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RESEARCH ARTICLE

Tactile perceptual learning: learning curves and transfer to the contralateral finger

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Abstract Tactile perceptual learning has been shown to improve performance on tactile tasks, but there is no agreement about the extent of transfer to untrained skin locations. The lack of such transfer is often seen as a behavioral index of the contribution of early somatosensory brain regions. Moreover, the time course of improvements has never been described explicitly. Sixteen subjects were trained on the Ludvigh task (a tactile vernier task) on four subsequent days. On the fifth day, transfer of learning to the non-trained contralateral hand was tested. In five subjects, we explored to what extent training effects were retained approximately 1.5 years after the final training session, expecting to find long-term retention of learning effects after training. Results showed that tactile perceptual learning mainly occurred offline, between sessions. Training effects did not transfer initially, but became fully available to the untrained contralateral hand after a few additional training runs. After 1.5 years, training effects were not fully washed out and could be recuperated within a single training session. Interpreted in the light of theories of visual perceptual learning, these results suggest that tactile perceptual learning is not fundamentally different from visual perceptual learning, but might proceed at a slower pace due to procedural and task differences, thus explaining the apparent divergence in the amount of transfer and long-term retention.

Keywords Human · Perceptual learning · Somatosensory · Vernier

Abbreviations

ANOVA	Analysis of variance
BSRD	Between Session Relative Decrease
LI	Learning Index
RA	Rapidly adapting
RHT	Reverse hierarchy theory
SA1	Slowly adapting type 1
S1	Primary somatosensory cortex
S2	Secondary somatosensory cortex
WSRD	Within-Session Relative Decrease

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Introduction

Studies in healthy human subjects showed that performance on tactile perceptual tasks can improve over the course of one or several practice sessions (Harris et al. 2001; Pleger et al. 2003; Sathian and Zangaladze 1997, 1998; Spengler et al. 1997). A lack of transfer of behavioral effects to untrained locations could indicate that learning includes brain plasticity in early somatosensory cortex.

However, there is currently no agreement about the extent of transfer to untrained locations and underlying contribution of early somatosensory regions (Harris et al. 2001; Sathian and Zangaladze 1997, 1998).

Findings on transfer to untrained locations range from complete transfer to no transfer at all, although most tactile learning studies showed substantial transfer to untrained locations. Spengler et al. (1997) found complete transfer to the contralateral hand in their tactile learning experiment involving tactile stimulation of multiple finger segments by two bars. Subjects learned to discriminate two consecutive stimulations by the same bar from the background pattern of alternating stimulation. In accordance with this lack of somatosensory specificity, magnetic source imaging revealed that primary somatosensory cortex was not involved. In a similar vein, Nagarajan et al. (1998) found that practice-related improvements in somatosensory interval discrimination generalized across skin location, hemisphere, and modality. Sathian and Zangaladze (1997) also found transfer between fingers on the same task. In a second study (Sathian and Zangaladze 1998), transfer to the index finger contralateral to the trained index finger was confirmed. Based on these findings, they suggested that learning effects in the tactile modality are less location specific than in the visual modality. Similar thresholds for the untrained finger were only reached after additional training sessions, but the required number of training sessions was less than for the originally trained finger. However, pre-training thresholds were unavailable for the untrained finger, so it is unclear whether the relative improvement was comparable across fingers. To accommodate disparate findings, some authors suggested a somatotopic transfer gradient, that is, improved performance after training of a finger transfers to its first neighbor of the same hand and to the symmetrically opposite finger in the other hand, but less so for the second neighbor in either hand. The results in a punctuate pressure and a roughness discrimination task indeed showed such a pattern (Harris et al. 2001). However, clear somatotopic specificity was found in a frequency discrimination task using the same procedure (Harris et al. 2001). Somatotopically specific improvements in tactile discrimination thresholds were also reported after 20 min–3 h of synchronous passive vibrotactile activation of a $\sim$50 mm^2 or larger skin area (Dinse et al. 2006; Kalisch et al. 2007; Pleger et al. 2003; Ragert et al. 2008). Threshold improvements correlated with enlargements of corresponding finger representations in SI and SII (Pleger et al. 2003) and lasted for about 24 h (Ragert et al. 2008).

One possible way to unify conflicting findings is to compare the effects of tactile learning with those of learning a visual skill. There is ample evidence that visual skill learning is topographically, or even retinotopically organized (Karni and Sagi 1991, 1993; Schoups et al. 1995, 2001; Dill and Fahle 1997; De Weerd et al. 2012). If tactile learning is somatotopically organized, it could be governed by similar organizational principles as visual learning. Thus, the occurrence (or lack) of location-specific learning effects might be explained by similar mechanisms. The reverse hierarchy theory (RHT) of visual perceptual learning proposes that learning-related changes first occur in areas higher up in the cortical hierarchy (Ahissar and Hochstein 2004). When these changes no longer suffice to further improve on the task, the adjustments progress backward toward the input levels (Ahissar and Hochstein 2004). As a prerequisite for topographic specificity or “global-to-local” transfer to occur, local cues should be important to the task and accessible to learning, that is, show a consistent relationship with the task. If this is the case, RHT predicts that transfer of learning effects to untrained regions of retinotopic or somatotopic space will be limited. The performance of highly trained subjects on tasks requiring high precision or high signal-to-noise is predicted to be based on low-level representations and to demonstrate specificity to low-level aspects.

The time course of visual perceptual learning often shows a fast and rapidly saturating improvement in the first learning session followed by relatively stable performance within sessions but large improvements between sessions (Karni and Sagi 1993). The fast within-session improvements were readily transferred between the eyes (Karni and Sagi 1991) and were interpreted as related to setting up a task-specific routine at higher levels of the perceptual hierarchy. The slower asymptotic learning phase of between session improvements was suggested to reflect offline consolidation in low-level perceptual modules (Karni and Sagi 1993) demonstrating topographic specificity (Karni and Sagi 1991). Topographic specificity of learning was indeed found after extensive training (Adini et al. 2002; Ball and Sekuler 1987; Crist et al. 1997; Karni and Sagi 1993; Saarinen and Levi 1995; Watanabe et al. 2002). The improvements after extensive training on a visual perceptual task have been shown to be retained for months (Watanabe et al. 2002) or years (Karni and Sagi 1993).

However, the parameters of visual learning may be highly dependent on the training procedure. Within-session improvement was smooth when the visual location varied slightly over trials (Otto et al. 2006). Changing the amount of trials per session with an identical total amount of training also influenced transfer in a nonlinear way (Aberg et al. 2009). Finally, a “double training paradigm” induced transfer of feature learning after unrelated training at the transfer location, suggesting that location specificity merely reflects feature-unspecific local factors (Xiao et al. 2008; Zhang et al. 2010b). These findings could suggest an alternative scenario in which perceptual learning may induce a selective re-weighting of the read-out of the most informative sensory outputs, rather than altering the low-level sensory representations (Huang et al. 2012; Petrov et al. 2005; Bejjanki et al. 2011; Law and Gold 2008; Zhang et al. 2010a).

In keeping with RHT and the time course and retention of visual perceptual learning, the different findings for the extent of somatotopic transfer in tactile learning might be explained by differences in the level of training or in the precision demands of the tasks. Sathian and Zangaladze (1997, 1998) used several training sessions with a 1–3 day interval, whereas Harris et al. (2001) used one training session on a single day. Fast improvements obtained in a single day most likely have a different neuronal correlate than slow incremental learning over several days (Karni and Bertini 1997; Karni and Sagi 1993). Moreover, RHT predicts that learning in primary sensory cortex will only occur for tasks requiring high spatial signal-to-noise for the detection of low-level features. The detection of a pattern of repeated stimulations against a background of alternating multidigit stimulations at proximal or distal phalanges as used by Sprengler et al. might not fulfill this criterion. It might rather promote integration of signals from different somatotopic locations at higher cortical levels, thus facilitating transfer to different somatotopic locations. The frequency discrimination task showing somatotopic specificity in the study by Harris et al. involved a much smaller skin region, and subjects showed a more gradual rate of improvement and larger number of trials to reach criterion on this task than on the punctuate pressure and roughness discrimination tasks, suggesting high-precision demands on low-level features (frequency). However, an average of four daily training sessions on the Ludvigh task, a tactile vernier task (Loomis 1979), did not yield somatotopically specific results (Sathian and Zangaladze 1998). This is at odds with its apparent low-level high-precision demands, evidence for a correlation of Ludvigh thresholds with the distance between finger representations in primary somatosensory cortex (S1, Brodmann areas 3b and 1) (Duncan and Boynton 2007) and the finding that training on visual vernier tasks leads to retinotopically specific learning effects already within 1 h of training (Fahle et al. 1995) and would suggest that perceptual learning proceeds differently in the tactile modality, compared to the visual domain.

To further investigate perceptual learning in the tactile modality, the present study focused on the time course and topographic specificity of tactile perceptual learning. Sixteen subjects were trained on the Ludvigh task (tactile vernier task) on four subsequent days. On the fifth day, the transfer of learning effects to the non-trained contralateral hand was tested. The hypothesis was that tactile perceptual learning would follow a similar time course as visual perceptual learning and shows similar topographic specificity and retention. We therefore expected that (1) the initial strong within-session improvement during the first training would decrease to a stable level for consecutive sessions, (2) between-session improvements would decrease for later sessions, and (3) learning effects would be somatotopically specific, i.e., stronger improvements for the trained hand than the non-trained hand. In five subjects, we explored to what extent training effects were retained approximately 20 months after the final training session, expecting to find long-term retention of learning effects after training.

Materials and methods

Subjects

Sixteen participants (6 males, mean (SD) age 28 (7) years) took part in this study. Two participants were left-handed (one male, score −79 %, one female, score −74 %), the others were right-handed [mean (SD) score 86 % (16 %)] as determined by the Edinburgh Handedness Inventory (Oldfield 1971). All were university undergraduate or graduate students, without injuries to the hands or neurological problems. All participants signed an informed consent form before the start of the experiment and obtained gift certificates for their efforts. The study was approved by the local ethics committee and was conducted according to the standards of the Helsinki declaration.

Stimuli and setup

The stimulus setup (Fig. 1) was based on the one used in a study by Loomis (1979). Thirty-eight triplets of identical raised dots (1.3 mm diameter at the base, 0.05 mm at the top, 0.89 mm height) were attached to a round metal plate. The distance between the top and bottom dot was 6 mm for all triplets. The triplets only varied in the direction (left or right) and size of the orthogonal offset of the middle dot with respect to the virtual line connecting the top and bottom dots (Fig. 1b, c). Offset size varied from 3.75 to 0 mm (in steps of 0.25 mm from 3.75 to 0.25 mm, and in steps of 0.05 mm below 0.25 mm). The 0 mm offsets were not used in the current experiment.

The round metal stimulus plate of 30 cm diameter (Fig. 1a, 4) was mounted between two fiberboard plates (Fig. 1a, 5 and 6) and could rotate around a steel axle. The covering plate had a 27 by 50 mm cut-away at the border for the participant's finger (Fig. 1a, 2). A patch of foam was attached over the cut-away at the border of the covering plate and served as a rest and a guide for the tip of the

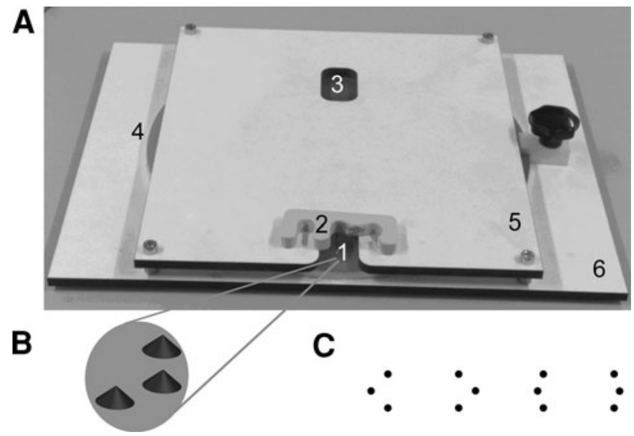

Fig. 1 Setup. **a** The stimulus setup consisted of a metal plate that could rotate around a steel axle between two fiberboard plates. *1* cut-away for current stimulus and participant's finger, *2* patch of foam to guide the finger, *3* cut-away for experimenter to monitor stimulus presentation and positioning, *4* round metal stimulus plate, *5* covering plate, *6* bottom plate. **b** An enlarged artistic impression of the tactile dot pattern. **c** Four examples of *dot patterns* at their actual size, from left to right a pattern with a 3 mm offset to the left, to the right and a pattern with a 1 mm offset to the left and to the right

stretched index finger. Its position was individually adjusted for each participant and finger to make sure that the finger would be positioned correctly when it was moved down onto the stimulus plate.

There was another cut-away on the opposite side of the covering plate, near the center, allowing the experimenter to monitor the stimulus code as well as a radial positioning line on the turn table (Fig. 1a, 3). Alignment of this line with two markers at the top and bottom of the cut-away ensured accurate positioning of the stimuli, aligning the virtual line between the top and bottom dot with the center of the cut-away and the longitudinal axis of the participant's finger.

Stimulus presentation and data acquisition were controlled using Presentation 14.4 software (Neurobehavioral Systems Inc., Albany CA, USA; nbs.neuro-bs.com). A tone of 1,000 Hz (200 ms) indicated the start of each trial. Subjects pressed a keyboard button to the left for "offset to the left", and vice versa. They subsequently received feedback on their performance by two tones, a high 1,500 Hz tone (200 ms) for a correct response and a low 500 Hz tone (200 ms) for an incorrect one. The experimenter pressed a mouse button to play the starting sound for the next trial.

Procedure

All participants took part in five sessions on five consecutive days (supplementary table 1). Each session started with the completion of a subjective sleep quality questionnaire (Mulder-Hajonides van der Meulen 1981). In the first session, participants also completed the Edinburgh Handedness Inventory (Oldfield 1971).

Each session included a short practice run of the perceptual task with the hand(s) that were to be trained during that session. The dominant hand was used to perform the perceptual task in all five sessions. The non-dominant hand was used in session one and five only. During session two, three, and four, subjects performed four tactile discrimination staircases (see below). During session one and five, subjects performed a total of six staircases. In session one, subjects completed two staircases with the non-dominant hand and four with the dominant hand. This was done to obtain a reliable baseline value for the threshold of the non-dominant hand while restricting the opportunity for learning. The order of the staircases for the two hands was balanced across subjects (see Table 1).

In session five, subjects completed two staircases with the dominant hand and four with the non-dominant hand. The first two for each hand were used to obtain a reliable post-learning threshold. Two more staircases were added for the non-dominant hand to asses whether further learning would occur. We did not add additional staircases for the dominant hand to limit the length of the session.

During the task, participants were blindfolded and sat comfortably in a quiet room. The experimenter saw the stimulus ID (related to a specific offset size and direction) for the upcoming trial on his computer monitor. He turned the stimulus plate to the corresponding position. The starting tone was played when the experimenter pressed a button. Upon hearing this tone, participants moved their finger straight down from the resting position and put the index finger pad of the dominant or non-dominant hand onto the pattern. Participants were instructed not to apply pressure nor move their finger across the stimulus (static touch). In case of misplacement, they were allowed to replace the finger once. This happened only rarely. The participants then lifted their finger from the stimulus and reported the direction of the displacement as soon as possible, based on their first impression, pressing a button with the contralateral hand. A feedback sound was played, and the experimenter received visual instruction about the stimulus offset that was to be presented in the next trial. He pressed a button as soon as he had turned the stimulus plate to the right position. Then, the starting tone was played again, signaling the participants to start the next trial.

The direction of stimulus offset (left or right) was randomized from trial to trial. The experimenter would introduce random rotations of the disk to make sure that the participant could not use auditory or temporal cues to solve the task.

The stimuli were presented in a staircase procedure. In the first session, the first staircase for each index finger

Table 1 Handedness based on the Edinburgh Handedness Inventory (Oldfield 1971)

Subject	Gender	Handedness score	Pre-training threshold (mm)		Post-training threshold (mm)			Retention threshold (mm)		Learning Index (% post–pre change)			Retention Index (% retention-pre change)	
			D	ND	D	ND (initial)	ND (final)	D (initial)	D (final)	D	ND (initial)	ND (final)	D (initial)	D (final)
1	F	100	1.23	1.04	0.71	1.01	0.93			−42.68	−2.90	−10.63		
2	M	−79	3.53	1.92	1.58	0.34	0.35			−55.38	−82.55	−81.77		
4	F	100	3.54	3.63	2.42	3.43	3.54			−31.78	−5.65	−2.48		
5	M	89	1.40	2.24	0.51	0.92	0.73	1.29	0.55	−63.44	−59.15	−67.41	−7.35	−60.58
6	F	−74	1.28	1.23	0.32	0.96	0.69	0.65	0.33	−74.90	−22.67	−44.13	−49.19	−73.78
7	F	82	2.47	3.43	2.09	1.50	1.07			−15.38	−56.33	−68.85		
8	F	57	2.11	2.40	0.78	1.01	0.87	0.71	1.55	−63.27	−58.12	−63.75	−66.59	−26.78
10	F	100	3.21	2.12	0.35	0.45	0.49			−89.08	−78.54	−77.12		
11	F	59	3.34	2.85	0.87	2.07	0.92	2.94	2.24	−73.99	−27.24	−67.84	−12.11	−33.04
12	F	67	3.18	3.41	2.23	3.27	2.49	2.03	2.07	−29.76	−4.25	−27.13	−36.06	−34.8
13	F	100	3.63	3.70	3.33	3.67	3.55			−8.26	−0.95	−4.19		
15	M	100	0.87	0.77	0.69	0.89	0.31			−20.23	15.69	−59.48		
16	M	90	3.64	3.54	0.92	2.95	0.91			−74.69	−16.67	−74.44		
Mean (best learners)		84	2.57	2.48	1.29	1.73	1.30	1.52	1.35	−49.45	−30.72	−49.94	−34.26	−45.80
SD		16	1.06	1.04	0.95	1.20	1.13	0.97	0.87	26.36	32.41	28.96	24.93	20.29
3	M	68	2.32	3.69	2.71	3.24	1.84			17.06	−12.08	−50.2		
9	F	100	3.36	3.42	3.57	3.53	3.62			6.41	3.07	5.7		
14	M	90	3.33	3.21	3.42	3.62	3.58			2.55	12.95	11.7		
Mean (worst learners)		86	3.00	3.44	3.23	3.46	3.01			8.67	1.31	−10.93		
SD		16	0.59	0.24	0.46	0.20	1.02			7.52	12.60	34.14		
Mean (all)		85	2.65	2.66	1.66	2.05	2.61			−38.55	−24.71	−42.63		
SD		16	0.99	1.01	1.16	1.28	1.28			33.35	32.07	32.76		

The pre-training threshold was based on the average of the first two staircases on the first day. The (initial) post-training threshold was based on the average of the first two staircases on the fifth day. The final post-training threshold for the non-dominant hand was based on the average of the last two staircases on the fifth day. The Learning Indices were computed as a percentage of the pre-training threshold

F female, *M* male, *D* dominant index finger, *ND* non-dominant index finger

started with the largest offset (i.e. 3.75 mm). The offset was subsequently changed using a 3-down/1-up procedure. Three correct responses in a row led to a one-step decrease in offset and a single incorrect response led to a one-step increase in offset. The first staircase for each finger on the first day was an exception: there, the first twenty trials had a step size of two for both upward and downward steps. The staircase ended after 100 trials or at the 20th reversal. A reversal was defined as a turning point in the sequence of offsets, that is: an increase in the offset after a trial with a decreasing offset or a decrease after a trial with an increasing offset. After each staircase, the perceptual threshold was computed by averaging over all presented offsets after the sixth reversal. The starting value for the next staircase for the same finger on the same day was derived from the threshold of the previous staircase by taking the nearest larger offset and then increasing by one step (e.g. a threshold of 1.15 was rounded to 1.25, and thus 1.50, the next stimulus level above was chosen as the first offset for the following block). The starting value for the first staircase on a subsequent day was based on the average threshold across all staircases of the preceding day on which the finger was trained, taking the nearest larger offset and then increasing by one step. This way the subject was likely to receive motivating positive feedback on the first trials, while the vast majority of the trials would likely be spent close to the 75 % threshold just like in the study of Sathian and Zangaladze (1998). Details about the exact order and number of staircases can be found in supplementary table 1. The practice run served to familiarize the participants with the whole stimulus range and consisted of 15 trials. The offsets in the first five trials were randomly chosen from the stimuli from 3.75 to 2.25 mm, the offsets in the next five trials from the stimuli from 2.00 to 0.50 mm, and the last five trials from 0.25 to 0.05 mm.

Retention test

Five subjects (one male, one left-handed, mean age 24 years, SD = 1 at time of first training) could participate in a retention test approximately 1.5 years after the original training session. The test consisted of the short practice session followed by six staircases with the dominant hand. The first staircase started at the largest offset (3.75 mm); the starting value for subsequent staircases was derived from the previous staircase in the way described above.

Analysis

For each staircase, the perceptual threshold was computed by averaging over all offsets presented after the sixth reversal. The perceptual threshold obtained in this way corresponded to a percentage correct of approximately 75 %.

Correlations were computed between the subjective sleep quality score and the percentage change in the average threshold with respect to the previous day as well as the percentage change with respect to the first staircase of that day's session (i.e., the within-session decrease score, see computation below).

We wanted to assess the relative decrease within and across sessions. Relative decrease measures yield a larger value when the same absolute decrease is achieved relative to a lower initial threshold.

For the within-session relative decreases (WSRD), the percentage change was computed for each subject, session, and staircase by taking the threshold from each staircase relative to the first staircase of the same session:

$$\mathrm{WSRD}_x = \frac{(T_{xi} - T_{x1})}{T_{x1}} \times 100\,\% \qquad (1)$$

where x denotes the session and T_{xi} the threshold of the ith staircase of the xth session.

To assess the relative decrease of the session average with respect to the first session baseline (BSRD), the percentage change in the average tactile threshold was computed for each subject and session with respect to the average threshold of the two baseline measurements of the first session:

$$\mathrm{BSRD}_x = \frac{\left(\frac{\sum_{i=1}^{N_x} T_{xi}}{N_x} - \frac{\sum_{j=1}^{2} T_{1j}}{2}\right)}{\frac{\sum_{j=1}^{2} T_{1j}}{2}} \times 100\,\% \qquad (2)$$

where x indicates the session (with $x > 1$), N_x the number of staircases in the xth session, T_{xi} the threshold of the ith staircase of the xth session, and T_{1j} the threshold of the jth staircase of the first session. The average of two staircases was taken to obtain a more stable measurement, unaffected by the predefined initial offset of the staircase procedure.

To assess the decrease in thresholds after training for the dominant and non-dominant hand, we computed the Learning Index (LI), the difference between the pre- and post-training thresholds for each hand:

$$\mathrm{LI}_h = \frac{\left(\frac{\sum_{i=1}^{2} T_{h5i}}{2} - \frac{\sum_{i=1}^{2} T_{h1i}}{2}\right)}{\frac{\sum_{i=1}^{2} T_{h1i}}{2}} \times 100\,\% \qquad (3)$$

where h indicates the hand (dominant or non-dominant) and T_{hDi} the threshold of the ith staircase of the Dth day for hand h. Note that a negative LI indicates improvement from pre- to post-test.

To exclude potential initial differences in the thresholds for the dominant and non-dominant index finger which could affect the ability to improve, a paired t test was performed on the average of the two first staircases from the first day for each finger.

The first hypothesis was that there would be a strong within-session improvement during the first session and stable within-session performance for later sessions. The within-session decreases for the dominant hand were entered in a Session (4) by Staircase (3) repeated measurements ANOVA. Planned repeated measures and polynomial contrasts were used to further investigate the nature of the potential session by staircase interaction.

The second hypothesis concerned the presence of between-session improvements, which would become smaller for subsequent sessions. To test for a significant improvement between the first and second session, a one-sided one-sample t test was performed, testing whether the BSRD score (between-session relative decrease with respect to the first session baseline) for the second session was significantly lower than zero. To test whether the BSRD scores were significantly different for subsequent days, the BSRDs for the dominant hand were entered in a Session (4) repeated measurements analysis of variance (ANOVA). One-tailed planned repeated measurement contrasts were used to test whether training effects leveled off for later sessions.

The third hypothesis was related to the presence of somatotopic specificity of learning. This was evaluated with a one-sided paired t test on the Learning Index for each hand, testing whether the relative decrease of the non-trained hand was smaller than the relative decrease of the trained dominant hand. As a more lenient test of transfer, we also compared the relative decrease of the non-trained hand to the relative decrease of the trained dominant hand taking the second session for both hands, i.e., data from day 5 for the non-dominant hand and day 2 for the dominant hand. A larger relative decrease for the non-dominant hand in this test would indicate transfer of learning effects. To also assess whether the learning rate for the non-dominant hand was the same as the learning rate for the non-dominant hand, the slopes of the best fitting lines to the within-session relative decrease scores were compared in a one-sided paired *t* test, taking the data from the second session (second day) of the dominant hand and comparing it to the data from the second session (last day) of the non-dominant hand.

Finally, an explorative analysis was performed to evaluate the extent to which learning effects were retained in the five subjects that could participate in the retention test 543 days (SD 33; ~1.5 years) post-training. Retention scores were computed for the initial retention thresholds by taking the average of the first two staircases of the retention test as the "post" score and computing the relative improvement compared to the pre-training baseline using the previously defined formula (3). The Retention scores for the retention test were subsequently entered in a Wilcoxon signed rank test to test whether they were significantly different from zero and to subsequently compare them to the Learning Index from the original training data for the dominant hand. No difference on the second test would indicate full retention.

Results

The average number of trials per staircase was 88 for the 6 staircases with the non-dominant hand and 88 for the 18 staircases with the dominant hand (paired samples *t* test $t(15) = 0.006$, $p = 0.995$). There were no significant correlations (at $\alpha = 0.05$, one-tailed, Bonferroni corrected for multiple comparisons) between the subjective sleep quality scores and the relative decrease of the average threshold compared to the threshold the previous day, nor between the sleep scores and the within-session relative decrease scores. The average pre-training thresholds (based on the average of the first two staircases for each hand on the first day) did not differ between hands (dominant hand 2.65 mm, non-dominant hand 2.66 mm, paired samples *t* test: $t(15) = 0.063$, $p = 0.951$; Table 1). A Hand (2) by Order (2) split plot analysis on the Learning Index showed no significant effects of Order ($F(1, 14) = 2.167$, $p = 0.163$), nor a Hand by Order interaction ($F(1, 14) = 0.709$, $p = 0.414$).

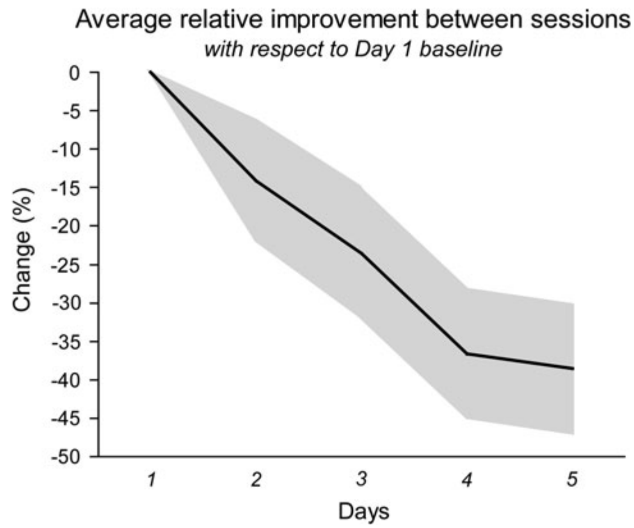

Fig. 2 Between-session relative improvement dominant hand. The estimated marginal means for the relative decrease with respect to the first session average (*black line*) of the dominant hand index finger on session two to five, expressed as percentage change in threshold with respect to the pre-training baseline on the first day (first two staircases). The value for the percentage change on the first session was set to zero for illustration purposes. The *gray lines* indicate the 95 % (between subject) confidence interval

Relative decrease in threshold between and within sessions

The Session (4) by Staircase (3) repeated measurement ANOVA on the within-session decreases of the dominant hand showed no significant effects at $\alpha = 0.05$ (supplementary figure 1). The same result was obtained when only the best learners (defined as those subjects with a negative Learning Index, indicating improvement from pre- to post-test for the dominant hand, see Table 1) were considered.

The one-sample *t* test on the BSRD score (between-session relative decrease scores with respect to the first session baseline) for the second session showed that there was a significant relative decrease with respect to the first session baseline for the dominant hand ($t(15) = -1.810$, $p = 0.045$, one-tailed). The Session (4) repeated measurements ANOVA on the BSRDs for the dominant hand revealed a significant main effect of Session ($F(3, 45) = 8.415$, $p = 0.000$). Planned repeated measures contrasts showed a trend toward a larger BSRD for day 2 compared to day 3 ($F(1, 15) = 2.277$, $p = 0.076$, one-sided) and a significantly greater BSRD for day 3 compared to day 4 ($F(1, 15) = 5.743$, $p = 0.015$, one-tailed), whereas the BSRD for day 4 was not significantly larger than for day 5 ($F(1, 15) = 0.460$, $p = 0.254$, one-tailed; Fig. 2).

Somatotopic specificity: transfer to the non-dominant hand

The paired t test on the Learning Index (representing the relative decrease between pre- and post-training thresholds for each hand) showed a larger decrease for the dominant (trained) hand ($t(15) = 1.879$, $p = 0.040$, one-tailed). When excluding those subjects who did not show any decrease on the dominant hand, the effect became stronger ($t(12) = 2.278$, $p = 0.021$, one-tailed). The average decrease for the dominant hand was −38.55 % (best learners: −49.45 %), while the average decrease for the non-dominant hand was −24.71 % (best learners: −30.72 %; Table 1). A more lenient test for transfer comparing the relative improvement for session 2 (day 2) for the dominant hand and session 2 (day 5) for the non-dominant hand) showed no significant difference between the dominant and non-dominant hand ($t(15) = -1.244$, $p = 0.117$, one-tailed; best learners: $t(12) = -1.13$, $p = 0.141$, one-tailed). The average improvement for the second session compared to the pre-training baseline was −14.1 % (best learners: −19.8 %) for the dominant and −24.71 % (best learners: −30.72 %) for the non-dominant hand. The paired t test on the regression slopes of the within-session relative decrease scores of the second session of the dominant (day 2) and non-dominant hand (day 5) yielded a strong trend toward a more negative slope for the non-dominant hand (average slope dominant hand: −3.49, non-dominant hand: −11.89; t(14[1]) = 1.744, $p = 0.052$; one-tailed, supplementary figure 2). The trend was weaker when only the best learners were taken into account (average slope dominant hand: −4.00, average slope non-dominant hand: −13.43; $t(11) = 1.605$, $p = 0.068$; see Footnote 1). The relative decrease of the average threshold of the last two staircases with respect to the pre-training baseline was 42.63 %, which was not different from the −38.55 % average decrease between pre- and post-training threshold for the dominant hand (paired t test: $t(15) = 0.565$, $p = 0.581$). Thus, the relative improvement of the non-dominant, untrained hand on the fifth day was comparable to the relative improvement of the dominant, trained hand across 4 days even though the training interval was substantially compressed.

Long-term retention

Thresholds and Retention scores for the retention test can be found in Table 1. The explorative Wilcoxon signed rank test of the retention data revealed that the Retention score was significantly different from 0 ($p = 0.022$, one-tailed). A second Wilcoxon signed rank test revealed no significant difference between the average Retention score (−34.26 %) and the average Learning Index (−61.07 %) for the sample of five subjects from the original training ($z = -1.214$, $p = 0.225$), probably due to the small sample size and large variability. When the Retention scores for the retention session were based on the last two staircases instead of the first two staircases, the average was −45.80 %, much closer to the −61.07 % dominant hand Learning Index obtained in the original training.

[1] One subject (subject 15) was excluded from the analysis due to a missing value for the last staircase of the non-dominant hand on the fifth day.

Discussion

Four days of training of the dominant index finger on a tactile perceptual task yielded significant threshold reductions. No significant effects were found within sessions. Contrary to our hypothesis, this was also true for the first session. As expected, the largest improvements occurred between sessions, an effect that levelled off in the last session. There was no complete transfer of learning effects: pre- to post-training threshold improvements were larger for the trained than for the untrained index finger. This effect was stronger when only the best learners were considered. When equating the amount of training by comparing the relative improvement for the dominant hand on day 2 and the non-dominant hand on day 5, we did not find significant transfer effects either: the relative improvement did not differ for the dominant and non-dominant hand. However, there was a strong trend toward a faster learning rate for the untrained index finger after training of its dominant counterpart. After a single training session, the relative improvement for the non-trained hand was at the same level as that of the trained hand. Finally, an explorative analysis showed limited retention of training effects in the dominant hand after 1.5 years.

Differences in tactile thresholds reported in previous studies

The average perceptual threshold for the dominant index finger (2.65 mm) reported in the current study is higher than the average of approximately 0.43–0.56 mm reported by previous studies of tactile hyperacuity (Duncan and Boynton 2007; Loomis 1979; Sathian and Zangaladze 1998). There could be several explanations for these differences. First, the thresholds reported by Loomis came from a sample of three subjects, and most likely do not reflect naïve, untrained performance. Furthermore, the experimenters were also the participants and had extensive experience in tactile discrimination tasks, obtained during the experiment itself (∼1,000 trials on the tactile hyperacuity task, and about the same number on other similar tasks) and during 20–30 h of pilot work (for comparison: the total time subjects spent on the current learning study was about 6 h). Given the expected intrinsic motivation of these subjects, it seems reasonable to compare them to our best subjects after training. Our best subject reached a threshold of 0.32 mm which is in the same range as the threshold obtained by the best subject from Loomis' study (0.31 mm). Second, the dot stimuli and spacing differed slightly between studies. The dots in the current study were 0.05 mm at the top, 1.3 mm diameter at the base, 0.89 mm height, with 3 mm center-to-center distance. When comparing this to the previous study by Sathian and Zangaladze (1998), the dot diameter in our study is a striking factor 6 smaller at the top. It could be that small displacements of dots with a diameter far below the receptive field size induce smaller changes in the neural response profiles than dots that are larger. This would be in accordance with the reported U-shape relationship between vernier thresholds and spatial frequency in vision (Wilson 1986). Third, it is known from visual and auditory research that attaining low thresholds critically depends on the assessment procedure. Using fixed cross-trial reference stimuli yielded lower thresholds (Ahissar et al. 2009). Sathian and Zangaladze (1998) used such a reference: stimuli with an offset were compared to a reference stimulus with zero offset. Stimuli with the same offset were presented in blocks. The staircase procedure used here did not proceed randomly through the stimulus levels, but the presented offsets varied based on the response given and there was no stable cross-trial reference stimulus. Judging the direction of an offset based on a single stimulus as in the current study may be more difficult than judging which of two sequentially presented stimuli contains an offset. Indeed, the former procedure (Sathian and Zangaladze 1998; Stilla et al. 2008) leads to a fourfold to fivefold increase in thresholds compared to the latter (Grant et al. 2000) in (two different samples of) blind participants. Another contributing factor might be the starting level of the learning procedure. The current study started with an offset of 3.75 mm for the pre-test on the first day and the retention test. Sathian and Zangaladze (1998) started testing from an offset value (1.04 mm) which was below the final threshold for the 13 best learners (defined as those participants showing improvement for the dominant hand after training) in the current study (1.29 mm). Finally, the samples in all studies are rather small (3, 10, 10 and 16 subjects in the current study) which could lead to substantial variability in the average estimated threshold sizes.

Whatever the cause of the discrepancy, the fact remains that a threshold of 2.65 mm most likely does not reflect hyperacuity, as the estimated innervation density for SA1 (slowly adapting type 1) and RA (rapidly adapting) fibers in the fingertips is around 1 mm (Johansson 1978; Johansson and Vallbo 1979). This could suggest that training was not continued long enough to push early sensory areas to their precision limits. However, the precision demands of the task are high enough to engage early sensory areas and to warrant a contribution of these areas to learning, given the fine resolution of the stimuli and the difficulty of the task.

Pattern of improvements within and between sessions

The lack of significant within-session learning effects is in agreement with previous findings in visual learning (De Weerd et al. 2012; Karni and Sagi 1991; 1993; Schoups et al. 1995), except for the first session, for which previous visual studies showed significant improvements (e.g. Fahle et al. 1995). A trend for within-session learning effects was reported in a side note for all sessions in a previous tactile learning study, although this study did not set out to provide a systematic investigation (Sathian and Zangaladze 1997).

The significant relative between-session improvement for the second session is in accordance with previous findings in the visual domain (Karni and Sagi 1993). However, the effects did not become increasingly smaller; in fact, the largest relative improvement occurred in the fourth session. These results could still reflect a two-stage learning process in accordance with Karni and Sagi (1993), but with a slower initial learning phase. However, we did not test explicitly whether such a model yields a better fit than an exponential one. In the visual domain, Dosher and Lu (2007) found that a single exponential model provided a better fit to the shape of the learning curve than a two-component model.

Somatotopic specificity

We did not find complete transfer of learning effects: there was a stronger improvement from pre- to post-test for the trained than for the non-trained hand. This indicates that tactile perceptual learning has a somatotopically specific component, just like perceptual learning of vibration, punctuate pressure, or roughness (Harris et al. 2001). An equivalent visual vernier task showed retinotopically specific learning effects already within 1 h of training, which partly transferred to the untrained eye and different offsets (Fahle et al. 1995).

The presence of topographically specific training effects suggests involvement of topographically organized neuronal populations in tactile perceptual learning. Functional magnetic resonance imaging already showed that tactile perceptual thresholds are correlated with the distances between finger representations in the primary somatosensory cortex (Duncan and Boynton 2007). This finding suggests the involvement of area 3b and area 1. Sathian and Zangaladze (1998) also interpreted their findings as evidence for the involvement of somatotopically organized brain regions, such as S1 or S2. Studies on visual perceptual learning using human magnetic resonance imaging (Schwartz et al. 2002; Yotsumoto et al. 2008, 2009) and transcranial magnetic stimulation on the visual cortex (De Weerd et al. 2012) demonstrated that changes in early sensory regions can already occur during the early stages of learning.

Somatotopic specificity of learning effects was visible in the first two threshold measurements for the non-dominant hand after dominant hand training. A more lenient test of transfer equating the amount of training (comparing to the dominant hand on day 2) pointed in the same direction: there was no significantly larger relative improvement for the non-dominant hand. However, there was a trend toward a faster learning rate for the untrained finger, and after only one session, the relative improvement with respect to the pre-training baseline did not differ anymore between hands. Sathian and Zangaladze (1997, 1998) also found that there was an increased learning rate for the untrained contralateral index finger, evidenced by the fact that fewer sessions were required to obtain a stable threshold. We found similar results, looking at the relative improvement with respect to a pre-training baseline, thus precluding that any initial differences between the acuity of the fingers would affect our results.

In light of results from visual perceptual learning, it is striking that we still found some degree of somatotopic specificity: Zhang et al. (2010b) found that location specificity of orientation learning as previously reported (Schoups et al. 1995) was abolished by a short pre-training baseline measurement (200 trials) at the untrained retinal location. As it cannot be ruled out that learning and transfer occur during the pre-training threshold measurement, we assume that the relative decrease from pre- to post-training will always be an underestimation of the actual learning effects. This could especially affect the hand whose threshold is measured second. Such order effects were ruled out in the current study by counterbalancing the order of the pre-training threshold measurements across subjects.

Long-term retention

In five subjects, we tested to what extent training effects were retained approximately 1.5 years after the final training session and found significant retention of learning effects compared to the pre-training baseline. Previously, the results of asymptotic visual learning were shown to be retained up to several months (Zhou et al. 2006) and even years after training (Karni and Sagi 1993). In tactile learning, long-term retention was found to be limited: 7 ± 9 months after first stimulus exposure, Sathian and Zangaladze (1998) found that initial thresholds were lower and slightly fewer sessions were required to attain the final threshold. In the current study, the average relative improvement (with respect to the pre-training baseline) of the first two staircases of the retention test was lower than the average relative improvement recorded right after the original training, suggesting that at least initially, retention was not complete. This effect did not reach significance, probably due to the limited amount of five subjects that were willing and able to participate in the retention test.

Interpretation in light of perceptual learning theories

In the context of RHT, the fact that we did not find complete transfer indicates that learning went beyond procedural task aspects and effects were somatotopically specific. However, our data also show that learning effects could transfer to the untrained hand within a single session, whereas no signs of within-session learning were found in the initial dominant hand training. The faster time course of the improvements for the non-dominant hand suggests that they are more related to changes in the overall strategy and readout routine, and less to plasticity of the representation in primary somatosensory cortex. It also suggests that somatotopic specificity could have been even more pronounced if dominant hand training had been pursued even further along the asymptote. The extent of training effects and their specificity have been found to be dependent on the amount of trials per session, with optimal numbers differing between visual (Aberg et al. 2009) and auditory paradigms, as well as between specific tasks (Wright and Sabin 2007).

It might be that the characteristics of the tactile staircase procedure slowed down the learning process. Firstly, in the staircase procedure, different offset sizes were presented interleaved and the step sizes were fixed and not relative. The latter is due to the mechanical nature of the stimulus setup which only allows presentation of a predetermined set of stimuli. Some (small) additional variability could have arisen due to differences in the amount of pressure applied and in the touch duration. This variability might have effectively resulted in a "roving" procedure of slightly different stimuli, involving synaptic changes in overlapping but not identical populations of neurons. This type of presentation was shown to reduce perceptual learning (Herzog et al. 2012; Tartaglia et al. 2009).

The heterogeneity in results of visual learning complicates a direct comparison between visual and tactile learning. This heterogeneity appears to be at least partly attributable to variations in task parameters. Nevertheless, we argue that tactile learning appears to have commonalities with visual learning in several respects, which is in line with the idea that general mechanisms govern human procedural learning (Censor et al. 2012; Seitz and Dinse 2007). For the tactile domain, our results indeed provide support for a somatotopic aspect, because initially, transfer is not complete. This initial performance difference cannot be attributed to a lack of experience with the procedural aspects of the task, because subjects trained the procedural aspects of the task in the pre-training threshold measurement and in several practice runs before each session with both hands. It therefore appears that some aspects of perceptual learning are tied to the somatotopic location and might involve early somatotopic regions such as S1. However, it might be that this involvement is expressed in setting up and fine-tuning changes in synaptic connectivity for readout routines by higher order regions, rather than in changes in the representation. Similar accounts have also been put forward for visual perceptual learning (Huang et al. 2012; Petrov et al. 2005; Bejjanki et al. 2011). These changes in the readout of early sensory regions can apparently be remapped to another, contralateral location within the same session, possibly through the influence of connections with higher order regions with bilateral receptive fields, or cross-callosal connections with the corresponding contralateral region in S1.

Conclusion

The current study shows that tactile perceptual learning of the dominant hand mainly occurred offline, between sessions. Initially, transfer to the untrained contralateral hand was not complete, but training effects became available at the untrained location after a few additional training runs. After 1.5 years, dominant hand training effects were not fully washed out and could be recuperated completely with a single training session. Interpreted in light of theories of visual perceptual learning, these results do not suggest that tactile perceptual learning is fundamentally different from visual perceptually learning, because procedural and task difference might explain the apparent differences in the amount of transfer and retention in both visual and tactile paradigms.

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