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Brief article

Movement preparation improves touch perception without awareness

Freek van Ede, Thomas I. van Doren, Jochem Damhuis, Floris P. de Lange, Eric Maris *

Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, The Netherlands

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ABSTRACT

Movements are often directed at external objects, such as when reaching out for a glass to drink from. Surprisingly, however, it is largely unknown how movement plans influence the identification of such external somatosensory stimuli. To address this, we cued participants to prepare for a speeded button press with their left/right thumb and presented a spatially-patterned somatosensory stimulus at either the same or the opposite thumb with equal probability. In contrast to many previous investigations that focused on self-produced somatosensory input and reported attenuated perception, we show that the identification of external stimuli (touch perception) is facilitated by movement preparation. In line with analogous studies in vision, this suggests that movement preparation automatically allocates processing resources (attention) to the location and/or body part of the planned movement. We further show that, in contrast to deliberate somatosensory preparation, participants do not become more confident in their touch perception following movement preparation. These data suggest that the perceptual improvement during movement preparation occurs outside of awareness. Such an unconscious facilitatory process will ensure that relevant parts of the environment are processed with high fidelity, while sparing conscious resources for monitoring other processes in the course of action.

1. Introduction

Movements are often directed at objects that are relevant for current goals, such as when reaching out to a glass when thirsty. To ensure optimal processing of goal-relevant information, it has been hypothesized that movements are associated with the automatic allocation of processing resources (attention) to movement-relevant locations, and that this may already start during movement preparation (e.g. Baldauf & Deubel, 2010). This is also referred to as the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987).

Evidence in support of the hypothesis that movement preparation facilitates perception at movement-relevant locations comes from studies into visual perception. In particular, preparation for goal-directed eye (Deubel & Schneider, 1996; Rolfs & Carrasco, 2012) and reaching (Baldauf & Deubel, 2010; Rolfs, Lawrence, & Carrasco, 2013) movements improves identification and enhances perceived contrast for visual stimuli that are presented at the location of the saccade- or reach goal.

Many previous studies have also investigated how movement preparation influences somatosensory perception. In striking contrast with the studies in the visual modality, the majority of these studies have concluded that movement preparation *attenuates* the perception of sensory input at the body part for which the movement

* Corresponding author at: Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Centre for Cognition, Montessorilaan 3, 6525 HR Nijmegen, The Netherlands. Tel.: +31 (0)243612651.

E-mail address: e.maris@donders.ru.nl (E. Maris).

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is prepared. This has been interpreted in the context of forward models of motor control (Wolpert & Flanagan, 2001) and predictive coding models of perception (Clark, 2013; Friston & Kiebel, 2009), in which predicted sensory input is subtracted from the actual sensory input. Indeed, in these studies, the spatiotemporal patterns of somatosensory input were highly predictable, as with tickling oneself (Blakemore, Frith, & Wolpert, 1999), self-produced force (Shergill, Bays, Frith, & Wolpert, 2003), or electrical stimulation of fixed positions on the skin (Chapman & Beauchamp, 2006; Voss, Ingram, Haggard, & Wolpert, 2006).

In goal-directed movements, external objects provide a source of somatosensory input whose precise spatiotemporal nature can often not be fully predicted. In fact, an important role of somatosensory processing is to resolve the precise identity of these objects. Surprisingly, however, it has remained largely unexplored how movement plans influence this type of touch perception.

Analogous to the observations for visual perception, we hypothesize that movement preparation will improve the identification of somatosensory stimuli whose precise spatiotemporal nature cannot be predicted (i.e. external objects). This hypothesis is further supported by the identification of a physiological substrate through which movement preparation may improve touch perception. Movement preparation is associated with the suppression of beta oscillations (15–30 Hz) throughout a distributed somatomotor network (e.g. Paradiso et al., 2004; Pfurtscheller & Lopes da Silva, 1999). Critically, suppressed beta oscillations in this same network (van Ede & Maris, 2013) have also been associated with improved touch perception (Jones et al., 2010; van Ede, Köster, & Maris, 2012).

2. Materials and methods

2.1. Participants

19 Naïve participants (7 male, 1 left handed, age range: 18–33 year) took part in the experiment. All participants provided written informed consent. The experiment followed guidelines of the local ethics committee and the declaration of Helsinki. We aimed at a sample size of approximately 20 participants based on a previous study from our lab (van Ede, de Lange, & Maris, 2012) that, with $n = 19$, demonstrated a robust influence of somatosensory preparation on the identification of similar stimuli (which serves as a reference here). We stopped at 19 because we had run out of lab time, and not because the effect of interest (Fig. 3b) had reached significance. In fact, retrospective analysis showed that this effect had already reached significance after 12 participants.

2.2. Set-up

A custom-built device (Fig. 1) allowed us to present somatosensory stimuli and to collect motor responses at the same body site. Two somatosensory stimulators (braille cells) were each mounted on a response button. Participants held the device such that the left and right thumb each rested on a braille cell (left above right). A braille cell (Metec, Stuttgart, Germany) contains eight plastic pins (diameter 1.5 mm, inter-pin spacing 2.5 mm) that can be raised and lowered individually. Pins rise 1 mm out of their casing and produce the sensation of a tap to the skin.

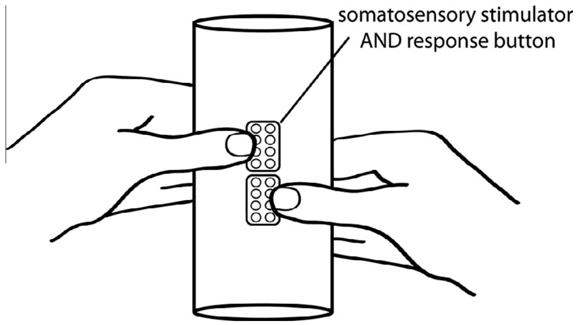

Fig. 1. Combined somatosensory stimulator and response device. Two braille cells were each mounted on a response sensor, thereby also serving as response buttons. In this schematic, braille cells are disproportionally large and thumbs are depicted to the side of these cells. In reality, thumbs covered the braille cells completely.

2.3. Design

Participants performed a combined motor/somatosensory task in which the side of either the upcoming motor response or the upcoming somatosensory stimulus could be anticipated. In each trial, participants consecutively responded to the motor task and thereafter to the somatosensory task.

In *movement preparation blocks* (Fig. 2a), we cued participants to prepare for a speeded button press with their left or right thumb. 1.5 s after the preparatory cue (an arrow pointing left- or rightward), the response signal for the motor task (the word "LEFT", "RIGHT" or "NO"), indicated to either press the left- or the right-thumb button as fast as possible, or to refrain from a response. In case of a go trial ("LEFT" or "RIGHT"), the preparatory cue correctly indicated the side of the required button press in 80% of the trials; in 20% of the go trials, the required button press was invalidly cued.

To probe somatosensory perception, we presented a somatosensory stimulus simultaneous with the response signal for the motor task. Somatosensory stimuli were equally likely to occur at the same (congruent) or the opposite (incongruent) thumb as the thumb for which a movement was prepared. Participants' task was to identify whether the upper or the lower two pins of the braille cell on the stimulated thumb were raised (see inset Fig. 2a). To increase difficulty, targets were followed by a mask in which all pins were raised. Target and mask each lasted for 20 ms, and were 100 ms apart. Participants indicated an upper/lower target by pressing the left/right-thumb button, respectively. Participants also indicated confidence in their perceptual report by varying the duration of their response. A visual analogue confidence bar was filled for as long as the button remained pressed (max 600 ms).

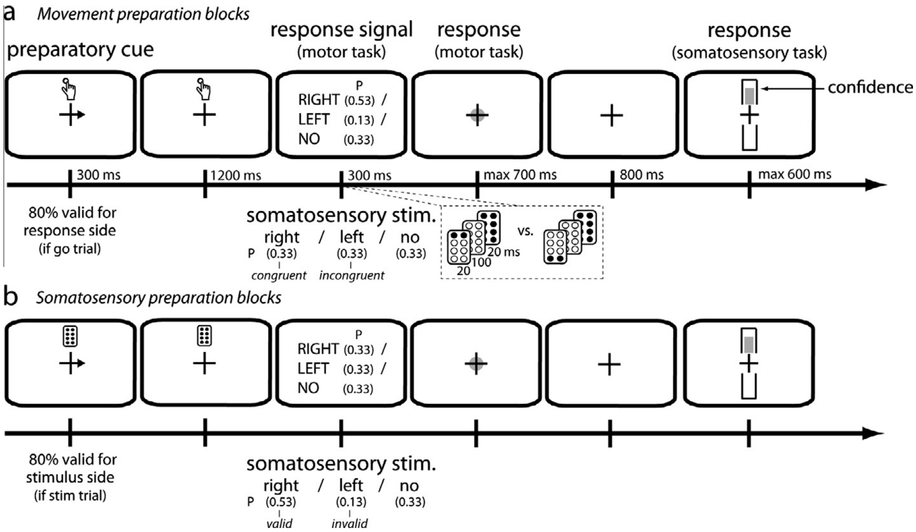

Fig. 2. Trial structures in movement (a) and somatosensory (b) preparation blocks. (a) The preparatory cue consists of a right- (as depicted) or leftward pointing arrow that is appended to the fixation cross. Above the arrow, a schematic of a button press indicates that the cue is informative for the side of the upcoming response signal of the motor task. After a preparatory interval, the response signal for the motor task is presented simultaneous with a somatosensory stimulus. Response signals instruct to press the left/right thumb button as fast as possible (go trials) or to refrain from responding (no go trials). Preparatory cues predict the side of the required button press (left/right thumb) with 80% validity, in case of a go trial (because 1/3 of the trials are no go trials, the probability for a response signal for the prepared side is 0.53 vs. 0.13 for the opposite side). Somatosensory stimuli are equally likely at the same thumb for which the movement is prepared (congruent), or at the opposite thumb (incongruent). Participants first respond to the response signal. To emphasize a speeded response, an ellipsoid increases in size, until it reaches the boundaries of the fixation cross at the maximum response time of 700 ms. A second response screen (with placeholders for confidence bars; rightmost display) indicates to report which of two possible somatosensory stimuli (see inset) was perceived at the time of the motor response signal. Upper (lower) somatosensory stimuli require a left (right) button press. Confidence is reported through button press duration. (b) Identical to A, except preparatory cues are informative for the side (again: left/right thumb) of the upcoming somatosensory stimulus. This is indicated by the schematic of a braille cell.

800 ms after the response to the motor task (or after refraining from a response for the max response time of 700 ms), a second response screen appeared and participants indicated their perceptual report and confidence. In 1/3 of the trials no stimulus was presented (analogous to no-go trials in the motor task) and the latter screen was skipped. Inter-trial-intervals were uniformly distributed between 1000 and 2000 ms.

To compare movement and somatosensory preparation with respect to their effect on touch perception, we included *somatosensory preparation blocks* (Fig. 2b) in which the preparatory cue was informative for the side of the upcoming somatosensory stimulus, instead of the upcoming response signal for the motor task. Again, participants first responded to the response signal for the motor task and thereafter indicated their perceptual report and confidence. Cued modality (motor/somatosensory) remained indicated on the screen throughout the preparatory interval (Fig. 2).

2.4. Procedure

Participants first practiced the motor and the somatosensory tasks separately (in different trials) and then integrated (in the same trials), for approximately five minutes each. For the somatosensory task, we titrated the difficulty in several participants to an accuracy of approximately 75%. For five participants we increased difficulty by using four instead of two pins for the upper/lower patterns and for four participants we decreased difficulty by prolonging the target-mask interval to 125 ms. Each participant completed two consecutive sessions of one hour, each containing 10 blocks of 60 trials each. The modality for which the preparatory cue was informative (motor/somatosensory) changed once per session, after five blocks. At this point, the experimenter carefully instructed the participant to use the preparatory cue for the other modality. Order of the modality blocks were counterbalanced across sessions and participants.

2.5. Analysis

For the motor task, we analyzed accuracy and reaction times (RTs). For the somatosensory task, we analyzed identification accuracy and confidence. We did not analyze RTs of the somatosensory reports because the motor task occurred in between the stimulus and the report. To quantify the effects of preparation, we calculated the following effect size percentages: [(valid–invalid)/invalid $*$ 100] and [(congruent–incongruent)/incongruent $*$ 100]. Percentages were calculated for each participant and tested at the group level against the null hypothesis of no difference using one-sample *t*-tests (alpha = 0.05, two-tailed). Reported measures of spread represent the 95% confidence interval.

3. Results

3.1. Movement preparation improves performance in the motor task

We first ascertained that participants adequately engaged in the speeded reaction time task. Participants performed this task with high accuracy, pressing the left or right button correctly (and in time) in 88.99 ± 3.31% of all go trials, and correctly withholding a button press in 96.47 ± 1.56% of all no go trials. In movement preparation blocks (Fig. 2a), responses to validly cued response signals (392 ± 24 ms) were 25 ± 12 ms faster than responses to invalidly cued response signals (417 ± 20 ms) and this difference was highly significant: $t(18) = 4.31$, $p < 0.001$, $d = 0.99$. This shows that movement preparation was effectively induced and paves way to investigate how movement preparation influences somatosensory identification accuracy and confidence.

3.2. Both somatosensory and movement preparation improve touch perception

We first ascertained that our somatosensory task was sensitive to preparatory influences by focusing on identification accuracy in somatosensory preparation blocks (Fig. 2b). As depicted in Fig. 3a, stimuli were better identified when presented to the hand at which these were expected (validly cued stimuli) compared to the opposite hand (invalidly cued stimuli): $t(18) = 3.30$, $p = 0.004$, $d = 0.76$. This is in line with a previous study that used similar stimuli (van Ede, de Lange et al., 2012) and serves as a reference for evaluating the influence of movement preparation on the performance in this task.

For evaluating the influence of movement preparation on touch perception, we focused on somatosensory identification in movement preparation blocks (Fig. 2a). Specifically, we contrasted trials in which somatosensory stimuli occurred at the same (congruent) vs. the opposite (incongruent) thumb as the thumb for which the movement was prepared. Fig. 3b depicts our main observation: stimuli presented to the thumb for which the movement was prepared were better identified than stimuli presented to the opposite thumb: $t(18) = 2.58$, $p = 0.019$, $d = 0.59$ (despite the fact that congruent and incongruent stimuli were equally likely; see Fig. 2a).

The influence of movement preparation on somatosensory identification accuracy was not as large as the influence of somatosensory preparation (compare Fig. 3b with 3a). This was confirmed by a significant interaction between the factors cued-side (same/opposite as the side of the somatosensory stimulus) and cued-modality (motor/somatosensory): $F(1,18) = 4.64$, $p = 0.045$, $\eta_p^2 = 0.21$. However, the central point is that we here demonstrate the existence and facilitatory nature of the former influence.

To isolate the influence of movement preparation from movement execution, we performed the same analysis as above but now only included no go trials in which the

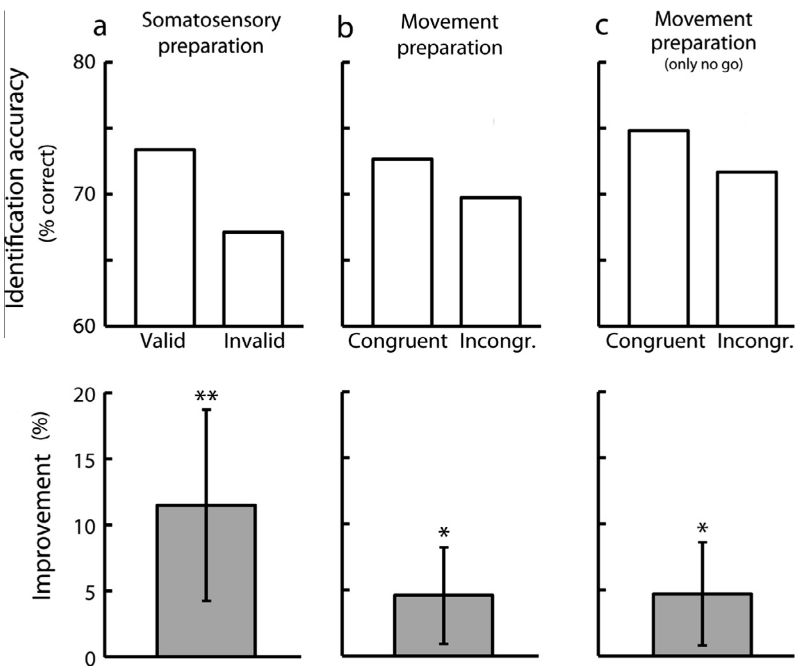

Fig. 3. Somatosensory identification accuracy following somatosensory and movement preparation. (a) Top panel: identification accuracy for somatosensory stimuli that followed a valid or invalid preparatory cue in somatosensory preparation blocks. Lower panel: percentage improvement due to valid somatosensory preparation. (b) Similar to panel A, except for somatosensory stimuli that occurred congruent or incongruent with the side of the preparatory cue in movement preparation blocks. Lower panel depicts improvement in somatosensory identification due to congruent movement preparation. (c) Similar to panel B, except only no go trials were analyzed in which the response in the motor task was correctly withheld. Error bars represent 95% confidence intervals. $^{*}p < 0.05$, $^{**}p < 0.005$.

response to the motor response signal "NO" (Fig. 2) was correctly withheld. As depicted in Fig. 3c, in these trials, we observed a highly similar facilitatory effect of movement preparation on somatosensory identification accuracy: $t(18) = 2.47$, $p = 0.024$, $d = 0.57$.

Finally, in our Supplementary material, we exclude the possibility that the observed facilitation of touch perception in movement preparation blocks reflects a carry-over effect from previous somatosensory preparation blocks.

3.3. Somatosensory but not movement preparation increases somatosensory identification confidence

We also analyzed how somatosensory and movement preparation influenced identification confidence. As depicted in Fig. 4a, somatosensory preparation resulted in higher confidence in the perceptual report for validly compared to invalidly cued somatosensory stimuli: $t(18) = 3.15$, $p = 0.006$, $d = 0.72$. Strikingly, this was not the case for movement preparation (Fig. 4b): $t(18) = 0.24$, $p = 0.810$, $d = 0.05$. Thus, responses to congruent somatosensory stimuli were not rated with higher confidence than responses to incongruent somatosensory stimuli, despite the facilitatory effect in accuracy (Fig. 3b). This was also true when focusing exclusively on no go trials (Fig. 4c): $t(18) = -1.37$, $p = 0.188$, $d = -0.31$. This dissociation between the influence of somatosensory and movement preparation was further supported by a significant interaction between the factors cued-side (same/opposite as the side of the somatosensory stimulus) and cued-modality (motor/somatosensory): $F(1,18) = 9.52$, $p = 0.006$, $\eta_p^2 = 0.35$.

These results were highly similar when we only included correct responses: somatosensory preparation: $t(18) = 2.56$, $p = 0.198$, $d = 0.59$; movement preparation: $t(18) = 0.54$, $p = 0.597$, $d = 0.12$; movement preparation only no go: $t(18) = -1.50$, $p = 0.152$, $d = -0.34$.

Importantly, the dissociation between the influences of somatosensory preparation and movement preparation on identification confidence could not be explained by the notion that participants only engaged in reporting their confidence in the somatosensory preparation blocks. In fact, average confidence did not differ between the somatosensory and the movement preparation blocks: $t(18) = -0.11$, $p = 0.913$, $d = 0.03$.

4. Discussion

We show that movement preparation improves perceptual accuracy at the body part for which the movement is prepared. This builds on previous work that had already shown that movement preparation can speed up reactions (Juravle & Deubel, 2009) and amplify neural responses (e.g. Eimer, Forster, Velzen, & Prabu, 2005) to somatosensory stimuli. We further show that, in contrast to explicitly cued somatosensory preparation, participants do not become more confident in their touch perception following movement preparation, suggesting that this improvement occurs outside of awareness.

To date, the notion that movement preparation improves perception at movement-relevant locations has been supported primarily by studies on visual perception (e.g. Baldauf & Deubel, 2010; Deubel & Schneider, 1996; Rolfs & Carrasco, 2012; Rolfs et al., 2013). The current work shows that this notion is more generally applicable. Thus, when planning a movement, processing resources are allocated to improve both vision and touch.

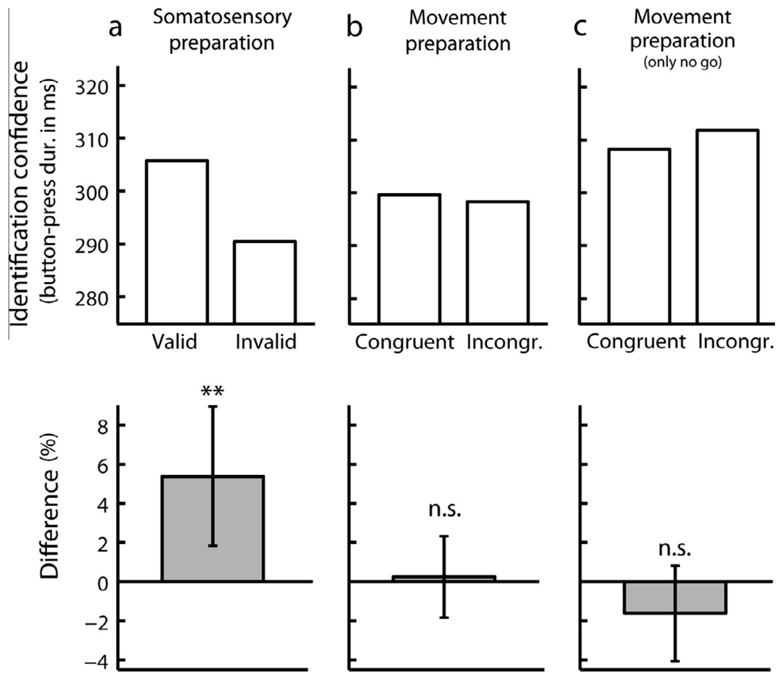

Fig. 4. Somatosensory identification confidence following somatosensory and movement preparation. Same conventions as in Fig. 3. Confidence was reported through button press duration. A bar filled up on the screen as long as the button remained pressed (up to max 600 ms). $^{**}p < 0.01$.

There are two relevant differences between the preparatory allocation of visual–spatial attention with eye movements and the preparatory allocation of somatosensory attention with manual movements. First, the allocation of attention prior to manual (but not eye) movements may occur either at the moving body part or at the location of the movement goal. Unfortunately, our experiment did not allow for distinguishing between these alternatives (but see Forster & Eimer, 2007). Second, Attention shifts prior to eye (but not manual) movements may also serve a "previewing" function of future foveal input, although it has been argued that facilitation of (non-foveal) target processing may be the main purpose of such shifts too (Cavanagh, Hunt, Afraz, & Rolfs, 2010).

What physiological substrate may underlie the observed facilitatory influence of movement preparation on touch perception? Recent studies have suggested that the somatosensory and motor cortices undergo collective changes in state (van Ede & Maris, 2013; Zagha, Casale, Sachdev, McGinley, & McCormick, 2013). Accordingly, movement preparation may automatically change the state of somatosensory cortices to facilitate somatosensory identification. Indeed, activation of the primary motor cortex has been shown to increase the discriminability of responses to somatosensory stimuli in the primary somatosensory cortex of rodent (Zagha et al., 2013).

Most prior studies on the influence of movement preparation on somatosensory perception have demonstrated attenuated perception. This has been interpreted in the context of forward models of motor control (Wolpert & Flanagan, 2001) and predictive coding models of perception (Clark, 2013; Friston & Kiebel, 2009) in which expected sensory input is 'explained away'. This may indeed account for attenuated perception of self-produced force (Shergill et al., 2003), self-tickle (Blakemore et al., 1999) and electrical stimulation of fixed positions of the skin (Chapman & Beauchamp, 2006; Voss et al., 2006). In contrast, we have here studied somatosensory identification of external objects. External objects generate input whose precise pattern can often not be predicted, but rather must be identified. As we have shown here, such identification is facilitated by movement preparation. Thus, whether somatosensory perception will be attenuated or facilitated by movement preparation may depend critically on the predictability of the somatosensory input. In addition, this may also depend on the time-period in which somatosensory perception is probed, such as before or during the movement (see e.g. Juravle, Deubel, & Spence, 2011), although during the movement one must deal with the influence of re-afferent somatosensory input that may mask the perception of external stimuli (Chapman & Beauchamp, 2006).

We observed that, while movement preparation improved participants' identification accuracy, it did not increase their perceptual confidence. This suggests that this improvement occurs outside of awareness. To our knowledge, this is the first demonstration that the influence of movement preparation on perception may be unconscious. In contrast, we observed that explicitly cued somatosensory preparation did increase perceptual confidence. This dissociation may be explained by the notion that participants only monitor their perceptual performance when cues instruct deliberate perceptual preparation.

Given that a great deal of our perception results from movement, perceptual facilitation by preparatory processes might more often occur unconsciously as a result of movement preparation, rather than consciously as a result of deliberate perceptual preparation. Such an unconscious facilitatory process may ensure that relevant parts of the environment are processed with high fidelity, while sparing conscious resources for monitoring other processes in the course of action.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2015.01.009.

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