al., 2001, 2002; Fang et al., 2005; Jin et al., 2005; Solomon & Kohn, 2014). With regard to touch, orientation information of afferent neurons is directly projected onto S1 cortical neurons (Bensmaia, Denchev, et al., 2008). Notably, it has been pointed out that shared mechanisms exist for orientation processing

between vision and touch (Sathian & Zangaladze, 2002; Yau et al., 2009; Zangaladze et al., 1999). Also, a visual TAE was reported to transfer to tactile stimulation on the forehead (Krystallidou & Thompson, 2016). These findings suggest that analogous neural mechanisms could underlie visual and tactile TAEs. Thus, it is likely that TAEs are elicited by the suppression of neural activity and changes in neural population coding in SI neurons.

Receptive fields of V2 neurons are reported to respond to multiple orientations (Anzai et al., 2007). Also, visual tilt adaptation induces similar suppressive neural responses both in V1 and V2 (Fang et al., 2005). Interestingly, neurons in SII show orientation selectivity for tactile stimulations across different finger pads (Fitzgerald et al., 2006). Moreover, it has been suggested that SII neurons can represent larger-scale spatial features of tactile stimuli by integrating information from different skin locations (Serino et al., 2008). Based on these findings and our current results on the transfer TAEs across palm and dorsum, we predict that SII, as well as SI, is involved in the TAEs on the hand.

Studies regarding tactile orientation processing have focused on basic aspects such as detection and discrimination on a single body part (i.e., finger pads) (Bensmaia, Denchev, et al., 2008; Bensmaia, Hsiao, et al., 2008; Fitzgerald et al., 2006; Hsiao et al., 2002; Pruszynski & Johansson, 2014; Silver, 1969; Suresh et al., 2016; Thakur et al., 2006) or representations in haptic space (Kappers, 1999; Postma et al., 2008). The existence of the TAE itself and the orientation-specific aspect of the observed tactile TAEs in the current study indicate that neural orientation tuning is not limited to fingers, but is a general property across body surfaces including the hand. The perceptual characteristics of the tactile TAE, such as independence from hand rotation, inter-surface transfer, and no transfer between hands, suggest the existence of hand-centered representations in the processing of basic tactile

orientation information. Adaptation aftereffects reflect ecologically-important functions of perceptual adaptive modulation processes toward changes from moment to moment in the external world (Gibson, 1937; Thompson & Burr, 2009). Our findings of tactile TAE on the hand likely reflect a fundamental characteristic in tactile orientation perception contributing to the perception of external objects and events like shapes and motion of objects.

Acknowledgments

This research was supported by a Grant-in-Aid for Scientific Research (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.

References

- Anzai, A., Peng, X., & Van Essen, D. C. (2007). Neurons in monkey visual area V2 encode combinations of orientations. *Nature Neuroscience*, *10*(10), 1313–1321.
<https://doi.org/10.1038/nn1975>
- Azañón, E., & Soto-Faraco, S. (2008a). Changing reference frames during the encoding of tactile events. *Current Biology*, *18*(14), 1044–1049.
<https://doi.org/10.1016/j.cub.2008.06.045>
- Azañón, E., & Soto-Faraco, S. (2008b). Spatial remapping of tactile events: Assessing the effects of frequent posture changes. *Communicative & Integrative Biology*, *1*(1), 45–46.
<https://doi.org/10.4161/cib.1.1.6724>
- Bensmaia, S. J., Denchev, P. V., Dammann, J. F., Craig, J. C., & Hsiao, S. S. (2008). The representation of stimulus orientation in the early stages of somatosensory processing. *Journal of Neuroscience*, *28*(3), 776–786. <https://doi.org/10.1523/JNEUROSCI.4162-07.2008>
- Bensmaia, S. J., Hsiao, S. S., Denchev, P. V., Killebrew, J. H., & Craig, J. C. (2008). The tactile perception of stimulus orientation. *Somatosensory and Motor Research*, *25*(1), 49–59. <https://doi.org/10.1080/08990220701830662>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
<https://doi.org/10.1163/156856897X00357>
- Calzolari, E., Azañón, E., Danvers, M., Vallar, G., & Longo, M. R. (2017). Adaptation aftereffects reveal that tactile distance is a basic somatosensory feature. *Proceedings of the National Academy of Sciences*, *114*(17), 4555–4560.
<https://doi.org/10.1073/pnas.1614979114>

- Campbell, F. W., & Maffei, L. (1971). The tilt after-effect: A fresh look. *Vision Research*, 11(8), 833–840. [https://doi.org/10.1016/0042-6989\(71\)90005-8](https://doi.org/10.1016/0042-6989(71)90005-8)
- Clifford, C. W. G. (2014). The tilt illusion: Phenomenology and functional implications. *Vision Research*, 104, 3–11. <https://doi.org/10.1016/j.visres.2014.06.009>
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd Ed.). Lawrence Erlbaum Associates.
- Coltheart, M. (1971). Visual feature-analyzers and aftereffects of tilt and curvature. *Psychological Review*, 78(2), 114–121. <https://doi.org/10.1037/h0030639>
- Delemos, K. A., & Hollins, M. (1996). Adaptation-induced enhancement of vibrotactile amplitude discrimination: The role of adapting frequency. *The Journal of the Acoustical Society of America*, 99(1), 508–516. <https://doi.org/10.1121/1.414509>
- Dragoi, V., Rivadulla, C., & Sur, M. (2001). Foci of orientation plasticity in visual cortex. *Nature*, 411(6833), 80–86. <https://doi.org/10.1038/35075070>
- Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience*, 5(9), 883–891. <https://doi.org/10.1038/nn900>
- Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *Journal of Neurophysiology*, 94(6), 4188–4195. <https://doi.org/10.1152/jn.00378.2005>
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, 41(4), 1149–1160. <https://doi.org/10.3758/BRM.41.4.1149>

- 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>
- Fitzgerald, P. J., Lane, J. W., Thakur, P. H., & Hsiao, S. S. (2006). Receptive field properties of the macaque second somatosensory cortex: Representation of orientation on different finger pads. *Journal of Neuroscience*, *26*(24), 6473–6484.
<https://doi.org/10.1523/JNEUROSCI.5057-05.2006>
- Gibson, J. J. (1937). Adaptation with negative after-effect. *Psychological Review*, *44*(3), 222–244. <https://doi.org/10.1037/h0061358>
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*(5), 453–467.
<https://doi.org/10.1037/h0059826>
- He, D., Kersten, D., & Fang, F. (2012). Opposite modulation of high- and low-level visual aftereffects by perceptual grouping. *Current Biology*, *22*(11), 1040–1045.
<https://doi.org/10.1016/j.cub.2012.04.026>
- He, S., & MacLeod, D. I. A. (2001). Orientation-selective adaptation and tilt after-effect from invisible patterns. *Nature*, *411*(6836), 473–476. <https://doi.org/10.1038/35078072>
- Hsiao, S. S., Lane, J., & Fitzgerald, P. (2002). Representation of orientation in the somatosensory system. *Behavioural Brain Research*, *135*(1–2), 93–103.
[https://doi.org/10.1016/S0166-4328\(02\)00160-2](https://doi.org/10.1016/S0166-4328(02)00160-2)
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, *160*(1), 106–154.
<https://doi.org/10.1113/jphysiol.1962.sp006837>

- Iwamura, Y. (2000). Bilateral receptive field neurons and callosal connections in the somatosensory cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 355(1394), 267–273. <https://doi.org/10.1098/rstb.2000.0563>
- JASP Team. (2018). *JASP (Version 0.9)*.
- Jin, D. Z., Dragoi, V., Sur, M., & Seung, H. S. (2005). Tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex. *Journal of Neurophysiology*, 94(6), 4038–4050. <https://doi.org/10.1152/jn.00571.2004>
- Kaas, J., Nelson, R., Sur, M., Lin, C., & Merzenich, M. M. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science*, 204(4392), 521–523. <https://doi.org/10.1126/science.107591>
- Kappers, A. M. L. (1999). Large systematic deviations in the haptic perception of parallelity. *Perception*, 28(8), 1001–1012. <https://doi.org/10.1068/p281001>
- Kappers, A. M. L., & Bergmann Tiest, W. M. (2013). Haptic size aftereffects revisited. 2013 *World Haptics Conference, WHC 2013*, 335–339. <https://doi.org/10.1109/WHC.2013.6548431>
- Knapen, T., Rolfs, M., Wexler, M., & Cavanagh, P. (2011). The reference frame of the tilt aftereffect. *Journal of Vision*, 10(1), 8. <https://doi.org/10.1167/10.1.8>
- Krystallidou, D., & Thompson, P. (2016). Cross-modal transfer of the tilt aftereffect from vision to touch. *I-Perception*, 7(5), 1–10. <https://doi.org/10.1177/2041669516668888>
- 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>

- Li, L., Chan, A., Iqbal, S. M., & Goldreich, D. (2017). An adaptation-induced repulsion illusion in tactile spatial perception. *Frontiers in Human Neuroscience*, *11*, 1–15.
<https://doi.org/10.3389/fnhum.2017.00331>
- Longo, M. R. (2020). Tactile distance anisotropy on the palm: A meta-analysis. *Attention, Perception, & Psychophysics*, *82*(4), 2137–2146. <https://doi.org/10.3758/s13414-019-01951-w>
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences*, *107*(26), 11727–11732. <https://doi.org/10.1073/pnas.1003483107>
- 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., & Haggard, P. (2012). A 2.5-D Representation of the human hand. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(1), 9–13.
<https://doi.org/10.1037/a0025428>
- Magnussen, S., & Kurtenbach, W. (1980a). Linear summation of tilt illusion and tilt aftereffect. *Vision Research*, *20*(1), 39–42. [https://doi.org/10.1016/0042-6989\(80\)90139-X](https://doi.org/10.1016/0042-6989(80)90139-X)
- Magnussen, S., & Kurtenbach, W. (1980b). Adapting to two orientations: Disinhibition in a visual aftereffect. *Science*, *207*(4433), 908–909.
<https://doi.org/10.1126/SCIENCE.7355271>
- Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C. A., Haggard, P., & Iannetti, G. D. (2014). Whole-body mapping of spatial acuity for pain and touch. *Annals of Neurology*, *75*(6), 917–924. <https://doi.org/10.1002/ana.24179>

- Manser-Smith, K., Tamè, L., & Longo, M. R. (2018). Tactile confusions of the fingers and toes. *Journal of Experimental Psychology: Human Perception and Performance*, 44(11), 1727–1738. <https://doi.org/10.1037/xhp0000566>
- Maravita, A. (1997). Implicit processing of somatosensory stimuli disclosed by a perceptual after-effect. *NeuroReport*, 8(7), 1671–167. <https://doi.org/10.1097/00001756-199705060-00022>
- Marr, D. (1982). *Vision*. Cambridge, MA: MIT Press.
- Mathôt, S., & Theeuwes, J. (2013). A reinvestigation of the reference frame of the tilt-adaptation aftereffect. *Scientific Reports*, 3(1), 1152. <https://doi.org/10.1038/srep01152>
- May, K. A., & Zhaoping, L. (2016). Efficient coding theory predicts a tilt aftereffect from viewing untilted patterns. *Current Biology*, 26(12), 1571–1576. <https://doi.org/10.1016/j.cub.2016.04.037>
- Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Current Biology*, 15(19), 1745–1748. <https://doi.org/10.1016/j.cub.2005.08.044>
- Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, 10(7), 903–907. <https://doi.org/10.1038/nn1917>
- Merzenich, M. M., Kaas, J. H., Sur, M., & Lin, C.-S. (1978). Double representation of the body surface within cytoarchitectonic area 3b and 1 in “SI” in the owl monkey (*aotus trivirgatus*). *The Journal of Comparative Neurology*, 181(1), 41–73. <https://doi.org/10.1002/cne.901810104>
- Merzenich, M. M., Kaas, J. H., Wall, J., Nelson, R. J., Sur, M., & Felleman, D. (1983). Topographic reorganization of somatosensory cortical areas 3b and 1 in adult monkeys

following restricted deafferentation. *Neuroscience*, 8(1), 33–55.

[https://doi.org/10.1016/0306-4522\(83\)90024-6](https://doi.org/10.1016/0306-4522(83)90024-6)

Merzenich, M. M., Nelson, R. J., Kaas, J. H., Stryker, M. P., Jenkins, W. M., Zook, J. M., Cynader, M. S., & Schoppmann, A. (1987). Variability in hand surface representations in areas 3b and 1 in adult owl and squirrel monkeys. *The Journal of Comparative Neurology*, 258(2), 281–296. <https://doi.org/10.1002/cne.902580208>

Mountcastle, V. B., & Powell, T. P. (1959). Central nervous mechanisms subserving position sense and kinesthesia. *Bulletin of the Johns Hopkins Hospital*, 105, 173–200.

Movshon, J. A., Chambers, B. E. I., & Blakemore, C. (1972). Interocular transfer in normal humans, and those who lack stereopsis. *Perception*, 1(4), 483–490.

<https://doi.org/10.1068/p010483>

Nakashima, Y., & Sugita, Y. (2017). The reference frame of the tilt aftereffect measured by differential Pavlovian conditioning. *Scientific Reports*, 7(1), 40525.

<https://doi.org/10.1038/srep40525>

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](https://doi.org/10.1016/0028-3932(71)90067-4)

Oliva, A., & Torralba, A. (2007). The role of context in object recognition. *Trends in Cognitive Sciences*, 11(12), 520–527. <https://doi.org/10.1016/j.tics.2007.09.009>

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>

- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, *60*(4), 389–443.
<https://doi.org/10.1093/brain/60.4.389>
- Pons, T. P., Wall, J. T., Garraghty, P. E., Cusick, C. G., & Kaas, J. H. (1987). Consistent features of the representation of the hand in area 3b of macaque monkeys. *Somatosensory Research*, *4*(4), 309–331. <https://doi.org/10.3109/07367228709144612>
- Postma, A., Zuidhoek, S., Noordzij, M. L., & Kappers, A. M. L. (2008). Keep an eye on your hands: On the role of visual mechanisms in processing of haptic space. *Cognitive Processing*, *9*(1), 63–68. <https://doi.org/10.1007/s10339-007-0201-z>
- 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.
- Pruszynski, J. A., & Johansson, R. S. (2014). Edge-orientation processing in first-order tactile neurons. *Nature Neuroscience*, *17*(10), 1404–1409. <https://doi.org/10.1038/nn.3804>
- Saad, E., & Silvanto, J. (2013). How visual short-term memory maintenance modulates subsequent visual aftereffects. *Psychological Science*, *24*(5), 803–808.
<https://doi.org/10.1177/0956797612462140>
- Sathian, K., & Zangaladze, A. (2002). Feeling with the mind's eye: Contribution of visual cortex to tactile perception. *Behavioural Brain Research*, *135*(1–2), 127–132.
[https://doi.org/10.1016/S0166-4328\(02\)00141-9](https://doi.org/10.1016/S0166-4328(02)00141-9)

- Serino, A., Giovagnoli, G., de Vignemont, F., & Haggard, P. (2008). Spatial organisation in passive tactile perception: Is there a tactile field? *Acta Psychologica*, *128*(2), 355–360.
<https://doi.org/10.1016/J.ACTPSY.2008.03.013>
- Silver, R. J. (1969). *Tilt after-effects in touch*. Brandeis University.
- Solomon, S. G., & Kohn, A. (2014). Moving sensory adaptation beyond suppressive effects in single neurons. *Current Biology*, *24*(20), R1012–R1022.
<https://doi.org/10.1016/j.cub.2014.09.001>
- Suresh, A. K., Saal, H. P., & Bensmaia, S. J. (2016). Edge orientation signals in tactile afferents of macaques. *Journal of Neurophysiology*, *116*(6), 2647–2655.
<https://doi.org/10.1152/jn.00588.2016>
- Tannan, V., Whitsel, B. L., & Tommerdahl, M. A. (2006). Vibrotactile adaptation enhances spatial localization. *Brain Research*, *1102*(1), 109–116.
<https://doi.org/10.1016/J.BRAINRES.2006.05.037>
- Thakur, P. H., Fitzgerald, P. J., Lane, J. W., & Hsiao, S. S. (2006). Receptive field properties of the macaque second somatosensory cortex: Nonlinear mechanisms underlying the representation of orientation within a finger pad. *Journal of Neuroscience*, *26*(52), 13567–13575. <https://doi.org/10.1523/JNEUROSCI.3990-06.2006>
- Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology*, *19*(1), R11–R14.
<https://doi.org/10.1016/j.cub.2008.10.014>
- Tommerdahl, M., Hester, K. D., Felix, E. R., Hollins, M., Favorov, O. V., Quibrera, P. M., & Whitsel, B. L. (2005). Human vibrotactile frequency discriminative capacity after adaptation to 25 Hz or 200 Hz stimulation. *Brain Research*, *1057*(1–2), 1–9.
<https://doi.org/10.1016/J.BRAINRES.2005.04.031>

- Tong, J., Mao, O., & Goldreich, D. (2013). Two-point orientation discrimination versus the traditional two-point test for tactile spatial acuity assessment. *Frontiers in Human Neuroscience*, 7, 1–11. <https://doi.org/10.3389/fnhum.2013.00579>
- Uznadze, D. N. (1966). *The psychology of set*. Consultants Bureau.
- Vallbo, Å., & Johansson, R. S. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Human Neurobiology*, 3(1), 3–14. <https://doi.org/10.1007/s00406-006-0654-6>
- Van Der Horst, B. J., Duijndam, M. J. A., Ketels, M. F. M., Wilbers, M. T. J. M., Zwijsen, S. A., & Kappers, A. M. L. (2008). Intramanual and intermanual transfer of the curvature aftereffect. *Experimental Brain Research*, 187(3), 491–496. <https://doi.org/10.1007/s00221-008-1390-0>
- van der Horst, B. J., Willebrands, W. P., & Kappers, A. M. L. (2008). Transfer of the curvature aftereffect in dynamic touch. *Neuropsychologia*, 46(12), 2966–2972. <https://doi.org/10.1016/j.neuropsychologia.2008.06.003>
- Vidyasagar, T. R., & Urbas, J. V. (1982). Orientation sensitivity of cat LGN neurones with and without inputs from visual cortical areas 17 and 18. *Experimental Brain Research*, 46(2), 157–169. <https://doi.org/10.1007/BF00237172>
- Vogels, I. M. L. C., Kappers, A. M. L., & Koenderink, J. J. (1997). Investigation into the origin of the haptic aftereffect of curved surfaces. *Perception*, 26(1), 101–117. <https://doi.org/10.1068/p260101>
- 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). Charles C. Thomas.

- Yau, J. M., Pasupathy, A., Fitzgerald, P. J., Hsiao, S. S., & Connor, C. E. (2009). Analogous intermediate shape coding in vision and touch. *Proceedings of the National Academy of Sciences*, *106*(38), 16457–16462. <https://doi.org/10.1073/pnas.0904186106>
- Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, *401*(6753), 587–590. <https://doi.org/10.1038/44139>
- Zimmermann, E., Morrone, M. C., Fink, G. R., & Burr, D. (2013). Spatiotopic neural representations develop slowly across saccades. *Current Biology*, *23*(5), R193–R194. <https://doi.org/10.1016/J.CUB.2013.01.065>