

OBSERVATION

Topographic Generalization of Tactile Perceptual Learning

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Perceptual learning can improve our sensory abilities. Understanding its underlying mechanisms, in particular, when perceptual learning generalizes, has become a focus of research and controversy. Specifically, there is little consensus regarding the extent to which tactile perceptual learning generalizes across fingers. We measured tactile orientation discrimination abilities on 4 fingers (index and middle fingers of both hands), using psychophysical measures, before and after 4 training sessions on 1 finger. Given the somatotopic organization of the hand representation in the somatosensory cortex, the topography of the cortical areas underlying tactile perceptual learning can be inferred from the pattern of generalization across fingers; only fingers sharing cortical representation with the trained finger ought to improve with it. Following training, performance improved not only for the trained finger but also for its adjacent and homologous fingers. Although these fingers were not exposed to training, they nevertheless demonstrated similar levels of learning as the trained finger. Conversely, the performance of the finger that was neither adjacent nor homologous to the trained finger was unaffected by training, despite the fact that our procedure was designed to enhance generalization, as described in recent visual perceptual learning research. This pattern of improved performance is compatible with previous reports of neuronal receptive fields (RFs) in the primary somatosensory cortex (S1) spanning adjacent and homologous digits. We conclude that perceptual learning rooted in low-level cortex can still generalize, and suggest potential applications for the neurorehabilitation of syndromes associated with maladaptive plasticity in S1.

Keywords: touch, acuity, oriented gratings, training, somatotopic

Sensory perception is learned, though mostly passively. This learning depends critically on exposure to, and experience with, the environment. The ability to extract new sensory information from the environment following training is termed “perceptual learning.” Because aging and many nervous system syndromes and injuries (e.g., amblyopia, macular degeneration) result in a decline in perceptual acuity, training-induced perceptual learning represents a promising new approach in assisting rehabilitation (e.g., Levi & Li, 2009). Understanding the mechanisms underlying perceptual learning, in particular, when perceptual learning generalizes, has therefore become an important focus of neuroscience research and controversy.

Behavioral experiments using visual stimuli originally demonstrated highly specific benefits of perceptual learning. Training failed to generalize beyond the trained retinal location, spatial frequency, and/or orientation (Fiorentini & Berardi, 1980; Karni & Sagi, 1991; Poggio, Fahle, & Edelman, 1992; see Sagi, 2011, for a review). Based on these observations, perceptual learning was thought to be driven by plasticity in low-level sensory brain areas, which display those features of specificity (see Gilbert, Sigman, & Crist, 2001; Schoups, Vogels, & Orban, 1995, for a review; see also Recanzone, Merzenich, & Schreiner, 1992, for a discussion of tactile perceptual learning and plasticity in S1). The involvement of low-level visual cortex in perceptual learning has since been supported by single-cell recordings (Adab & Vogels, 2011; Schoups, Vogels, Qian, & Orban, 2001) as well as fMRI studies in humans (Jehee, Ling, Swisher, van Bergen, & Tong, 2012). Recently, Shibata, Watanabe, Sasaki, and Kawato (2011) provided some of the first evidence of a causal relationship between activity in the primary visual cortex and visual perceptual learning (using real-time fMRI neurofeedback, in which there is no visual stimulus and thus no awareness of learning). More recent neural models have demonstrated that plasticity in sensory cortex can explain not only patterns of specificity of perceptual learning but also certain conditions of generalization (Bejjanki, Beck, Lu, & Pouget, 2011).

Alternatively, a growing number of behavioral studies have challenged this notion and instead suggested that generalization of perceptual learning involves plasticity in a sensory cortex, such as those areas involved in attention and decision making.

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Xiao et al. (2008) were among the first to demonstrate that, under particular circumstances (e.g., “double training”), learning generalizes beyond the local visual features of the trained stimuli: When distinct stimulus features (in their case, the contrast and orientation of Gabor patches) were trained separately, and in different spatial locations, participants’ performance improved on both tasks, in both locations, resulting in complete generalization of learning of visual features to untrained locations (see also Wang, Zhang, Klein, Levi, & Yu, 2012). Similarly, T. Zhang, Xiao, Klein, Levi, and Yu (2010) and J. Y. Zhang et al. (2010) reported that the generalization of perceptual learning to untrained retinal locations can be achieved following brief exposure to the trained stimulus in an untrained location, such as when measuring baseline performance at additional locations to the trained one. It has therefore been proposed that perceptual learning is achieved by the improved interpretation of sensory information guiding decisions, rather than improving the representation of sensory information. In support of this notion, over the past decade, visual perceptual learning has been shown to influence neural activity and connectivity across multiple levels of visual cortex, as well as parietal and frontal areas (Byers & Serences, 2012; Law & Gold, 2008).

In the present study, we utilized the hand’s topographic organization in the somatosensory system (Merzenich, Kaas, Sur, & Lin, 1978) in order to test the mechanisms underlying tactile perceptual learning, which are still debated. Tactile orientation discrimination was practiced on the distal pad (hereafter “fingertip”) of one finger over the course of multiple training sessions. Thresholds for tactile orientation discrimination were measured on the trained and adjacent fingers, as well as their intermanual homologues (see Figure 1), both prior to and following the training sessions. Assuming that the degree of generalization can inform us about the underlying neural circuitry, there are four potential outcomes for the present study (see depictions of these options in Figure 1c-f). If learning of grating orientation occurs in areas with no topographic representation of the fingers (or no direct readout of somatotopic areas), then improvements from training should transfer equally across the untrained fingers (see Figure 1c; see results in Sathian & Zangaladze, 1997; Spengler et al., 1997). Alternatively, learning may involve somatosensory areas, or higher order (nonprimary) areas that are not necessarily topographically organized but receive direct inputs from somatotopic areas (see Discussion). In this case, learning should either not transfer at all (see Figure 1d; e.g., see results in Dinse et al., 2006) or else transferral should follow a topographic pattern. At least two topographic generalization patterns are possible: If the transfer to other fingers is partial, and its amplitude is based on the extent of the overlap with the trained finger’s representation, a transfer gradient is expected (see Figure 1e; see results in Harris, Harris, & Diamond, 2001; Kaas, van de Ven, Reithler, & Goebel, 2013) or training should transfer fully and equally to fingers that overlap with the trained finger’s representation, but not to other fingers (i.e., complete topographic transfer; see Figure 1f).

Adjacent fingers are represented adjacently in the primary somatosensory cortex (SI), and tactile receptive fields (RFs) span a single finger (Brodmann area [BA] 3b; Iwamura, Tanaka, Saka-

moto, & Hikosaka, 1993), adjacent fingers (BA 3b and 1; Iwamura et al., 1993), or adjacent and homologous fingers (BA 2; Iwamura, Iriki, & Tanaka, 1994). By comparing the pattern of learning across fingers known to share cortical representations, our aim was to characterize the perceptual learning mechanisms underlying improved tactile orientation discrimination.

Method

Participants

Thirty-five participants were initially tested in the study (22 females; median age 23 years). Participants showing reliable performance ($n = 24$, see Statistical Analysis) were equally and randomly assigned to the trained or the control group. Six of the participants assigned to the trained group were trained on their left hand (two were left-hand dominant, based on self-report), and the other six were trained on their right hand. Handedness was not taken into account because, unlike acquisition and transfer of motor skill (Chase & Seidler, 2008), tactile acuity (as well as the generalization of temporal tactile acuity) is independent of handedness (Nagarajan, Blake, Wright, Byl, & Merzenich, 1998; Vega-Bermudez & Johnson, 2001). The study was approved by the Central University Research Ethics Committee of the University of Oxford. Participants gave their informed consent before taking part in the study. The experiment consisted of two testing sessions (Sessions 1 and 6), spaced 1 week apart. The trained group was also given four training sessions (Sessions 2 through 5), over consecutive days between the two testing sessions.

Tactile Stimuli

Tactile stimuli were applied using JVP dome gratings (Stoelting Co., Wood Dale, IL), with varying spatial frequencies corresponding to 3.5, 3.0, 2.5, 2.0, 1.5, 1.2, 1.0, 0.75, 0.50, 0.35 mm. Oriented discrimination provides a stable and reliable measure of tactile acuity, and overcomes the pitfalls associated with other tactile acuity measures, such as two-point discrimination (Bleyenheuft & Thonnard, 2007; Johnson & Phillips, 1981; Sathian & Zangaladze, 1996; Van Boven & Johnson, 1994). In the present study, the gratings were applied in a semi-automated fashion using a custom built device, which allowed for the consistent presentation of vertical and horizontal orientations. Instructions were presented to the experimenter via a computer screen. At the beginning of each block of trials, the hand to be tested was placed in a prone position on a raised surface, with the fingertip to be tested centered and fixed above a 15-mm aperture. The relevant grating was placed on a rotating disk underneath the fingertip (see Figure 1a). For each trial, the experimenter positioned the grating either parallel (vertical) or orthogonal (horizontal) to the axis of the finger, and lowered the hand to enable contact between the tested fingertip and the grating for approximately 1 s. The participants were blindfolded throughout the experiment.

Threshold Estimation Procedure

The participant’s task in testing Sessions 1 and 6 was to determine the orientation of tactile gratings of varying groove widths (all of those described, except for 3.0 mm), selected in

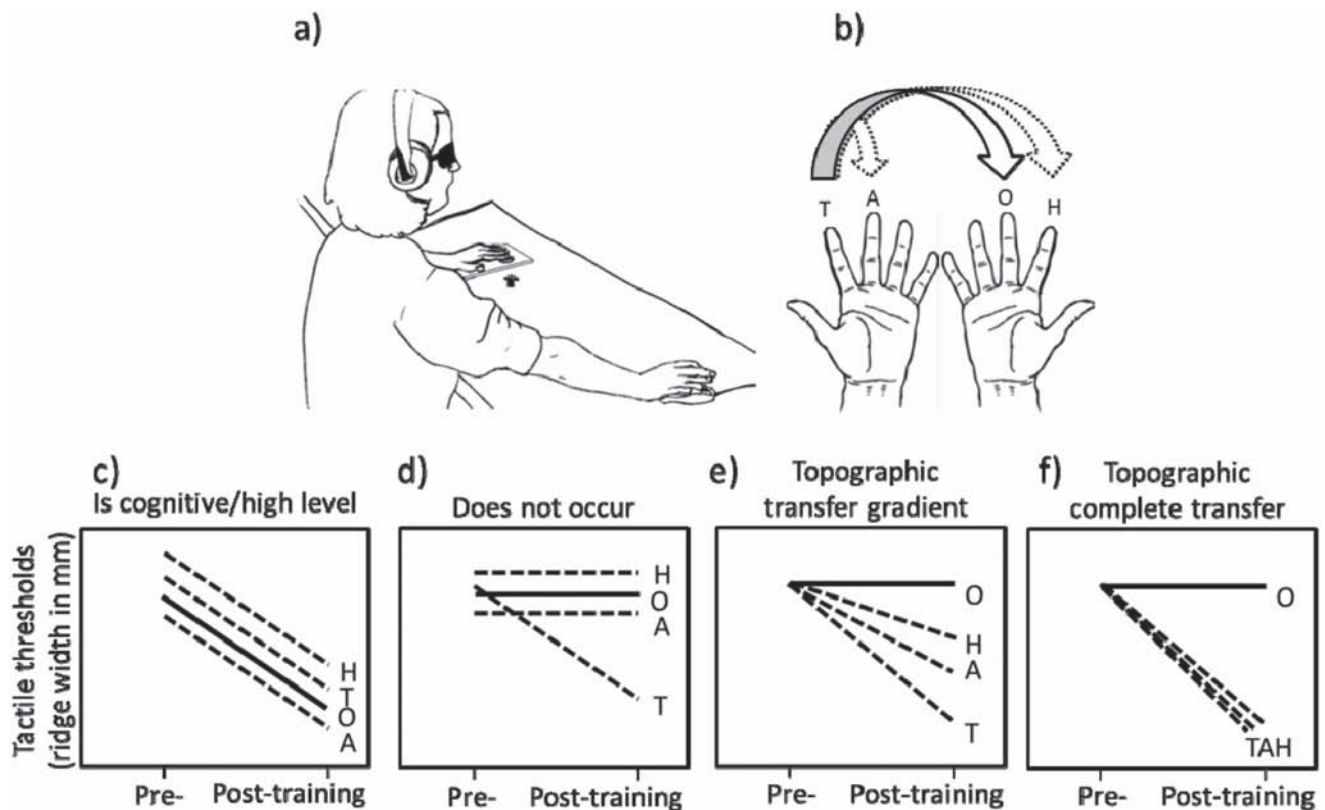


Figure 1. Experimental setup and predictions for generalization of perceptual learning. (a) A schematic diagram of the apparatus. The participants were blindfolded and wore headphones while resting their tested hand on a plate, with the finger to be tested placed over an aperture under which the experimenter positioned the appropriate grating at the appropriate orientation. The plate was controlled by the experimenter, ensuring that the gratings' orientation was presented with precision, and with a constant force across sessions. (b) The relationship of the four fingers tested is shown. One of four fingers was chosen as the trained finger "T" (for diagrammatic purposes only, the index finger on the left hand is depicted here as "T"). Relative to T, the finger next to it was labeled adjacent "A"; the same finger as the trained one, but on the opposite hand, was labeled homologous "H"; and the finger labeled the other finger "O" was neither adjacent nor homologous to the trained finger. (c) One possible outcome is that training lead to *complete generalization* in learning, where all tested fingers show similar improvements. This would be interpreted as providing evidence that perceptual learning engages high-level brain areas. (d) An alternative outcome is that there is *no generalization* of tactile perceptual learning. In this case, only the trained finger ("T") would show improved acuity (shown here as declined threshold following training), whereas the threshold of the other tested fingers would remain unchanged. (e-f) A final prediction is that if the neuronal population underlying improvement in the trained finger is shared between the trained and the untrained fingers, then perceptual learning will *generalize topographically*. In this case, improved acuity will be transferred only to the fingers that share cortical representation with the trained finger. Transfer in SI may therefore occur to the adjacent "A" and the homologous "H" fingers. This transferral could be either partial (where untrained fingers improve significantly, but less than the trained finger, as depicted in e) or full (as depicted in f).

a pseudorandom order with two blocks of 10 trials each (five at each orientation). We chose to present the predetermined set of gratings in a random order (i.e., the traditional method of constant stimuli), as it has been shown to be advantageous over other methods in which stimuli are ordered based on difficulty. The latter design, frequently used with tactile oriented gratings (see, e.g., Craig, 1999), is likely to cause varied effort over the course of the testing session (see Guilford, 1954), thereby violating underlying assumptions of the psychometric function. Gratings were applied to each of four fingertips (right index,

left index, right middle, left middle; see sample data in Figure 2a). The total of 72 blocks took about 50 min to complete. Responses were reported by pressing one of two mouse buttons (using the untested hand). The order of presentation of the stimuli and the recording of responses were controlled by E-Prime (Psychology Software Tools Inc., Pittsburgh, PA; www.psnet.com/eprime). White noise was played over headphones to mask any auditory cues arising from the apparatus. For each block, one finger and one grating width were pseudorandomly chosen and presented. At the beginning of the two first blocks

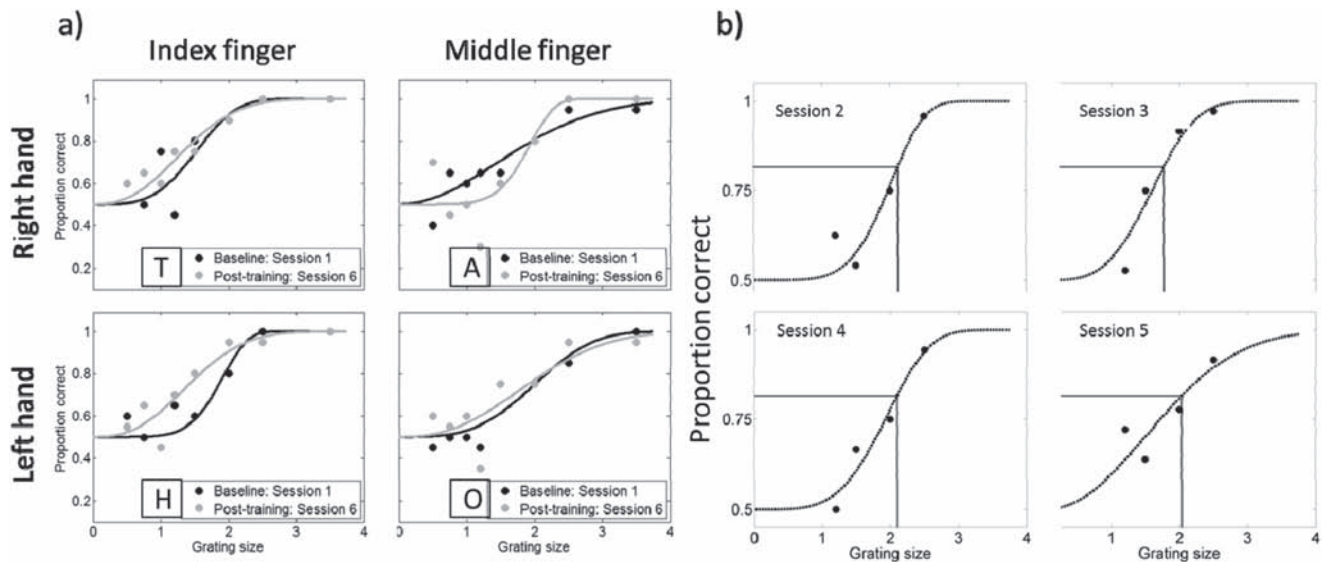


Figure 2. Sample participant data. The first participant’s data and fitted functions are depicted as sample data. This participant was initially tested on all four fingers (2a) and was trained on the left index finger (see “T” in legend on the left, from which the adjacent “A,” homologous “H,” and other “O” digits can be labeled). (a) Participant’s correct response rate (circles) across the 8 gratings and fitted plots (lines) during testing Session 1 (baseline, black) and Session 6 (posttraining, gray). The psychometric functions were used to calculate tactile orientation acuity thresholds for each finger and session. During the four training sessions (Sessions 2 through 5), only the right index finger was tested for this particular participant, data shown in b. (b) Participant’s performance (filled circles) and estimated function (dotted line) during training (Sessions 2 through 5) is plotted. Horizontal lines are drawn at one standard deviation above the inflection point, such that vertical lines down depict the threshold estimated from the data accumulated across each training session.

for each finger, the participants were refamiliarized with the two orientations and the corresponding response buttons. The participants were instructed to respond accurately, and no time constraints were imposed.

Training Procedure

Sessions 2 through 5 were used for training (see Figure 2b for sample data). For the 12 participants in the trained group, one of the four tested fingers was pseudorandomly assigned for training, such that three participants were trained on each of the four possible fingers (see Figure 1b). Four tactile gratings were chosen, based on the threshold calculated from the first testing session initially, and based on performance in the previous training sessions (Sessions 2 through 4) thereafter. When possible, two gratings above and two below the threshold were used for training.

To encourage participants to train on features of the stimulus (the orientation of the gratings), rather than the task, the task for training Sessions 2 through 5 consisted of a modified version of the task used to estimate the threshold (described previously): Each trial consisted of the presentation of two consecutive gratings, either at the same or orthogonal orientations. The participants had to determine whether the two orientations were the same or different (i.e., orthogonal). As before, accuracy was stressed and no time constraints were imposed. Following incorrect responses, negative feedback was given in the form of a loud noise, presented over headphones (the loudness was ad-

justed to a comfortable level for each participant). Each block consisted of 12 trials (half with the same orientation [3-both vertical, 3-both horizontal] and half with different orientations [3-vertical first, 3-horizontal first]), presented randomly. The total of 12 blocks (four gratings widths \times three block repetitions) took about 25 min to complete. Participants’ performance was assessed at the end of each training session (by fitting a psychometric function to the four data points as described in Statistical Analysis).

Statistical Analysis

Cumulative Gaussian psychometric functions were fit to the proportion of correct responses for each tested fingertip as a function of the grating width (see Gibson & Craig, 2006; Van Boven & Johnson, 1994, for a similar method). The reliability of each curve was assessed for goodness of fit using a coefficient of determination (r^2). Participants were discarded from the study if their thresholds functions (data from Session 1 or Session 6) had an $r^2 < 0.5$. This resulted in 11 participants being discarded from the study (eight of whom were discarded based on their baseline performance in Session 1). As the goodness of fit to the psychometric function was generally low (the average r^2 was $0.74 \pm SE$ 0.01), we subsequently fitted the data with a three-parameter Weibull psychometric function (Nachmias, 1981; Weibull, 1951, see Equation 1) using MATLAB (release 2010b) with the Palamedes toolbox.

$$y = \gamma + (1 - \gamma - \lambda) \left(1 - \frac{1}{e^{(\frac{x}{\alpha})^\beta}} \right) \quad (1)$$

The fitting procedure followed Wichmann and Hill (2001). Maximum likelihood estimation was used to determine the best fitting function (rather than least squares) because the experimental errors were not expected to be equally and normally distributed across the gratings. Gamma (γ) was fixed to 0.5 (consistent with a two-alternative forced-choice threshold detection task). Alpha (α) is the estimated discrimination threshold presented in the results, and beta (β) is the estimated slope of the psychometric function (same analysis methods as in Harris, Gliksberg, & Sagi, 2012). Results presented are for lambda (λ – attention lapse) fixed to zero (though the same pattern of results was seen if it was not fixed). Figure 2 plots these functions for a representative participant with the average threshold at about 2 mm. Using this fitting procedure, 93% of the deviance values from simulations ($n = 20$) were larger than the deviance value of the data (100% would indicate a perfect fit). The data from the three participants who completed the study but were excluded was also poorly fit with a Weibull function (e.g., deviance values of 0.15, .04, and 0.45) and was therefore not included in the analysis reported here.

Between- and within-group comparisons were assessed using ANOVA. One data point was discarded from the between-groups ANOVA and another from the within-group ANOVA because the values were greater than three standard deviations above the rest. Bidirectional dependent samples t tests were used to follow up significant effects.

Results

To determine whether training affected the ability of participants to correctly detect grating orientation, two within-group

variables—finger tested (right index, left index, right middle, left middle) and testing times (Session 1 or 6)—and one between-groups variable—group (trained or control)—were assessed using a mixed-model ANOVA. The ANOVA revealed a significant main effect of the finger tested, $F(3,63) = 4.865$, $p = .004$, $\eta_p^2 = .197$, indicating that, as previously observed, thresholds were lower for index fingers compared with middle fingers (Vega-Bermudez & Johnson, 2001; see also differences between index and middle finger threshold functions of a typical participant in Figure 2a). Similar results were obtained in an additional ANOVA replicating the one described, but in which finger tested was split into hand (left and right) and finger identity (index and middle). In this $2 \times 2 \times 2 \times 2$ ANOVA, there was a main effect of finger identity, $F(1,21) = 16.889$, $p = .001$, but no significant main effect or interaction effect of hand ($p > .05$). The significant effect of finger can be used to interpret the seemingly high thresholds documented in Figure 3 (which represent the average thresholds across index and middle fingers), compared with previous reports using a similar interpolation analysis but which tested the acuity of the index finger alone (e.g., Craig, 1999; Craig & Lyle, 2001). Further, the threshold presented here (α in Equation 1) represents the ridge width at which 82% of the responses are estimated to be correct (as in Harris et al., 2012, but unlike Craig and others, who have interpolated the grating size necessary for 75% correct detection).

A significant interaction effect of Testing Time \times Group, $F(1,21) = 5.148$, $p = .034$, $\eta_p^2 = .197$, was also observed. As shown in Figure 3a, this interaction was driven by a significant increase in tactile orientation discrimination performance (reduced threshold) in the trained group's second testing session compared with the controls. This result confirms that the trained group exhibited an improvement in their performance beyond what could be explained based on their exposure of the stimuli during initial threshold estimation session.

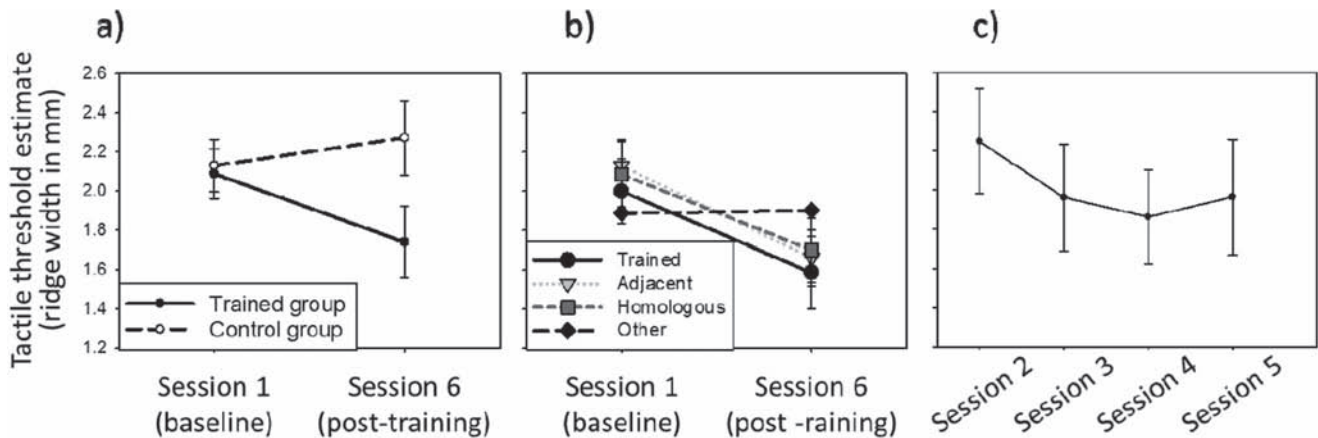


Figure 3. Results. (a) Mean thresholds, obtained from the two testing sessions, are shown for both the trained group (solid line) and the control group (dashed line), averaged across the four fingers tested. (b) Thresholds for the trained group are shown for each of the fingers tested. Trained, adjacent, and homologous fingers significantly improved (decreased thresholds—see inserted legend), whereas the finger which was neither adjacent nor homologous (“Other,” black long-dash horizontal line) did not improve significantly. (c) Average thresholds obtained from data collected from 12 trained participants (see Footnote 2) plotted as function of training sessions. For all panels, lower threshold values indicate better performance, and errors bars represent ± 1 standard error.

In light of the significant Testing Time \times Group interaction, we looked at the effects of time on specific fingers separately for the trained and control groups. Two repeated measures ANOVAs were conducted, one for control participants and the other for trained participants, with two within-group variables: finger tested (right index, left index, right middle, left middle) and testing times (Session 1 or 6). For the control group, no significant main effects or interaction effects were found. For the trained group, there was a significant main effect of testing time, $F(1,11) = 9.577$, $p = .010$, $\eta_p^2 = .465$, and a significant main effect of finger, $F(3,33) = 4.533$, $p = .034$, $\eta_p^2 = .292$, thus replicating the initial main effect of finger reported earlier. Importantly, there was no interaction between finger type and testing time for the trained group or the control group, that is, across the group, there was no significant difference in the amount of improvement (or lack of improvement) for the four types of fingers tested.

To study the patterns of perceptual learning in the trained group, the fingers were labeled according to their position with respect to the trained finger. The repeated measures ANOVA was conducted with fingers tested (trained, adjacent, homologous, and other) and testing times (Session 1 or 6). A significant main effect of testing time was observed, $F(1,10) = 7.148$, $p = .023$, $\eta_p^2 = .417$, such that thresholds were significantly lower on Session 6 compared with Session 1. A significant interaction term was also observed, $F(3,30) = 3.760$, $p = .021$, $\eta_p^2 = .273$ (Figure 3b). This interaction contradicts the nontopographic global account shown in Figure 1c, which predicts generalization across all fingers.

Post hoc pairwise comparisons revealed significant improvements not only for the trained finger, $t(11) = 2.718$, $p = .020$, 95% CI [0.08, 0.77] (Figure 3b, solid black line, filled black circles) but also for its adjacent finger, $t(11) = 4.054$, $p = .002$, 95% CI [0.23, 0.78] (Figure 3b, dotted light gray line) and its homologous finger, $t(11) = 2.353$, $p = .038$, 95% CI [0.02, 0.611] (Figure 3b, dashed dark gray line). Importantly, no improvement was observed for the “other” finger (i.e., the finger that was neither adjacent nor homologous to the trained finger), $t(10) < 1$, 95% CI [-0.41, 0.38] (Figure 3b, solid line).¹ These results contradict the prediction outlined in Figure 1d (no generalization) and instead are in line with the prediction depicted in Figures 1e and 1f, in which training transfers topographically.

Is there a difference in the amount of improvement/generalization in the trained, adjacent, and homologous fingers? A subsequent ANOVA was conducted on the trained group’s data, but this time only comparing fingers that have been shown to improve following training. A 2×3 repeated measures ANOVA revealed a significant main effect of testing times, $F(1,11) = 17.015$, $p = .002$, $\eta_p^2 = .607$, but no significant main effect of, or interaction effect with, finger tested, $F(2,22) < 1$, n.s. Thus, the adjacent and homologous fingers improved by a comparable amount to the trained finger (supporting the prediction depicted in Figure 1f). The same pattern was also revealed when using mean accuracy scores (i.e., without fitting psychometric functions).

While examining the psychometric functions of individual participants, it was observed that, for some participants, the slopes might have changed (see sample participant data depicted in Figure 2). The slopes of the psychometric functions were therefore also analyzed, using the same ANOVAs as described. However, no significant main effects of finger or time, or interaction effects between these variables, or with group, were observed. This result

suggests that changes in the slopes of participants’ psychometric functions were not reliably reproduced across the group. This finding supports the conclusion that changes in the pattern of responding are evidence for changes in the tactile acuity threshold.

To explore the pattern of improvement, the data collected during the four consecutive training sessions were also analyzed using Weibull functions (see sample data in Figure 2b, and means in Figure 3c).² A within-participants ANOVA revealed a trend toward a quadratic contrast effect, $F(1,6) = 3.77$, $p = .10$, $\eta_p^2 = .386$, in which the largest improvement (decrease in threshold) is observed between the first and second training sessions. However, given the limitations of function fitting to this data, this result requires further validation.

Discussion

We have demonstrated that multiple training sessions lead to similar gains in tactile orientation discrimination for the trained finger and its adjacent and homologous fingers. The other finger showed no improvement despite the fact that baseline measurements were taken (see further discussion in the following paragraphs). Generalization of tactile perceptual learning was therefore topographic; only skin surfaces that are thought to share cortical representations with the trained finger in SI (henceforth, “topographically related”) improved with training. Transferral was complete, such that topographically related fingers showed the same magnitude of improvement as the trained finger.

Although touch was the modality of choice for the seminal research in perceptual learning (Volkman, 1858), and SI was among the first to demonstrate a relationship between cortical plasticity and perceptual learning (Recanzone et al., 1992), most of our knowledge concerning mechanisms of perceptual learning now comes from visual and, to a lesser extent, auditory research (e.g., Seitz & Dinse, 2007). The dominance of visual research is particularly evident with regard to discussions of generalization in perceptual learning (see Fahle, 2005; Seitz, 2011). And yet tactile discrimination is an ideal paradigm for studying the mechanisms of generalization of perceptual learning because of the somatotopic organization of SI, and evidence showing that the cortical representation of a finger can increase with improved tactile acuity and use (Duncan & Boynton, 2007; Lissek et al., 2009; Pleger et al., 2003).

Previous results demonstrating generalization of tactile perceptual learning have been inconclusive with respect to the pattern of topographic transfer of learning. For instance, Sathian and Zangladze (1997) trained participants over several sessions and ob-

¹ To verify that the lack of training effect in the “other” finger was not due to a lower initial threshold, we performed an additional contrast analysis comparing the Session 6 threshold on the “other” finger with the Session 6 thresholds for the control group. There was no significant difference between the two, $t_{22} = 1.3$, $p = .243$, $MD = .327 + SE.272$, suggesting that the lack of improvement in the “other” finger is not due to a potential outlier baseline result. Furthermore, no significant difference between the four baseline thresholds (trained, adjacent, homologous, and other fingers) was found, as demonstrated by a one-way repeated measures ANOVA, $F < 1$, $p = .42$.

² As these training thresholds were estimated from only four points, thresholds were excluded either if the functions did not converge ($n = 3$ out of 48 threshold estimates), or if the functions suggested thresholds beyond the range of the stimuli ($n = 3$).

served improved acuity on several fingers that were trained in turn. They reported that thresholds started out significantly lower on (as yet) untrained fingers than on the first-trained finger, and therefore concluded global generalization of tactile learning, that is, across all fingers. More recently, Kaas and colleagues (2013) concluded that partial generalization of tactile perceptual learning occurred using a similar stimulus but with an updated method and analysis procedure. However, these experimental designs do not account for the contribution of global learning (see Figure 1c) compared with topographic (see Figure 1e; see Nagarajan et al., 1998, for similar confounding results using vibrotactile discrimination training). Harris et al. (2001) removed this confound by testing generalization patterns from a single trained finger to multiple fingers, only some of which were topographically related. Relevant to the question of tactile spatial acuity, Harris and colleagues demonstrated that improvements in tactile roughness discrimination transferred almost completely to the adjacent and homologous fingers, and partially to a topographically nonrelevant finger (termed “Other” in the present study), suggesting a topographic transfer gradient (see Figure 1e; see similar transfer gradient results observed by Volkman, 1858). Given the latest developments in perceptual learning, Harris et al.’s design still cannot clarify the relative contribution of topographic and global generalization mechanisms in tactile perceptual learning.

Our experimental design accounts for a number of factors that have recently been shown to impact the generalization of perceptual learning, and that could have confounded the interpretation of the pattern of partial generalization reported previously. Harris and colleagues (2012) demonstrated that generalization of visual perceptual learning is more likely to occur following short training sessions, comprised of varied stimuli. T. Zhang et al. (2010) and J. Y. Zhang et al. (2010) demonstrated that baseline measurements in untrained locations also facilitate generalization of visual perceptual learning. Based on these developments, our use of multiple short training sessions, involving gratings of multiple spatial frequencies and orthogonal orientations, as well as our baseline measurements of the untrained fingers, should have resulted in a greater contribution of nontopographic mechanisms, and consequently *more* global generalization. Although these considerations seem to have resulted in more efficient (and in our case complete) transfer to the topographically relevant fingers, the fact that the topographically irrelevant finger showed no improvement in our study suggests that only specific topographic cortical regions were involved in tactile perceptual learning. Thus, our results are also consistent with the reverse hierarchy theory (Ahissar & Hochstein, 1997, 2004) suggesting that greater amounts of training will involve plasticity of low-level processes. The relationship between double-training and topographic representation in tactile acuity will therefore require further study.

As mentioned previously, the pattern of generalization observed in the present study may be consistent with the topography of primary somatotopic brain areas. Indeed, tactile RFs in SI often span multiple digits, both within the hand (Chen, Friedman, & Roe, 2005; Reed et al., 2006; Thakur, Fitzgerald, & Hsiao, 2012) and across the hands (Iwamura et al., 1994). In contrast, the organization of RFs in the secondary somatosensory cortex (SII) is more complex and often not somatotopic (Iwamura, Tanaka, Iriki, Taoka, & Toda, 2002). In humans, a recent fMRI adaptation study revealed that SI (as well as SII) integrates somatosensory inputs

across homologous fingers (Tamè et al., 2012). We thus hypothesize that the effects reported here for tactile perceptual learning are strongly linked with somatotopic representations in SI, and may be even due to plastic changes in neuronal populations with RFs spanning multiple fingers, such as BA 2. According to Bejjanki et al. (2011), plasticity in sensory cortex underlying perceptual learning would likely include a combination of a change in the shape of the tuning curve and a change in the pattern or correlations between the cells. This view is supported by an electrophysiology study (Adab & Vogels, 2011) demonstrating that generalization of visual orientation training to untrained retinal locations was associated with changes in the macaques’ area V4 (which is hierarchically homologous to BA 2).

Alternatively, the topographic generalization reported here can be attributed to an improvement in the selective read-out of early sensory signals by nonsensory area (at the decision-making stage; Law & Gold, 2008, 2009; Petrov, Doshier, & Lu, 2005). According to this account, better tuning of high-level cortex responsive to neuronal populations in SI with RFs spanning multiple fingers would result in improved spatial acuity in the fingers with overlapping RFs. Let us assume that improvement in tactile acuity depends on better tuning of “read-out” areas, receiving inputs from the sensory neuron that is representing the trained finger. Now let us assume that the same neuron also represents the finger adjacent to the trained finger. Better tuning to this neuron will result in improved performance of the adjacent finger. Therefore, even if learning occurs in a nontopographic area, the generalization pattern of improved performance is still rooted to representation patterns of a somatotopic area. Although further research is required to determine the relationship between sensory gain and sensory read-out, our results demonstrate that contrary to present views, transferral of learning can still be restricted to the topographic boundaries of low-level sensory cortex (see also Seitz, 2011).

As tactile discrimination appears to show predictable improvements following training, beyond the specific features of training (i.e., the trained skin surface), our findings may have exciting potential applications for neurorehabilitation. For example, tactile acuity training to reverse age-related sensory decline (Dinse et al., 2006) can benefit from generalization to nontrained fingers, as shown here. Generalization of tactile perceptual learning might also be applied to reverse maladaptive plasticity in SI, which is thought to play a causal role in a range of chronic pain conditions (e.g., phantom pain, complex regional pain syndrome, writer’s cramp; see Nava & Röder, 2011, for review).

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