Enhancement and suppression of tactile signals during reaching

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Running title: Tactile sensitivity during reaching

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Abstract

The perception of tactile stimuli presented on a moving hand is systematically suppressed. Such suppression has been attributed to the limited capacity of the brain to process task-irrelevant sensory information. Here, we examined whether humans do not only suppress movement-irrelevant but also enhance in parallel movement-relevant tactile signals when performing a goal-directed reaching movement. Participants reached to either a visual (LED) or somatosensory target (thumb or index finger of their unseen static hand) and discriminated two simultaneously presented tactile stimuli: a reference stimulus on the little finger of their static hand and a comparison stimulus on the index finger of their moving hand. Thus, during somatosensory reaching the location of the reference stimulus was task-relevant. Tactile suppression, as reflected by the increased points-of-subjective-equality (PSE) and just-noticeable-differences (JND), was stronger during reaching to somatosensory than visual targets. In experiment 2, we presented the reference stimulus at a task-irrelevant location (sternum) and found similar suppression for somatosensory and visual reaching. This suggests that participants enhanced the sensation of the reference stimulus at the target hand during somatosensory reaching in experiment 1. This suggestion was confirmed in experiment 3 using a detection task in which we found lower detection thresholds on the target hand during somatosensory but not during visual reaching. We postulate that humans can flexibly modulate their tactile sensitivity by suppressing movement-irrelevant and enhancing movement-relevant signals in parallel when executing a reaching movement.

Keywords: tactile perception, suppression, gating, enhancement, reaching, discrimination, detection, sensory thresholds

Introduction

Tactile information that arises on a body part just before or during its movement is misperceived or even suppressed. For example, tactile stimuli are perceived weaker (Chapman et al., 1987; Williams and Chapman, 2002) and later in time (Jackson et al., 2011; Parkinson et al., 2011) at a moving than a static limb. Similarly, humans feel their self-tickling actions (Blakemore et al., 1999; 2000; Claxton, 1975; Weiskrantz et al., 1971) and self-produced forces (Bays et al., 2005; Shergill et al., 2003) as less intense as when produced by others.

Tactile suppression is considered to occur due to a central feed-forward mechanism that predicts the sensory consequences of the planned movement and cancels the expected afferent signals (Bays et al., 2006; Wolpert and Flanagan, 2001). This is also supported by studies showing that tactile signals are even attenuated during movement planning, up to approximately 150 ms before movement onset (Buckingham et al., 2010). Alternatively, it has been proposed that tactile suppression is caused by movement-related reafferent signals that mask external, task-irrelevant somatosensory input (Williams and Chapman, 2002). Such cancelation processes are assumed to prevent the system from sensory overload and increase its capacity to process more relevant information.

Suppression of externally presented tactile stimuli has been found for simple single-joint (Chapman and Beauchamp, 2006; Voss et al., 2008; Williams and Chapman, 2002) as well as more complex goal-directed movements (Buckingham et al., 2010; Juravle et al., 2011). It is typically reflected by increased detection (Buckingham et al., 2010; Chapman and Beauchamp, 2006; Williams et al., 2002) or discrimination thresholds (Juravle et al., 2010, 2013). Although such suppression may arise from the execution of the movement itself, discrimination thresholds are increased even when a movement is expected but eventually not performed (Voss et al., 2008). This suggests that tactile suppression relies on the existence of a movement plan and not on the movement itself. However, tactile stimuli are also suppressed during passive movements (Williams and Chapman, 2002) indicating that they are modulated not only by central efferent but also peripheral afferent information.

Humans can modulate the strength of tactile suppression depending on whether somatosensory information is relevant for the task. For instance, when reaching to grasp an object between thumb and index finger, the sensitivity to unpredictable tactile stimuli on the forearm or little finger of the moving arm is decreased, while sensitivity on the grasp-relevant index finger is only barely reduced (Colino et al., 2014). Similarly, afferent somatosensory information from a limb is less suppressed when cutaneous signals arising at that limb are task-relevant (Staines et al., 2000). The degree to which somatosensory information is relevant for a particular movement seems to modulate how strong tactile stimuli are suppressed.

Movement planning and execution can also enhance the perception of sensory events (Huttunen et al., 1996; Tremblay and Nguyen, 2010). For instance, humans are less prone to audio-visual fusion illusions during reaching, as they may enhance the processing of reach–related visual information; although they may also attenuate the movement-irrelevant auditory information (Tremblay and Nguyen, 2010). Moreover, tactile sensitivity is increased when it is advantageous for the task, e.g. when performing slow exploratory finger movements to discriminate different surface properties (Juravle et al., 2013), and sensitivity is reduced with higher movement speeds (Cybulska-Klosowicz et al., 2011).

The above mentioned findings suggest that movement planning and execution may in some cases lead to suppression and in other cases to enhancement of sensory information. Yet, there are situations in which one may need to suppress irrelevant and in parallel enhance relevant sensory events. Here, we examined whether humans can suppress movement-irrelevant and at the same time enhance movement-relevant somatosensory information when performing a goal-directed movement task. We asked participants to reach to either a *visual* (LED) or a *somatosensory* target (thumb or index finger of their left hand) and discriminate two tactile stimuli presented simultaneously during either movement planning or execution. A reference stimulus was presented on the little finger of the left, static hand, and a comparison stimulus on the index finger of the right, moving hand. Since no visual information about either of the hands was available, the left target hand, to which we presented the reference stimuli, became task-relevant for somatosensory but not for visual reaching. Based on previous findings (Williams and Chapman, 2002; Buckingham et al., 2010; Juravle et al., 2010), we expected tactile suppression during both visual and somatosensory reaching. Importantly, if humans can also enhance movement-relevant information in parallel, this would be evident during somatosensory reaching: a stronger suppression during somatosensory than visual reaching would be indirect evidence for enhancement of the relevant somatosensory information at the target hand in order to accurately guide the hand to the reach goal (= left target hand).

Methods

Participants

Sixteen healthy volunteers (3 males; mean age ± SD: 25 ± 4 years, range between 19-32 years old) participated in experiment 1, with one of them being an author. The rest were naive as to the precise purpose of the study. Participants were right-handed according to the German translation of the Edinburgh Handedness

Inventory (Oldfield, 1971; mean ± SD: 83 ± 22). Prior to the experiment, participants gave their written informed consent. The protocol was approved by the local ethics committee. They were paid 8 euro/hour for their effort.

Apparatus

The experiment was performed in a dark room. A schematic top view of the setup is shown in Figure 1. Participants sat in front of a table with their head resting on a chin-rest and their right wrist on a start button, 10 cm in front of their body and 20 cm to their right. A black cardboard was attached to the chin-rest and occluded the view to both hands during the whole experiment. A transparent touch screen was placed vertically, 50 cm in front of the participants, and was aligned with their body midline. A horizontal array of light emitting diodes (LEDs) was attached to a rail placed directly behind the touch screen, 5 cm above the table surface. Thus, LEDs could be seen through the touch screen, but not felt when the participant made contact with the touch screen. Brief suprathreshold tactile stimuli (250 Hz, 50 ms) were generated by custom-made vibrotactile stimulation devices (Engineer Acoustics Inc., Florida, USA). Muscular activity of the right deltoid muscle was measured with bipolar recording using surface electrodes at 2000 Hz (BrainVision LLC, North Carolina, USA).

Procedure

Participants placed their left hand in front of the touch screen, with their digits wide apart but still at a comfortable posture. The thumb and index fingertips were approximately 45 cm away from the participant’s body. Participants were instructed to discriminate the intensity of two simultaneously presented tactile stimuli: a reference stimulus on the dorsal surface of their left static little finger and a comparison stimulus on the dorsal surface of their right moving index finger. We used two reference stimuli differing in their intensity in order to prevent participants from memorizing the reference intensity: a *weak* (peak-to-peak displacement of 0.25 mm) and a *strong* (peak-to-peak displacement of 0.35 mm) reference tactile stimulus. Each reference stimulus was combined with one of 13 comparison tactile stimuli (peak-to-peak displacement of 0.06, 0.11, 0.16, 0.21, 0.25, 0.30, 0.35, 0.40, 0.44, 0.49, 0.54, 0.58 and 0.63 mm).

Each trial started with the participant pressing and holding the start button with their right wrist. After a delay of 200 ms the target location was cued: in the *visual* condition one of the two LEDs was illuminated, whereas in the *somatosensory* condition the word “index” or “thumb” was announced by speakers. Three consecutive auditory tones (800 Hz, 50 ms) were then presented, separated by 450 ms. Participants were instructed to initiate their movement, and thus release the start button, with the onset of the third tone (*Go cue*). The LED was extinguished with the release of the start button; therefore, the duration of the presentation of the visual stimulus depended on the time when participants released the start button. Participants then reached with their right index finger to the location of the previously illuminated LED (*visual*) or the nail of their left thumb or index finger (*somatosensory*). Finally, participants brought their hand back to the start button to get ready for the next trial.

Tactile stimuli were presented simultaneously at one of three different stimulation times during the trial: with the first tone, with the *Go cue* (both stimulation times during movement planning), or 150 ms *after* the release of the start button (stimulation time always during movement execution). After the end of the reaching movement, participants had to respond by a button press with their right hand which of the two stimuli was stronger.

In a different block of trials, we ran a *baseline condition* that only consisted of the tactile discrimination task. The procedure was kept identical to the experimental conditions except that no reaching movement had to be executed. Participants relaxed their right wrist at the start button and tried to avoid any muscle tension in the fingers. After the three consecutive tones, the two tactile stimuli were presented simultaneously. Participants were instructed to keep their hands still until the stimuli were presented, and then respond by a button press which of the two stimuli was felt stronger.

The 3 tactile stimulation times, combined with the 2 reference stimuli and the 13 comparison stimuli resulted in 78 combinations; each was presented 12 times resulting in a total of 936 trials for each experimental (*visual* or *somatosensory*) condition. The baseline condition comprised of 26 combinations (2 reference stimuli x 13 comparison stimuli) each one presented again 12 times, resulting in a total of 312 trials (both conditions presented with the method of constant stimuli). Participants performed 2 blocks of trials for each target modality (*visual* or *somatosensory*), thus 4 experimental blocks in total. The baseline condition was also presented in 4 blocks, either preceding or following an experimental block. Participants performed the two experimental conditions separately on two consecutive days. Each combination of stimuli was presented in a random order within each block, with the restriction that the same combination was not presented on two consecutive trials. Each of the two targets in each (visual or somatosensory) block was presented in an equal amount of trials. The presentation of the blocks was counterbalanced across participants. The experiment took approximately 4 hours for each participant.

Data analysis

We first calculated the proportion of comparison stimuli that were judged as stronger than the reference stimulus for each individual participant. We then fitted these data of each participant to a logistic function using the maximum-likelihood estimation with the function *psignifit* in Matlab (Wichmann and Hill, 2001). This function estimated the point-of-subjective-equality (PSE) and the just-noticeable-difference (JND) for each of the 2 reference stimuli in each of the 3 conditions (visual, somatosensory, baseline) and for each of the 3 stimulation times. The PSE was defined as the 50% point of the psychometric function and the JND as the difference between the PSE and the 84% point of the psychometric function, which corresponds to one standard deviation of the Gaussian distribution. In order to examine how discrimination accuracy and precision were influenced by movement planning and execution we subtracted each participant's baseline PSE and JND from his or her respective values in each of the two experimental conditions (visual, somatosensory) and for each of the 3 stimulation times. This was done separately for each of the two reference stimuli, and the obtained PSE and JND differences (PSE_{diff}, JND_{diff}) represent the strength of the tactile suppression for each participant. Therefore, when interpreting the results, stronger suppression is represented with larger positive differences from zero, while zero represents no suppression with respect to the baseline.

We also examined whether and how the strength of the tactile suppression differed between the phases of movement planning and execution. Because tactile suppression has been found to occur up to approximately 150 ms prior to the movement onset (Williams and Chapman, 2002; Buckingham et al., 2010), we also determined the latencies of the reaching movement. In order to do so we first determined the onset of the reaching movement in each trial as the moment that the absolute muscular activity on the deltoid muscle was greater than 3 standard deviations of its average absolute activity during the first 500 ms of each trial. We then determined the reaching latency as the time difference between the onset of the reaching movement and the moment of the *Go cue*. The median reaching latency was calculated across all trials performed by each participant for each of the 3 stimulation times, and was later averaged across the median latencies of the 16 participants.

We obtained PSE_{diff}, JND_{diff} and reaching latencies for each individual participant, which were then averaged across participants. Effects of the stimulation times, target modality and intensity of the reference stimulus on PSE_{diff} and JND_{diff} were examined with a 3 (stimulation time) x 2 (target modality) x 2 (reference intensity) repeated measures analysis of variance ($p < 0.05$). When sphericity was violated, the Greenhouse-Geisser correction was applied. The accuracy with which participants discriminated the stimuli in the baseline condition, as well as differences in reaching latencies between the 3 stimulation times, were evaluated with one-sample *t*-tests for each reference stimulus separately. The discrimination accuracy in the baseline was tested against 0.25 and 0.35 for the weak and the strong reference stimulus, respectively. Variations of the baseline PSEs and JNDs within the 4 blocks were examined with a 4 (blocks) x 2 (reference intensity) repeated measures analysis of variance ($p < 0.05$). For investigating the stability of the baseline PSEs and JNDs across the 2 sessions, we performed a 2 (sessions) x 2 (reference intensity) repeated measures analyses of variance ($p < 0.05$). Significant differences between the conditions were examined using post-hoc *t*-tests and multiple comparisons were Bonferroni-corrected.

Results

Figure 2 shows an example of the psychometric curves for comparison stimuli that were judged as stronger than the weak reference stimulus presented in the baseline condition (tactile discrimination only) and in the reaching conditions for each of the three stimulation times and the two target modalities.

The baseline PSEs remained stable within the 4 blocks of trials ($F_{3,45} = 0.20$, $p = 0.8$, $\eta^2 = 0.01$) and across the 2 sessions ($F_{1,15} = 0.001$, $p = 0.9$, $\eta^2 = 0.001$). The variability of the baseline PSE for the weak and strong reference was the same (0.05 mm within the 4 blocks and 0.03 mm across the 2 sessions). Similarly, the baseline JNDs were also stable within the 4 blocks ($F_{3,45} = 0.50$, $p = 0.6$, $\eta^2 = 0.03$) and across the 2 sessions ($F_{1,15} = 0.9$, $p = 0.3$, $\eta^2 = 0.06$). The variability (standard deviation) of the baseline JNDs was 0.02 mm and 0.03 mm for the weak and strong reference within blocks, respectively, and 0.02 mm across sessions (for both references).

The average baseline PSE for trials with the weak reference was 0.32 mm (± 0.02 mm) and was significantly higher than the intensity of the weak reference stimulus (0.25 mm; $t_{15} = 3.7$, $p = 0.002$). This may reflect a general decrease in sensitivity for weaker stimuli on the left little finger. Participants were more accurate with respect to the strong reference: the baseline PSE was 0.37 mm (± 0.02 mm) and was not different from the intensity of the strong reference stimulus (0.35 mm; $t_{15} = 1.2$, $p = 0.21$). The precision of the discrimination judgments in the baseline condition, as reflected by the baseline JND, was 0.10 mm (± 0.003 mm) and 0.12 mm (± 0.008 mm) for the weak and strong reference stimuli, respectively, which differed from each other ($t_{15} = -2.9$, $p = 0.009$).

We first calculated the difference between the baseline PSEs and the PSEs obtained in the experimental condition for each of the two references separately, and then averaged the difference values across the two references (PSE_{diff}; see Methods). In the two experimental conditions, PSE_{diff} varied with stimulation time ($F_{1, 15} = 20.1$, $p < 0.001$, $\eta^2 = 0.57$; Fig. 3a) being larger than their corresponding baselines during movement execution (*visual target*: $t_{15} = 4.3$, $p = 0.001$; *somatosensory target*: $t_{15} = 8.6$, $p < 0.001$), but not during movement planning (before and with the *Go cue*; p's > 0.14). There was also an interaction between the stimulation time and the target modality ($F_{2, 30} = 6.5$, $p < 0.005$, $\eta^2 = 0.31$): only during movement execution, PSE_{diff} were larger when reaching to somatosensory than visual targets ($t_{15} = -2.7$, $p = 0.016$).

JND_{diff} were also influenced by the stimulation time ($F_{1, 15} = 12.8$, $p < 0.001$, $\eta^2 = 0.46$; Fig. 3b): they were larger with respect to their corresponding baselines when the tactile stimulation occurred during movement for both visual ($t_{15} = 2.5$, $p = 0.02$) and somatosensory targets ($t_{15} = 3.7$, $p < 0.001$), but not during movement planning (p's > 0.12). We also found an interaction between the intensity of the reference stimulus and the target modality ($F_{2, 30} = 5.6$, $p = 0.03$, $\eta^2 = 0.27$) with JND_{diff} for the strong reference being slightly larger when reaching to somatosensory than visual targets ($t_{15} = -2.6$, $p = 0.009$).

The latencies of the reaching movements were influenced by the stimulation time ($F_{2, 30} = 12.1$, $p < 0.001$, $\eta^2 = 0.44$): they were 299 ms (± 67 ms), 350 ms (± 72 ms) and 395 ms (± 71 ms) for tactile stimuli presented well before, with the *Go cue* or during movement, respectively. The differences between the 3 stimulation times were significant (t's > 2.4, p's < 0.001). No effects of target modality were found ($F_{1,15} = 1.3$, $p = 0.26$, $\eta^2 = 0.08$).

Discussion

In line with previous findings (Buckingham et al., 2010; Williams and Chapman, 2002), tactile stimuli presented during movement execution on the right moving hand were perceived weaker (stronger suppression) than during the baseline, when the right hand was static. One might have also expected stronger suppression of tactile stimuli during movement planning (Williams and Chapman, 2002). The lack of such effect in our study is presumably due to the reach latencies, which were much longer (~350 ms) than the latencies reported in other studies that found tactile suppression before the start of the movement (tactile suppression was evident up to 150 ms before movement onset; Buckingham et al., 2010; Williams and Chapman, 2002). Reach latencies were also influenced by the stimulation time, with tactile stimuli presented earlier in the trial leading to shorter latencies. This might be due to the tactile stimulation serving as a preparation cue to start the movement; the earlier the stimulation is presented, the greater may be the benefit.

Importantly, we did find stronger suppression during reaching to somatosensory than visual targets. In the somatosensory condition, participants needed to infer the position of their thumb or index finger from somatosensory signals, and thus must rely purely on somatosensory information from the target hand. Therefore, somatosensory information arising at the target hand was particularly important for the task. The need to use such information in the somatosensory condition may have increased the sensitivity on the target hand, leading to a stronger perception of the reference stimulus, and thus lower tactile thresholds for perceiving the reference stimulus on that hand. As a consequence, the intensity of the comparison stimulus on the moving hand must have been even stronger (compared to the visual condition) to be perceived as equal to the perceived intensity of the reference stimulus. Therefore, reaching to one’s own hand may have caused stimuli presented to the target hand to be perceived as stronger than when that hand is not relevant for the movement, like in visual reaching.

Experiment 2

In the first experiment we found stronger suppression when reaching to somatosensory than visual targets. This might be due to increased sensitivity on the target hand, which led participants to perceive the reference stimulus as stronger than when that hand was not important for the reaching task. In this case, the comparison stimulus would need to be even stronger, compared to the visual condition, in order to be perceived as equal to the perceived intensity of the reference. To test this hypothesis, we asked the same group of participants to take part in a second experiment. This experiment was identical to the first with the only difference that the reference stimulus was now presented to a movement-irrelevant location. Therefore, we did not present the reference stimulus to one of the fingers of the moving right hand, as it was expected to be suppressed, nor to one of the fingers of the left static hand, as the possible enhancement we hypothesized in experiment 1 might generalize across the whole target hand. Instead, we presented the reference stimulus to the sternum because this location is task-irrelevant, can hardly be affected by any muscular activity, and is aligned to the body midline reducing laterality effects. If the stronger suppression during somatosensory than visual reaching in experiment 1 was due to participants enhancing sensory signals at their target hand, we expected to find no differences in tactile suppression between reaching to somatosensory and visual targets.

Methods

The same 16 participants took part also in experiment 2. Except for the details mentioned below, the apparatus, procedure, and data analysis were identical to those of experiment 1. The two reference stimuli were now presented to the participant's sternum. Because in experiment 1 the differences between the two target modalities were found only during movement execution, we now specifically focused on this stimulation time. In order to prevent participants from anticipating the moment of the tactile stimulation, we also presented half of the stimuli during one of the two stimulation times during movement planning. The other half of the stimuli were presented during movement execution. More precisely, each of the 26 combinations (2 reference stimuli x 13 comparison stimuli) occurred 6 times at each of the two moments during movement planning (first tone, *Go cue*), and 12 times during movement execution (identical to experiment 1). This resulted in a total of 624 trials. Because we focused on possible effects during movement execution, we examined the influence of the target modality and of the reference stimulus' intensity on $\mathrm{PSE}_{\mathrm{diff}}$ and $\mathrm{JND}_{\mathrm{diff}}$ with a 2 (target modality) x 2 (reference intensity) repeated measures analysis of variance ($p < 0.05$).

Results

Again, PSEs in the baseline condition were stable within the 4 blocks ($F_{3,\,45} = 0.85$, $p = 0.47$, $\eta^2 = 0.05$) and across the 2 sessions ($F_{1,\,15} = 0.14$, $p = 0.71$, $\eta^2 = 0.009$). The variability of the baseline PSEs was 0.05 mm within the 4 blocks and 0.04 across sessions, for both the weak and strong reference. Similarly, the baseline JNDs were stable both within the 4 blocks ($F_{3,\,45} = 0.39$, $p = 0.7$, $\eta^2 = 0.02$) and across the 2 sessions ($F_{1,15} = 0.2$, $p = 0.6$, $\eta^2 = 0.01$). The average variability of the baseline

JNDs was 0.03 mm within blocks and 0.02 mm across sessions, for both the weak and the strong reference.

In the baseline condition, participants misperceived the intensity of both the weak and the strong reference stimuli: baseline PSEs were 0.37 mm (± 0.02) and 0.47 mm (± 0.02) for the weak and strong reference, respectively, and were both different from the intensities of their respective reference stimuli (weak, 0.25 mm: $t_{15} = 5.7$, $p < 0.001$; strong, 0.35 mm: $t_{15} = 5.6$, $p < 0.001$). Baseline JNDs were 0.13 mm (± 0.006 mm) and 0.12 mm (± 0.006 mm) for the weak and strong reference stimuli, respectively, and did not differ from each other ($t_{15} = 0.5$, $p = 0.6$).

Importantly, the $\mathrm{PSE}_{\mathrm{diff}}$ were not influenced by the target modality ($F_{1,\,15} = 0.16$, $p = 0.70$, $\eta^2 = 0.01$; Fig. 4a): they increased by 0.05 mm (± 0.02 mm) with respect to the baseline for both visual and somatosensory reaching. $\mathrm{PSE}_{\mathrm{diff}}$ varied with the reference intensity ($F_{1,\,15} = 6.67$, $p = 0.02$, $\eta^2 = 0.32$; Fig. 4a): stimuli on the moving hand were perceived as weaker when they had to be compared with the strong than the weak reference.

The $\mathrm{JND}_{\mathrm{diff}}$ were not influenced by the target modality ($F_{1,\,15} = 0.29$, $p = 0.59$, $\eta^2 = 0.19$; Fig. 4b), but were affected by the reference intensity ($F_{1,\,15} = 6.09$, $p = 0.02$, $\eta^2 = 0.28$; Fig. 4b): discrimination judgments were more precise when the stimuli on the moving hand were compared to the weak than the strong reference.

The average reaching latencies for the trials in which the stimuli were presented during movement execution was 272 ms (± 23 ms). Note that the reaching latencies for these trials in experiment 1 were 395 ms. Because participants took part in both experiments, the shorter reaching latencies in experiment 2 might result from a training effect leading to improved predictability of the Go cue (based on the three tones). No effect of the target modality was found for latencies ($F_{1,15} = 2.6$, $p = 0.12$, $\eta^2 = 0.16$).

Discussion

We again found suppression of stimuli presented during movement execution. However, this time, there were no differences in the PSE_{diff} between somatosensory and visual reaching. We attribute the absence of this effect to the reference stimulus being now presented at a task-irrelevant location. This supports the idea that the stronger suppression when reaching to somatosensory targets in experiment 1 is due to the perception of the reference stimulus being enhanced when it is presented at a movement-relevant location (i.e., at the target hand that served as movement goal in somatosensory reaching).

Experiment 3

The results of experiments 1 and 2 confirm previous findings on movement-related suppression. The difference in tactile suppression we observed for somatosensory and visual reaching in experiment 1 vanished in experiment 2. We interpret this as participants having perceived the reference stimulus on their target hand (experiment 1) as stronger when reaching to that hand. In the third experiment, we aim to provide direct evidence for tactile enhancement at movement-relevant locations. We instructed participants to detect a vibrotactile stimulus presented on the dorsal surface of their left little or right index finger. They were asked to do so while they hold both hands static (baseline) or reached with the right index finger to the static left thumb (*somatosensory reaching)* or an LED (*visual reaching)*. Based on previous findings and the results of experiment 1 and 2, we expect that the detection thresholds for stimuli at the moving index finger will increase during reaching compared to baseline independent of the target modality, reflecting tactile suppression on the moving hand. If tactile sensitivity is enhanced at movement-relevant location, we expect that stimuli on the left little finger will be perceived as stronger during somatosensory reaching than during baseline, while we expect no difference in tactile sensitivity between visual reaching and baseline.

Methods

Eighteen healthy volunteers (7 males; mean age ± SD: 24 ± 4 years, range between 18-33 years old) participated in the study, with one of them being author, and the rest being naïve. Participants were right-handed according to the German translation of the Edinburgh Handedness Inventory (Oldfield, 1971; mean ± SD: 83 ± 15). Prior to the experiment, participants gave their written informed consent. The study and its protocol were approved by the local ethics committee.

Except for the details mentioned below, the apparatus, procedure, and data analysis were identical to those of experiment 1. Participants had to detect a brief vibrotactile target stimulus (50 ms, 250 Hz) on the dorsal surface of either their left little or right index finger. In addition, we simultaneously presented a noise vibrotactile stimulus (500 ms, 250 Hz) to the ventral surface of both the left little and right index fingers. As detection requires distinguishing a relevant signal from noise, we presented the relevant target stimulus during the presentation of the irrelevant noise stimulus, precisely 150 ms after the onset of the noise stimulus. Note that we always presented the noise stimulus to the ventral surface of both fingers, while only one target stimulus was presented to the dorsal surface of one of these fingers. We introduced this change in order to increase the detection thresholds during baseline (no movement). Indeed, when we only presented the target stimulus alone (50 ms, 250 Hz) the detection thresholds reached a ceiling effect, i.e., participants were able to detect the weakest tactile stimuli that could be presented, thus leaving no room to examine tactile enhancement. Therefore, we added noise to the target stimulus by presenting noise stimuli together with the target stimulus. This change led to an increase of the baseline detection thresholds so that we could test for enhanced tactile sensitivity during reaching compared to baseline.

Each participant performed 2 baseline and 2 reaching blocks in alternating order. During the reaching block, participants reached to either their unseen left thumb or an LED behind the touch screen. The target location was specified either with the word “thumb” being announced by the speakers or the LED being illuminated (and remaining illuminated until movement onset). During the baseline blocks, the noise stimuli were presented together with the last auditory tone, and during the reaching blocks together with movement onset. In both baseline and reaching blocks, the target stimulus was presented 150 ms after the onset of the noise stimuli. Care was taken that the movement direction was similar for the two targets, despite the visual target being ~5 cm farther than the somatosensory target. The target stimuli had a peak-to-peak displacement of 0 (no-stimulation) to a maximum peak-to-peak displacement of 0.091 mm, in steps of 0.003 mm. The irrelevant noise stimuli had a fixed displacement of 0.012 mm. Participants were instructed to report whether they felt a target stimulus on the dorsal part of one of either their left little or right index finger. They were explicitly told that the noise stimulus would be present in each trial and on both digits, while the target stimulus, if present, would occur on one of these two digits.

In the baseline condition, each of the 30 target stimuli differing in intensity was presented 4 times for each of the 2 digits, resulting in a total of 240 trials over both sessions. In the reaching condition, each of the 30 target stimuli was presented 4 times for each of the 2 digits and the 2 target modalities, resulting in a total of 480 trials over both sessions (both conditions presented with the method of constant stimuli). We calculated the proportion of stimuli that were detected for each individual participant, and we then fitted the data to a logistic function using the maximum-likelihood estimation. Then, we calculated the detection threshold as the 50% point of the logistic function, and the precision of the stimulus detectability as the difference in stimulus intensity between the 50% and the 84% points of the function. Effects of the stimulation site and target modality on the change in detection thresholds and the change in precision of stimulus' detectability of the reaching condition relative to baseline were evaluated with a 2 (stimulation site) x 2 (target modality) repeated measures analysis of variance ($p < 0.05$).

Results

The detection thresholds in the baseline condition did not differ between the 2 blocks ($F_{1, 17} = 0.88$, $p = 0.36$, $\eta^2 = 0.05$). The variability of the baseline detection thresholds within the 2 blocks was 0.005 mm for both the left little and right index finger. Similarly, the precision of the stimulus' detectability was stable within the 2 blocks ($F_{1, 17} = 1.41$, $p = 0.25$, $\eta^2 = 0.07$): its average variability within the 2 blocks was 0.007 mm for the left little and 0.004 mm for the right index finger.

The detection thresholds in the baseline condition were 0.046 mm (± 0.005 mm) and 0.039 mm (± 0.003 mm) for the left little and right index finger, respectively, and did not differ between the two digits ($t_{17} = 1.69$, $p = 0.11$).

As expected, the change in detection thresholds was influenced by the stimulation site ($F_{1,\,17} = 20.06$, $p < 0.001$, $\eta^2 = 0.54$; Fig. 5a): the change in detection thresholds relative to baseline was greater on the right moving index finger (0.015 mm ± 0.004 mm) than on the left static little finger (-0.007 mm ± 0.004 mm). We also found an interaction between stimulation site and target modality ($F_{1,\,17} = 4.67$, $p = 0.045$, $\eta^2 = 0.21$; Fig. 5a): the change in detection thresholds relative to baseline on the moving hand did not differ between somatosensory and visual reaching ($t_{17} = 0.39$, $p = 0.69$), whereas on the static hand the thresholds relative to baseline were smaller during somatosensory than visual reaching ($t_{17} = -2.44$, $p = 0.026$). As expected, the detection thresholds on the moving hand were greater than baseline during both somatosensory ($t_{17} = 3.59$, $p = 0.002$) and visual reaching ($t_{17} = 3.47$ $p = 0.003$). Importantly, the detection thresholds on the static hand were smaller than baseline only during somatosensory ($t_{17} = -3.41$, $p = 0.003$) but not during visual reaching ($t_{17} = -0.33$, $p = 0.74$). Note that the suppression and enhancement effects were similar in strength: participants suppressed their sensitivity on their moving index finger by 0.015 and 0.014 mm during somatosensory and visual reaching, respectively, while they enhanced it on their static little finger by 0.013 mm only during somatosensory. The modulation on the static little finger during visual reaching was of 0.001 mm with respect to the baseline.

Regarding the precision of the stimulus' detectability, participants were less precise when detecting stimuli on their right moving hand 0.012 mm (± 0.004 mm) than their left static hand -0.001 mm (± 0.003 mm) ($F_{1,\,17} = 7.33$, $p = 0.015$, $\eta^2 = 0.30$; Fig. 5b). This effect was not influenced by the target modality ($p = 0.54$).

Discussion

The results of experiment 3 support our previous findings suggesting that tactile sensitivity is enhanced at movement-relevant locations. Participants suppressed the target stimulus on the right moving hand independent of the target modality. Importantly, the detection threshold of the target stimulus on the left static little finger during somatosensory reaching was reduced as compared to baseline. This decrease was not observed at this hand during visual reaching. Although the changes in tactile sensitivity we observed were rather small (suppression of 0.0145 and enhancement of 0.0013 mm), the results were very systematic and consistent across participants and confirm those obtained in our previous experiments 1 and 2.

Tactile enhancement at the target hand during somatosensory reaching could not only be caused by a change of tactile sensitivity of the target stimulus, but also of the noise stimulus. It is conceivable that both the target and the noise stimuli were enhanced or that the noise stimulus was even suppressed in order to increase the signal-to-noise ratio. However, in both cases the detectability of the target stimulus would be enhanced at movement-relevant locations. How multiple somatosensory signals are processed at movement-relevant locations, and how location-specific these effects are, are questions beyond the purpose of this study and should be addressed in future work.

General discussion

In this study we examined whether humans can suppress movement-irrelevant and, in parallel, enhance movement-relevant somatosensory signals during reaching. We found stronger tactile suppression of a stimulus on the moving hand during reaching to a somatosensory (thumb or index finger of the static hand) than a visual target (LED). Importantly, this effect occurred only when the stimulus had to be compared with a reference stimulus at a movement-relevant location (movement goal), but not when it was at a movement-irrelevant location (sternum). This may suggest that humans do not only suppress movement-irrelevant stimuli on their moving hand, but at the same time also enhance movement-relevant signals on their target hand. In order to provide direct evidence for the latter possibility, we performed a detection task in experiment 3 and observed better tactile detectability of stimuli at the movement-relevant target hand and worse tactile detectability of stimuli at the moving hand, supporting our results of experiment 1 and 2.

In experiment 1, participants reached to either a somatosensory or a visual target and discriminated the strength of a tactile stimulus on their moving hand from a reference stimulus that was simultaneously presented on their static hand. As expected, tactile stimuli were suppressed during movement execution, as has been demonstrated in previous studies for simple finger movements (Chapman et al., 1987; Williams and Chapman, 2002) as well as for reaching (Buckingham et al., 2010) and grasping (Colino et al., 2014; Juravle et al., 2010) movements. We did not find tactile suppression when the stimuli were presented during movement planning, probably because the reaching latencies in our study were considerably longer (~350 ms) than the time window shown to be sensitive to tactile suppression (up to ~150 ms before movement onset; Buckingham et al., 2010; Chapman and Williams, 2002).

Importantly, the strength of tactile suppression was modulated by the modality of the target in experiment 1. While tactile stimuli were suppressed during movement execution irrespective of the target modality, tactile suppression was 1.7 times stronger when reaching to somatosensory than to visual targets. The stronger suppression during somatosensory reaching may arise from either (i) suppressing the stimulus on the moving hand more strongly, or (ii) enhancing the stimulus on the static hand, or (iii) suppressing signals on the moving hand and in parallel enhancing signals on the static hand. Below, we discuss these possibilities and argue why the latter one is the most suitable explanation.

The stronger suppression during somatosensory than visual reaching is unlikely to be caused by an additional reduction of tactile sensitivity on the moving hand. Since participants had no visual feedback of their hands and arms, somatosensory information was important for determining key aspects of the movement, such as the location of the movement target (Smeets and Brenner, 1999; Voudouris et al., 2013), the time when to stop the movement and its accuracy. Assuming limitations in processing a plethora of incoming somatosensory information (Williams and Chapman, 2002), it might be reasonable that the sensitivity on the moving hand will be reduced in order to have more resources for processing the relevant information from the target hand. The results of experiment 2, however, argue against this idea.

In experiment 2, participants performed the exact same reaching tasks as in experiment 1, but with the reference stimulus presented at a movement-irrelevant location (i.e., sternum). Tactile stimuli on the moving hand were again suppressed during reaching, but most importantly the strength of the suppression was comparable between somatosensory and visual reaching and similar to that during visual reaching in experiment 1 (cf., Fig. 3a and 4a; no effect of experiment: $F_{1,15} = 2.44$, $p = 0.14$, not reported in the *Results*). This suggests that the higher PSEs during somatosensory reaching in experiment 1 are most likely caused by additional tactile enhancement of the reference stimulus at the task-relevant location. Previous studies suggest that humans can modulate the strength of tactile suppression in a context-dependent manner (e.g., less suppression of tactile signals at digits engaged in a grasping movement; Colino et al., 2014). Our results demonstrate that humans not only flexibly adjust the strength of suppression but, in parallel, also enhance movement-relevant somatosensory signals.

The enhancement of somatosensory signals at the target hand could be explained by prioritizing and selectively processing of that information when reaching to an unseen part of the own body than to a visual target. There is evidence that humans show superior visual discrimination performance at a location to which they plan a goal-directed eye or hand movement (Deubel et al., 1998; Moehler and Fiehler, 2014; 2015). Moreover, they detect tactile stimuli faster if the stimuli are presented at a body location to which a saccade is being planned, or which will move (Juravle and Deubel, 2009). However, when humans prepare a reaching movement towards their own other hand, early somatosensory event-related potential (ERP) signals have larger amplitudes for tactile stimuli presented at the hand that is prepared to move but not at the hand serving as movement goal (Eimer et al., 2005; Foster and Eimer, 2007). This finding argues against enhanced processing of somatosensory information at the reach goal (at least) during movement planning. Here, we demonstrate that during movement execution tactile enhancement can occur for sensory signals arising from the target hand.

The differences we found between somatosensory and visual reaching are unlikely to be caused by the movement itself. Tactile sensitivity is reduced for larger movement amplitudes (Williams et al., 1998) and seems to increase at the end of the movement (Juravle et al., 2010). In the present study, reaches to somatosensory targets were slightly shorter in amplitude and thus possibly in duration because the target hand was placed approximately 5 cm closer to the start location than the visual target. Importantly, we did not find differences between somatosensory and visual reaching in experiment 2 suggesting that differences in the movement itself cannot account for our results. Moreover, somatosensory and visual reaching differed in the availability of online sensory feedback of the target location. While participants were able to rely on online somatosensory information when reaching to their own hand, online feedback of the visual target was not available as the target LED was extinguished at movement onset. The lack of online visual feedback during reaching to visual targets may have limited external validity and influenced hand movement kinematics (Westwood et al., 2003; Hesse and Franz, 2009; Voudouris et al., 2010). However, because visual information was always absent, this manipulation cannot account for our findings of parallel processes of tactile suppression and enhancement.

Our findings of experiment 3 confirm the results of experiments 1 and 2. Detection thresholds were increased on the moving hand during reaching compared to baseline and this suppression was independent of the target modality, as we found in experiment 2. Importantly, detection thresholds on the static hand were decreased during somatosensory but not during visual reaching compared to baseline. This supports our combined findings of experiments 1 and 2 suggesting that tactile sensitivity is enhanced at movement-relevant locations and at the same time suppressed at the moving hand.

We conclude that humans flexibly tailor their tactile sensitivity depending on what information is necessary for the task. Our results provide evidence that humans do not only suppress irrelevant somatosensory signals, but, in parallel, also enhance relevant somatosensory information in order to successfully perform a goal-directed movement. This is an important step in understanding the concepts underlying tactile perception, as it suggests that the paradoxical mechanism of tactile suppression may become inactive, or even reversed, if beneficial.

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Acknowledgements

We thank Hanna Gertz and Frieder Hartmann for their valuable assistance in piloting and data collection. This work was supported by the German Research Foundation (DFG) TRR 135 assigned to K.F..

Figure captions

Figure 1. Top view of the setup and timeline. Participants had their left hand in front of the touch screen and placed the two target fingers above the target zones marked with fabric (green/dark gray circles). The sight on the workspace in front of the participant was occluded by a black cardboard (here drawn transparent for illustration). Tactile stimulators (gray boxes) were attached to the right index finger and the left little finger. Participants reached from a start button to either one of two visual (blue /gray circles on the touch screen) or somatosensory (green/gray circles below the fingers of the left hand) targets after the Go cue. The target location was cued at the start of each trial. The tactile stimulation was presented at one of three time points (thick black lines): with the first tone, with the Go cue, or 150 ms after movement onset (always during movement execution).

Figure 2. Psychometric curves of a representative participant in the baseline and the visual and somatosensory reaching conditions. Data points reflect the proportion of responses participants judged the stimulus on the moving hand as stronger than on the static hand. Larger PSEs indicate stronger tactile suppression. In the baseline condition (black curves in all panels), the PSE (black vertical line) is slightly increased compared to the intensity of the reference stimulus (0.25 mm; indicated with the thick line on the x-axis). **(a)** The PSEs for the reaching conditions remain similar when the stimuli are presented *before* (blue/light gray curve for visual reaching and green/dark gray curve for somatosensory reaching) and **(b)** *with* the *Go cue* (cyan/gray curve for visual reaching and green/gray curve for somatosensory reaching). **(c)** The PSEs during reaching increases and the psychometric curves

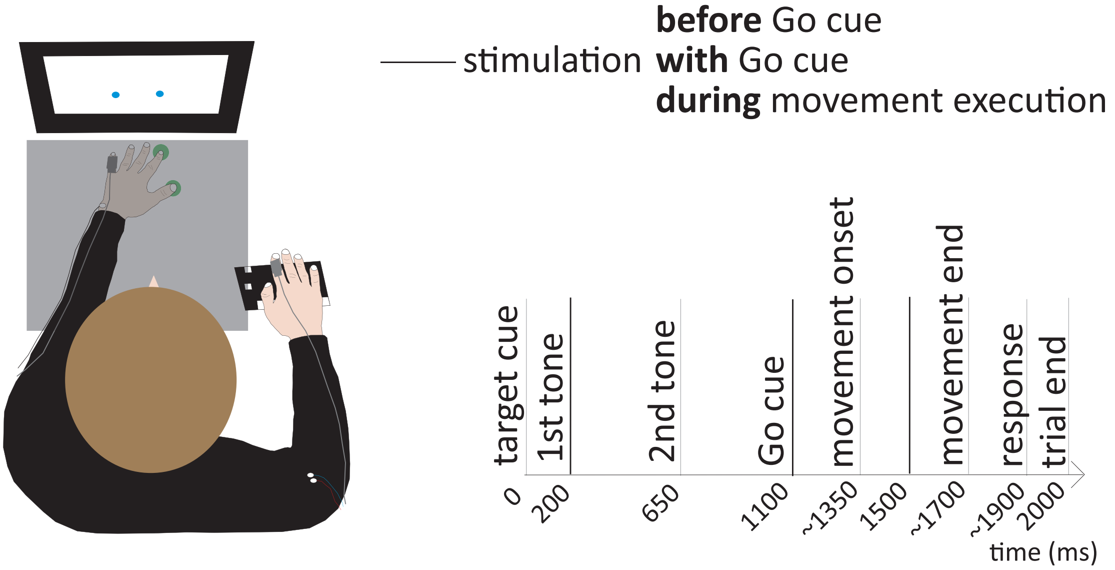
become shallower when the tactile stimuli are presented after the Go cue (i.e. *during movement*; blue/light gray curve for visual reaching and green/dark gray curve for somatosensory reaching). All curves are obtained from trials with the weak reference stimulus (0.25 mm).

Figure 3. Results of experiment 1. Effects of the stimulation time and target modality on **(a)** PSE_{diff} (PSE reaching – PSE baseline) and **(b)** JND_{diff} (JND reaching – JND baseline), averaged across the two intensities of the reference stimulus. PSE_{diff} and JND_{diff} were only influenced during movement. Importantly, PSE_{diff} were higher during somatosensory than visual reaching. Transparent blue and green circles show the effects of the conditions on PSE_{diff} and JND_{diff} for each individual participant. Error bars represent the standard error of the mean. For grayscale illustration, the first and the second dot of each dot pair indicate visual and somatosensory reaching, respectively.

Figure 4. Results of experiment 2. Effects of the stimulation time and target modality on **(a)** PSE_{diff} (PSE reaching – PSE baseline) and **(b)** JND_{diff} (JND reaching – JND baseline). PSE_{diff} and JND_{diff} did not differ between the two target modalities. Stimuli on the moving hand were more accurately and precisely discriminated when they were compared with the weak (densely dotted lines, leftmost of each triple) than with the strong reference (sparsely dotted lines, middle of each triple). Transparent blue and green circles show the effects of the conditions on PSE_{diff} and JND_{diff} for each individual participant. Error bars represent the standard error of the mean. For grayscale illustration, the left and the right triple of dots in figure (a) and (b) indicate visual and somatosensory reaching, respectively.

Figure 5. Results of experiment 3. Effects of the stimulation site and target modality on **(a)** the change in detection thresholds, and **(b)** the change in precision of stimulus detectability between reaching and baseline. The detection thresholds are lower than baseline at the static hand during somatosensory (dark green) but not during visual reaching (dark blue). The detection thresholds at the moving hand are higher than baseline during both somatosensory (light green) and visual reaching (light blue). Target stimuli on the moving hand were less precisely detected during reaching compared to baseline. The precision of detecting a stimulus on the target hand did not differ between reaching and baseline. Transparent blue and green circles show the effects of each individual participant. Error bars represent the standard error of the mean. For grayscale illustration, the left and right pairs of dots for each hand in figure (a) and (b) indicate somatosensory and visual reaching, respectively.

Figure 1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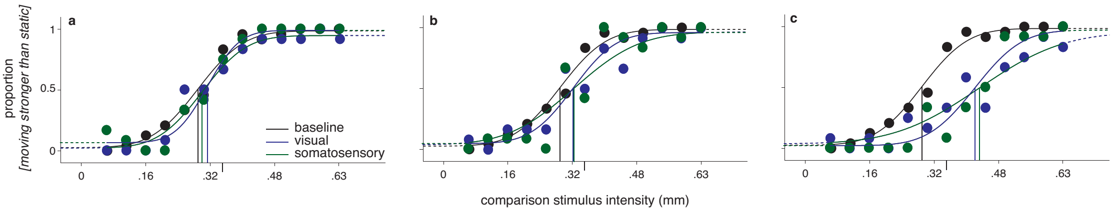
before Go cue
with Go cue
during movement execution
target cue
1st tone
2nd tone
Go cue
movement onset
movement end
response
trial end
0
200
650
1100
~1350
1500
~1700
~1900
2000
time (ms)

Figure 2


a
b
c
proportion
[moving stronger than static]
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0.5
0
baseline
visual
somatosensory
0
.16
.32
.48
.63
comparison stimulus intensity (mm)

Figure 3

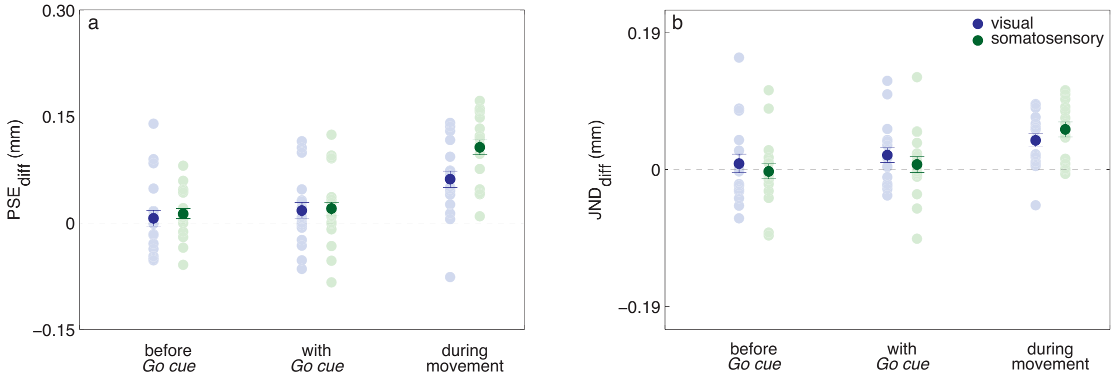
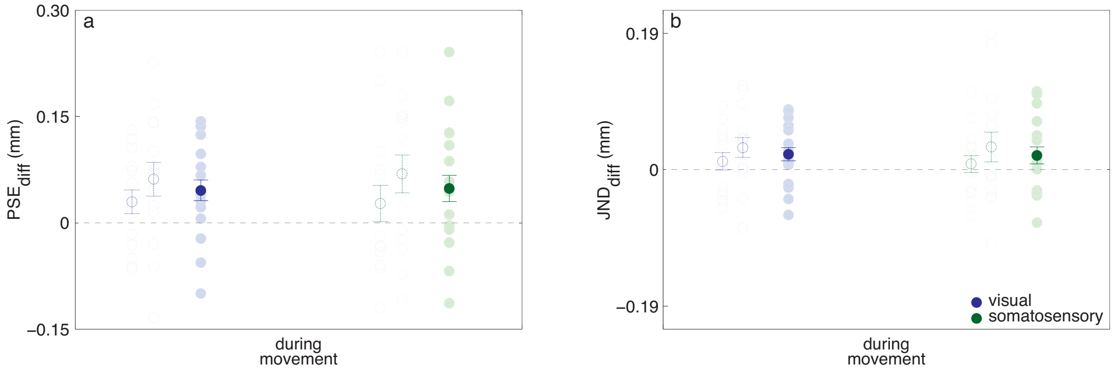

a
0.30
0.15
0
−0.15
PSE$_{diff}$ (mm)
before *Go cue*
with *Go cue*
during movement
b
● visual
● somatosensory
0.19
0
−0.19
JND$_{diff}$ (mm)
before *Go cue*
with *Go cue*
during movement

Figure 4


a
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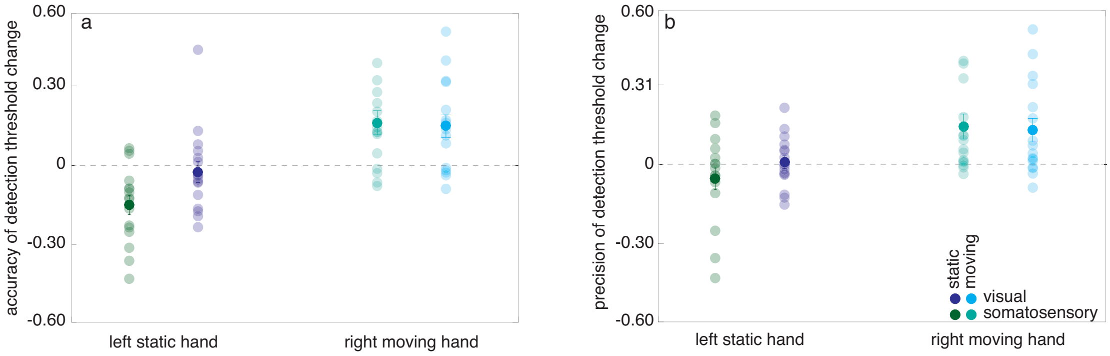
0.15
0
−0.15
PSE$_{diff}$ (mm)
during movement
b
0.19
0
−0.19
JND$_{diff}$ (mm)
during movement
● visual
● somatosensory

Figure 5


a
accuracy of detection threshold change
0.60
0.30
0
-0.30
-0.60
left static hand
right moving hand
b
precision of detection threshold change
0.60
0.31
0
-0.30
-0.60
left static hand
right moving hand
static
moving
visual
somatosensory