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Effect of Haptic Feedback From Self-Touch on Limb Movement Coordination

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Touching one's own body provides haptic feedback about the spatial configuration and movement of body parts. However, the influence of self-touch on movement performance has not been investigated so far. The authors evaluated the contribution of self-touch by asking participants to perform cyclic movement sequences with their feet while touching them with their hands, or vice versa. Hands and feet were either crossed or uncrossed (parallel), manipulating anatomical congruency of haptic feedback. The effects of self-touch (vs. object-touch), active limb (feet vs. hands) and sequence complexity were assessed in three separate experiments. Task performance was strongly and specifically disrupted in one of the anatomically incongruent conditions (hands-parallel/feet-crossed). This disruption occurred only with self-touch (Experiment 1), with the feet active (Experiment 2), and was more pronounced for the more complex movement sequence (Experiment 3). Thus, incongruent self-touch can strongly interfere with motor performance, showing that haptic information is automatically integrated in the online control of movement. The observed asymmetry between hands and feet indicates limb-specific differences regarding the use of spatial frames of reference and/or regarding the weighting of sensory information. The results emphasize the intimate connection between programming of action sequences and the anticipation of somatic feedback from self-touch.

Keywords: self-touch, body representation, coordination, motor control, haptic

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Sensory feedback from self-generated action is necessary for correction of ongoing movements and motor learning. Indeed, it has been shown that sensory input is automatically integrated in the online control of movement, as shown in studies experimentally manipulating visual (Franklin & Wolpert, 2008), tactile (Jeka & Lackner, 1994), proprioceptive (Cordo, Gurfinkel, Bevan, & Kerr, 1995), or auditory feedback (Lee, 1950; Yates, 1965). When two body parts are in direct contact with one another during an action (such as fingers touching with each other while manipulating an object, or the elbow touching one's torso while swinging a tennis racket), the combined tactile and proprioceptive (i.e., haptic) sensory information provides strong cues for the spatial location and movement of the respective body parts. Therefore, self-touch can also provide strong feedback signals relevant for the ongoing action. However, the influence of self-touch on online movement control in healthy individuals has not been studied in detail. In the present study, we demonstrate that haptic feedback from self-touch is automatically integrated in online control of movement, by showing that making haptic feedback anatomically incongruent by crossing limbs (e.g., touching the right foot with the left hand) can strongly disrupt performance of a cyclic limb movement task.

Most previous research on self-touch has focused on its capacity to modulate the representation of the size, structure and current configuration of one's body. In a classical paradigm (Lackner, 1988), participants touch their nose with their finger tip, whereas a proprioceptive illusion of arm extension is induced by means of tendon vibration. In many participants, this induces the illusion of a lengthening nose ("Pinocchio illusion"). This illusion also occurs, when self-touching the contralateral finger, and it also affects more implicit measures of perceived body size, such as tactile distance judgments (de Vignemont, Ehrsson, & Haggard, 2005). These studies show that self-touch induces a rapid integration between touch and proprioception, and provides linked spatial

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information about the touching and the touched effectors. However, it is not clear whether the apparent influence of self-touch on body representations also affects movement performance.

Preliminary evidence that self-touch may indeed be integrated in movement control comes from studies with neurological patients. Single-case studies with stroke survivors have demonstrated beneficial effects of self-touch for grip force control (Aruin, 2005) and hand movement kinematics (Stevens, Cole, & Vishton, 2012). Moreover, in a sample of eight patients with multiple sclerosis, it was recently shown that light self-touch with the contralateral index finger could help reduce exaggerated grip forces during object lifting (Iyengar, Santos, Ko, & Aruin, 2009). As discussed by the authors, the beneficial effect of self-touch on movement in this study may be due to the enhancement of sensory information about movement and position through the added haptic feedback.

Unusual body configurations, in particular those involving crossing of limbs in space, have been shown to affect the perceived temporal order of tactile stimuli. This indicates that the tactile input is processed in parallel in an anatomical and a spatial frame of reference, and crossing of the limbs induces a conflict between the two kinds of representations (Yamamoto & Kitazawa, 2001). Body configuration has also been shown to influence the identification of body parts based on tactile stimuli (Haggard, Kitadono, Press, & Taylor-Clarke, 2006). In that study, interweaving the fingers of one's hands in an extended posture affects identification of the touched hand (but not the touched finger). Finally, Riggio, De Gonzaga Gawryszewski, and Umilta (1986) found that responses were generally delayed with crossed compared to noncrossed limbs, suggesting that conflicting information (spatial and anatomical) needs to be integrated to execute the movement. Thus, unusual body configurations may affect the ability of the central nervous system to process location and timing of tactile stimuli as well as identification of body parts for action.

Summing up, sensory information from self-touch and unusual body configurations have been shown to modulate perceptual aspects of body representation in healthy participants. Moreover, there is preliminary evidence, that self-touch may modulate movement performance in neurological patients. In the present study, we systematically vary body configuration and anatomical congruency of haptic feedback to directly evaluate the effect of self-touch on movement performance in healthy participants.

To assess the integration of self-touch in motor performance, we devised a task in which upper and lower limbs (hands and feet) are touching one another, such that the central nervous system receives haptic feedback of the movement of one body part via the touch of another body part. By systematically varying body configuration (limb crossing), the association between movement and haptic feedback can be manipulated. If haptic feedback is automatically integrated into movement control, motor performance should be degraded under conditions in which the performed (or intended) movement and the resulting (or predicted) haptic feedback are difficult to integrate. According to the literature reviewed above, this may be the case when (a) tactile information is made difficult to interpret by crossing the touching limbs (Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001), (b) limb identification or movement initiation is compromised by crossing of the active limbs (Haggard et al., 2006; Riggio et al., 1986), or (c) haptic feedback is made anatomically incongruent by crossing only one pair of limbs (touch the left foot with the right hand, and vice versa).

We predicted that anatomically incongruent self-touch (but not incongruent body configurations as such) can lead to degraded motor performance. We moreover predicted that a detrimental effect of incongruent self-touch could most likely be demonstrated for movements performed with less "skillful" limb (i.e., with the feet rather than the hands), and that interference of self-touch is more likely to be observed in self-generated movements of a certain complexity, requiring maintenance and continuous updating of the current body state. These predictions are tested in three independent experiments.

Experiment 1

The goal of Experiment 1 was to assess potential interference effects of haptic feedback from self-touch by the hands on performance of a cyclic foot movement sequence. Crossing of feet and hands was systematically varied to assess the potential influence of three mechanisms discussed in the Introduction. If anatomical-spatial confusion of tactile information (Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001) affects motor control, degraded performance should be observed when the hands (nonactive limbs) are crossed, irrespective of the crossing of the feet (active limbs). If unusual position of the active limbs leads to problems with limb identification (Haggard et al., 2006) or delays in movement initiation (Riggio et al., 1986), degraded performance should be observed when the feet are crossed, irrespective of hand crossing. Finally, if the anatomical congruence of haptic feedback (left hand touching the left vs. the right foot) is decisive, motor performance should be degraded when either the hands or the feet are crossed, such that the central nervous system receives haptic feedback from the right foot via the left hand and vice versa. Furthermore, we assess whether any observed interference of incongruent haptic feedback is due to actual self-touch or can also be induced by positioning the hands close to the feet (e.g., due to modulation of spatial attention). We predicted that motor performance would be degraded only with self-touch and only in anatomically incongruent conditions.

Method

Participants. Twelve healthy, right-handed young adults (22–31 years, eight female) participated in the study after giving informed written consent. All were tested according to the guidelines of the American Psychological Association and with the approval of the ethics committee of the Max Planck Institute of Human Development, Berlin. Participants received 10 Euros per hour. As the experiment involved a potentially uncomfortable body posture (see below), particular care was taken throughout the experiment to ensure the participants' well-being. Individuals with extended experience (more than 5 years of training) in a musical instrument or dance were not included in the study, as they likely have specific expertise in interlimb coordination.

Procedure and design. Participants were seated on a height-adjustable bench in a bent-forward position, with the fingertips of index, middle, and ring finger touching the top of their feet (self-touch condition) or a piece of wood placed next to their feet (object-touch condition; see Figure 2A). In the self-touch condi-

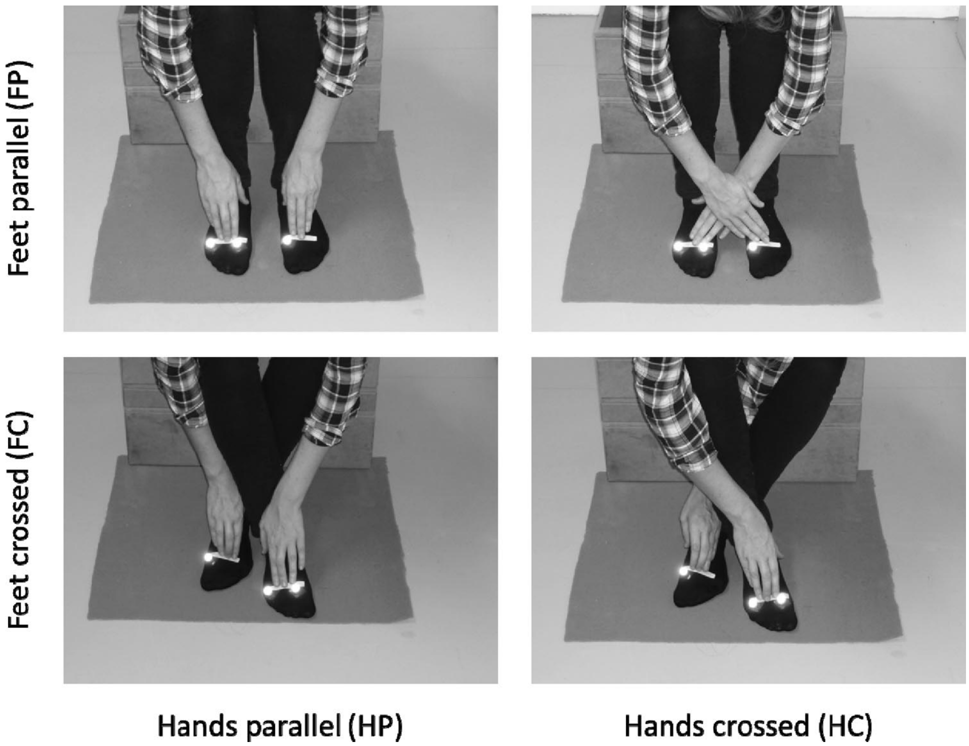

Figure 1. Basic hand and foot configurations used in the three experiments.

tion, participants were instructed to touch their feet at the position indicated by a strip of adhesive tape attached to the foot at the level of the metacarpophalangeal joints. In the object-touch condition, they touched two pieces of wood positioned laterally to the feet. Participants were wearing socks but no shoes during the experiment. The self-touch and object-touch conditions were combined with four body postures, with arms and legs either crossed or uncrossed (see Figure 1), resulting in a total of eight experimental conditions. Thus, Experiment 1 had a three-way factorial design with factors Touch (self-touch, object-touch), Hand Position (parallel [HP], crossed [HC]), and Foot Position (parallel [FP], crossed [FC]). As the aim was to investigate the influence of haptic feedback on motor performance, participants performed the movement tasks with closed eyes to avoid potential visuomotor effects.

The task consisted of producing a cyclic sequence with the feet, consisting of four movements of lifting and lowering one of the fore-feet, with a phase-lag of 90° (see below). Participant chose the foot crossing (left or right leg in front) according to their preference, and the same crossing was used for the arms. Participants were instructed to position their feet with the heels comfortably resting on the floor, to ensure the forefeet could be lifted without destabilizing body equilibrium. Participants were also asked to

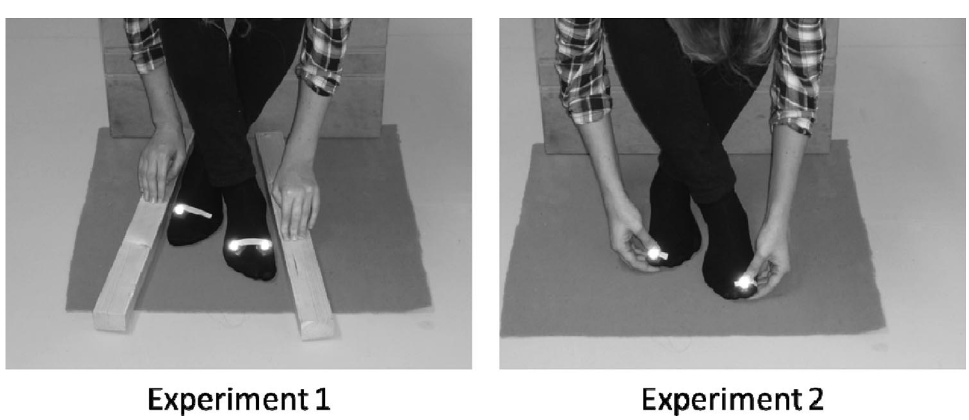

Figure 2. Control conditions used in Experiment 1 (assessing the effect of self-touch vs. object-touch) and Experiment 2 (allowing either the foot or the hand to be the active limb), illustrated for one of the hand-foot configurations (hands parallel, feet crossed; HPFC).

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make sure their arms did not touch one another in the HC condition. For the HCFC condition, this was ensured by asking participants to cross the back arm behind the front leg (see Figure 1).

Prior to the actual experiment, participants were familiarized with the task. To avoid prior learning, the foot movements and the body configurations were instructed separately. The foot movement sequences and foot positions were demonstrated by the experimenter and practiced by the participant (without self-touch) in an upright sitting. The body configurations (with self-touch but without foot movement) were instructed verbally. The movement sequence started either with the left foot (left-up, right-up, left-down, right-down) or with the right foot (right-up, left-up, right-down, left-down). A metronome beat (interbeat interval: 700 ms) was used to time the participants' movements, with one movement per beat. Participants were explicitly instructed that the feet were to perform the movement actively while the hands should be as passive as possible. They were also instructed to try and return to the movement pattern whenever they lost track.

Before each trial, the next position, movement task, and starting foot were shown (e.g., "Hands crossed, feet parallel, hands on feet, right foot starts") on a screen placed on the ground at 1 m distance from the participants' feet. During the trials, participants closed their eyes. Each trial comprised of 36 metronome beats with 700 ms interbeat interval. Participants were instructed to start the movement sequence with the fifth beat. Any movements made accidentally before the fifth beat were not analyzed.

The experiment consisted of eight blocks, one for each experimental condition. The sequence of conditions was chosen pseudorandomly for each participant, with the additional constraints that (a) the touch condition (self-touch, object touch) alternated between blocks, and that (b) the two blocks of the same body configuration (hand and foot crossing) never occurred in direct succession. Each block consisted of four trials, with alternating starting foot (left, right). The starting foot of the first trial in each block was determined pseudorandomly. Between trials and blocks, resting periods were given.

Movement data acquisition and analysis. Foot movements were recorded at 100 frames per second by a motion capture system (Vicon MX, Oxford, UK). To simplify preprocessing of the data, two reflective markers were placed on the right foot and one on the left foot, on the metatarsophalangeal articulations (see Figure 1). Only the two medial markers were used for further analysis. The vertical component of the kinematic data was analyzed in two ways: (2) number of correct four-element sequences and (b) cross-correlation at the prescribed time lag (700 ms).

For the number of correct sequences (Figure 3A and 3C), the vertical position data of each foot were rescaled such that the interdecile range (10% to 90%, determined separately for each

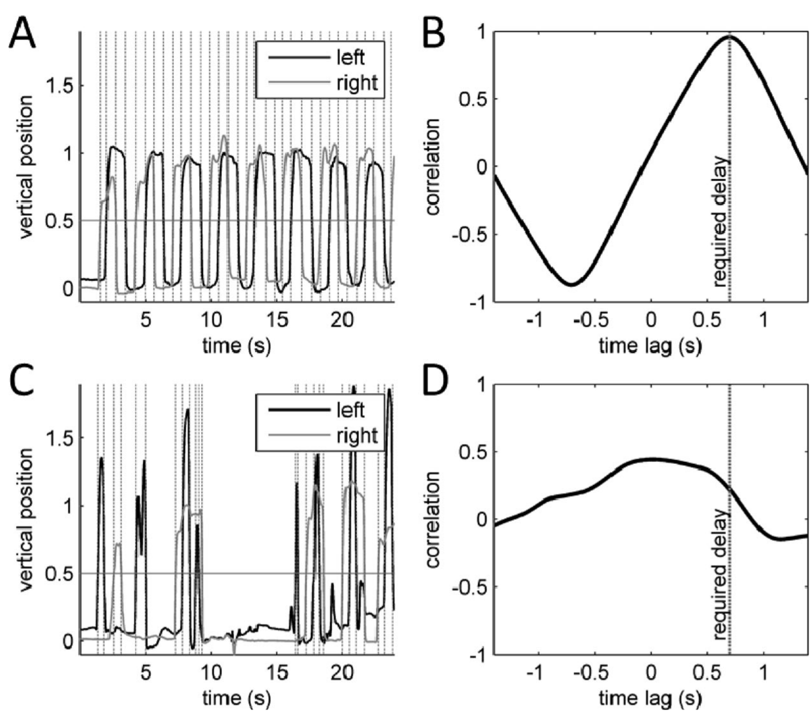

Figure 3. Sample data and illustration of the kinematic analysis for two experimental conditions from Experiment 1: hands crossed, feet crossed (HCFC)/self-touch (A, B) and hands parallel, feet crossed (HPFC)/self-touch (C, D). A, C: Kinematic (vertical movement) data from each foot were linearly rescaled (A, C) such that the interdecile range (10%–90%) was mapped to the interval (0,1). A threshold criterion (0.5, horizontal line) was used to detect foot movements (left/right, up/down; vertical lines). In the data shown here, the number of correct four-element sequences was 8 (A) and 0 (C), respectively. C, D: Lagged cross-correlation of the kinematic data of left and right foot. As the instructed bipedal sequence consists of the same movements with a time-lag of 700 ms, the correlation coefficient at that time lag (vertical line) is high when the movement sequence is performed correctly (B; $r = .96$) and low for poor performance (D; $r = .21$).

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trial) corresponded to the interval (0,1). Foot movements (left/right, up/down) were detected by a threshold criterion (0.5). The number of correct sequences was defined as the number of occurrences of the required four-element sequences (e.g., right-up, left-up, right-down, left-down) within the actually performed movement sequence, which had 32 elements if performed correctly. As the required sequence consisted of four different movements, each actual movement could only contribute to one correct four-element sequence. Hence, the resulting number of correct sequences ranged between 0 and 8.

For the time-lagged cross-correlation (Figure 3B and 3D), the correlation coefficient of the vertical position data of the left and right foot was computed at the required time lag (700 ms). As the required movement sequence of the left and right foot was identical but shifted in time by this delay, higher (positive) correlation coefficients correspond to better performance. The time-lagged correlation was Fisher z transformed for statistical analysis. In combination, the number of correct sequences and the time-lagged cross-correlation address both the sequential and the timing aspect of the task. (Other performance measures, such as the variability of the intermovement interval or the number of correct movement pairs, showed the same pattern of results).

Subjective rating. Between blocks, participants were asked to respond to rate a number of statements concerning their subjective experience of the task on range between −3 (completely disagree) and +3 (completely agree). The order of statements was chosen pseudorandomly for each participant. We report the subjective performance (“I was able to perform the movement task”) and subjective comfort (“The position was comfortable”). The first rating reflects participants’ insight into a potential coordinative challenge. The second rating allows controlling for potential influence of postural comfort on task performance. In addition, participants were asked after completing the experiment if they had any comments on the relative difficulty or comfort of the different conditions.

Statistical analysis. Statistical analysis was performed in R (R Development Core Team, 2008). Dependent variables were analyzed by means of a three-way repeated measures analysis of variance (ANOVA) with factors Touch (self-touch, object-touch), Hand Position (parallel, crossed), Foot Position (parallel, crossed). To control for potential influences of postural comfort on performance, the ANOVAs were repeated for the two objective performance measures after accounting for variance explained by the subjective rating of comfort.

As the main prediction involved a three-way interaction and as additional pairwise comparisons were performed to assess differences between conditions in detail (see below), only the three-way interaction is reported for the performance variables. For subjective comfort, all significant effects are reported. Complete ANOVA tables are reported in the Supplementary Materials.

Pairwise comparisons between conditions were performed between the four hand-foot configurations (six comparisons), separately for each level of the factor Touch; and between the two levels of the factor Touch, separately for each hand-foot configuration (four comparisons). Pairwise comparisons were done by permutation tests, correcting for multiple comparisons (Holm, 1979). The level for statistical significance testing was set to 0.05.

Results and Discussion

Sample kinematic data from one participant are shown in Figure 3, for the HCFC and HPFC conditions, both with self-touch. As illustrated by the kinematic data, performance of the foot movement sequence is strongly disrupted in the HPFC condition, and this is reflected both in the number of correct sequences (Figure 3A and 3C) and the time-lagged correlation (Figure 3B and 3D). The performance of one participant in the self-touch conditions of Experiment 1 is shown in Video 1 (Supplementary Materials). The effect of self-touch (vs. object touch) in the HPFC condition is shown in the first part of Video 2 (Supplementary Materials).

The performance measures and subjective ratings are plotted in Figure 4. The ANOVA results show significant three-way interactions of Hand Position, Foot Position, and Touch, for both objective performance measures (Figure 4A and 4B), number of correct sequences, $F(1, 11) = 16.49$, $p = .002$, and lagged correlation, $F(1, 11) = 12.45$, $p = .005$. Pairwise comparisons showed lower performance scores (a) only in the self-touch condition, of HPFC compared to the other three hand-foot configurations, for the number of correct sequences (all $p < .01$) and lagged correlation (all $p < .01$), and (b) between the self- and object-touch conditions in the HPFC-configuration for sequences ($p = .006$), and correlation ($p = .004$).

Subjective performance ratings (Figure 4C, “I was able to perform the task”) were in line with the objective measures, with a significant three-way interaction, $F(1, 11) = 34.24$, $p < .001$, and the same pairwise comparisons yielding significant differences: (a) HPFC with self-touch versus other hand-foot configurations with self-touch (all $p < .01$) and (b) HPFC with self-touch versus object-touch ($p = .004$).

Importantly, these effects in measured and self-reported performance are not explained by subjective postural comfort (Figure 4D, “The position was comfortable”). First, subjective comfort did not show an analogous three-way interaction, $F(1, 11) < 1$. Instead, main effects of Hand Position, $F(1, 11) = 30.51$, $p < .001$, and Foot Position, $F(1, 11) = 26.40$, $p < .001$, were found. Second, the performance effects reported above remained after accounting for variance explained by subjective comfort, with significant three-way interactions for the number of correct sequences, $F(1, 11) = 16.85$, $p = .002$, lagged correlation, $F(1, 11) = 13.04$, $p = .004$, and subjective performance, $F(1, 11) = 29.79$, $p < .001$.

The results of Experiment 1 indicate that haptic feedback from the hands during self-touch can interfere with performance in a sequential foot movement task. This demonstrates that haptic feedback is automatically integrated in online movement control in this task, and, at a more general level, underlines the intimate connection between programming of action sequences and the anticipation of somatic feedback. Interference was only observed in the self-touch condition, indicating that actual haptic feedback (and not spatial proximity of hands and feet as such) is necessary for it to occur. Moreover, the interference occurred only in one of four self-touch conditions, the HPFC condition, which combines the crossed position of the feet with incongruent haptic feedback from the hands (i.e., touching the right foot with the left hand, and vice versa). Neither crossed hand or foot position alone (which were also present in HCFP and HCFC), nor incongruent feedback as such (which was present in HCFP) were sufficient to elicit the interference effect. The fact that interference was only observed in

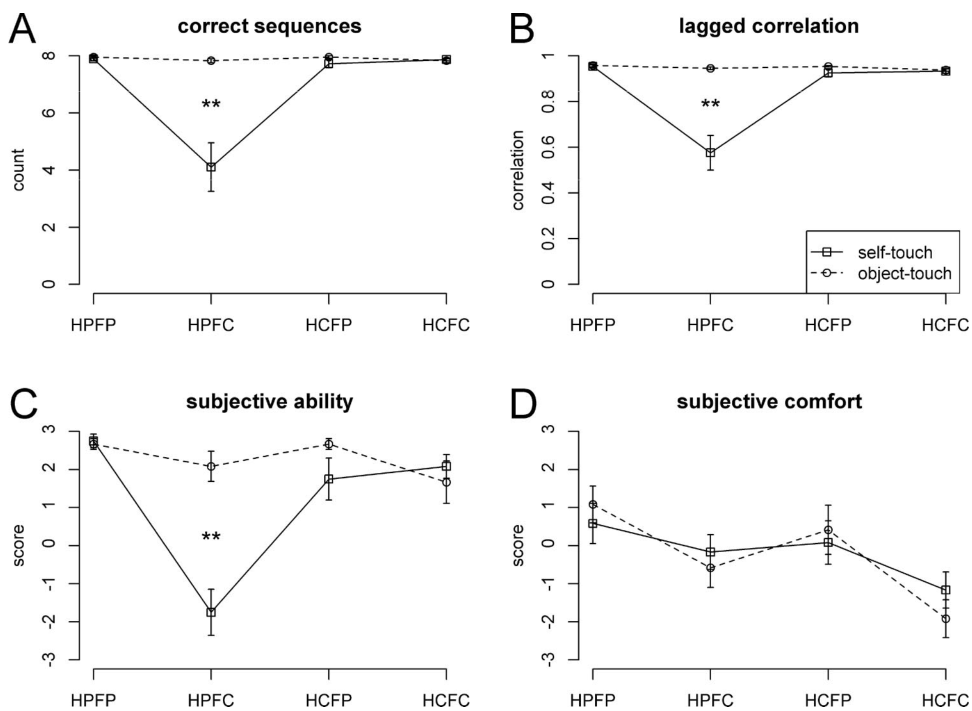

Figure 4. Results of Experiment 1, showing objective performance measures, based on kinematic data (A, B), and subjective ratings of ability (C) and comfort (D). Error bars represent SEM. Significant simple effects of touch are indicated ($^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$).

one of the two anatomically incongruent conditions (HPFC) may be due to differences between hands and feet in remapping spatial and anatomical frames of reference, or to a specific effect of crossing the actively moving limb. These alternative hypotheses are addressed in Experiment 2.

Experiment 2

In Experiment 1, disruption of the movement sequence was only found in the specific hand/feet posture relationship (HPFC), and only when their hands were touching the feet (self-touch). Also, in this experiment, participants were instructed to move their feet while touching them with the hands. In Experiment 2, we examined if the limb actively engaged in this task has any role in the observed effect. Participants assumed the same four postures (with self-touch) as in Experiment 1, but performed the movement sequence actively with the feet or with the hands while following passively with the other pair of limbs. If the posture itself (HPFC) is the cause of the degraded performance, the same pattern of poor performance will be also observed for the active hand condition. Alternatively, interference might depend on the crossing of the actively moving limb, in combination with incongruent feedback. If this is the case, interference should be found in HPFC when the feet are active (as in Experiment 1) and in HCFP when the hands are active. As a third alternative, if the interference was due to the interaction between the specific posture and the actively moving limb, the poor performance would be only observed in the feet active condition performed under the specific posture (HPFC).

Method

Participants. Twelve healthy young participants (20–34 years, six female) volunteered according to the same criteria and conditions as for Experiment 1, after giving informed written consent and with the approval of the local ethics committee. None of the participants had taken part in Experiment 1.

Procedure and design. Participants performed the sequential movement task of Experiment 1 (e.g., left-up, right-up, left-down, right-down) either with their hands or with their feet being the active limbs, with the instruction to let the other limbs follow as passively as possible. This experimental manipulation was combined with the same four hand and foot configurations as in Experiment 1 (see Figure 1), resulting in a total of eight experimental conditions. Thus, Experiment 2 had a three-way factorial design with factors Active Limb (feet, hands), Hand Position (parallel, crossed), and Foot Position (parallel, crossed).

Because of the biomechanical difficulty of moving the feet through the hands' action, the task was modified to require only movement of the big toes. Participants were bent forward holding the big toes of their feet between their thumb and index/middle fingers (see Figure 2B). The difference between moving actively with the feet versus with the hands was emphasized in the instructions and familiarization prior to the experiment and before each block of trials.

Conditions were presented in blocks of four trials as in Experiment 1. The conditions were presented in pseudorandom order, with the additional constraint that the Active Limb conditions

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alternate and that the same body configuration did not occur in successive blocks of trials.

Movement data acquisition and analysis. Movement of the big toes (whether moved actively from the feet or from the hands) were recorded by reflective markers placed on the toe nails. The kinematic analysis was the same as in Experiment 1. Task performance was quantified by the number of correct sequences and the lagged cross-correlation at 700 ms.

Subjective rating. In addition to the two statements from Experiment 1 ("I was able to perform the movement task" and "The position was comfortable"), two additional statements were used to assess the subjective experience of the hands versus feet being active ("The feet were leading the movement" and "The hands were leading the movement"). A new measure was defined by subtracting the response to the first question (feet leading) from the response to the second question (hands leading) in the active hands condition, and vice versa in the active feet condition.

This measure captures potential differences between the subjective experience of leading the movement with the hands versus the feet.

Statistical analysis. The statistical analysis was the same as for Experiment 1, with the factor Touch replaced by Active Limb.

Results and Discussion

Performance scores from Experiment 2 are plotted in Figure 5. Performance in three of the conditions of Experiment 2 (feet active, HPFC; hands active, HPFC; hands active, HCFP) related to the three hypotheses discussed above, is illustrated in the second part of Video 2 (Supplementary Materials).

The ANOVA revealed a three-way interaction of Active Limb, Hand Position, and Foot Position, both for the number of correct sequences, $F(1, 11) = 17.24$, $p = .002$, and the lagged correlation, $F(1, 11) = 16.79$, $p = .002$. Pairwise comparisons revealed lower performance scores (a) only in the Feet Active condition, of HPFC compared to the other three hand-foot configurations, for the number of correct sequences (all $p < .01$) and lagged correlation (all $p < .05$); and (b) between the Active Feet and Active Hands conditions in the HPFC-configuration, for sequences ($p = .008$), and correlation ($p = .008$). As in Experiment 1, the findings are not explained by subjective postural comfort, as (1) no corresponding statistical effects were found for that dependent variable, (2) removing the variance explained by postural comfort from the performance measures did not change the pattern of statistically significant effects.

Subjective ratings of which limb was leading the movement indicated that subjects were sensitive to the instruction. Regarding the statement "the hands were leading the movement," a main effect of instructed Active Limb, $F(1, 11) = 57.48$, $p < .001$, was found. Pairwise comparisons showed greater scores (i.e., stronger agreement) in the conditions in which the hands were instructed to be active, for all four hand-foot configurations (all $p < .005$). Regarding the statement "the feet were leading the movement," a main effect of instructed Active Limb, $F(1, 11) = 89.52$, $p < .001$, and a three-way interaction, $F(1, 11) = 6.83$, $p = .024$, were found. Pairwise comparisons showed greater scores (i.e., more agreement with the statement) in the conditions in which the feet were instructed to be active, for all four hand-foot configurations (all $p < .005$). The difference score, directly assessing the subjective experience of leading the movement with the hands versus the feet, did not show any significant effects (all $F(1, 11) < 3$, $p > .1$). This shows that the specific interference effect in the HPFC configuration with active feet is not explained by differences in subjective ability to lead the movement with hands versus the feet.

Summing up, the results of Experiment 2 are incompatible with the first two hypotheses discussed above, namely that the interference effect depends only on the crossing of the feet, or only on the crossing of the active limb. Instead, the fact that interference was observed only in the active feet but not the active hands condition points at an asymmetry between hands and feet in remapping anatomical and spatial frames of reference and/or in the integration of haptic feedback from the other limb in movement control.

Experiment 3

The goal of Experiment 3 was to assess the influence of sequence complexity on the interference effect. This was done under the same four postural configurations (hand/feet crossing) as in the first two experiments, with self-touch (Experiment 1) and with active feet (Experiment 2), but with two sequences of differing complexity. The sequence used in Experiments 1 and 2 consists of identical cyclical movements performed with the left and right foot with a phase lag of 90° (one movement in a four-movement sequence), which involves temporally overlapping movements of the two feet. In Experiment 3, performance for this sequence was compared to a simpler sequence of alternating movements of the

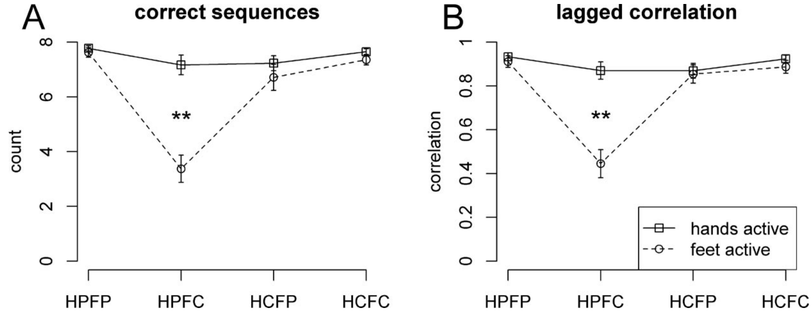

Figure 5. Results of Experiment 2, showing objective performance measures based on kinematic data. Error bars represent SEM. Significant simple effects of active limb are indicated (* $p < .05$, ** $p < .01$, *** $p < .001$).

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left and right foot (e.g., left-up, left-down, right-up, right-down), which has a phase lag of 180° between the feet and has no overlapping actions of the two feet. We hypothesized that performing the simpler sequence involves lower demands concerning representation and continuous updating of foot position (up vs. down), as it can—in principle—be performed by alternating two-element movements of the left and right foot. Thus, we predicted the interference effect observed in Experiment 1 and 2 for the HPFC configuration to be more pronounced in the complex versus simple movement condition.

Method

Participants. Twelve healthy young participants (23–34 years, four female) volunteered according to the same criteria and conditions as for Experiments 1 and 2, after giving informed written consent and with the approval of the local ethics committee. None of the participants had taken part in Experiments 1 or 2.

Procedure and design. Participants performed two sequential movement tasks of different complexity with their feet. The more complex task was the same as in Experiments 1 and 2 (e.g., left-up, right-up, left-down, right-down). The simpler sequence consisted of alternating a two-element sequence (up, down) between the two feet (left-up, left-down, right-up, right-down). This experimental manipulation was combined with the same four different combinations of hand and foot crossing as in Experiment 1 (see Figure 1), resulting in a total of eight experimental conditions. Thus, Experiment 3 had a factorial design with factors Sequence (simple, complex), Hand Position (parallel, crossed), and Foot Position (parallel, crossed).

The difference between the two movement sequences was emphasized in the instructions and familiarization prior to the experiment and before each block of trials. When instructing the participants, the sequences were labeled as "up-up-down-down" (complex) and "up-down-up-down" (simple), rather than "complex" and "simple" to avoid effects due to expected difficulty.

Conditions were presented in blocks of four trials as in Experiment 1. The conditions were presented in pseudorandom order, with the additional requirement that the Sequence conditions alternate and that the same body configuration did not occur in successive blocks of trials.

Movement data acquisition and analysis. Movement data were acquired and analyzed in the same way as in Experiment 1 (with two markers on the right foot). Task performance was quantified by the number of correct sequences and the lagged cross-correlation at 700 ms.

Subjective rating. The same two statements from Experiment 1 ("I was able to perform the movement task" and "The position was comfortable") were rated after each block of trials.

Statistical analysis. The statistical analysis was the same as for Experiment 1, with the factor Touch replaced by Sequence Complexity.

Results and Discussion

Performance scores from Experiment 3 are plotted in Figure 6. The effect of sequence complexity in the HPFC condition is illustrated in the third part of Video 2 (Supplementary Materials).

Analysis of variance revealed a three-way interaction of Sequence Complexity, Hand Position and Foot Position, both for the number of correct sequences, $F(1, 11) = 9.17$, $p = .011$, and the lagged correlation, $F(1, 11) = 10.34$, $p = .009$. Pairwise comparisons for the number of correct sequences showed lower performance in the complex sequence condition for HPFC compared to the other three configurations (all $p < .05$), and for HCFC compared to HCFP ($p = .05$). The number of correct sequences was also lower for the complex compared to the simple sequence in the HPFC ($p = .008$) and HCFC ($p = .05$) configuration. For the lagged correlation, lower performance was found in the complex sequence conditions for HPFC compared to the other three hand-foot configurations (all $p < .03$) and for HCFC compared to HCFP and HPFP (both $p < .05$). The lagged correlation was also lower for the simple sequence for HCFC compared to both the HCFP and the HPFC condition (both $p < .05$). In addition, the lagged correlation revealed lower performance for the complex compared to the simple sequence in the HPFC configuration ($p < .01$) and in the HCFC configuration ($p = .02$). Like in Experiments 1 and 2, the findings are not explained by subjective postural comfort, as (a) no corresponding statistical effects (three-way interaction) were found for that dependent variable, (b) removing the variance explained by postural comfort from the performance measures did not change the pattern of statistically significant effects.

According to the results of Experiment 3, interference in the HPFC condition mainly occurs in the condition involving a complex self-generated sequence. This emphasizes the importance maintenance and continuous updating of the internal representation of the current state of the feet (up or down). In contrast, the simpler sequence may be performed according to a more elemen-

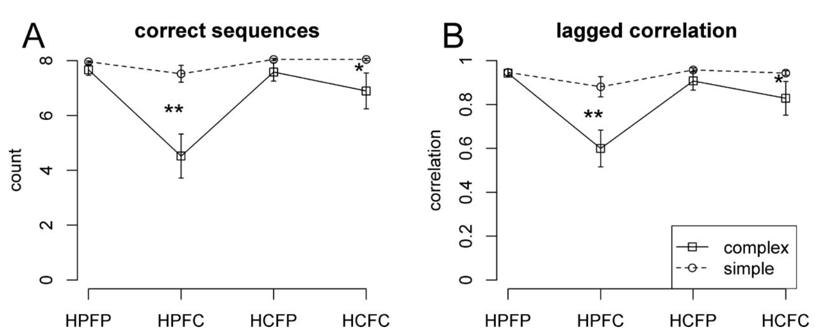

Figure 6. Results of Experiment 3, showing objective performance measures, based on kinematic data. Error bars represent SEM. Significant effects of Sequence are indicated ($^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$).

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tary "switching rule," which may be less susceptible to interference of incongruent haptic feedback as it poses lower demands on internal representation and updating of the current body state.

General Discussion

We investigated the influence of haptic feedback on the performance of limb movements by experimentally manipulating the anatomical congruence between touched and moving limbs. Strong interference could be demonstrated in one particular incongruent feedback condition, in which a complex movement sequence was performed by the crossed feet touched with the uncrossed hands. This demonstrates, for the first time to our knowledge, the automatic integration of haptic feedback in the online control of movements. The interference effect was independently replicated in each of the Experiments 1–3, which further scrutinized the conditions under which it occurs.

The results of Experiment 1 show that, as hypothesized, interference depends on anatomical incongruency (left hand touching the right foot) of haptic feedback, rather than crossed position of moving or touching limbs alone (Haggard et al., 2006; Riggio et al., 1986; Schicke & Röder, 2006; Yamamoto & Kitazawa, 2001). Moreover, Experiment 1 also demonstrates that interference is due to actual self-touch and cannot be explained by mechanisms of spatial attention or peripersonal space (Holmes & Spence, 2004; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). In particular, merely placing the hands in close spatial proximity of the feet, but without touching them, was not sufficient to elicit the interference effect. Unexpectedly, interference from self-touch was only found for one of the two anatomically incongruent conditions, with hands parallel and feet crossed (HPFC). This specificity was replicated in all three experiments. The reasons why this anatomical configuration may be special are discussed below. As all the experiments were performed with eyes closed, the interference cannot readily be explained by potential effects of visual feedback, as has been suggested for some other somatic illusions (Van Riper, 1935).

Experiment 2 shows that the interference is specific to foot movements, suggesting a functional asymmetry between hands and feet in remapping anatomical and spatial frames of reference and/or in the integration of haptic feedback from the other limb in movement control. Finally, in Experiment 3, interference due to anatomically incongruent haptic feedback was only observed when using a complex foot movement sequence (the same as in Experiments 1 and 2), but not for a simpler sequence which does not involve temporally overlapping actions of the feet. This underlines the importance of complex self-generated movements, presumably requiring the maintenance and updating of the representation of the current state of the motor system, for the interference effect demonstrated here.

Altering the sensorimotor loop often leads to a corresponding adaptation of motor performance, for instance when laterally shifting the visual scene by prism goggles (Redding, Rossetti, & Wallace, 2005) or shifting the fundamental frequencies or particular formants in speech (Houde & Jordan, 1998). After being exposed to altered feedback, motor commands are adjusted in order to restore the original sensory effects (reaching end positions, speech sounds). More dramatic effects of altered sensory feedback have been demonstrated by introducing manipulations that are hard (or impossible) to compensate by adapting motor performance. Manipulating temporal delays of auditory feedback during speaking can induce severe articulatory dysfluencies, termed artificial stuttering (Lee, 1950; Yates, 1963). Interestingly, comparable dysfluencies have been found in skilled Morse coding, when auditory feedback of the tapping movements was delayed (Yates, 1965). In the well-known Japanese illusion (Burnett, 1904; Henri, 1898), in which visuomotor feedback is confused by putting the hands in an unusual position, individuals are "frequently unable to move a designated finger, or [are] able to move it only after one or more false starts" (Van Riper, 1935, p.252).

The effect documented in the present study seems to belong to these latter examples of more dramatic inability to generate the appropriate motor command. Indeed, some participants were unable to perform even a single correct four-element sequence under the condition with incongruent haptic feedback and with the feet in unfamiliar position (HPFC). This is complemented by spontaneous statements of some participants, informally noted after the experiment, such as "I knew which foot I wanted to move, but it didn't go up or down," "the correct foot went up, but the wrong one went down," or "It felt as if I was not in control." These observations are consistent with the following interpretation: haptic feedback from the hand occurring as a result of foot movement was automatically integrated in the online control of the foot movement. However, when the feet were crossed, yet the hands were not, this haptic feedback would arrive in the "wrong" hand. This incongruent feedback appeared to be automatically integrated and could apparently not be ignored by the majority of participants.

In all three experiments, the interference effect occurred only in the HPFC condition, but neither in the other anatomically incongruent condition (HCFP) nor in the other condition with crossed feet (HCFC). Thus, the effect depends both on the crossed foot position and the incongruent haptic feedback. For the hands, it has been shown that touch is rapidly and automatically remapped into external space by using proprioception (Azañón, Longo, Soto-Faraco, & Haggard, 2010). While tactile remapping has also been demonstrated for the feet and even across hands and feet (Schicke & Röder, 2006), the concurrent use of two different remapping schemes (as presumably required in the HPFC and HCFP conditions) may lead to processing conflicts. Remapping for the hand may be expected to dominate over that of feet, as crossed hands are more frequently actively used in everyday actions than crossed feet, which may explain why interference only occurs in the incongruent crossed-feet (HPFC) condition.

The interference effect specifically in the feet active condition (Experiment 2) may also be explained in a Bayesian framework (Knill & Pouget, 2004), by assuming strong priors of default foot position (the right foot is usually on the right side in space) in combination with limb and modality specific weighting of sensory information, namely low weighting of proprioceptive information from the leg (due to the unfamiliar position) and strong weighting of haptic information from the hands (according to everyday usage). The former two (strong prior and weak proprioceptive weighting for the feet) may have led to the illusion of the right foot being touched by the right hand, and the latter (strong weighting of haptic information from the hand) to actual movement interference. In line with this, the absence of manifest interference in the second anatomically incongruent condition (HCFP) may be explained by the default position of the feet, and reduced positional priors and increased proprioceptive weighting for the hands (as a

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result of everyday usage). Similarly, the absence of interference in the hands active condition (Experiment 2) could be explained by weaker priors of default limb position and stronger use of proprioceptive information for the hands, as well as weak weighting of haptic information from the feet (all in line with everyday usage of the limbs).

The proposed differences between hands and feet in terms of use of self-touch information are compatible with a neurological case study on the effect of self-touch on tactile extinction (Coslett & Lie, 2004). In that study, touching the left knee with the own right hands led to an significant reduction of left tactile extinction, whereas touching the left knee with the right foot had no such effect. This points to a difference between hands and feet in terms of processing self-touch information, which is in line with the observed difference between active hands and active feet conditions observed in Experiment 2. On the other hand, spatial remapping of tactile information has been found to be comparable between hands and feet and to occur even between hands and feet (Schicke & Röder, 2006). This latter finding indicates that the asymmetry between hands and feet is not present for tactile perception as such, but is more specific to the integration of self-touch into perceptual or motor processes. Clearly, the observed asymmetry between hands and feet requires further investigation.

The fact that the interference effect was more pronounced when a relatively complex sequence was performed (Experiment 3) suggests that it may be related to the requirement of continuously maintaining and updating the internal representation of the current state (up or down) of both feet. This requirement is much reduced when performing the simple alternating sequence, which can probably be performed with a "switching" strategy, allowing the subjects to focus on one foot at a time. In addition, in the complex sequence task, the movement of the hands is shifted by a quarter cycle (90°), whereas it is shifted by a half-cycle (180°) in the simple sequence. Research on interlimb coordination indicates that in-phase and antiphase coordination patterns are more stable than intermediate patterns (Tuller & Kelso, 1989).

All three experiments involved the instruction to move one pair of limbs actively while passively following the movement with the other pair of limbs. Unfortunately, our setup did not allow directly controlling adherence to this instruction. However, we do not think this is problematic for the evaluation of the present results. First, the mere instruction in Experiment 2 to perform (kinematically very similar) movements either with active feet versus hands produced measurable and statistically significant differences in performance, indicating that participants were sensitive to the instructions. Second, there is not a priori reason why following the instructions would be specifically more difficult in one hand-foot configuration (HPFC), in which interference effects were found. Third, directly comparing subjective evaluation of the movement being led by either the feet or the hands (Experiment 2) did not reveal significant differences between conditions.

Based on the current findings, we can only speculate about potential neural mechanisms underlying the observed interference effects. At a peripheral level, nerve conduction times are unlikely to account for the observed hand-foot asymmetry as it has been shown that, in endogenously triggered simultaneous hand-foot movements, conduction delays are compensated for (Bard et al., 1992). The cerebellum has been implicated in temporally predicting tactile consequences of self-directed motor action (Blakemore, Frith, & Wolpert, 2001). However, in contrast to the study by Blakemore et al., which manipulated temporal congruency, we manipulated anatomical congruency of haptic feedback, which may involve different neural processes. At the cortical level, the task used in the present study certainly involves functions such as representation of limb position (premotor cortex; Lloyd, Shore, Spence, & Calvert, 2003), generation of movement sequences (supplementary motor areas; Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994), and spatial remapping of touch (posterior parietal cortex; Azañón et al., 2010). Evidently, further study is needed to elucidate the neural underpinnings of the present results.

In conclusion, the results of the present study demonstrate, for the first time to our knowledge, that incongruent self-touch can strongly interfere with motor performance. This indicates that, when present, haptic information is automatically integrated in movement performance and hence is an essential modality for motor control. Further study is needed to assess to what extent beneficial effects of self-touch, as previously found with neurological patients, can also be demonstrated in healthy participants.

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