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Touch automatically upregulates motor readiness in humans

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van Ede F, Winner T, Maris E. Touch automatically upregulates motor readiness in humans. J Neurophysiol 114: 3121–3130, 2015. First published September 23, 2015; doi:10.1152/jn.00504.2015.—Goal-directed movements require effective integration of tactile input with ongoing movement. Here we investigated the functional consequences of such integration in healthy humans by probing the influence of spatially congruent and incongruent tactile stimuli on performance in a speeded button-press task. In addition, using magnetoencephalography (MEG), we evaluated whether the modulation of somato-motor beta (13–30 Hz) oscillations following tactile input—which has been shown to propagate to motor areas—could underlie this influence. We demonstrate that congruent tactile stimuli, despite being irrelevant to the motor task, lead to both faster and more accurate responses. We further show that this automatic upregulation of lateralized motor readiness 1) is specific to tactile input, 2) is independent of the spatial separation of the hands in peripersonal space, and 3) lasts (and remains facilitatory) for up to a second after the tactile input. This pattern of behavioral results is in line with recent physiological investigations showing that somatosensory and motor areas directly influence each other’s processing capacity through joint changes in brain state. At the same time, however, the tactile-induced modulation of beta oscillations (one particular index of such a somato-motor state change) could not account for the observed movement facilitation, because it had a different time course.

tactile stimuli; movement; sensorimotor integration; beta oscillations; automatic facilitation

GOAL-DIRECTED MOVEMENTS require effective interactions between the brain’s somatosensory and motor areas. Recent physiological studies have suggested that such interactions are facilitated by the direct influence of somatosensory areas on motor areas, and vice versa. For example, stimulation of rodent primary motor cortex (M1) influences the physiological state of the primary somatosensory cortex (S1) through a direct pathway from M1 to S1, and this improves sensory processing (Lee et al. 2013; Zagha et al. 2013). Likewise, sensory responses and state changes in S1 propagate to M1 (Ferezou et al. 2007) as well as the spinal cord (van Ede and Maris 2013) and may even contribute to motor control directly (Coulter and Jones 1977; Matyas et al. 2010). To date, however, the behavioral consequences of such tactile-induced state changes of the motor system have remained largely unexplored. Moreover, most previous inferences on the integration between touch and movement (including the involvement of somato-motor state changes) have been based on animal (i.e., rodent) models. In the present work, we therefore aimed at characterizing the influence of touch on movement in healthy humans. In particular, we investigated the influence of external tactile stimuli on motor readiness: the ability to respond quickly to an arbitrary response signal (imperative cue).

Our objectives were threefold. First, we wanted to demonstrate the existence of an automatic and facilitatory influence of tactile input on motor readiness. We hypothesized that if tactile stimuli automatically upregulate motor readiness, then such stimuli should speed up movements at the stimulated effector, even when they are irrelevant to the movement task. Second, we wanted to characterize the time course of this hypothesized influence. Finally, we wanted to assess whether this tactile-induced movement facilitation could be accounted for by a tactile-induced neural state change in the motor system.

We approached our third and most challenging objective in two ways, using both behavioral and electrophysiological data. First, we reasoned that if tactile-induced motor state changes underlie the hypothesized movement facilitation, then this facilitation should be specific to tactile (as opposed to nontactile) stimuli. Moreover, it should be independent of the positioning of the (stimulated) effector in peripersonal space. Second, we also directly assessed the involvement of one particular index of tactile-induced state changes in the motor system: the tactile-induced modulation of somato-motor beta oscillations (13–30 Hz). Ample studies have demonstrated that these oscillations are inversely related to motor readiness, whereby their suppression is associated with enhanced readiness (e.g., Gilbertson et al. 2005; Pogosyan et al. 2009; Zhang et al. 2008). Importantly, the same beta oscillations are also suppressed by tactile input (Cheyne et al. 2003; Gaetz and Cheyne 2006; Hari and Salmelin 1997), with the suppression propagating from somatosensory to motor areas of the nervous system (van Ede and Maris 2013; see also Brovelli et al. 2004). Accordingly, we hypothesized that the tactile-induced suppression of beta oscillations may underlie the hypothesized movement facilitation. Moreover, because beta oscillations are also known to rebound after their suppression, we also hypothesized that the initial movement facilitation following tactile
input will change into movement inhibition during the beta rebound.

MATERIALS AND METHODS

Participants. Eighteen healthy human volunteers (9 men, 9 women; mean age 25 yr, range 20–33 yr; all right-handed with 1 exception) participated in the study after giving informed consent. The experiment was conducted according to protocols reviewed and approved by the local ethics committee (Committee on Research Involving Human Subjects, Region Arnhem-Nijmegen, The Netherlands). Data of one male participant were excluded because of malfunctioning of the tactile stimulators at the time of the experiment.

Materials. For tactile stimulation, we used two piezoelectric braille cell (Metec, Stuttgart, Germany)—one for each thumb—that were each built into a graspable plastic cylinder (see Fig. 1A). Each braille cell contains eight pins (pin diameter: 1.5 mm; pin spacing: 2.5 mm) aligned in two columns of four. Tactile stimulation was achieved by simultaneously raising all eight pins of either braille cell. When raised, pins stood 1 mm out of their casings. Twenty milliseconds after being raised, all pins were retracted into the casing again. Stimulation was well above detection threshold.

Each tactile stimulator was mounted onto a response sensor, such that button presses could be made with the left and right thumbs without participants having to displace their thumbs.

As depicted in Fig. 1A, the tactile stimulation/response devices could be held in two configurations, referred to as the close and far configurations. When in the close configuration, the hands would be held in front of the body midline (with the left thumb placed above the right thumb; Fig. 1A) and the distance between the centers of both braille cells would be as little as 2 cm. To transition from the close to the far configuration, participants inserted a tube between the two tactile stimulator/response units to create a horizontal distance between the braille cells of 81 cm.

For control purposes, we also presented lateralized auditory and visual stimuli. For auditory stimulation, we used [magnetoencephalography (MEG) compatible] earplugs through which we presented a 500-Hz pure tone to the left or right ear. For visual stimulation, we positioned a screen ~70 cm in front of the eyes and presented a white disk of 2-cm diameter (1.6° visual angle) to the left or right of the fixation cross with a horizontal offset of 15 cm (12.2° visual angle). Like the tactile stimuli, the visual and auditory stimuli lasted for a short time (16.7 and 20 ms, respectively) and were well above detection threshold.

Experimental design and procedure. We employed a speeded button-press task in which we probed the influence of side-congruent and side-incongruent tactile, visual, and auditory stimuli that were irrelevant to the motor task.

Figure 1B shows the trial design. A white fixation cross centered on a black display was presented throughout the experiment. Participants were instructed to respond as fast as possible to a blue/yellow color change of this fixation cross (defined as the “imperative cue”) by pressing either the left- or right-thumb button, depending on the presented color. Color-response side pairings were counterbalanced across participants. The color of the fixation cross remained blue or yellow either until a response was made or until the maximal time for responding of 700 ms was exceeded. After incorrect responses (either when the wrong button was pressed or when no response was registered within 700 ms), the fixation cross turned red for 300 ms. To encourage fast responses, a gradually expanding white disk around the fixation cross was presented, indicating elapsed time. After the response (and the feedback) the fixation cross remained on the screen. Therefore, the fixation cross did not mark the onset of a trial.

To probe the influence of task-irrelevant stimuli on performance in the speeded button-press task, we presented task-irrelevant tactile, auditory, or visual stimuli around the time of the imperative cue to the left or right hand/ear/side of the screen. Because we primarily aimed at comparing the influence of tactile with nontactile task-irrelevant stimuli, 50% of these stimulus-containing trials contained a tactile stimulus, while the other half contained either a visual (25%) or an auditory (25%) stimulus. Stimulus presence, side, and modality were randomly drawn on a trial-by-trial basis. Crucially, the side of the task-irrelevant stimulus was uninformative about the side of the required button press, resulting in 50% of trials in which the side of the task-irrelevant stimulus was congruent with the side of the required button press and 50% of trials in which it was incongruent. Participants were instructed to neglect the task-irrelevant stimuli and to focus exclusively on the color change of the fixation cross.

To investigate the time course of the influence of the task-irrelevant stimuli on performance in the speeded button-press task, we varied the interval between the task-irrelevant stimulus and the imperative cue. The task-irrelevant stimulus (which lasted ~20 ms) would occur in an interval ranging from 1,000 ms before to 200 ms after the onset of the imperative cue, with intervals drawn randomly from a uniform distribution on a trial-by-trial basis.
As control trials, in 5% of the trials no task-irrelevant stimulus was presented (allowing us to evaluate behavioral performance without task-irrelevant stimuli) and in another 10% task-irrelevant stimuli were presented that were not followed by an imperative cue (allowing us to investigate the neural response to these stimuli without contamination by imperative cues and button presses). Control trials were randomly interleaved with regular task trials. The interval between the last event in a trial and the first event in the next trial (the intertrial interval) was randomly drawn between 300 and 800 ms, except in the task-irrelevant stimulus-only trials, in which 1,500 ms passed before the next event.

Hand positioning (being in the close or far configuration; Fig. 1A) was manipulated blockwise and was counterbalanced across blocks. Critically, in the close configuration the left and right thumbs were very close to each other, whereas in the far configuration they were very far from each other (Fig. 1A). Accordingly, this manipulation allowed us to investigate whether the influence of the task-irrelevant stimuli (in particular the differential influence between side-congruent and -incongruent stimuli) depended on the distance between the hands in peripersonal space.

Data were collected in two experimental sessions of ~1 h each. Both sessions were scheduled on a single day and separated by a 15-min break. Each session consisted of 16 experimental blocks containing 84 trials. In total, ~1,200 tactile and 1,200 nontactile trials were collected from each participant.

**Analysis of behavioral data.** We analyzed two dependent variables: reaction time (RT) and accuracy in the speeded button-press task. For all analyses on RT, we only included trials with a correct response.

We estimated the influence of tactile and nontactile (visual and auditory) stimuli on performance in the speeded button-press task as a function of the interval between the task-irrelevant stimulus and the imperative cue. For this, we employed a sliding time window approach (as adopted from van Ede et al. 2012). First, we sorted trials based on the interval between the task-irrelevant stimulus and the imperative cue. We then calculated average RT and accuracy scores for intervals within a 250-ms window that we advanced in 12 steps of 100 ms over the interval range from −225 to 975 ms (i.e., from imperative cues presented 225 ± 125 ms before the task-irrelevant stimulus to 975 ± 125 ms after this stimulus).

For statistical evaluation, we contrasted trials in which the task-irrelevant stimulus occurred on the same (congruent) or opposite (incongruent) side as the required button press. For our main statistical inferences, we collapsed across all task-irrelevant stimulus–response intervals and evaluated this congruency effect with paired-samples t-tests. We also employed two 2 × 2 ANOVAs to evaluate the interactions between the factors 1) congruency and task-irrelevant stimulus modality (tactile/nontactile) and 2) congruency and hand position (close/far configuration). In addition, we also statistically evaluated the congruency effect jointly at all tested intervals between the task-irrelevant stimuli and the imperative cues. To circumvent the multiple-comparison problem introduced by evaluating the congruency effect at multiple intervals, we made use of a cluster-based permutation approach, as described in Maris and Oostenveld (2007). In short, in this approach thresholded univariate t-values for adjacent intervals are clustered and collectively evaluated under a single permutation distribution.

**Analysis of MEG data.** During the experiment, we also collected electrophysiological data with MEG. This allowed us to assess whether the tactile-induced modulation of beta oscillations (suppression followed by rebound) over the contralateral primary somato-motor areas (see, e.g., van Ede and Maris 2013) could account for the hypothesized tactile-induced influence on performance in the speeded button-press task. To evaluate this hypothesis, we extracted the time course of this beta modulation and compared it to the time courses of the tactile congruency effects obtained for RT and accuracy (as described above).

Data acquisition and analyses were very similar to van Ede et al. (2011, 2012) and van Ede and Maris (2013), and we here limit ourselves to repeating the essential details of the present analysis. Data were collected with a CTF MEG system that contained 275 axial gradiometers. Data were sampled at 1,200 Hz and were analyzed in MATLAB with FieldTrip (Oostenveld et al. 2011). As part of our preprocessing pipeline, we removed line noise with a discrete Fourier transform filter and cut out our epochs of interest and demeaned them. Next, we removed excessively noisy trials by visual inspection of the data. Finally, we calculated the planar gradients of the signal that are known to be maximal above the sources (Bastiaansen and Knosche 2000). Horizontal and vertical gradients were combined (summed) after power was calculated. Having cleaned our data and calculated the planar gradients of the signal, we first selected channel clusters above the left and right primary somato-motor areas based on the strongest difference in beta (13–30 Hz) power following left and right tactile stimuli in the poststimulus window between 150 and 400 ms (the window in which the beta suppression is most pronounced). We made this selection per participant and always selected 10 left and 10 right somato-motor channels. We next used a short-time Fourier transform to calculate the time-resolved modulation of oscillatory power in each channel and averaged across the 10 channels in each channel cluster. As for the behavioral time courses, we used a 250-ms sliding time window that was advanced in 100-ms steps. To avoid contamination of neural activity induced by subsequent imperative cues and/or responses, we only included time windows after the tactile stimulation for which the imperative cue and the response had not yet occurred. Because we had included control trials in which tactile stimuli were not followed by an imperative cue for 1,500 ms, we were able to map the time course of the beta modulation in an uncontaminated way for this sufficiently long interval. Finally, we normalized the power following contralateral tactile stimulation as a percent change from the power following ipsilateral stimulation (cf. van Ede et al. 2012; van Ede and Maris 2013). This resulted in a spatially specific metric whose time course could be compared to the time courses of the spatially specific congruency effects calculated for RT and accuracy.

We analyzed time-resolved power both with and without frequency resolution. For the analysis with frequency resolution, we applied a Hanning taper to the data before doing the spectral analysis. In contrast, when zooming in on the beta modulation we used a multitaper approach (Percival and Walden 1993) that allowed us to control spectral smoothing and thereby to estimate power in the beta frequency band between 13 and 30 Hz.

**RESULTS**

To probe whether tactile input automatically facilitates movement at the stimulated effector, we employed a speeded button-press task in which we presented task-irrelevant tactile stimuli at the same (congruent) or opposite (incongruent) thumb as the required button press (Fig. 1B). Moreover, to map several properties of this hypothesized influence, we also 1) varied the interval between the task-irrelevant stimulus and the task-relevant imperative cue in order to characterize its time course, 2) manipulated the positioning of the hands to assess its dependence on the spatial separation of the thumbs, and 3) included task-irrelevant congruent and incongruent visual and auditory stimuli to assess its modality specificity. Because the visual and auditory stimuli served the same control purpose—and because we did not observe significant differences between them—we collapsed across them and refer to them jointly as nontactile stimuli (but see Fig. 4A).

Tactile input automatically facilitates movement at the stimulated effector. Figure 2A depicts average RTs as a function of the interval between the task-irrelevant stimulus and the im-
The zero point on the x-axis in Fig. 2A corresponds to the time of the task-irrelevant stimulus, with negative time points signifying trials in which imperative cues preceded these stimuli and positive time points signifying trials in which imperative cues followed these stimuli. Open circle on left depicts average RT in trials without task-irrelevant stimuli. B: identical to A, except for accuracy. C: congruency effect (congruent minus incongruent) time courses for RT, separately for trials with tactile and nontactile task-irrelevant stimuli. D: identical to C, except for accuracy. E: congruency effect time courses for RT in trials with tactile stimuli, separately for blocks in which the hands were held in the close and far configurations. F: identical to E, except for accuracy. Colored shadings represent ±1 SE, calculated across participants. Horizontal lines indicate significant temporal clusters as revealed by a cluster-based permutation analysis. All significant clusters had a P value < 0.005.

In the present study, we were specifically interested in a more specific type of facilitation that may dissociate between tactile and nontactile stimuli. For this, we made use of spatially congruent and incongruent stimuli. We reasoned that, while both congruent and incongruent stimuli would have the same “alerting effect,” their influences may dissociate by virtue of an additional influence, such as state changes that propagate from somatosensory to motor areas of the brain. Critically, this influence would be expected to occur only for spatially congruent stimuli and only for stimuli that are tactile. In the following, we therefore focused on the RT difference between congruent and incongruent stimuli, because this subtraction removed the general alerting effect.

Thus the central phenomenon of this report pertains to the differential response to spatially congruent vs. spatially incongruent tactile stimuli. As can be seen in Fig. 2A, for most tested intervals, RTs are shorter in trials with congruent compared with incongruent tactile stimuli. Collapsed across all tested intervals, this pertains to a 9.8 ± 1.4-ms (mean ± 1 SE) benefit.
that is highly significant \( t_{1(6)} = -7.26, P < 0.001 \). In comparison, no such congruency effect is observed for non-tactile stimuli \( (P = 0.23) \), giving way to an interaction between the factors congruency and stimulus modality that is also highly significant \( F_{1,1(6)} = 24.9, P < 0.001 \).

Figure 2C zooms in on the time course of this congruency effect and reveals that tactile stimuli facilitate RTs most when presented around the time of the imperative cue, which is on average \( >400 \text{ ms} \) before the actual response (given an average RT \( >400 \text{ ms} \)). While this facilitatory influence decays thereafter, it is noteworthy that a significant facilitation is still observed for responses to imperative cues that are presented up to 500 ms after the transient \( (20 \text{ ms}) \) task-irrelevant tactile input \( (\text{significant temporal cluster from } -225 \text{ to } 675 \text{ ms}; P < 0.005; \text{ also indicated in Fig. 2C}) \). This corresponds to overt responses that are registered on average \( >900 \text{ ms} \) after this input.

Figure 2, B and D, depict the corresponding results for accuracy in the speeded button-press task and reveal that congruent tactile stimuli also lead to a higher percentage of accurate responses. In contrast to the RT effect, however, the accuracy benefit appears to last for a shorter time \( (\text{significant temporal cluster from } -225 \text{ to } 75 \text{ ms}; P < 0.005; \text{ also indicated in Fig. 2D}) \) and to be present also after nontactile stimuli \( (\text{albeit to a lesser extent}) \). However, this latter trend did not reach significance and, moreover, did not generalize to an RT effect \( (\text{despite the fact that the RT effect was far more robust}) \).

Tactile-induced movement facilitation is independent of spatial separation of the hands. We next evaluated whether the observed tactile congruency effects depend on the spatial separation of the hands. To assess this, we compared the time courses of the tactile congruency effects between blocks in which the hands were held in the close and the far configurations \( (\text{see Fig. 1A}) \). As evident from Fig. 2, E and F, congruency benefits were highly comparable between these different postural configurations, and this was the case for both the RT and the accuracy benefit. In fact, for none of the intervals did we observe a significant interaction between the factors congruency and hand position.

Tactile-induced modulation of beta oscillations cannot account for the tactile-induced movement facilitation because it follows a different time course. Finally, we assessed whether the time course of the tactile-induced movement facilitation \( (\text{i.e., the congruency effect}) \) might be matched by the time course of the tactile-induced modulation of the amplitude of beta oscillations. To this end, we extracted the time course of this beta modulation and compared this to the behavioral congruency time courses. To extract the time course of the beta modulation, for each participant we selected 10 channels above the left and right somato-motor cortices based on the topography of the initial beta suppression that was calculated by contrasting responses to left and right tactile stimuli. The grand-average topography of this contrast is depicted in Fig. 3A. After this channel selection, we were able to contrast contralateral with ipsilateral tactile stimulation, which resulted in a spatially specific measure that could be compared with the spatially specific behavioral congruency effect. Figure 3B depicts the time-frequency representation of this spatially specific tactile-induced response and confirms that the modulation of beta-band \( (13–30 \text{ Hz}) \) oscillations is the most prominent spatial state change in the MEG signal following tactile input.

In the following, we focus on the time course of this beta-band modulation.

Figure 3C shows the time course of the tactile-induced beta modulation that we aimed to compare to the observed behavioral congruency time courses. Critically, the beta modulation shows a biphasic response \( (\text{suppression followed by rebound}) \) that is unparalleled by the behavioral congruency effect time courses of both RT and accuracy. Specifically, whereas the influence of tactile input on the amplitude of beta oscillations reverses sign after \( ~500 \text{ ms} \), the influence on RT \( (\text{Fig. 3D}) \) and accuracy \( (\text{Fig. 3E}) \) remains of the same sign, i.e., facilitatory.

This observation cannot be reconciled with the hypothesis that the beta modulation is responsible for the behavioral congruency effect. There are two ways to demonstrate this, one that explicitly considers the time that is required to interpret the imperative cue and another that does not. Starting with the latter, consider imperative cues that were presented during the beta rebound \( (\text{say, } 600 \text{ ms after the task-irrelevant tactile stimulus}) \). For these trials, as a result of the tactile stimulus, beta amplitude is higher over the contralateral compared with the ipsilateral somato-motor cortex \( (\text{with contra- and ipsilateral being defined relative to the tactile stimulus}) \). This is the case not only at the time of the imperative cue but also at the time of the subsequent response preparation and execution \( (\text{given that the rebound persists for at least } 500 \text{ ms}) \) and that the average RT is \( ~420 \text{ ms} \). As a consequence, for these trials, we expect that responses to congruent imperative cues \( (\text{made with the motor cortex contralateral to the tactile stimulus}) \) would be slower and/or less accurate than responses to incongruent imperative cues \( (\text{made with the motor cortex ipsilateral to the tactile stimulus}) \). However, even for these imperative cues that occurred during the beta rebound, we observed faster responses to congruent compared with incongruent imperative cues \( (\text{Fig. 3D}) \).

For our second demonstration, we explicitly take into account that it takes time to interpret the imperative cue before a movement can be prepared and executed. Because of this, the time at which the movement will be most susceptible to nonmotor influences \( (\text{such as brain states induced by the tactile stimulus}) \) will always be after the onset of the imperative cue. We denote this as the time until the maximal motor susceptibility, with time here defined relative to the onset of the imperative cue. For the sake of argument, assume that the beta modulation does explain the behavioral congruency effect. In this case, the time of maximal motor susceptibility equals the difference in latency between the maximum beta suppression and the maximum behavioral congruency facilitation. Given that the former peaks at \( ~250 \text{ ms} \) and the latter at \( ~0 \text{ ms} \), the time until the maximal motor susceptibility is estimated to be \( ~250 \text{ ms} \) after the imperative cue. Now, for imperative cues that are presented from as early as \( 250 \text{ ms} \) after the tactile stimulus, the time of the maximal motor susceptibility \( (250 \text{ ms after the imperative cue}) \) coincides with the beta rebound, which emerges \( ~500 \text{ ms} \) after the tactile stimulus. Nevertheless, also for these trials, we observe a congruency benefit. We thus conclude that the behavioral congruency effect cannot be explained by the tactile-induced modulation of beta amplitude.

Additional analyses. Having described our main observations, we now briefly turn to the outcomes of several additional analyses before returning to our main results in \textit{Discussion}. 

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First, in previous analyses of the behavioral data we had collapsed across task-irrelevant visual and auditory stimuli. Figure 4A shows our main behavioral result (the congruency effect on RT) when visual and auditory task-irrelevant stimuli were kept separate. This confirmed that, especially at the interval at which the tactile congruency effect is most pronounced, there is no clear congruency effect following either visual or auditory task-irrelevant stimuli.

Second, when comparing the behavioral data to the MEG data, we had evaluated whether the difference in RT following congruent and incongruent tactile stimuli could be accounted for by the difference in beta power following contralateral tactile stimulation, expressed as % change from ipsilateral stimulation. C: time course of the tactile-induced modulation of beta (13–30 Hz) power in MEG channels above the primary somato-motor cortices after contralateral tactile stimulation, expressed as % change from ipsilateral stimulation. D: time course of the tactile congruency effect for RT (identical to Fig. 2C). E: identical to D, except for accuracy. Colored shadings represent ±1 SE, calculated across participants.

Third, in exploring the neural substrate of the tactile-induced movement facilitation, we particularly focused on beta power, and the reasons for this are outlined in the introduction. Although we had less clear hypotheses about this, we also analyzed event-related fields (ERFs) after the task-irrelevant stimuli and investigated both nonlateralized [contingent negative variation (CNV)-like] and lateralized [lateralized readiness potential (LRP)-like] components (Fig. 4C). As for the analysis of beta oscillations, we only included segments in which the imperative cue and response had not yet occurred. Apart from confirming the presence of a clear tactile-evoked ERF (Fig. 4C), these time-domain components also did not match the time courses of the behavioral movement facilitation. First, although there was an upward drift in field strength following
all stimuli (Fig. 4C, left), this was unlikely to be introduced by the stimuli because it had already started ~250 ms prior to stimulus onset. It is therefore also unlikely to account for the general alerting effect. Second, when focusing on the difference between contralateral and ipsilateral fields (Fig. 4C, right), no clear LRP-like pattern emerged that could account for the congruency effect time courses observed in behavior. Finally, the MEG analyses were based on channels that were selected on the basis of the tactile-induced response (see MATERIALS AND METHODS for details) and that were assumed to be sensitive to somatosensory as well as motor-related activity. To confirm the latter, we also evaluated the modulation of power in these channels during contra- and ipsilateral motor responses. As depicted in Fig. 4D, right, these channels were also highly sensitive to movement-related changes in power. This analysis further confirmed that tactile input and motor output result in highly similar time-frequency profiles, in line with the suggestion that these modulations reflect state changes within the same underlying somato-motor network (see van Ede and Maris 2013).

**DISCUSSION**

We have demonstrated that tactile input automatically facilitates movement at the stimulated effector, as reflected in faster and more accurate responses in a button-press task. This central observation complements a large body of physiological studies in the rodent vibrissal system on the integration of touch and movement (e.g., Ferezou et al. 2007; Lee et al. 2013; Matyas et al. 2010; Zagha et al. 2013) by demonstrating a clear functional consequence of such integration in healthy humans.

In the present study, we probed the influence of touch on movement using tactile stimuli that were irrelevant to the
motor task. However, in everyday life most tactile input received by the brain is highly relevant to, and produced by, ongoing movement. Hence, the reported facilitatory influence is likely to support efficient integration of relevant touch sensations with ongoing movement.

To our knowledge, only a single other study has demonstrated that task-irrelevant tactile stimuli facilitate movement (Frith and Done 1986, experiment II), and that was in the context of a different experimental question. Here we replicate this observation and extend it in at least two ways. First, we also characterized the time course of this facilitation and observed that it remained facilitatory up to 1 s after the tactile input. Second, we also assessed the origin of this influence, and we elaborate on this in the following.

Whereas the existence of several pathways for somatosensory processing in humans had previously been reported (see Dijkerman and de Haan 2007), we were particularly inspired by recent physiological evidence in rodents supporting additional, more direct, pathways between somatosensory and motor areas of the brain (see Ferezou et al. 2007; Lee et al. 2013; Matyas et al. 2010; Zagha et al. 2013). We hypothesized that through state changes propagating along these pathways (see van Ede and Maris 2013 and Zagha et al. 2013) tactile input may automatically influence the corresponding motor areas and thereby facilitate movements of the stimulated effector. We evaluated this hypothesis in two ways. First, we evaluated its compatibility with the pattern of movement facilitation observed in the behavioral data. Second, we investigated one particular index of somato-motor state changes (tactile-induced modulation of beta oscillations; van Ede and Maris 2013) and assessed whether its time course matched that of the behavioral modulation.

The behavioral data revealed that the influence of body side-congruent sensory input on movement 1) is specific to tactile input, 2) is independent of the positioning of the hands in peripersonal space, and 3) lasts (and remains facilitatory) for up to 1 s after the tactile input. This pattern of results is compatible with the somato-motor state change account. However, is it equally compatible with alternative accounts, such as the capture of spatial attention or (spinal) reflexes?

Ample studies have shown that salient stimuli can lead to the automatic allocation of processing resources (spatial attention) to the side of the salient stimulus (e.g., Carrasco 2011; Corbetta and Shulman 2002; Macaluso et al. 2000; Posner 1980). Such allocation of exogenous spatial attention is thought to be mediated by supramodal spatial representations that are thought to be contained in the brain’s ventral fronto-parietal network (Corbetta and Shulman 2002). This is supported by studies showing that salient stimuli in one sensory modality can facilitate perception of stimuli in other sensory modalities, when presented at the same side in peripersonal space (Kennett et al. 2002; Macaluso et al. 2000), and by the identification of parietal regions that code for peripersonal space independently of stimulus and response modalities (Macaluso et al. 2003). It is thus conceivable that our tactile stimuli facilitated movements at the stimulated side through attentional allocation to this side in peripersonal space. However, if this were the case, then 1) a similar congruency effect would be expected for congruent visual and auditory stimuli and 2) a stronger influence would be expected when the hands were further separated in peripersonal space. In contrast, we observed that the congruency effect was 1) highly specific to tactile stimuli and 2) independent of hand positioning. Of course, it could still be maintained that the observed movement facilitation reflects a form of attentional allocation that is specific for cueing particular body parts. Using behavioral data alone, it is unclear how such a highly specific form of attentional allocation can be distinguished from a nonattentional mechanism that only depends on direct somato-motor coupling. Nevertheless, if attentional mechanisms were responsible for the observed movement facilitation, it seems unlikely that attention would not also be deployed to locations in peripersonal space and in response to nontactile stimuli (and thus show at least some dependence on hand positioning as well as some facilitation for congruent nontactile stimuli).

Related to a possible attentional account of our results, we should also consider inhibition of return. This is a classical feature of exogenous spatial attention, involving behavioral facilitation that turns into inhibition a few hundred milliseconds after the congruent exogenous cue (e.g., Klein 2000). Importantly, the observed movement facilitation time courses in Fig. 2 showed no sign of inhibition of return, further arguing against an attentional account of the observed movement facilitation.

Under certain circumstances, tactile input is also known to trigger overt movements directly, as exemplified by the well-known patellar (knee jerk) reflex. However, if a reflex accounted for the movement facilitation reported here, then this facilitation should lead to many incorrect responses on incongruent trials and should be short-lived. However, even in incongruent trials, participants correctly responded with the hand opposite to the stimulated one in >90% of the trials. Moreover, the facilitation lasted up to 1 s after the tactile input. Instead of a reflex, our data thus show that tactile input leads to a relatively prolonged upregulation of lateralized motor readiness that modulates (rather than determines) movements. In this regard, it is interesting to note that in the neuropathological condition of cortical myoclonus tactile input of the type studied here has been associated with triggering overt movements (Shibasaki and Thompson 2011). This is possibly related to the present work, with tactile input in the pathological condition affecting motor output directly, rather than via a modulation of motor readiness.

Having discussed viable alternative accounts of the observed movement facilitation, we conclude that a tactile-induced state change in motor areas offers a plausible account of the behavioral data. While the existence and functional relevance of propagating state changes between S1 and M1 have been convincingly demonstrated in rodents (see Zagha et al. 2013), the present work suggests that such joint state changes between somatosensory and motor areas of the brain may also exist and impact on behavior in humans (see also van Ede and Maris 2013). Interestingly, such state changes have been documented in both directions (i.e., from somatosensory to motor areas and reverse; e.g., van Ede and Maris 2013; Zagha et al. 2013) and may thus play a central role in the bidirectional integration between touch and movement. In this light, it is noteworthy that we have recently also reported an automatic facilitatory influence in the complementary direction, whereby movement preparation improves touch perception automatically (without conscious awareness; van Ede et al. 2015).
One index of tactile-induced state change in motor areas of the brain is the tactile-induced modulation of beta oscillations (see van Ede and Maris 2013). To evaluate whether this particular index could provide the substrate for the tactile-induced movement facilitation, we compared their time courses and found that these did not match. In particular, whereas the beta modulation reversed in sign (i.e., rebounded) ~500 ms after the tactile input, the behavioral influence of this input remained facilitatory. This was the case for all trials in which the beta rebound overlapped with motor preparation and execution. Thus, whereas the behavioral data favored the somato-motor state change interpretation, this could not be related to this particular index of such state changes. We speculate on the possible reasons for this discrepancy. First, additional processes may be involved, and, assuming their influence remains facilitatory, they may counteract the inhibition that results from the rebound. To identify these processes, it may be that other indexes of somato-motor states must be considered, such as those recorded at finer spatial scales. Unlike the states reflected by the amplitude of beta oscillations (between 13 and 30 Hz), invasive recordings have identified such states in electrophysiological activity below 5 Hz (Harris and Thiele 2011; Zaghia et al. 2013). To our knowledge, such states have not been identified with MEG in humans, and it is currently unknown whether they follow a similar time course after tactile input. Likewise, it may be that the relevant brain states that are modulated by tactile input occur at the subcortical level, whose states may be invisible to MEG. Second, it is possible that the beta suppression and rebound originate from different sources and that only activity in the former source explains the behavioral facilitation. However, as a result of mixing of the signals, activity of this explanatory source may become occluded when the nonexplanatory rebound source becomes active.

As alluded to above, several previous studies demonstrated that beta oscillations are correlated with motor output (e.g., Gilbertson et al. 2005; Pogosyan et al. 2009). We want to point out that our data do not argue against this interesting relation but, instead, demonstrate that changes in motor performance (i.e., movement facilitation by task-irrelevant tactile input) are not always paralleled by changes in beta amplitude.

In conclusion, the present work has demonstrated a highly robust and spatially specific facilitatory influence of tactile input on movement in healthy humans. This influence involves an upregulation of lateralized motor readiness that proceeds automatically and that likely contributes to efficient integration of touch sensations with ongoing movement. While the behavioral data favored the involvement of a direct tactile-induced change in the processing capacity of motor areas of the brain, the tactile-induced modulation of beta oscillations (one index of somato-motor state changes) could not account for this behavioral facilitation in a straightforward way. Substantiating the physiological substrate(s) of the tactile-induced movement facilitation therefore remains an important target for future research.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: F.v.E., T.W., and E.M. conception and design of research; F.v.E. and T.W. performed experiments; F.v.E. and T.W. analyzed data; F.v.E., T.W., and E.M. interpreted results of experiments; F.v.E. prepared figures; F.v.E. drafted manuscript; F.v.E., T.W., and E.M. edited and revised manuscript; F.v.E., T.W., and E.M. approved final version of manuscript.

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