



Transfer of Tactile Learning from Trained to Untrained Body Parts Supported by Cortical Coactivation in Primary Somatosensory Cortex

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A pioneering study by [Volkman \(1858\)](#) revealed that training on a tactile discrimination task improved task performance, indicative of tactile learning, and that such tactile learning transferred from trained to untrained body parts. However, the neural mechanisms underlying tactile learning and transfer of tactile learning have remained unclear. We trained groups of human subjects (female and male) in daily sessions on a tactile discrimination task either by stimulating the palm of the right hand or the sole of the right foot. Task performance before training was similar between the palm and sole. Posttraining transfer of tactile learning was greater from the trained right sole to the untrained right palm than from the trained right palm to the untrained right sole. Functional magnetic resonance imaging (fMRI) and multivariate pattern classification analysis revealed that the somatotopic representation of the right palm in contralateral primary somatosensory cortex (SI) was coactivated during tactile stimulation of the right sole. More pronounced coactivation in the cortical representation of the right palm was associated with lower tactile performance for tactile stimulation of the right sole and more pronounced subsequent transfer of tactile learning from the trained right sole to the untrained right palm. In contrast, coactivation of the cortical sole representation during tactile stimulation of the palm was less pronounced and no association with tactile performance and subsequent transfer of tactile learning was found. These results indicate that tactile learning may transfer to untrained body parts that are coactivated to support tactile learning with the trained body part.

Key words: coactivation; perceptual learning; primary somatosensory cortex; somatosensory system; tactile plasticity; transfer

Significance Statement

Perceptual skills such as the discrimination of tactile cues can improve by means of training, indicative of perceptual learning and sensory plasticity. However, it has remained unclear whether and if so, how such perceptual learning can occur if the training task is very difficult. Here, we show for tactile perceptual learning that the representation of the palm of the hand in primary somatosensory cortex (SI) is coactivated to support learning of a difficult tactile discrimination task with tactile stimulation of the sole of the foot. Such cortical coactivation of an untrained body part to support tactile learning with a trained body part might be critically involved in the subsequent transfer of tactile learning between the trained and untrained body parts.

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Introduction

Psychophysical investigations in the mid-19th century showed that training on a tactile discrimination task with a given body part (e.g., the hand) increased task performance with the trained body part (Volkman, 1858), indicative of tactile learning (Seitz and Dinse, 2007). Interestingly, it was found that tactile learning is not restricted to the trained body part but can transfer to untrained body parts (Volkman, 1858; Sathian and Zangaladze, 1998; Kaas et al., 2013; Arnold and Auvray, 2014; Muret et al., 2014). Surprisingly, however, transfer of tactile learning appears to be specific for certain body parts (Volkman, 1858; Harris et al., 1999, 2001; Godde et al., 2000; Harris and Diamond, 2000; Harrar et al., 2014; Muret et al., 2014; Dempsey-Jones et al., 2016; Muret and Dinse, 2018). For instance, some studies reported that tactile learning transferred from the trained hand to the untrained face (Muret et al., 2014) but not from the trained hand to the untrained forearm (Volkman, 1858; Muret and Dinse, 2018). The mechanisms underlying transfer of tactile learning from trained to untrained body parts remain unclear, and are the focus of the current investigation.

If transfer of tactile learning from trained to untrained body parts or locations is specific, it should occur in specific directions, that is, tactile learning should transfer from one trained body part or location to another untrained one, but not to a similar extent vice versa. To test this possibility, tactile learning and transfer of tactile learning should be compared between body parts or locations that share anatomic and functional features, yet differ sufficiently enough, such that they are not simply homologous body parts or locations on different sides of the body (e.g., left and right hands).

Here, we measured transfer of tactile learning between two body parts that exhibit multiple commonalities but also differ in some aspects: the right hand and the right foot. Hand and foot are serially homologous structures that have co-evolved (Rolian et al., 2010), exhibit similar anatomic features including their number of digits, bone structures, and type of skin surface (glabrous vs hairy) on alternate sides, and they are both distal portions of a limb. Although hand and foot have separate representations in primary somatosensory cortex (SI; Penfield and Rasmussen, 1950; Hashimoto et al., 2013; Akselrod et al., 2017; Roux et al., 2018; Germann et al., 2020), there might be a common high-level representation of the hand and foot in cortical areas beyond SI (Manser-Smith et al., 2018, 2019). There are even indications that the representations of hand and foot in SI share information content in healthy human subjects (Muret et al., 2022). This is corroborated by results in one-handed subjects who have been found to represent tactile information from their intact foot in the cortical representation of their missing hand in SI (Hahamy et al., 2017). A functional relationship between hand and foot is also suggested by results showing that touch to the hand may be misattributed to the foot and vice versa (Schicke and Röder, 2006; Badde et al., 2019). Notwithstanding these commonalities, there are also obvious differences between hand and foot in terms of function, shape, total number of mechanoreceptors (Taube Navaraj et al., 2017), innervation densities (Corniani and Saal, 2020), receptor activation thresholds (Johansson et al., 1980; Kennedy and Inglis, 2002), and potentially also tactile spatial resolutions (Weinstein, 1968; Mancini et al., 2014).

Using the palm of the right hand and the sole of the right foot for tactile stimulation, we conducted a series of behavioral and functional magnetic resonance imaging (fMRI) experiments to investigate mechanisms underlying transfer of tactile learning. We hypothesized that if transfer of tactile learning were specific,

it should occur to a greater extent from one trained body part (e.g., the right sole) to the untrained one (the right palm) than vice versa. Alternatively, if transfer of tactile learning were not specific, it should occur to a similar extent in each direction.

Materials and Methods

Subjects

Overall, 80 subjects (64 females and 16 males, mean age = 22.1 ± 0.48 SEM years) participated in different experiments of this study (including pilot experiments, behavioral experiments and fMRI experiment; see below, Experimental design). Only right-handed and right-footed subjects were recruited. Subjects had a mean \pm SEM right-handedness score of 86.6 ± 2.54 and a mean \pm SEM right-footedness score of 60.2 ± 3.81 as determined by handedness (Oldfield, 1971) and footedness questionnaires (Chapman et al., 1987). Subjects gave informed consent before participation. Participation was rewarded either by course credit or monetary compensation. The study was approved by the local internal review board.

Experimental design

The study consisted of behavioral and fMRI experiments. Before these experiments, several pilot experiments were conducted.

In a first pilot experiment, the two-point-discrimination (2-PD) thresholds were measured for the right palm and sole in each of six subjects (within-subject design). In a second pilot experiment, pretraining performance in the tactile discrimination task used for training with the right palm and sole was measured in each of 16 new subjects (within-subject design). In a third pilot experiment, six new subjects trained on the tactile discrimination task with the right palm until they achieved a predefined learning criterion (within-subject design).

In the behavioral experiment, two groups of 12 new subjects each trained on the tactile discrimination task either with the right palm or sole until they achieved a predefined learning criterion. Thereafter, they performed a posttraining transfer test in the trained task with the untrained right sole or palm (depending on training group). Posttraining transfer performance was compared between the two training groups (between-subject design).

Two behavioral control experiments were conducted. In the first behavioral control experiment, a group of 12 new subjects trained on the tactile discrimination task with the right sole for 11 training sessions and thereafter performed a posttraining transfer test in the trained task with the untrained right palm. Posttraining transfer performance was compared between subjects in this control experiment and subjects trained with the right palm from the behavioral experiment who performed a posttraining transfer test to the untrained right sole (between-subject design). In the second behavioral control experiment, a subset of 12 subjects from the second pilot experiment trained on the tactile discrimination task either with the right palm or sole (six subjects for each training group) until they achieved a predefined learning criterion. Thereafter, they performed a posttraining transfer test in the trained task to the untrained right sole or palm (depending on training group). For each subject, pretraining performance with the untrained body part was subtracted from posttraining transfer performance with the untrained body part to correct for pretraining performance with the untrained body part. The corrected transfer performance with the untrained body part was compared between the two training groups (between-subject design).

Finally, a group of 16 new subjects first completed an fMRI experiment in which brain activations in the representations of the right palm and sole in contralateral SI were measured during tactile stimulation. The performance in a tactile control task conducted during fMRI was correlated with brain activations across subjects (within-subject design, correlational approach). Thereafter, subjects trained on the tactile discrimination task for ten behavioral training sessions outside the scanner either with the right palm or sole (eight subjects for each training group). After training ended, trained subjects performed a posttraining transfer test, again outside the scanner, in the trained task with the untrained right sole or palm (depending on training group). Posttraining transfer

performance between the two training groups was compared (between-subject design). Furthermore, activations in the fMRI experiment were used to predict performance in the tactile discrimination task in an early stage of training and in the subsequent posttraining transfer test separately for each training group (within-subject design, correlational approach). The design of this experiment (i.e., using activations in an fMRI experiment to predict subsequent behavioral learning results) followed the approach of a previous study (Reavis et al., 2015).

Tactile stimulation device

The tactile stimulation device used in this study consisted of a 2-by-2 matrix of air-jets, each of which directed an air stream onto the skin surface to create a discernable tactile movement pattern (Fig. 1*a*). The air-jets moved independently in linear directions within a square-shaped field (each subtending 2.5×2.5 cm). The jets were mounted within a plastic container (length = 25 cm, width = 20 cm, height = 8 cm). Subjects positioned the right palm or sole over the air-jets (Fig. 1*b*). The air-jets themselves never touched the surface of the skin. Air jet nozzles were always at least 1 cm away from the skin. Tactile movement patterns were presented by highly focused air streams on the underlying skin surface. The device was connected to an air pressure system. Air streamed through the jets with an average of 5.2 mN. This stimulus intensity was chosen to assure that the stimuli were suprathreshold and were experienced by all subjects as light touch, which was confirmed in pilot trials in all cases. A compressed air regulator and a vacuum pump were interposed between the air pressure system and the tactile stimulation device. The compressed air regulator was controlled by solenoid valves, which were connected to a circuit board equipped with a 32-bit microcontroller module (Cypress Semiconductor CY8KIT-049-42xx PSOC 4 Prototyping kit). The adjusted air pressure was fed into the air-jets of the tactile stimulation device via air pressure lines (length = 6 m). The movements of the jets were driven by alterations in air pressure, which in turn was controlled by a custom-made software package written in MATLAB (The MathWorks) and C++ using the SharpDevelop software tool. The tactile stimulation device was MRI-safe, as all electronics, pumps and regulators were outside of the MRI recording chamber. The air pressure lines passed through the MRI waveguide to the tactile stimulation device inside the scanner.

Tactile discrimination task for learning

A tactile discrimination task was designed in which subjects were asked to discriminate between different tactile movement patterns (Fig. 1*c*). On each trial the tactile stimulation device directed an air stream to create four independent tactile stimuli simultaneously onto the surface of the skin. Each stimulus was presented in a different quadrant and consisted of a pattern moving either in a “v”-shaped trajectory or an inverted “v”-shaped trajectory from left to right (Fig. 1*c*). The “v”-shaped trajectory served as a target while inverted “v”-shaped trajectories served as distractors.

Each trajectory took 1.5 s to complete, followed by a break of the same duration during which time the air-jet returned to the starting position without emitting any air. Each air-jet started to present a stimulus after one of four on-ramps (0, 250, 500, and 750 ms, referenced to trajectory onset), which were assigned to each air-jet in a counterbalanced order across trials. By using on-ramps the trajectories were presented asynchronously across the four stimulus quadrants. Because of these phase shifts, the target could not be identified by having a unique instantaneous direction compared with the distractors. Indeed, the movement, pressure, and direction features that comprised the target and distractors were the same. Instead, the target could only be identified by virtue of its unique conjunction of downward and upward features in space and time.

Each trajectory was presented a total of four times per trial, resulting in a total trial duration of ~12 s. On each trial either one target was presented among three distractors (target-present condition; Fig. 1*c*, left panel) or four distractors were presented (target-absent condition; Fig. 1*c*, right panel). Subjects performed a five-alternative forced choice task. They were asked to indicate whether a target was present in one of the quadrants (buttons 1–4 on the computer keyboard corresponding to

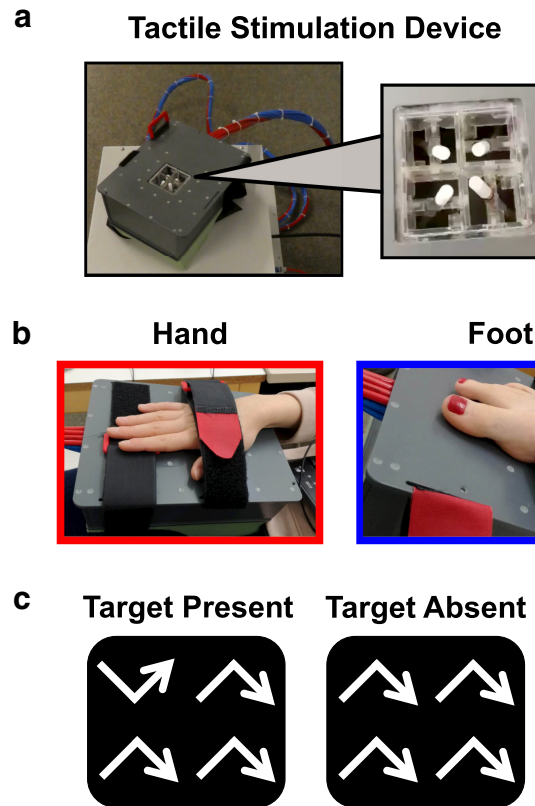


Figure 1. Tactile stimulation device and experimental conditions. *a*, MRI-safe tactile stimulation device. Tactile movement patterns were created by a continuous air stream directed to the surface of the skin by air-jets arranged in separate quadrants. *b*, Body parts used for tactile stimulation and learning in a sample subject. Left, Tactile stimulation of the palm of the right hand. Right, Tactile stimulation of the sole of the right foot. *c*, Schematic representation of tactile stimulus conditions in the tactile discrimination task used for learning. Left, Target-present condition. A tactile target trajectory was presented among three tactile distractor trajectories. The target moved in a “v”-shaped trajectory. Distractors moved in inverted “v”-shaped trajectories. In this example, the target is located in the upper left quadrant. Note that the white arrows signify the direction of the movement trajectories for the sake of illustration only. Right, Target-absent condition. All stimuli moved in inverted “v”-shaped trajectories.

target presence in respective quadrants, starting with button 1 for the lower left quadrant and continuing with buttons 2–4 for other quadrants in a clockwise direction) or whether the target was absent (button “v” on the keyboard).

Subjects sensed the stimuli with the right palm or sole and used the left hand to give a response on the keyboard. Subjects were instructed to respond as accurately as possible. They could respond at any time during a trial. After subjects responded, the trial was terminated. If the response was correct, a beep tone was presented via headphones. If the response was incorrect, no tone was presented. In each session subjects performed a total of 120 trials (24 target-present trials for each quadrant and 24 target-absent trials), resulting in a session duration of ~30 min. Trials were presented in random order in each session.

We expected that this task would strongly activate the representations of the respective body parts in contralateral SI, given that neurons in SI are sensitive to tactile movement direction (Pei and Bensmaia, 2014; Sathian, 2016). Furthermore, visual learning experiments using a similar task showed that subjects exhibit low task performance at the beginning of training but greatly improve task performance over the course of daily training sessions, indicative of learning (Frank et al., 2016, 2018). Therefore, we predicted that subjects in this study would exhibit low task performance before and at the beginning of training, but improve task performance dramatically with daily training sessions, indicative of tactile learning. Although the palm and sole exhibit differences in their physiological properties

(Johansson et al., 1980; Kennedy and Inglis, 2002; Taube Navaraj et al., 2017; Corniani and Saal, 2020) and potentially also in their tactile spatial resolutions (Weinstein, 1968; Mancini et al., 2014; see below, 2-PD thresholds), we predicted that pretraining performance in the tactile discrimination task would be similar with the palm and sole because of the great complexity of the tactile stimuli and the novelty of the task, which both contributed to a high level of task difficulty.

General procedure

Behavioral experiments were conducted in a windowless testing room with lights turned off. Subjects rested in supine position on a reclining table and positioned their right palm or sole on the surface of the tactile stimulation device (Fig. 1*b*). The tactile device was attached to the right hand or foot with a nylon strap. Subjects were blindfolded and instructed to keep their eyes closed. They wore earplugs and headphones to minimize any perceived noise from the tactile stimulation device and the vacuum pump.

For the fMRI experiment subjects were in supine position on the MRI-gantry and the tactile stimulation device was attached to the right hand or foot with a nylon strap (Fig. 6*a*). Subjects were asked to keep their eyes closed and wore earplugs and MRI headphones. They responded by button press on the MRI-safe button box with the left hand. Room lights were turned off.

Pilot experiments

2-PD thresholds

In a first pilot experiment, the spatial resolutions of the right palm and sole were measured. Previous studies using the 2-PD method reported that the palm has a higher spatial resolution to discriminate tactile cues than the sole (Weinstein, 1968; Mancini et al., 2014). To replicate this result, we measured the spatial resolution of the right palm and sole by means of 2-PD thresholds in a sample of six subjects. Although the 2-PD method has been criticized for being an unreliable measure of tactile spatial resolution (Craig and Johnson, 2000), it was found that 2-PD thresholds correlate with innervation densities of different body parts and locations (Corniani and Saal, 2020). For instance, the palm has a higher innervation density (Corniani and Saal, 2020), a greater number of mechanoreceptors (Taube Navaraj et al., 2017) and lower receptor activation thresholds (Johansson et al., 1980; Kennedy and Inglis, 2002) than the sole, which agrees with lower 2-PD thresholds found in the palm than that found in the sole (Weinstein, 1968; Mancini et al., 2014). To replicate the 2-PD threshold results of the palm and sole for the purpose of this pilot experiment, a two-point-discriminator (Baseline 12-1480 Aesthesiometer, 3B Scientific GmbH) was manually operated by an experimenter, who was unaware of the purpose of the experiment and previously reported 2-PD threshold results for different body parts and locations. For each body part the 2-PD threshold was measured within each quadrant used for tactile stimulation in the learning experiment (Fig. 1*c*). The 2-PD measurements for each quadrant and body part were conducted in random order within a single session for each subject. Subjects were blindfolded during the measurements.

The following 2-PD testing procedure was used for each quadrant: at trial start, a beep tone was played to alert the subject. Shortly thereafter the experimenter briefly touched the skin with the pointer and the subject was asked to report whether they sensed one point or two points. Subjects did not receive any feedback about the correctness of the response. Based on previously reported 2-PD thresholds for the body parts examined in this study (see Weinstein, 1968; Mancini et al., 2014) we used the following distances between the two pointers (in millimeters): palm: 6, 7, 8, 9, 10, 11, 12, 13, 14; sole: 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24. There were a total of 10 trials for each distance. Trials were presented in random order. A total of 10 catch trials were randomly intermixed with the regular trials. In catch trials, only one pointer touched the skin. Catch trials were included to measure whether subjects were biased toward reporting the two-point response option when reporting their tactile sensations.

2-PD thresholds were calculated using the following procedure. For each distance and quadrant, the total number of two-point responses was divided by the total number of trials for this distance to obtain the

proportion of two-point responses. A psychometric function was then fit to the proportion scores across different distances (excluding catch trials). The 75% point on the fitted curve was used as the threshold. Thresholds were averaged across quadrants for each body part.

Pretraining performance

In a second pilot experiment, a group of 16 subjects performed two pretraining sessions of the tactile discrimination task (Fig. 1*c*) used for training in the behavioral learning experiment. One session was conducted with the right palm. The other session was conducted with the right sole. Sessions were conducted successively without any intermission on the same day for each subject. The order of sessions was counterbalanced across subjects. This pilot experiment served to measure pretraining performance in the tactile discrimination task with the right palm and sole. A subset of 12 subjects of this pilot experiment also participated in a later control experiment (see below, Behavioral control experiments).

Tactile learning

In a third pilot experiment, six subjects trained on the tactile discrimination task with the right palm until they achieved a response accuracy of 90% correct or greater in two training sessions, successive or nonsuccessive (henceforth referred to as the learning criterion). Each training session was conducted on a separate day. With this pilot experiment, we wanted to check whether subjects improved their performance in the tactile discrimination task by means of training, which would be indicative of tactile learning. Furthermore, we wanted to measure how many training sessions would be necessary in different subjects to achieve the learning criterion.

Behavioral learning experiment

In the behavioral learning experiment two groups of 12 subjects each trained in daily sessions either with the right palm or sole on the tactile discrimination task (Fig. 2*a*). Subjects were randomly assigned to one training group. For each subject, training was terminated when the learning criterion of 90% correct response accuracy in two training sessions was achieved. On a separate day after the last training session a posttraining transfer test of tactile learning to the untrained body part (either the right sole or palm, in different training groups) was conducted. The transfer test was conducted exactly as a training session except that subjects performed the tactile discrimination task with the untrained body part (i.e., with the sole after training with the palm or with the palm after training with the sole).

Behavioral control experiments

Two behavioral control experiments were conducted. In a first behavioral control experiment, a group of 12 subjects trained on the tactile discrimination task with the right sole for a total of 11 daily sessions (Fig. 2*b*). This number of training sessions was chosen based on the mean number of training sessions required to learn the task with tactile stimulation of the right palm across subjects in the behavioral learning experiment (Fig. 4*a,b*). On a separate day after the last training session, trained subjects performed a posttraining transfer test of the tactile discrimination task to the untrained right palm. This control experiment served to exclude the possibility that the greater number of training sessions required to learn the task with the sole than the palm (Fig. 4*a–d*) contributed to differences in the magnitude of transfer of tactile learning to the untrained body part.

In a second behavioral control experiment, a subset of 12 subjects who completed a pretraining test in the tactile discrimination task with the right palm and sole (see above, Pretraining performance, and Pilot experiments) continued to train on the tactile discrimination task in daily sessions until they achieved the predefined learning criterion (i.e., 90% correct response accuracy in two training sessions; Fig. 2*c*). Half of the subjects trained with the right palm while the other half trained with the right sole (subjects were randomly assigned to each training group). On a separate day after the last training session, trained subjects performed a posttraining transfer test to the untrained right sole or palm (depending on training group). Pretraining performance with the untrained body part was

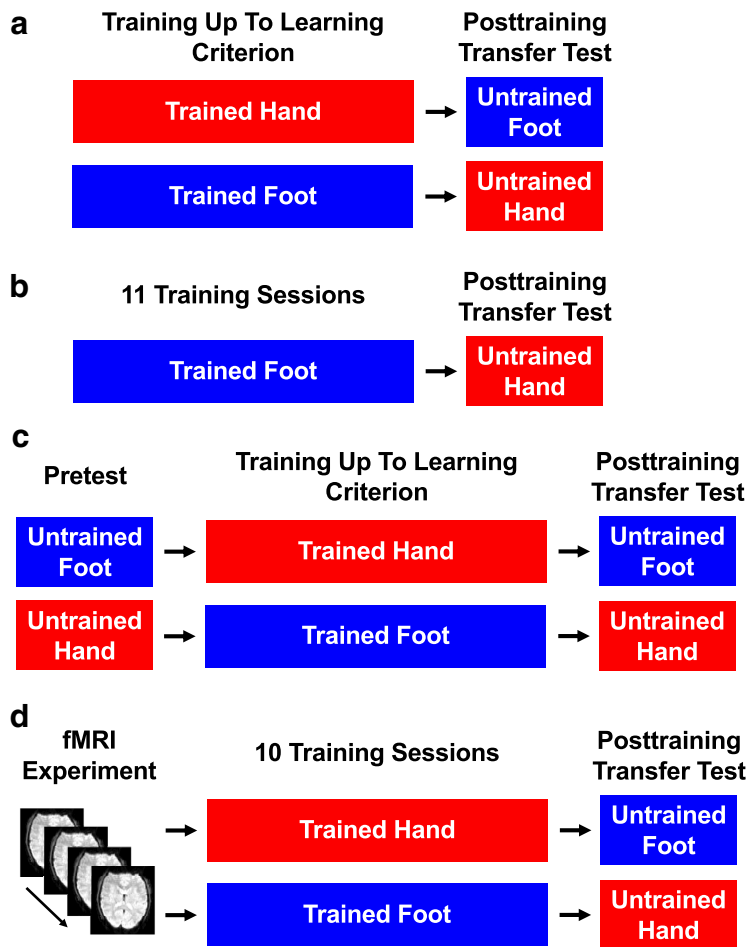


Figure 2. Experimental design. **a**, Behavioral learning experiment. Two groups of subjects trained on the tactile discrimination task in daily sessions either with the palm of the right hand (top panel) or with the sole of the right foot (bottom panel) until they achieved a learning criterion corresponding to a response accuracy of 90% or greater in two training sessions. After the end of training, subjects trained with the right palm performed a posttraining transfer test in the trained task with the untrained right sole, while subjects trained with the right sole performed a posttraining transfer test with the untrained right palm. **b**, Behavioral control experiment. Subjects trained for 11 daily sessions on the tactile discrimination task with the right sole. After the end of training, trained subjects performed a posttraining transfer test in the trained task with the untrained right palm. **c**, Behavioral control experiment. Two groups of subjects trained on the tactile discrimination task in daily sessions either with the right palm (top panel) or with the right sole (bottom panel) until they achieved the same learning criterion as in the behavioral learning experiment. Before the first training session, each subject performed a pretest in the trained task with the untrained right sole or palm (depending on training group). After the end of training, trained subjects performed a posttraining transfer test in the trained task with the untrained right sole or palm (depending on training group). **d**, fMRI experiment followed by behavioral training and posttraining transfer test. Subjects first completed an fMRI experiment in which brain activations during tactile stimulation of the right palm and sole were measured. Thereafter, they trained on the tactile discrimination task for ten daily sessions either with the right palm (top panel) or with the right sole (bottom panel). After the end of training, trained subjects performed a posttraining transfer test in the trained task with the untrained right sole or palm (depending on training group).

subtracted from posttraining transfer performance with the untrained body part. After this subtraction, the magnitude of transfer of tactile learning was compared between the two training groups. This control experiment served to exclude the possibility that pretraining differences in performance of the tactile discrimination task between the untrained palm and sole contributed to differences in posttraining transfer performance between the two body parts.

fMRI experiment followed by behavioral training

A total of 16 naive subjects volunteered to participate in the fMRI experiment in which brain activation was measured during tactile stimulation of the untrained right palm and sole, followed by behavioral training in the tactile discrimination task. Two types of tactile movement patterns

were presented with the tactile stimulation device during fMRI (Fig. 6b). The first type consisted of all stimuli moving in “v”-shaped trajectories. The second type consisted of all stimuli moving in inverted “v”-shaped trajectories. We selected these two types of tactile movement patterns for several reasons: first, to have two types of tactile stimuli that were identical except for the movement trajectory; second, to avoid biasing subjects for the tactile learning experiment, which they completed after the fMRI experiment (see below); and third, to increase the decodability of the fMRI activation patterns corresponding to the two types of tactile stimuli without any training. Stimuli were presented in desynchronized order across quadrants exactly as in the behavioral learning experiment. Within each quadrant the tactile stimulus was presented a total of four times within a 12-s-long tactile stimulation trial. Each trial with tactile stimulation was followed by a 12-s-long baseline without any stimulation. Trials with “v”-shaped and inverted “v”-shaped trajectories were presented in random order. A total of 12 trials for each tactile movement pattern were presented within each fMRI run. The first two trials for each type of tactile movement pattern were used for region of interest (ROI) definitions and these data were excluded from other analyses (see below, ROI definitions). Each subject completed two fMRI runs with tactile stimulation of the right palm and sole, respectively. fMRI runs for each of the two body parts were blocked and the order of blocked fMRI runs was counterbalanced across subjects.

In each fMRI run subjects performed a tactile oddball detection task. This task was included as a control to maintain subjects’ attention on the tactile movement patterns. Oddball trials were 12-s-long and identical to nonoddball trials except for the following aspect: during oddball trials only two randomly selected diagonal jets moved for half of the “v”-shaped (i.e., the downward stroke) or for half of the inverted “v”-shaped (i.e., the upward stroke) trajectories, while the second half of the trajectories was completed by the other two jets. Stimuli were presented a total of four times exactly as during nonoddball trials. Subjects were asked to respond only if they detected an oddball and to indicate by pressing one of two buttons on the MRI-safe button box with the left hand whether it was a “v”-shaped or an inverted “v”-shaped oddball. Subjects were asked to respond during stimulus presentation. No feedback was provided. Oddball trials were randomly intermixed among nonoddball trials. A total of five oddball trials were included in each fMRI run, resulting in a total fMRI run length of ~12 min.

Subjects’ performance on the tactile oddball detection task was calculated as observer sensitivity (d'). A response was considered a hit if the following

two conditions were met: the trial was an oddball trial and the subject correctly identified the tactile stimulation as a “v”-shaped pattern or an inverted “v”-shaped pattern. If the subject identified the incorrect type of pattern on an oddball trial or if the subject did not respond on an oddball trial, the response was considered a miss. If the subject responded during a nonoddball trial, the response was considered a false alarm. If the trial was a nonoddball trial and the subject did not respond, this was considered a correct rejection. Hit and false alarm rates were calculated and combined to determine the d' value (for a detailed description, see Frank et al., 2020).

Imaging data were collected using a 3 Tesla Siemens MAGNETOM Prisma MRI scanner (Siemens Healthcare) equipped with a 64-channel

head/neck coil. For the acquisition of the fMRI data a T2*-weighted echoplanar imaging sequence was used with the following parameters: time-to-repeat (TR) = 1 s, time-to-echo (TE) = 33 ms, multiband factor 4, flip angle (FA) = 59°, in-plane acquisition matrix (AM) = 96 × 96, 48 axial slices, voxel size = 2.5 × 2.5 × 2.5 mm, no interslice gap. A high-resolution T1-weighted anatomic scan of each subject's brain was collected using a magnetization prepared rapid gradient echo sequence: TR = 2.3 s, TE = 2.32 ms, FA = 8°, AM = 256 × 256, 192 sagittal slices, voxel size = 0.9 × 0.9 × 0.9 mm, interslice gap = 0.45 mm.

After completing the fMRI experiment subjects trained on the tactile discrimination task (Fig. 1c) exactly as in the behavioral learning experiment for ten daily sessions outside the scanner (Fig. 2d). Half of the subjects trained with the right palm, while the other half trained with the right sole. Subjects were randomly assigned to one training group. On a separate day after the last training session, trained subjects completed a posttraining transfer test of tactile learning to the untrained right sole or palm (depending on training group) exactly as in the behavioral learning experiment.

fMRI data analysis

Preprocessing

Anatomical and functional MRI data were preprocessed using Freesurfer and the FSLFAST toolbox (Martinos Center for Biomedical Imaging). Each subject's high-resolution anatomic scan was reconstructed and inflated (Dale et al., 1999; Fischl et al., 1999). fMRI data were motion-corrected, coregistered to the reconstructed anatomic brain, smoothed with a small three-dimensional Gaussian kernel (full-width at half-maximum = 3 mm) and intensity-normalized.

Univariate analysis

Preprocessed fMRI data were analyzed using a general linear model (GLM) approach. The BOLD response was modeled using the SPM canonical hemodynamic response function. Each 12-s-long nonoddball trial with tactile stimulation was modeled using a separate regressor. Oddball trials were modeled with a regressor-of-no-interest and data from these trials were not analyzed any further. Additional regressors-of-no-interest for motion correction parameters and a linear scanner drift were included in the GLM. The first five images of each run were excluded to secure MRI signal equilibrium.

The β weights of the first two trials for each type of tactile movement pattern in each fMRI run were excluded from any further multivariate analyses and used for ROI definitions only (see below, ROI definitions). The β weights of each of the remaining trials (10 trials for each type of tactile movement pattern in each fMRI run) and each tactile stimulation condition (right palm, right sole) were submitted to multivariate analyses (see below, Multivariate analysis). Furthermore, these β weights were used to calculate BOLD percent signal changes during tactile stimulation relative to baseline without any stimulation.

Multivariate analysis

Multivariate fMRI pattern classification analysis was conducted using the MATLAB-based CoSMoMVPA toolbox (Oosterhof et al., 2016). A two-way classification analysis was conducted between β weights corresponding to each type of tactile movement pattern (i.e., "v"-shaped and inverted "v"-shaped trajectories) using a linear support vector machine. For each subject there were a total of 20 trials for each type of tactile movement pattern and stimulated body part. The classification analysis between β weights corresponding to the two types of tactile movement patterns was conducted for each stimulated body part (right palm, right sole) and ROI (right palm representation in left SI, right sole representation in left SI; see below, ROI definitions). A leave-one-trial-out cross-validation was used. Chance level of classification accuracy was 50%.

A repeated measures ANOVA with the factors of stimulated body part (right palm, right sole) and ROI (right palm representation in left SI, right sole representation in left SI) on classification accuracy was conducted, followed by permutation testing to determine the statistical significance. Before entering the results into the ANOVA and only for the statistical analysis, classification accuracies were arcsin square-root transformed (see below, Statistical analysis). The statistical significance

of main effects and the interaction effect was calculated using permutation testing (Stelzer et al., 2013). To this end, classification analyses were conducted on shuffled condition labels. This permutation and classification procedure was reiterated 1000 times for each ROI in each subject. Classification accuracy at each iteration was arcsin square-root transformed. A chance distribution on the group-level for each ROI and stimulated body part was calculated by randomly selecting a classification result of each subject's permutation distribution. Then, the F values for main effects and the interaction effect were calculated. This random selection was reiterated 10,000 times with replacement. The resulting group-based permutation distributions of F values for main effects and the interaction effect were compared with F values from the ANOVA using classification results with correct condition labels. If F values resulting from classification with correct condition labels surpassed F values expected by chance (i.e., as determined by the 5% probability in the group-level permutation distribution), the result was considered significant. To assess the statistical significance of classification accuracy from chance level for each stimulated body part and ROI, the same permutation procedure as described above was used, except that transformed classification accuracies were averaged across subjects on each iteration of the group-level permutation procedure. If the mean classification accuracy using correct condition labels across subjects surpassed mean accuracy levels across subjects expected by chance (i.e., as determined by the 5% probability in the group-level permutation distribution), the result was considered significant.

ROI definitions

Univariate activations in the first two trials of tactile stimulation of the right palm and sole with each type of tactile movement pattern were used to define the somatotopic representations of these body parts in SI. Greater activation during tactile stimulation of the right palm compared with no-stimulation baseline was used to define the representation of the right palm in left SI. Greater activation during tactile stimulation of the right sole compared with no-stimulation baseline was used to define the representation of the right sole in left SI. ROIs were defined on the inflated cortical surface of each subject's brain using a threshold of $p < 0.001$ false discovery rate-corrected. ROIs for the respective body parts did not overlap in any subject. Figure 6d shows the location and size of each subject's ROIs remapped and overlaid onto the Freesurfer template brain. Across subjects the representation of the right palm was located in the superior portions of the postcentral gyrus and sulcus on the lateral side of the left hemisphere (Brodmann areas 1, 2, 3; Van Essen, 2005; Glasser et al., 2016). The representation of the right sole was located on the superior medial side of the left hemisphere and included the paracentral gyrus as well as partially the postcentral gyrus and sulcus (Brodmann areas 1, 2, 3, 4, 5; Van Essen, 2005; Glasser et al., 2016).

The mean \pm SEM MNI coordinates and number of voxels in functional space of the ROIs across subjects were: representation of the right palm in left SI: $X = -40 \pm 1$, $Y = -28 \pm 1$, $Z = 57 \pm 1$; 159 ± 22 voxels; representation of the right sole in left SI: $X = -13 \pm 1$, $Y = -41 \pm 1$, $Z = 68 \pm 1$; 94 ± 10 voxels (for similar coordinates in previous studies, see Akselrod et al., 2017; Roux et al., 2018). To exclude the possibility that differences in the number of voxels between ROIs influenced the classification results, we conducted a control classification analysis (see Results) for which ROIs were centered around the peak voxel with constant radius and thus exhibited similar sizes. The mean \pm SEM number of voxels in functional space for each ROI across subjects in this control analysis corresponded to the following: representation of the right palm in left SI: 110 ± 12 voxels; representation of the right sole in left SI: 107 ± 12 voxels.

Statistical analysis

The sample size of the experiments in this study was determined based on previous studies (Sathian and Zangaladze, 1998; Harris et al., 2001; Pleger et al., 2003; Kaas et al., 2013; Harrar et al., 2014; Muret et al., 2014; Dempsey-Jones et al., 2016; Muret and Dinse, 2018). The results of the pilot experiment with tactile training of the right palm were used to determine the learning criterion for the behavioral learning experiment. This learning criterion was used to ensure that all subjects learned the

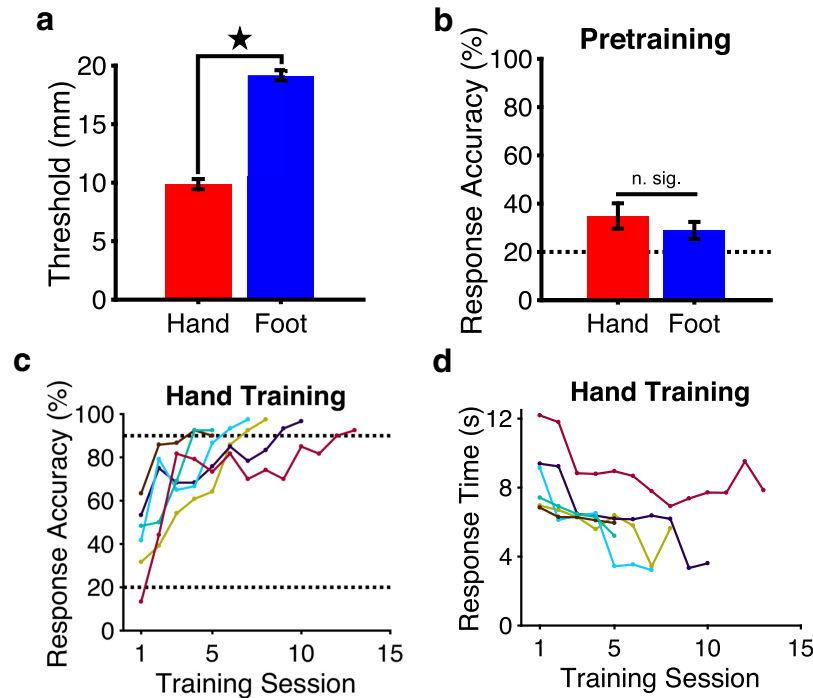


Figure 3. Results of pilot experiments. **a**, Mean \pm SEM 2-PD thresholds in millimeters of the palm of the right hand and the sole of the right foot across a sample of six subjects. The asterisk indicates a significant difference in thresholds between the palm and the sole; $*p < 0.05$. **b**, Mean \pm SEM response accuracy in the tactile discrimination task with the right palm and sole before training across 16 subjects. The dotted line shows performance chance level (corresponding to 20% correct). n. sig. = not significantly different. **c**, Response accuracy over the course of training in a group of six subjects who trained on the tactile discrimination task with the right palm until they achieved a learning criterion corresponding to a response accuracy of 90% correct or greater in two training sessions. The dotted lines show performance chance level (20% correct) and the learning criterion (90% correct), respectively. Each color shows the result of a different subject in this pilot experiment. **d**, Same as **c** but for response time in seconds.

task equally well before the posttraining transfer test to the untrained body part in each training group was conducted. Behavioral and univariate fMRI data were analyzed using parametric statistics (ANOVA and *post hoc t* tests). The assumption of normality was violated for response accuracy in the tactile discrimination task as shown by significant results using the Shapiro–Wilk test. Therefore, for the purpose of the statistical analysis, each subject's response accuracy (p) in each session of the tactile discrimination task (including training session, pretraining test session and posttraining transfer test session) was arcsin square-root transformed using the following formula: $p' = \arcsin(\sqrt{p})$. The transformed response accuracy results were submitted to statistical tests. Only for the purpose of the statistical analysis, the same transformation was applied to the fMRI classification results with correct and shuffled condition labels (see above). Response time results for each subject were calculated as median response time across trials for each session. The 2-PD thresholds for the right palm and sole were not normally distributed as shown by a significant result in the Shapiro–Wilk test and were analyzed using a nonparametric Wilcoxon signed-rank test. Furthermore, the results of the behavioral control experiment for which subjects completed a pretraining test and a posttraining transfer test with the untrained body part were analyzed using nonparametric Mann–Whitney U tests because of the smaller sample size in this experiment. Correlational analyses between fMRI results and tactile behavior were conducted using Pearson correlation. Since the fMRI classification results did not depend on the size of the ROIs (see Results, fMRI experiment followed by behavioral training), the original size of each ROI was used for the correlational analyses. For all statistical tests, the two-tailed α -level was set to 0.05. Partial η^2 , Cohen's d and r are reported as measures of effect size for ANOVA, t test and Pearson correlation, respectively. For the Wilcoxon signed-rank test and the Mann–Whitney U test, r is reported as a measure of effect size.

Results

Pilot experiments

2-PD thresholds

The results of a first pilot experiment showed that the mean \pm SEM 2-PD thresholds across subjects were 9.87 ± 0.43 mm for the right palm and 19.1 ± 0.42 mm for the right sole (Fig. 3a). The thresholds were significantly lower for the palm than the sole (Wilcoxon signed-rank test; $z = -2.20$, $p = 0.03$, $r = -0.64$), replicating previously reported results (Weinstein, 1968; Mancini et al., 2014). The mean \pm SEM proportion of two-point responses in catch trials across quadrants and subjects was $3.33 \pm 2.47\%$ for the right palm. No two-point responses were reported in catch-trials of any quadrant for the right sole in any subject.

Pretraining performance

The results of a second pilot experiment for which subjects performed the tactile discrimination task in separate sessions with the untrained right palm and sole showed that pretraining performance was not significantly different between the palm and sole (paired-sample t test; $t_{(15)} = 1.32$, $p = 0.21$; Fig. 3b). This indicates that subjects' baseline performance in the tactile discrimination task was similar between the two body parts.

Tactile learning

In a third pilot experiment subjects trained on the tactile discrimination task with the right palm until they achieved a response accuracy in the trained task of 90% correct or greater in two training sessions. The results of this pilot experiment showed that each subject achieved the learning criterion. However, there were differences in the number of training sessions required between subjects (ranging from 5 to 13 sessions in different subjects; Fig. 3c), similar to results in visual training using similar stimulus patterns (Frank et al., 2016, 2018). Therefore, we decided to use this learning criterion for the behavioral learning experiment (see below) to ensure that all subjects learned the task equally well before they performed a posttraining transfer test of tactile learning to the untrained body part. This pilot experiment also revealed that subjects tended to show improvements in their response time in the tactile discrimination task over the course of training (Fig. 3d), indicating that improvements in response accuracy were not driven by a speed-accuracy trade-off (see also Fig. 4 for similar results in the behavioral learning and control experiments and Fig. 7 for similar results in the behavioral learning experiment after fMRI).

Behavioral learning experiment

Figure 4a–d shows individual results in each training session for subjects who trained on the tactile discrimination task either with the right palm or with the right sole until they achieved a learning criterion corresponding to a response accuracy of 90% correct or greater in two training sessions (for mean response accuracy across subjects in the final training session, see Fig. 5a). No significant difference in response accuracy in the first and last training sessions was found between subjects trained with

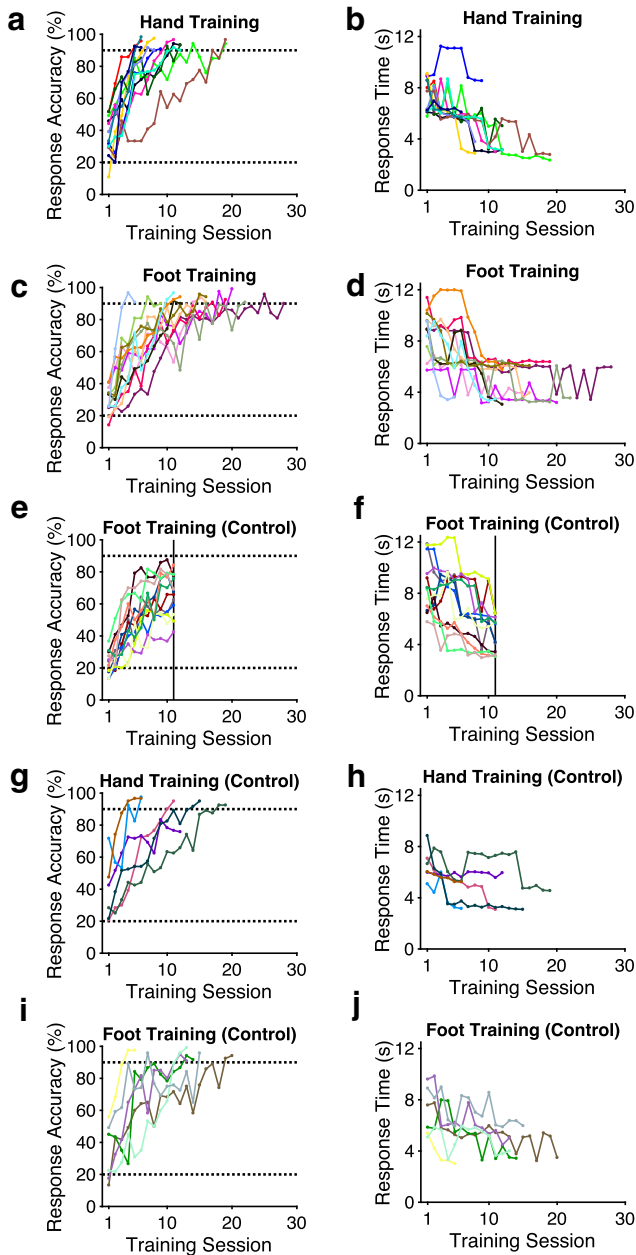


Figure 4. Tactile learning results with the trained body part. *a*, Response accuracy over the course of training in the behavioral learning experiment for 12 subjects who trained with the palm of the right hand. Otherwise, same as Figure 3*c*. *b*, Same as *a* but for response time in seconds. *c*, *d*, Same as *a*, *b*, but for a group of 12 subjects who trained with the sole of the right foot. *e*, *f*, Same as *c*, *d*, but for a group of 12 subjects in the first behavioral control experiment who trained for a total of 11 training sessions with the right sole. *g*, *h*, Same as *a*, *b* but for a group of six subjects in the second behavioral control experiment who trained with the right palm and performed a pretraining test and a posttraining transfer test with the untrained right sole. In one subject, training had to be terminated before the subject achieved the learning criterion of 90% correct response accuracy in two training sessions because of time constraints. *i*, *j*, Same as *g*, *h*, but for a group of six subjects who trained with the right sole and performed a pretraining test and a posttraining transfer test with the untrained right palm.

the palm and the sole (independent-sample *t* test; first training session: $t_{(22)} = 1.51$, $p = 0.15$; last training session: $t_{(22)} = 0.96$, $p = 0.35$). This result indicates that performance in the tactile discrimination task was similar between the two trained body parts at the beginning and end of training. Figure 5*d* shows response accuracy in the tactile discrimination task in the same subjects

during the posttraining transfer test with tactile stimulation of the untrained body part (i.e., the untrained right sole in the right palm training group and the untrained right palm in the right sole training group). An independent-sample *t* test on response accuracy in the transfer test showed that posttraining transfer of tactile learning to the untrained right palm after right sole training was significantly greater than to the untrained right sole after right palm training ($t_{(22)} = 7.56$, $p < 0.001$, $d = 3.08$).

Behavioral control experiments

A similar transfer result as in the behavioral learning experiment was obtained in the first behavioral control experiment in which subjects trained on the tactile discrimination task with the right sole for a total of 11 training sessions (see Fig. 4*e,f* for individual results in each training session and Fig. 5*b* for mean response accuracy across subjects in the final training session) and performed a posttraining transfer test in the trained task with the untrained right palm. Response accuracy of subjects in this control experiment was compared with that of subjects in the behavioral learning experiment who trained with the right palm until they achieved the learning criterion (i.e., a response accuracy of 90% correct or greater in two training sessions; Fig. 4*a,b*). Response accuracy in the first and last training sessions was significantly greater in subjects trained with the right palm than the right sole (independent-sample *t* test; first training session: $t_{(22)} = 3.14$, $p = 0.005$, $d = 1.28$; last training session: $t_{(22)} = 8.80$, $p < 0.001$, $d = 3.59$). Performance in the last training session was expected to be greater in subjects trained with the right palm because they trained up to the learning criterion whereas subjects in the right sole training group trained until they completed 11 training sessions regardless of performance in the final training session. Although performance in the first training session was lower in subjects trained with the right sole in this control experiment, we deem it unlikely that this reflects a systematic difference between pretraining performance of the right palm and sole, because pretraining performance with the right palm and sole was not significantly different in any of the other experiments of this study. Furthermore, importantly, posttraining transfer of tactile learning to the untrained right palm after training with the right sole in this control experiment was significantly greater than to the untrained right sole after training with the right palm (independent-sample *t* test on response accuracy in the transfer test; $t_{(22)} = 4.02$, $p < 0.001$, $d = 1.64$; Fig. 5*e*), corroborating results of the behavioral learning experiment (see above).

In a second behavioral control experiment, subjects trained on the tactile discrimination task either with the right palm or with the right sole until they achieved the same learning criterion as in the behavioral learning experiment (see Fig. 4*g-j* for individual results in each training session and Fig. 5*c* for mean response accuracy across subjects in the final training session). Before the first training session with the trained body part subjects performed a pretraining test in the tactile discrimination task with the untrained body part (i.e., the untrained right sole in the right palm training group and the untrained right palm in the right sole training group). No significant difference in pretraining response accuracy in the tactile discrimination task was found between the training groups (Mann–Whitney *U* test; $U = 17.0$, $p = 0.94$), indicating that task performance before training was similar between the untrained body parts. Furthermore, there was no significant difference in response accuracy in the first and last training sessions with the trained body part between the training groups (first training session:

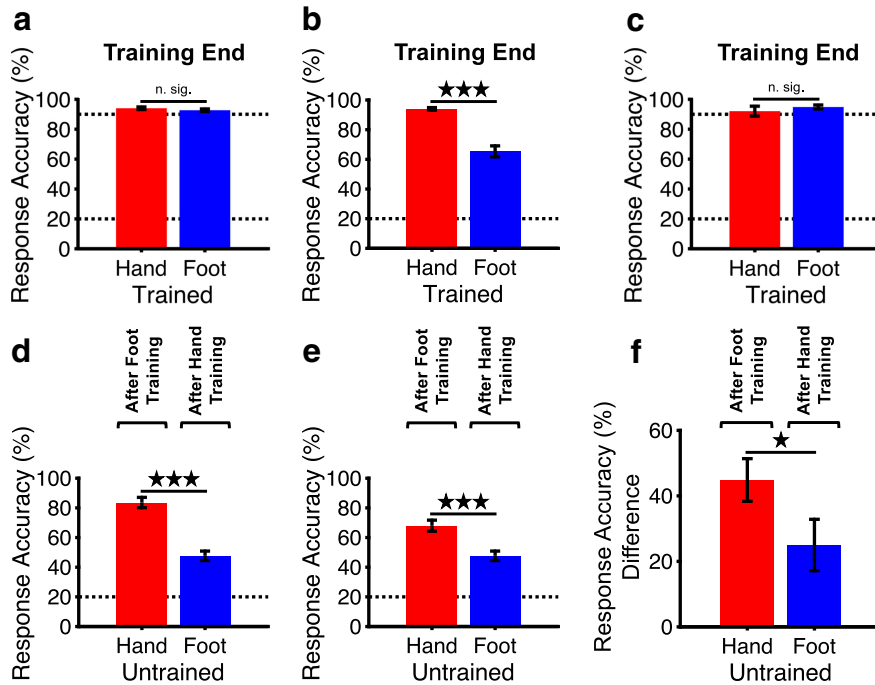


Figure 5. Performance at the end of training and posttraining transfer of tactile learning. *a*, Mean \pm SEM response accuracy in the final training session of the behavioral learning experiment with tactile stimulation of the palm of the right hand and the sole of the right foot for training, respectively, across subjects (12 subjects in each training group). The dotted lines show performance chance level (20% correct) and the learning criterion (90% correct), respectively. n. sig. = not significantly different. *b*, Same as *a* but for a group of 12 subjects in the first behavioral control experiment who trained for 11 training sessions with the right sole, regardless of performance in the final training session. Data for the trained right palm from *a*. The asterisks indicate a significant difference in response accuracy between the trained right palm and the trained right sole; $***p < 0.001$. *c*, Same as *a* but for groups of six subjects each in the second behavioral control experiment who trained either with the right palm or with the right sole. n. sig. = not significantly different. *d*, Same as *a* but for response accuracy in the posttraining transfer test of the behavioral learning experiment with tactile stimulation of the untrained right palm and sole after training with the right sole and palm, respectively. The asterisks indicate a significant difference in response accuracy between the untrained right palm and sole; $***p < 0.001$. *e*, Same as *d* but for transfer results in the first behavioral control experiment; $***p < 0.001$. *f*, Same as *d* but for transfer results in the second behavioral control experiment. The y-axis shows the difference in response accuracy with the untrained body part between the posttraining transfer test and the pretraining test (corresponding to performance in the posttraining transfer test minus performance in the pretraining test); $*p < 0.05$.

$U = 16.0$, $p = 0.82$; last training session: $U = 16.5$, $p = 0.82$), indicating that task performance was similar between the trained body parts at the beginning and end of training. After the last training session with the trained body part, subjects performed a posttraining transfer test in the trained task with tactile stimulation of the untrained body part. Response accuracy in the pretraining test was subtracted from response accuracy in the posttraining transfer test to correct for individual differences in pretraining performance with the untrained body part between subjects. The corrected posttraining transfer of tactile learning was significantly greater to the untrained right palm after training with the right sole than to the untrained right sole after training with the right palm ($U = 5.00$, $p = 0.04$, $r = -0.60$; Fig. 5f).

Taken together, the results of the behavioral learning and control experiments show that the trained body part strongly influenced the magnitude of transfer of tactile learning to the untrained body part. After training with the right sole, transfer of tactile learning to the untrained right palm was significantly greater than vice versa.

fMRI experiment followed by behavioral training

In the fMRI experiment, the right palm and sole of 16 subjects were stimulated with two types of tactile movement patterns

while activation was measured within the representations of the stimulated body parts in contralateral SI using fMRI (Fig. 6a,b,d). During tactile stimulation, a tactile oddball was occasionally presented and subjects were asked to detect the oddball (for details, see Materials and Methods). Detection performance (quantified as d') was significantly greater for tactile stimulation of the right palm than for tactile stimulation of the right sole (paired-sample t test; $t_{(15)} = 5.17$, $p < 0.001$, $d = 1.29$; Fig. 6c).

The transformed classification accuracies of fMRI activation patterns corresponding to the two types of tactile movement patterns (i.e., tactile movement pattern 1 vs tactile movement pattern 2) were submitted to a 2×2 repeated measures ANOVA with the within-subject factors of stimulated body part (right palm, right sole) and representation in contralateral SI (right palm, right sole). The statistical significance of main effects and the interaction effect was calculated using permutation testing (for details, see Materials and Methods). Most importantly, there was a significant interaction between stimulated body part and representation in contralateral SI ($p = 0.001$, partial $\eta^2 = 0.49$), indicating that classification accuracy was significantly greater in the cortical representation of the right palm during tactile stimulation of the right sole compared with the cortical representation of the right sole during tactile stimulation of the right palm (Fig. 6e). A similar result was obtained in a control analysis for which the size of the representations of the right palm and sole in contralateral SI (i.e., the number of voxels used in the analysis) was matched (henceforth referred to as control). Again, there was a significant interaction between stimulated body part and representation in contralateral SI ($p = 0.006$, partial $\eta^2 = 0.41$). The ANOVA also revealed a significant main effect of representation in contralateral SI ($p = 0.02$, partial $\eta^2 = 0.30$; control: $p = 0.04$, partial $\eta^2 = 0.28$), indicating that classification accuracy was greater in the cortical representation of the right palm than in that of the right sole across stimulated body parts (Fig. 6e). There was no significant main effect of stimulated body part ($p = 0.19$; control: $p = 0.64$). *Post hoc* analyses showed that classification accuracy was significantly above chance level for each stimulated body part and representation in contralateral SI (cortical representation of right palm during tactile stimulation of right palm: $p < 0.001$; control: $p < 0.001$; cortical representation of right palm during tactile stimulation of right sole: $p < 0.001$; control: $p < 0.001$; cortical representation of right sole during tactile stimulation of right sole: $p < 0.001$; control: $p < 0.001$; cortical representation of right sole during tactile stimulation of right palm: $p = 0.02$; control: $p = 0.01$).

The differential activations in contralateral SI during tactile stimulation of the nonrepresented body part were not evident in

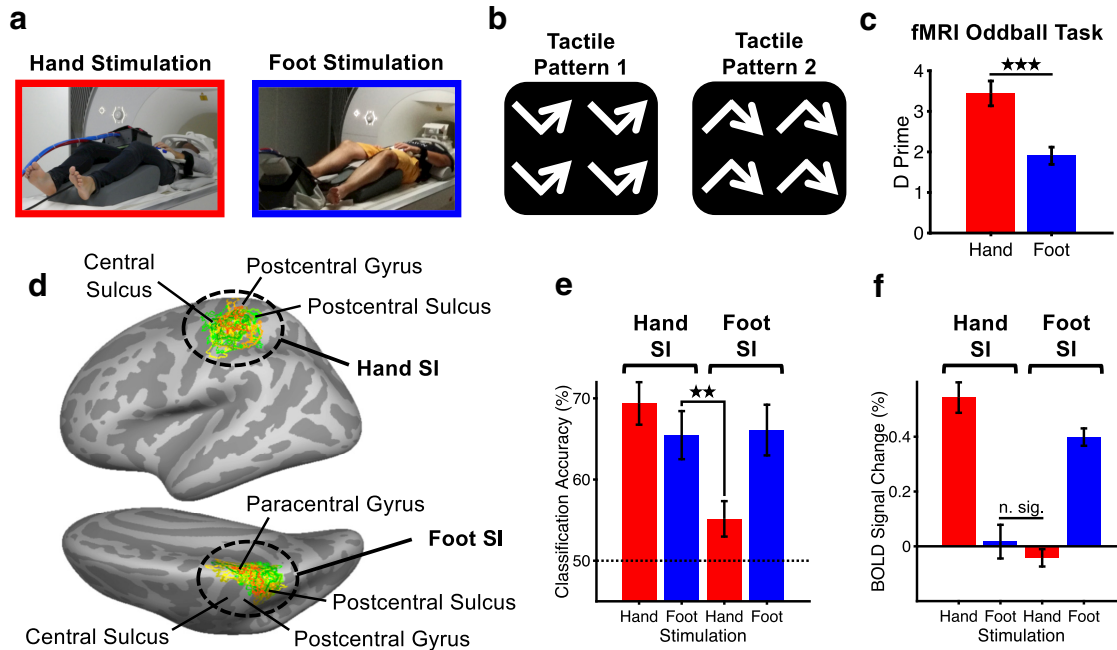


Figure 6. Setup and results of the fMRI experiment. **a**, Setup for tactile stimulation of the palm of the right hand and the sole of the right foot in two representative subjects. **b**, Tactile stimulus conditions. Tactile pattern 1 corresponded to all stimuli moving in “v”-shaped trajectories. Tactile pattern 2 corresponded to all stimuli moving in inverted “v”-shaped trajectories. Note that the white arrows signify the direction of the movement trajectories for the sake of illustration only. **c**, Mean \pm SEM performance (quantified as observer sensitivity, d') in the tactile oddball detection task for tactile stimulation of the right palm and sole during fMRI across 16 subjects. The asterisks indicate a significant difference in d' between the right palm and sole; *** $p < 0.001$. **d**, Representations of the right palm and sole in left SI shown by outline for each subject, remapped and overlaid on the Freesurfer average brain (dark gray = sulci, light gray = gyri). Each color shows the location based on the results for this subject. Top panel, Lateral view of the left hemisphere. Bottom panel, View from above the left hemisphere. **e**, Mean \pm SEM multivariate fMRI pattern classification accuracy between the two types of tactile movement patterns (see **b**) presented to the right palm and sole in the representations of these body parts in contralateral SI across subjects. The dotted line shows chance level of classification accuracy (corresponding to 50% correct). The asterisks indicate a significant interaction between stimulated body part and representation in contralateral SI; ** $p < 0.01$. **f**, Same as **e** but for univariate BOLD activation during tactile stimulation (corresponding to BOLD activation averaged across the two types of tactile movement patterns). Zero on the y-axis corresponds to the BOLD signal during baseline without any stimulation. n. sig. = not significantly different.

the univariate BOLD signal (Fig. 6f). A 2×2 repeated measures ANOVA with the within-subject factors of stimulated body part (right palm, right sole) and representation in contralateral SI (right palm, right sole) on univariate BOLD activation during tactile stimulation showed a significant interaction between stimulated body part and representation in contralateral SI ($F_{(1,15)} = 293.1$, $p < 0.001$, partial $\eta^2 = 0.95$). However, contrary to the results of the multivariate analysis, this interaction reflected that activation in SI occurred only during tactile stimulation of the represented body part, whereas activation during tactile stimulation of the nonrepresented body part was weak (Fig. 6f). This result was confirmed in *post hoc* one-sample t tests of univariate BOLD activation against zero corresponding to the BOLD signal during baseline without any stimulation. There was significant activation in the cortical representation of the right palm during tactile stimulation of the right palm ($t_{(15)} = 9.77$, $p < 0.001$, $d = 2.44$) and in the cortical representation of the right sole during tactile stimulation of the right sole ($t_{(15)} = 12.6$, $p < 0.001$, $d = 3.14$). In contrast, there were no significant activations in the cortical representation of the right palm during tactile stimulation of the right sole ($t_{(15)} = 0.28$, $p = 0.79$) and in the cortical representation of the right sole during tactile stimulation of the right palm ($t_{(15)} = -1.32$, $p = 0.21$). BOLD activations in the cortical representations of the right palm and sole during tactile stimulation of the nonrepresented body part did not differ significantly ($t_{(15)} = 0.97$, $p = 0.35$).

The ANOVA on univariate BOLD activation also revealed a nonsignificant trend for a main effect of representation in

contralateral SI ($F_{(1,15)} = 4.30$, $p = 0.06$, partial $\eta^2 = 0.22$), indicating that greater BOLD activation tended to occur in the cortical representation of the right palm than in that of the right sole across stimulated body parts (Fig. 6f). There was no significant main effect of stimulated body part ($F_{(1,15)} = 1.99$, $p = 0.18$).

Together, these results show that the activation pattern within the representation of the right palm in contralateral SI, before any training, contained significantly more information about tactile cues presented to the right sole than vice versa, indicating that the cortical representation of the right palm was more coactivated than that of the right sole. This result was only evident in the multivariate analysis (Fig. 6e), whereas no indication for coactivation was found in the univariate analysis (Fig. 6f).

If coactivation in the cortical representation of the right palm supports the processing of tactile cues presented to the right sole, then it should be more pronounced in subjects who have low tactile performance with tactile stimulation of the right sole, to augment the processing of tactile cues presented to the sole. Therefore, we predicted that subjects with lower performance in the tactile oddball detection task with tactile stimulation of the right sole would exhibit more pronounced coactivation in the cortical representation of the right palm while performing this task. To test this, a correlation analysis was conducted between the magnitude of coactivation (corresponding to fMRI classification accuracy in the representation of the right palm in contralateral SI during tactile stimulation of the right sole minus fMRI classification accuracy in the representation of the right sole in contralateral SI during tactile stimulation of the right palm; Fig. 6e) and task performance (corresponding to d' ; Fig. 6c) across

subjects. The results showed that subjects who tended to exhibit more pronounced coactivation in the cortical representation of the right palm during tactile stimulation of the right sole also tended to have lower performance in the tactile oddball detection task for the right sole (Pearson correlation; $r = -0.67$, $p = 0.005$; Fig. 8*a*). No such significant correlation was found between coactivation in the cortical representation of the right sole during tactile stimulation of the right palm and performance in the tactile oddball detection task with tactile stimulation of the right palm ($r = 0.27$, $p = 0.31$; Fig. 8*b*). These results agree with the hypothesis that coactivation in the cortical representation of the unstimulated right palm supports the processing of tactile cues presented to the right sole. Next, we investigated whether coactivation in the cortical representation of the right palm also supports learning of the tactile discrimination task with tactile stimulation of the right sole and modulates the magnitude of transfer of tactile learning from the trained right sole to the untrained right palm.

Subjects from the fMRI experiment trained on the tactile discrimination task either with the right palm or sole for a total of ten daily sessions outside the scanner and performed a post-training transfer test to the untrained right sole or palm (depending on training group) on a separate day after the last training session. Half of the subjects trained with the right palm, while the other half trained with the right sole (see Fig. 7*a–d* for individual results in each training session and Fig. 7*e* for mean response accuracy across subjects in the final training session). Independent-sample t tests did not show any significant differences in response accuracy in the tactile discrimination task in the first and last training sessions between the training groups (first training session: $t_{(14)} = -1.58$, $p = 0.14$; last training session: $t_{(14)} = -0.78$, $p = 0.45$). This indicates that subjects' performance in the tactile discrimination task at the beginning and end of training was similar between the trained right palm and sole. A correlation analysis between coactivation in the cortical representation of the right palm during tactile stimulation of the right sole (calculated as in the correlation analysis above) and performance in the early phase of training in the tactile discrimination task with tactile stimulation of the right sole (corresponding to the mean response accuracy across the first two training sessions for each subject) across subjects in the right sole training group was conducted. There was a significant correlation (Pearson correlation; $r = -0.74$, $p = 0.04$; Fig. 8*c*), such that subjects who tended to exhibit more pronounced coactivation in the cortical representation of the right palm also tended to have lower performance in the early phase of training with tactile stimulation of the right sole. There was no significant correlation between coactivation in the cortical representation of the right sole and performance in the early phase of training with tactile stimulation of the right palm across subjects in the right palm training group ($r = -0.22$, $p = 0.60$; Fig. 8*d*). These results agree with the hypothesis that coactivation in the cortical representation of the unstimulated right palm supports processing and learning of tactile cues presented to the right sole but not vice versa.

After the end of training, trained subjects performed a post-training transfer test in the tactile discrimination task with tactile stimulation of the untrained body part (either the untrained right sole or palm, depending on training group). The results of this transfer test (Fig. 7*f*) showed that response accuracy was significantly greater for the untrained right palm after training with the right sole than for the untrained right sole after training with the right palm (independent-sample t test; $t_{(14)} = 5.16$, $p < 0.001$, $d = 2.58$), comparable to the results of the behavioral experiments (see Fig. 5*d–f*).

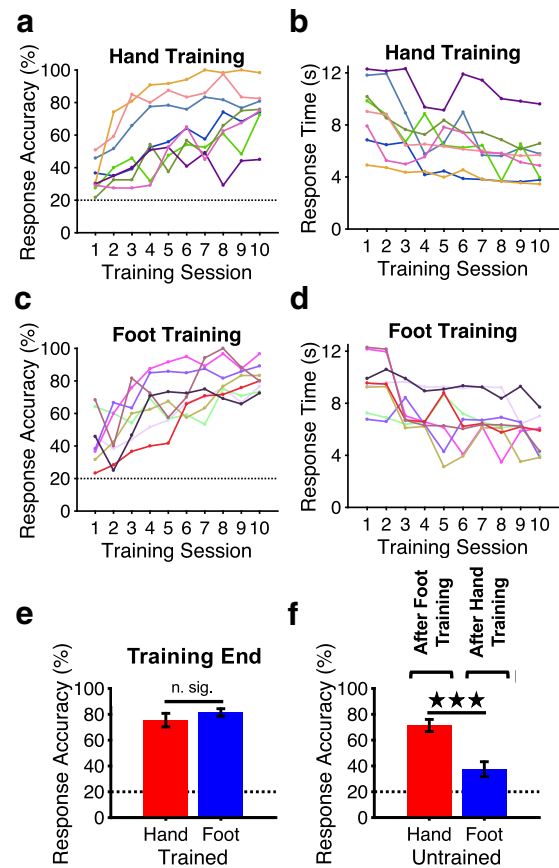


Figure 7. Results in the behavioral experiment after fMRI. *a*, Response accuracy over the course of ten training sessions in eight subjects who trained on the tactile discrimination task (Fig. 1*c*) with the palm of the right hand outside the scanner after completing the fMRI experiment. Otherwise, same as Figure 4*a*. *b*, Same as *a* but for response time in seconds. *c*, *d*, Same as *a*, *b* but for a group of eight subjects who trained with the sole of the right foot. *e*, Mean \pm SEM response accuracy in the final training session with tactile stimulation of the right palm and sole for training, respectively, across subjects (eight subjects in each training group). The dotted line shows performance chance level (corresponding to 20% correct). n. sig. = not significantly different. *f*, Same as *e* but for response accuracy in the posttraining transfer test with tactile stimulation of the untrained right palm and sole after training with the right sole and palm, respectively. The asterisks indicate a significant difference in response accuracy between the untrained right palm and sole. The dotted line shows performance chance level (corresponding to 20% correct); *** $p < 0.001$.

Next, we correlated subjects' coactivation in the cortical representation of the unstimulated body part (calculated as in the correlation analyses above) with the transfer of tactile learning to the untrained body part. The results showed that subjects who tended to exhibit more pronounced coactivation in the cortical representation of the right palm during tactile stimulation of the right sole also tended to have greater transfer of tactile learning to the untrained right palm after training with the right sole (that is, less difference between transfer performance with the untrained right palm and performance with the trained right sole in the final training session; Pearson correlation; $r = 0.77$, $p = 0.02$; Fig. 8*e*). In contrast, there was no significant correlation between coactivation in the cortical representation of the right sole during tactile stimulation of the right palm and transfer of tactile learning to the untrained right sole after training with the right palm ($r = 0.01$, $p = 0.98$; Fig. 8*f*). Together with the results of the previous correlational analyses, this indicates that coactivation in the cortical representation of the right palm in contralateral SI during tactile stimulation of the

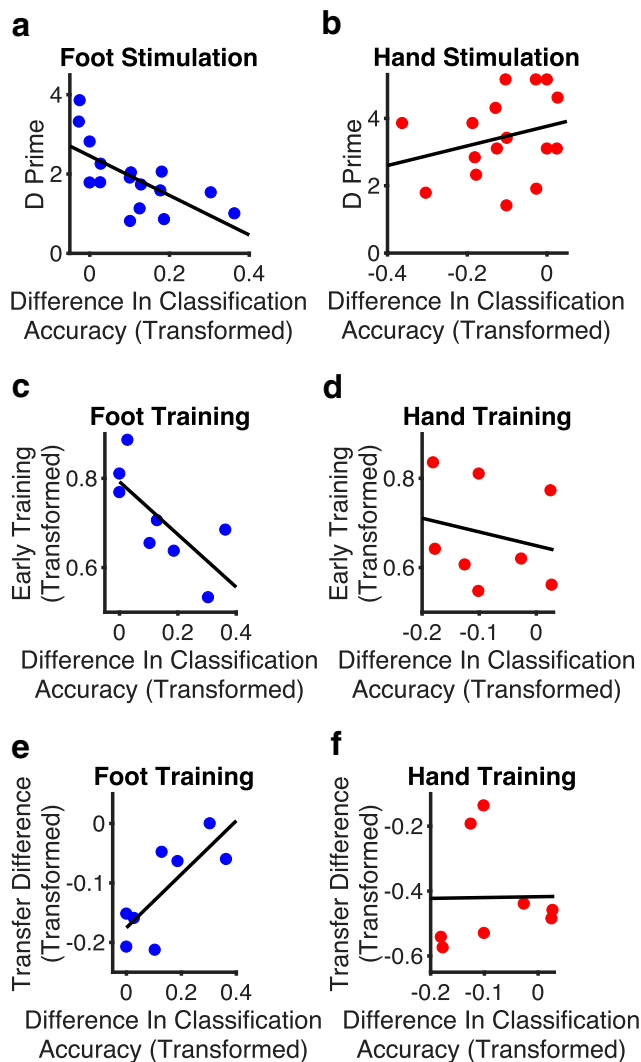


Figure 8. Correlation between fMRI results and behavioral results. **a**, Correlation between coactivation in the cortical representation of the palm of the right hand during tactile stimulation of the sole of the right foot in the fMRI experiment and performance in the tactile oddball detection task with the right sole. Each dot shows the result from a different subject. Results from all subjects ($n = 16$) in the fMRI experiment were used (regardless of their subsequent assignment to right palm and sole training groups). The x-axis shows fMRI classification accuracy in the representation of the right palm in contralateral SI during tactile stimulation of the right sole minus fMRI classification accuracy in the representation of the right sole in contralateral SI during tactile stimulation of the right palm (classification accuracies are arcsin square-root transformed). Zero on the x-axis indicates no difference in classification accuracies between the two conditions. Values greater than zero on the x-axis indicate that classification accuracy was greater for tactile stimulation of the right sole in the cortical representation of the right palm than of the same tactile stimulation of the right palm in the cortical representation of the right sole. The y-axis shows performance in the oddball detection task as observer sensitivity (d'). **b**, Same as **a** but for tactile performance with the right palm. The x-axis shows fMRI classification accuracy in the representation of the right sole in contralateral SI during tactile stimulation of the right palm minus classification accuracy in the representation of the right palm in contralateral SI during tactile stimulation of the right sole. Negative values on the x-axis indicate that classification accuracy was lower for tactile stimulation of the right palm in the cortical representation of the right sole than of the same tactile stimulation of the right sole in the cortical representation of the right palm. **c**, Correlation between coactivation in the cortical representation of the right palm during tactile stimulation of the right sole in the fMRI experiment and subsequent performance in the early phase of training in the tactile discrimination task with the right sole. Each dot shows the result from a different subject in the right sole training group ($n = 8$). The x-axis shows cortical coactivation of the right palm during tactile stimulation of the right sole in the same fashion as in **a**. The y-axis shows mean response accuracy across the first two training sessions with the right sole (response accuracies are arcsin square-root transformed). Greater

right sole supports processing and learning of tactile cues presented to the right sole and modulates the magnitude of transfer of tactile learning to the untrained right palm after training with the right sole. No such association was found between coactivation in the cortical representation of the right sole in contralateral SI during tactile stimulation of the right palm and tactile performance with the right palm or transfer of tactile learning to the untrained right sole after training with the right palm.

Discussion

Here, we examined neuronal mechanisms involved in the transfer of tactile learning from trained to untrained body parts. Subjects trained on a tactile discrimination task either with the palm of the right hand or with the sole of the right foot. After training ended, trained subjects performed the trained task with the untrained right sole or palm. The results showed that tactile learning transferred to a greater extent from the trained right sole to the untrained right palm than from the trained right palm to the untrained right sole. An fMRI experiment, conducted before training, showed that activation patterns in the cortical representation of the right palm in contralateral SI exhibited information about tactile cues presented to the right sole, indicating that the cortical palm area was coactivated during tactile stimulation of the sole. The more pronounced this coactivation was, the lower was tactile performance for tactile stimulation of the right sole and the greater was subsequent transfer of tactile learning to the untrained right palm after training with the right sole. These results indicate that an untrained body part (right palm) may be coactivated to support the processing of tactile cues presented to the trained body part (right sole). Furthermore, such coactivation may critically contribute to the transfer of tactile learning from the neural representation of the trained to the untrained body part in SI.

SI represents the human body as a somatotopic map in which adjacent portions of the skin are represented by the activity of adjacent neurons in the contralateral postcentral gyrus and sulcus (Penfield and Rasmussen, 1950; Hashimoto et al., 2013; Akselrod et al., 2017; Roux et al., 2018; Germann et al., 2020). More cortex is dedicated to processing those areas of the skin that have the highest spatial resolution to discriminate tactile

← values indicate better performance in the early phase of training. Note that for two subjects in the right sole training group performance only in the second training session was included for the purpose of this correlation analysis because of exceptionally high performance in the first training session in these two subjects (Fig. 7c). **d**, Same as **c** but for performance with tactile stimulation of the right palm in the right palm training group ($n = 8$). x-axis as in **b**. **e**, Correlation between coactivation in the cortical representation of the right palm during tactile stimulation of the right sole in the fMRI experiment and subsequent transfer of tactile learning to the untrained right palm after training with the right sole. Each dot shows the result from a different subject in the right sole training group ($n = 8$). The x-axis shows cortical coactivation of the right palm during tactile stimulation of the right sole in the same fashion as in **a**. The y-axis shows response accuracy with the untrained right palm in the posttraining transfer test minus response accuracy in the final training session with the trained right sole (response accuracies are arcsin square-root transformed). Zero on the y-axis indicates no difference in response accuracies between the posttraining transfer test and the final training session, corresponding to complete transfer of tactile learning. Values smaller than zero on the y-axis indicate lower performance in the posttraining transfer test than in the final training session. **f**, Same as **e** but for transfer of tactile learning to the untrained right sole in the right palm training group ($n = 8$). x-axis as in **b**. The y-axis shows response accuracy with the untrained right sole in the posttraining transfer test minus response accuracy in the final training session with the trained right palm.

cues (Penfield and Rasmussen, 1950). This is analogous to the cortical magnification of the foveal representation found in early visual cortex (Sereno et al., 1995; Dougherty et al., 2003). It has been reported that the fovea projection zone in early visual cortex may be coactivated by eccentric stimulation, potentially to support information processing taking part in the visual periphery by employing the higher spatial resolution of the foveal projection zone (Williams et al., 2008; Fan et al., 2016). Compared with the foot, the hand exhibits a greater number of mechanoreceptors (Taube Navaraj et al., 2017), a higher innervation density (Corniani and Saal, 2020), lower receptor activation thresholds (Johansson et al., 1980; Kennedy and Inglis, 2002) and also greater tactile spatial resolution, at least as measured by the 2-PD method (Weinstein, 1968; Mancini et al., 2014; Fig. 3a). Although there are obvious differences between the visual and somatosensory systems in terms of what can be considered center versus periphery and their interactions, we could speculate that the hand might play an analogous role to the fovea in that, in the case of touch, fine tactile discrimination will typically invoke manipulation of an object with the high-resolution hand, just as eye movements will typically bring the fovea to an object so that it can be processed with very high spatial resolution. The representation of the hand in SI might function as a buffer for tactile processing operations (for example, the discrimination of tactile movement patterns as in our study) that require such high spatial resolution. It is possible that other body locations with higher spatial resolution than the sole (e.g., the lips; Weinstein, 1968; Mancini et al., 2014) are also part of a tactile buffer in SI. In this case, the representations of these body locations in SI might have been coactivated during tactile stimulation of the sole as well. This possibility is supported by previous results showing that tactile learning transferred from the trained hand to the untrained face, which has a high spatial resolution, but not to the untrained forearm, which has a low spatial resolution (Muret et al., 2014; Muret and Dinse, 2018). Future studies are needed to investigate whether cortical coactivation and transfer of tactile learning are found from the trained sole to other untrained body locations with higher spatial resolution than the sole itself and which representations in SI might function as a putative buffer for tactile processing operations. In any case, our results, together with those of another recent report (Muret et al., 2022), indicate that tactile information might be more spread across distinct somatotopic representations in SI than previously assumed.

Our fMRI analysis focused on somatotopic representations of trained and untrained body parts in SI. The secondary somatosensory cortex (SII) is also organized somatotopically (Disbrow et al., 2000; Ruben et al., 2001), although separate representations of different body parts are more challenging to delineate in SII using fMRI in humans because of greater overlap between representations and larger intersubject variability (Ruben et al., 2001; Young et al., 2004; Bhatow et al., 2007). Previous results showed that SII is involved in tactile learning (Ridley and Ettlinger, 1976; Pleger et al., 2003). It would be interesting to examine in future studies whether representations of trained and untrained body parts in SII are coactivated in a similar fashion as in SI.

Our results suggest that the area of cortex recruited for performing and learning of a difficult tactile task may increase in terms of activation patterns across separate somatotopic representations. Previous studies found that when a body part is used frequently (for example, during physical training), it is represented over time by a larger cortical area, which can be accompanied by an increase in spatial resolution of the expanded body

part (Merzenich et al., 1984; Pascual-Leone and Torres, 1993; Elbert et al., 1995; Wang et al., 1995; van Boven et al., 2000; Pleger et al., 2003; Ragert et al., 2004; Valyear et al., 2020). Our results differ from these previous findings because the increase of cortical area occurred without any training and involved an extension of activation patterns across representations in SI, whereas the average (univariate) activation in the cortical area of the unstimulated body part was not significantly different from baseline without any tactile stimulation (Fig. 6f). Furthermore, the increase occurred between representations of body parts in SI, which did not share any cortical overlap. This result distinguishes our findings from studies, which found transfer of tactile learning between body parts that were coactivated because their cortical representations in SI (partially) overlapped (e.g., representations of adjacent fingers of the hand; Harris et al., 1999, 2001; Harris and Diamond, 2000; Harrar et al., 2014).

Taken together, the results of this study suggest that tactile learning with tactile stimulation of a trained body part might be supported by coactivation of the cortical representation of an untrained body part. This cortical coactivation might occur to increase the spatial resolution of the trained body part and might be critically involved in the transfer of tactile learning from the trained to the untrained body part. Future studies are necessary to determine whether cortical coactivation also occurs between other trained and untrained body parts and body locations and whether repeated coactivation leads to long-lasting changes of somatotopic representations in the cortex.

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