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Research report

Changes in tactile sensitivity over the time-course of a goal-directed movement

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ABSTRACT

We report three experiments designed to investigate changes in tactile sensitivity over the time-course of goal-directed movements. A dual-task paradigm involving a speeded movement task and a non-speeded perceptual task was utilized. In the movement task, participants grasped a start computer mouse with their right hand (RH) and, at the go signal, reached for and grasped a goal mouse placed 25 cm in front of it. In the perceptual task, a tactile (standard) pulse was presented to the middle finger of the left hand (LH) which was kept at rest throughout the experiment. A comparison pulse was delivered to the middle finger of the RH. In Experiment 1, this was delivered in the motor preparation period, at the release of the start mouse, during the reaching phase, at the grasp of the goal mouse, or shortly after the grasping action. In Experiment 2, the comparison pulse was delivered in the preparation period, in the early, mid or late execution periods, or in the post-movement period. In Experiment 3, participants only performed the perceptual task. The participants made an intensity comparison regarding the second pulse (i.e., stronger vs. weaker than the first). Significant changes in tactile sensitivity were observed, with decreased thresholds (i.e., better performance) during the motor preparation and post-movement periods and increased thresholds (i.e., poorer performance) during the execution period. These results are discussed in terms of *sensory suppression*.

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1. Introduction

The movements that we make in the space around our bodies constitute a central part of our daily lives. Depending on our intentions, we are able, through goal-directed actions, to interact with the surrounding environment. Suppose, for example, that as you are reading this paper, you decide that you would like to have a sip of coffee from the mug lying on the table beside you. For this, you will first have to locate the mug amongst the various papers stacked on your desk; you will reach for it, grasp it, and take a sip of the coffee in order to deliver the desired caffeine hit that will help you continue on to the next paragraph. Eye-movements to objects of interest, pointing, reaching, and grasping all constitute examples of goal-directed movements that one performs while awake. Of course, the majority of us are expert with vision and we rely on it, as we describe below, for many of the actions that we undertake in the space around our bodies. However, an interesting question concerns whether touch, a sense that has not been studied as extensively as vision, may be affected by goal-directed movements.

When we engage in purposeful actions, the visual system is the dominant motor system. An abundance of research has investigated eye-movements and their effect on (visual mostly, but also auditory and tactile) perception. Studies involving the *preparation* of saccadic eye-movements (e.g., [7,21,27,38]) clearly show enhanced perceptual performance at the target location or 'facilitation' prior to eye movements. Along similar lines, facilitation in discriminating visual targets at the goal location has been reported following manual reaching movements [8], as well as following grasping movements [41]. In the tactile domain, facilitation has been observed when participants have to discriminate tactile stimuli presented at the location of an upcoming saccade [39]. In a dual-task paradigm requiring the preparation and execution of a goal-directed saccade or a simple finger-lifting movement on every trial, Juravle and Deubel showed that tactile detection was enhanced for stimuli delivered both at the finger toward which the saccade was directed – the goal-location, as well as the finger that executed the action – the movement effector [24]. These studies, showing the facilitation of participants' behavioral performance in response to tactile stimuli delivered in the motor preparation period, have now been complemented by the results of event-related potential (ERP) studies showing enhanced somatosensory components (P90, N140) in response to tactile stimuli presented during the preparation of both eye-movements [17] and finger movements [10,12].

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In an elegant recent study, Brozzoli et al. [4] had their participants reach for, and grasp, targets positioned in different orientations. They delivered vibrotactile stimuli either in the motor preparation period, at the start of the movement, or during the execution phase of the movement. The participants had to indicate the elevation of the tactile target presented at either the index finger (up) or thumb (down), while trying to ignore a simultaneously presented visual distractor presented at either the same or different elevation on the to-be-grasped target object. The results showed that prior to the start of the movement, the interference from the visual distractor was minimal. This finding relates to the previous behavioral studies presented above (see [24,39]) and argues in favor of enhanced tactile discrimination performance in the motor preparation period. However, as soon as the movement started (*movement initiation*), interference from the visual distractor impaired participants' speeded discrimination performance significantly. Furthermore, the decline in performance continued over the course of the *execution* period. Although Brozzoli et al.'s [4] explanation of these findings involved an on-line remapping of peripersonal space as action unfolds over time (the integration of different sensory information at different spatial locations within peripersonal space), it may also be that tactile perception was suppressed during the execution of the goal-directed reach-to-grasp action and, in that case, vision 'took advantage', and significantly interfered with participants' tactile discrimination performance.

Thus far, the evidence concerning the facilitation in both tactile detection and discrimination performance during motor preparation has been reviewed. We have also reviewed the literature regarding visual interference at the start of the movement and over early-execution phases. But what exactly happens to the perception of tactile stimuli after the initiation of a movement? Studies concerned primarily with motor control have documented a phenomenon known as 'sensory suppression' which manifests itself as a decrease in tactile sensitivity in the movement effector starting shortly before movement initiation and continuing over the course of the movement execution phase.[1]

A clear demonstration of sensory suppression comes from the work of Voss et al. [51]. They measured the point of subjective equality (PSE) between a pulse delivered to a finger on the left hand which was kept at rest throughout the trial and a second pulse delivered to a finger on the right hand which, depending on the condition, participants had to lift following an auditory cue or else keep still. The results showed that the stimulation of the moving finger had to be 2.69 times stronger in order to be perceived as similar to the stimulus delivered to the finger that was at rest.

In another study [1], the participants initiated each trial by pressing a force sensor with their right index finger; the left index finger was always kept at rest beneath another force sensor. At the presentation of the go signal, the participants had to make a speeded reaching movement toward a third force sensor placed on top of the left force sensor. Therefore, at the end of the trial, participants actively tapped their left finger with their right finger. At variable time delays before or after the active tap [±300 ms], they also received a test tap on the right finger and the participants had to rate which of the taps they perceived as being more intense. The results highlighted the existence of sensory suppression, starting in the execution phase of the speeded movement (−300 ms), with a peak *at the contact* with the force sensor (active tap) and ending 100 ms after contact has been made.

By delivering tactile stimulation relative to muscle activity onset prior to the movement of the index finger, tactile suppression effects were shown to occur up to 120 ms prior the onset of the movement and to be localized on the moving limb or adjacent locations to this as compared to more distant body stimulation sites [55]. Subsequent studies have shown that the intensity of the tactile stimulation does not interfere with either the temporal or spatial pattern of sensory suppression manifested during movement [53].

In this context, one important point to note concerning the sensory suppression studies that have been discussed thus far is that such attenuating effects on tactile perception were found in either active or passive movements executed by independent digits of the hand, and not during more complex goal-directed movements, such as, for example, reach-to-grasp movements. In this respect, it is interesting to highlight a study that looked at reach-to-grasp movements under conditions of anaesthesia of the tactile receptors on the index finger and thumb [16]. The participants in this study were instructed to reach and grasp for either a small or large object, following a go signal. When no tactile input was available to the fingers of the reaching hand, the control of grasping was affected. More specifically, the finger-opening phase that preshapes the hand for grasping during the reaching movement was significantly delayed, as compared to the normal unanaesthesized condition. These results therefore suggest that we use the tactile input from our hands in order to compute and adjust the temporal parameters of grasping, as well as to extract and rely on proprioceptive feedback during movement.

To summarize, the studies reported thus far indicate facilitation in tactile performance in the motor preparation period and sensory suppression starting shortly before movement initiation and continuing until shortly after the termination of movement. Facilitation has been explained primarily in terms of shifts of (presumably visual) attention (but also combined visual and tactile attention) to either the goal location of the movement [7,8,17,21,27,39,41], or at the movement effector [10,12,24]. Prior to the start of movement, studies on tactile suppression have highlighted efferent or afferent processes of the central nervous system. According to the first account, when voluntarily preparing to move, feed-forward motor signals act on the activity elicited by the incoming sensory information, therefore the sensory suppression that is experienced in advance of the voluntary movement has a central origin and arises (most of the time) upstream from the primary motor cortex. Evidence in support of this account has been provided by Voss et al. [51]. Moreover, this account can also accommodate 'top-down' influences on sensory suppression, such as allowing for the motor system to modify the available sensory inputs as a function of expectation [52]. The second account, which is more physiologically based, states that sensory suppression arises from the afferent sensation resulting from bodily movements and could backwardly mask the new sensory stimulus; supporting evidence for this account comes from the equal sensory suppression observed during both passive and active movements [6,54].

In the present study, we wanted to examine the distribution of tactile sensitivity changes over the time-course of a goal-directed movement. Although the effects of motor preparation on tactile perception may have been well-documented in the literature, as well as there being some robust evidence regarding the start of the movement and the period before the actual contact with the goal-surface, there is a gap in the literature regarding the execution, grasp, as well as the post-movement phases. In the first experiment reported here, therefore, the participants had to prepare and execute a speeded reach-to-grasp movement following a go signal. At the beginning of the trial, a standard pulse was delivered to the participant's left hand (LH) that was kept at rest throughout each block of trials. The right hand (RH) received a comparison pulse that could be delivered, depending on the experimental condition, at one of five different points in time: motor preparation, start of the movement, execution, grasp, and post-movement. The partici-

[1] The phenomenon has also been referred to as 'tactile attenuation' [1], or 'tactile gating' [6].

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pants had to rate the intensity of the RH as being either stronger or weaker than that delivered to their LH.

Our hypothesis was that increased tactile sensitivity (i.e., better performance when comparing the tactile stimuli presented to the two hands) would be observed during the motor preparation period, as compared to an expected decline in performance during the execution of the movement. Moreover, we did not expect any difference in tactile sensitivity between the motor preparation and post-movement periods.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Nineteen participants (9 male, one left-handed) took part in this experiment. All of the participants reported normal touch, as well as normal or corrected to normal vision. The mean age of the participants was 27 years (age range 20–39 years). All of the participants gave their informed consent prior to their participation and the experiment was conducted in accordance with the Declaration of Helsinki. The experimental session lasted for approximately 75 min and participants received a £10 (British pounds) gift voucher in return for taking part in the study.

2.1.2. Apparatus

The participants were seated at a table in a darkened room with illumination provided centrally across the table surface by a single lamp positioned to their upper right side. Two computer mice were affixed to the surface of the table, to the right of the participant, with the mouse closest to the participant (the *start mouse*) positioned at a comfortable distance for the participant to interact with and the second mouse placed 25 cm in front of the start mouse (*goal mouse*; see Fig. 1a). Tactors (VBW32 skin stimulators, 1.6 cm × 2.4 cm vibrating surface, Audiological Engineering Corp., Somerville, MA, USA) were attached with tape to the middle fingers of each of the participant's hands. The tactors were covered in several layers of thin sponge in order to reduce the possibility that the participants would be able to hear their operation. The participants also wore disposable earplugs (3 M 1100), as well as over-the-head earmuffs (Peltor H7A) for the duration of the experiment for the same reason. The tactors were driven by means of a custom-built tactor box connected to the main computer (Dell Technologies) and interfaced through Matlab (Psychophysics Toolbox 3 [3,35]) on Windows XP. The participants rested their LH on an additional piece of soft sponge for the duration of the experiment; they placed their RH to the right of the start mouse at the beginning of each trial. The auditory stimuli were delivered from two loudspeaker cones, one placed on either side of the table. Participants responded by means of two foot-pedals connected to the computer.

2.1.3. Procedure

The dual-task experiment consisted of a speeded movement task paired with an unspeeded perceptual task. In each trial of the *movement task*, the participants were instructed to listen out for three auditory beeps (450 Hz, 100 ms) presented from the two loudspeaker cones placed on the table. The participants were instructed, following the first beep, to grasp the start mouse with their RH and to keep the left mouse button depressed. They had to prepare and execute a goal-directed movement toward the goal mouse as soon as they heard the second beep (which acted as the go signal). The participants executed the speeded movement, grasped the goal mouse, and kept the left button on the goal mouse depressed until they heard the third beep. At that time, they had to release the mouse and return their RH to the starting position, to the right of the start mouse. For the *perceptual task*, a *standard* tactile pulse (250 Hz, 660 ms) was presented to the participant's left middle finger [200–300] ms after the first beep on each and every trial. This pulse was followed by another random time interval ([300–400] ms) before the delivery of the go signal. The *comparison* tactile pulse (250 Hz, 660 ms) was delivered to the participant's right middle finger. The comparison pulse for each trial was presented at a different point in time, depending on the experimental condition. In particular, RH stimulation could be delivered either during the *movement preparation period* (0 ms after the standard left hand pulse), at the *start* of the movement following the go signal (0 ms after the release of the start mouse), during the *movement execution* period (100 ms after the release of the start mouse), at *the grasp* of the goal mouse (0 ms after the grasp), or in the *post-movement* period (100 ms after the grasp of the goal mouse; see Fig. 1b for a depiction of the timeline in a typical trial).

The perceptual task involved participants having to make a tactile intensity discrimination response: That is, the participants had to compare the RH pulse to the LH pulse and decide whether the intensity of the RH stimulation was stronger or weaker than that of the comparison pulse once they had completed the movement task and returned to the starting position. The participants were instructed to press one foot-pedal whenever a stronger pulse was presented to the RH and the other foot-pedal whenever the RH pulse was weaker. Response assignments for the left and right foot-pedals were counterbalanced across participants. Once the participants had made their response, the experiment progressed on to the next trial following a random inter-trial interval of [1500–2500] ms.

2.1.4. Design

The experiment involved an adaptive procedure comprising five different interleaved staircases for each of the five conditions of the experimental factor TIME – timing of the RH tactile stimulation – (motor preparation, movement start, movement execution, grasp, and post-movement). Each of the five staircases consisted of a three-interval one-up three-down adaptive procedure [30,47], designed to keep performance at a level of 79.4% correct [31]. The standard pulse delivered to the LH in the first trial was kept constant for all trials and all staircases, throughout the experiment. The comparison pulse delivered to the RH was calculated by either subtracting or adding one step from the standard pulse delivered to the LH. For all staircases, the first comparison pulse delivered to the RH was more intense than the standard pulse delivered to the LH, hence all staircases converged on the upper thresholds. After one incorrect response or a sequence of three correct responses, the staircase changed direction: 'UP' (increasing the RH pulse by one step for an incorrect response) or 'DOWN' (decreasing the RH pulse by one step following three consecutive correct responses), respectively. Changes in the direction of the staircase are referred to as 'reversals'. The step-size was doubled for the first five reversals in order to approach the threshold more rapidly (e.g., see [45]). The first five reversals were excluded from the final threshold calculations (the average value of upward and downward reversals). The staircase for each condition terminated once the total number of reversals (17) or the total number of trials (120) had been reached.

The presentation of trials from each of the staircases was randomized throughout the experiment. After the completion of every 60 trials, the participants were informed by three consecutive beeps that the block has finished and that they could take a break, if they so desired. A progress bar was presented on the screen behind their chair. This provided an estimate of the number of trials remaining, calculated on the basis of the total number of possible reversals (85). The participants pressed a key on the keyboard in order to continue on to the next block. The experiment required the par-

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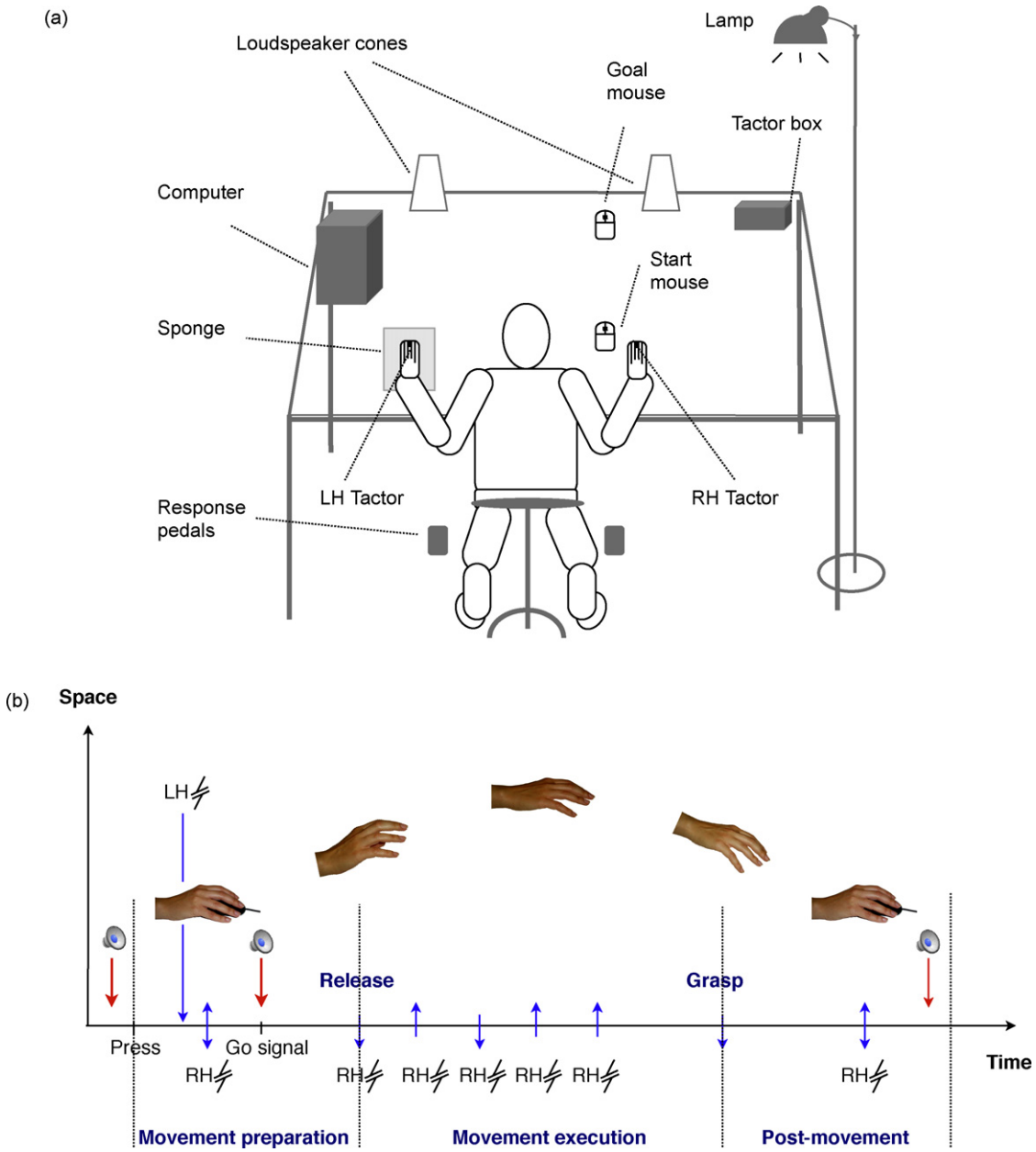

Fig. 1. (a) Bird's-eye view of the experimental set-up used in Experiments 1, 2 and 3. (b) Timeline of a single trial in Experiments 1 and 2. Upward arrows indicate the timing of the comparison pulse delivered to the RH at various points during the goal-directed movement in Experiment 1, whereas downward arrows indicate the timing of the comparison pulse delivered to the participants' RH in Experiment 2a.

ticipants to complete a maximum of 600 trials. It finished when all five staircases had terminated. The participants performed a short block of 10 practice trials at the beginning of the experiment. These practice data did not constitute part of the final analysis.

2.1.5. Data analysis

Three participants were excluded from the final data analysis as in the majority of trials they did not wait for the go signal before initiating their movement, or else they failed to keep the start mouse button depressed following the first beep. Due to the fact that the stimulation delivered during movement execution was triggered by the release of the start mouse, failure to keep the mouse depressed resulted in the delivery of the RH tactile comparison pulse while the participant's hand was still at rest. The remaining 16 participants were included in the final data analysis.

For the *perceptual task*, a one-way repeated measures ANOVA was conducted on the threshold data with the same factor TIME comprising the five levels corresponding to the different timings of tactile RH stimulation: movement preparation, start, execution, grasp, and post-movement.

2.2. Results

On average, the participants needed 380 trials in order to complete the experiment (approximately 78 per staircase). The average time to grasp (the time between the tactile stimulation of the RH and the grasp of the goal mouse), the average time difference between the stimulation of the RH relative to the LH, and the timing of RH stimulation relative to the start of the different movement phases (note that for the preparation period, the timing is provided relative to the LH and not the beginning of the preparation period

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Table 1
Experimental timings (in ms) for Experiments 1, 2, and 3. For each of the experiments, the first column (RH) represents the timing (in ms) of the RH pulse delivery relative to the start of the experimental conditions listed on the left side of the table. The second column (LH/RH) indicates the average time difference between the delivery of the pulses to the two hands. The third column (TTG) highlights the average time to grasp the goal mouse following the delivery of the RH pulse; negative values indicate that the grasp occurred first. Note that the RH is switched with the LH for Experiment 2b. In Experiment 1, Early stands for Start, Mid for Execution and Late for Grasp. In Experiment 3 Preparation stands for Short, Mid for Medium, and Post-move stands for Long.

	Experiment 1			Experiment 2a			Experiment 2b			Experiment 3		
	RH	LH/RH	TTG	RH	LH/RH	TTG	LH	RH/LH	TTG	RH	LH/RH	TTG
Preparation	0	0	993	100	100	928	100	100	1043	200	100	n.a.
Early	0	266	859	50	600	488	50	590	459	n.a.	n.a.	n.a.
Mid	100	692	634	150	699	434	150	692	382	998	699	n.a.
Late	0	1004	0	250	775	338	250	784	299	n.a.	n.a.	n.a.
Post-move	100	1142	−100	100	1145	−100	100	1188	−100	1442	1145	n.a.

which coincides with the beginning of the trial) are highlighted in Table 1.

2.2.1. Perceptual task

Mean thresholds and individual data from all participants are presented in Fig. 2a. Numerical values of the thresholds in the five conditions are presented in Table 2. The results show that the timing of tactile stimulation to the participant's RH significantly influenced the threshold data [$F(4,60) = 7.23$; $p < .001$]. Repeated contrasts showed thresholds to be significantly higher (i.e., poorer performance was observed) in the execution period as compared to the preparation period [$F(1,15) = 9.36$; $p = .008$], the start period [$F(1,15) = 5.97$; $p = .027$], the grasp period [$F(1,15) = 18.67$; $p = .001$], and the post-movement period [$F(1,15) = 35.54$; $p < .001$]. The thresholds were significantly lower (i.e., better performance was observed) in the post-movement period as compared to the preparation [$F(1,15) = 5.07$; $p = .04$] and grasp periods [$F(1,15) = 5.99$; $p = .027$]. The data allowed for a quadratic trend to be fitted [$F(1,15) = 6.75$; $p = .002$], with thresholds increasing from preparation to execution and decreasing from execution to post-movement.

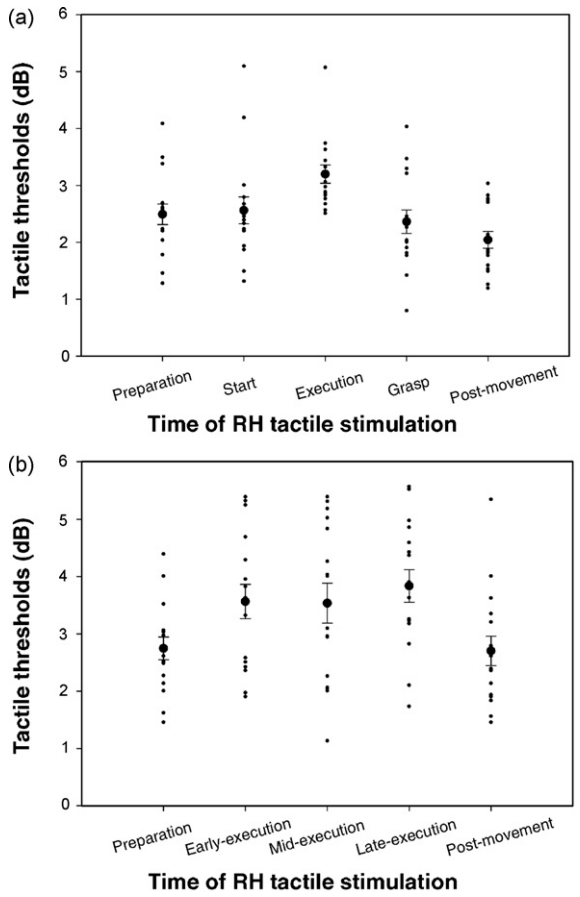

Fig. 2. Scatter-plots of the individual threshold data together with the means for the various timings of the RH pulse delivery for Experiment 1 (a) and Experiment 2a (b). Vertical error bars represent the standard errors of the means.

2.3. Discussion

The prediction for Experiment 1 had been that the tactile thresholds would be significantly higher in the execution period of the movement, as compared to when the participant was at rest. Consistent with this prediction, the results highlight a significant increase in participants' perceptual thresholds in this period as compared to the other phases of the movement. This finding supports the facilitation of tactile perception thought to occur during the motor preparation period (see [24,39]). Changes in tactile performance have been shown to occur during the start [4], execution [15,51,52], and contact [1] periods. Such results support the tactile suppression account of what happens during movement execution [1,51,52]. The results of Experiment 1 show that a facilitation of tactile performance can be observed once a movement has been terminated.

It should be noted that the duration of tactile stimulation may have had an effect on the sensitivity data. More specifically, it has been shown that the longer the stimulation, the more cues for discrimination would have been available to participants, and therefore, the better their performance [50]. Of course, visual spatial attention may also have played a role here [25,46].

In order to determine whether the duration of stimulation could have a significant effect in tactile sensitivity, we shortened the duration of tactile stimulation to 100 ms in Experiment 2a (for the stimulation presented to both hands).[2] RH tactile stimulation was delivered at one of five different time points referenced to the LH stimulation and the different movement phases: movement preparation, early-execution, mid-execution, late-execution, as well as post-movement. We hypothesized that tactile sensitivity would decrease during the execution period [1,51,52] and that it should be enhanced during the preparation [24,39] and post-movement periods. At the same time, we were concerned whether this sensory suppression phenomenon observed during reaching movements executed by the RH would be present during LH reaching as well. It has been argued by some researchers, primarily on the basis of the literature on spatial neglect and extinction, that space pro-

[2] At the time that this experiment was conducted, this was the shortest duration that the tactors could be programmed to turn on for. This serial-port lag, which only allowed a minimum duration of tactile stimulation of 660 ms vibration, may possibly have contaminated the data for the RTs recorded in the start condition (at the same time with the RH tactor stimulation), as well as the movement duration data in the start and execution condition (when the RH tactor vibrated while the RH was moving between the two mice).

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Table 2
Mean thresholds (dB) and SE for Experiments 1, 2, and 3, split according to the different experimental conditions. In Experiment 1, Early stands for Start, Mid for Execution and Late for Grasp. In Experiment 3 Preparation stands for Short, Mid for Medium, and Post-move stands for Long.

	Experiment 1		Experiment 2a		Experiment 2b		Experiment 3	
	Mean threshold	SE	Mean threshold	SE	Mean threshold	SE	Mean threshold	SE
Preparation	2.49	0.18	2.75	0.19	3.22	0.26	3.11	0.19
Early	2.56	0.23	3.56	0.29	4.12	0.27	n.a.	n.a.
Mid	3.20	0.15	3.53	0.34	3.79	0.26	2.49	0.27
Late	2.36	0.20	3.83	0.28	3.94	0.26	n.a.	n.a.
Post-move	2.04	0.14	2.70	0.25	3.33	0.27	2.19	0.16

cessing might primarily involve the right hemisphere [28,32,33], the same hemisphere that controls the movements, as well as the somatosensation, of the LH. Therefore, in Experiment 2b, participants had to perform the same reach-to-grasp movement as in Experiment 2a, this time using their left hand. We were interested in investigating, by comparing the performance of the two hands, whether the observed differences in tactile sensitivity were influenced by the active hand that performs the movement or the static comparison hand that receives the 'standard' stimulation.

3. Experiment 2

Experiment 2 was composed of two parts: a and b. The only methodological difference between the two parts was in terms of the hand that performed the movement: If, in Experiment 2a, the RH reached between the two computer mice, in Experiment 2b, it was the LH that performed the movement (with the computer mice affixed now on the left side of the table). For this reason, the methods for the two experiments are presented together.

3.1. Methods

3.1.1. Participants

All participants reported normal touch, as well as normal or corrected to normal vision. Nineteen participants (11 male, one left handed) took part in *Experiment 2a*. They had a mean age of 28 years old (age range 21–36 years). Six of the participants had already taken part in Experiment 1. Sixteen participants (7 male, one left-handed) participated in *Experiment 2b*. They had a mean age of 26 years old (age range 20–34 years). Six of the participants had already taken part in Experiment 2a.

The *apparatus*, *design*, and *procedure* were similar to those used in Experiment 1 with the following exceptions: (1) The duration of tactile stimulation was shortened to 100 ms for both the LH and RH pulses; (2) The auditory beeps in Experiment 2 were shortened and had a higher pitch (800 Hz, 50 ms) as we considered that a shorter duration might better serve their purpose as alerting sounds; (3) The third difference relates to *the timing* of the tactile stimuli. For *Experiment 2a*, just as for Experiment 1, the *standard* tactile pulse presented to the middle finger of the LH was followed by a random time interval [300–400] ms, after which time, the go signal was presented. The *comparison* tactile pulse was delivered to the RH either in the *movement preparation period* (100 ms after the standard LH pulse), at one of three points in time during the *movement execution* period (50 ms, 150 ms or 250 ms after the release of the start mouse), or in the *post-movement* period (100 ms after the grasp of the goal mouse). These different timings will be referred to as: motor preparation, early-execution, mid-execution, late-execution, and post-movement (see Fig. 1b for a depiction of the timeline of a typical trial). All the timings apply to *Experiment 2b*; note that for this experiment the RH receives the standard pulse, whereas the LH performed the movement and received the comparison pulse.

3.1.2. Data analysis

Three participants were excluded from the final data analysis of *Experiment 2a* as they either did not wait for the go signal before initiating their movement or else they did not keep the start mouse button depressed following the first beep. The remaining 16 participants were included in the final data analysis.

For the *movement task* of both Experiments 2a and 2b, a one-way repeated measures ANOVA was conducted on the RT data with the factor TIME comprising five levels of RH/LH tactile pulse delivery: movement preparation, early-execution, mid-execution, late-execution, and post-movement. A further one-way repeated measures ANOVA was conducted on the movement duration data. For the *perceptual task*, a one-way repeated measures ANOVA was conducted on the threshold data with the same factor TIME comprising the five levels corresponding to the different timings of tactile RH/LH stimulation.

Further repeated measures ANOVAs were then conducted on the RT data, the movement duration data, and the threshold data with a within-participants factor TIME (preparation, early-execution, mid-execution, late-execution, and post-movement) and a between-participants factor EXPERIMENT (2a vs. 2b).

3.2. Results

For each of Experiments 2a and 2b, the participants needed an average of 403 and 402 trials, respectively, in order to complete the experiment (i.e., approximately 80 per staircase). The results are highlighted in Table 1. Mean threshold data from both Experiments 2a and 2b are presented in Fig. 3a.

3.2.1. Movement task. RTs

3.2.1.1. Experiment 2a. Mauchly's test of sphericity on the RTs data indicated a violation of the sphericity assumption ($\chi^2(9) = 66.42$; $p = .007$). We therefore corrected the degrees of freedom using the Greenhouse-Geisser correction ($\varepsilon = .312$). The analysis of the results showed the timing of delivery of tactile stimulation to the participants' RH had a significant effect on RTs [$F(1.248; 18.719) = 9.76$; $p = .004$]. Pairwise post-hoc comparisons revealed that the effect was due to RTs ($M = 209$ ms; SE = 16 ms) in the preparation period being significantly faster than RTs ($M = 266$ ms; SE = 20 ms) in the early-execution period ($p = .002$) and in the post-movement period ($M = 271$ ms; SE = 21 ms; $p = .008$).

3.2.1.2. Experiment 2b. Mauchly's test of sphericity on the RT data indicated a violation of the sphericity assumption ($\chi^2(9) = 100.98$; $p < .001$). We therefore used the Greenhouse–Geisser correction ($\varepsilon = .283$) for the rest of the analysis. The results showed that the timing of delivery of tactile stimulation to the participants' LH had no significant effect on RTs [$F(1.131; 16.969) = 3.08$; $p = .094$].

3.2.2. Movement duration

3.2.2.1. Experiment 2a. Mauchly's test was significant on the movement duration data ($\chi^2(9) = 45.70$; $p < .001$). We therefore corrected

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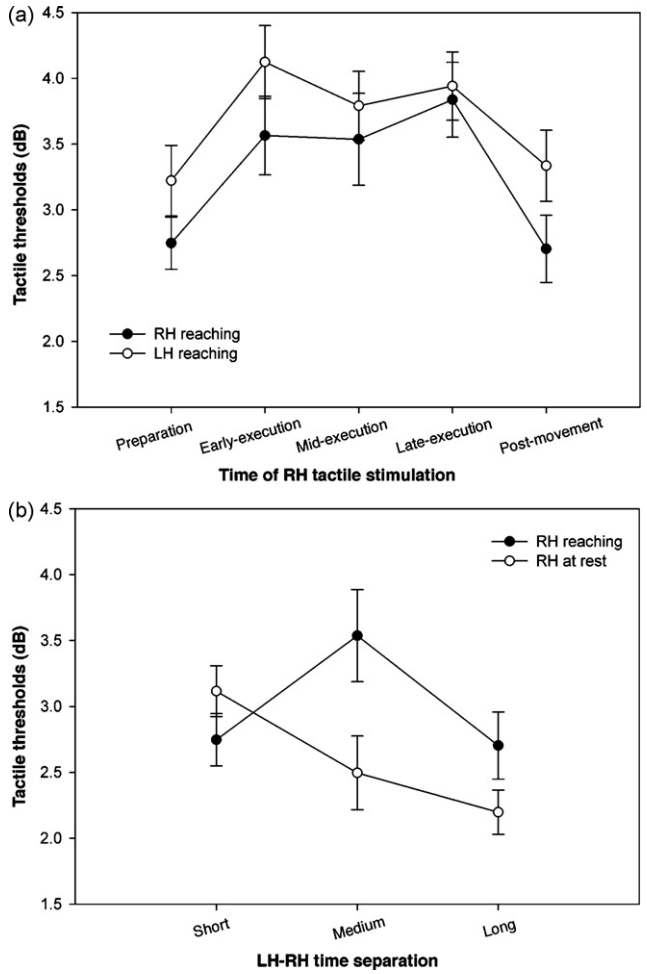

Fig. 3. Mean threshold data for the various timings of the RH pulse delivery for Experiment 2a vs. mean threshold data for the various timings of the LH pulse delivery for Experiment 2b (a); Mean threshold data for the short, medium, and long LH-RH time separation in Experiments 2a vs. 3 (b). Vertical error bars represent the standard errors of the means.

the degrees of freedom with the Greenhouse–Geisser correction ($\varepsilon = .465$). The results showed that the timing of the RH tactile stimulation did not have a significant influence on movement duration [$F(1.859; 27.887) = 1.46$; $p = .25$]

3.2.2.2. Experiment 2b. Mauchly's test was significant on the movement duration data ($\chi^2(9) = 31.19$; $p < .001$); we used the Greenhouse–Geisser correction ($\varepsilon = .574$) for the remaining analysis. The results showed that the timing of the LH tactile stimulation did not have a significant influence on movement duration [$F(2.295; 34.419) = .23$; $p = .825$].

3.2.3. Perceptual task

3.2.3.1. Experiment 2a. Mean thresholds and individual data from all participants are presented in Fig. 2b. Numerical values of the thresholds in the five conditions are presented in Table 2. The results show that the timing of tactile stimulation to the RH significantly influenced the threshold data [$F(4,60) = 10.87$; $p < .001$]. Repeated contrasts showed thresholds to be significantly lower (i.e., better performance was observed) in the movement preparation period as compared to the early-execution period [$F(1,15) = 13.37$; $p = .002$], the mid-execution period [$F(1,15) = 8.69$; $p = .01$], and the late-execution periods [$F(1,15) = 27.28$; $p < .001$]. Thresholds were significantly lower in the post-movement period as compared to the early-execution period [$F(1,15) = 12.87$; $p = .003$], the mid-execution period [$F(1,15) = 9.07$; $p = .009$], and the late-execution period [$F(1,15) = 22.72$; $p < .001$]. Participants were therefore significantly worse at comparing the two tactile pulses when one of them was delivered at any stage during the execution of the movement between the two mice. When tested with polynomial contrasts, the threshold data allowed a quadratic trend to be fitted with thresholds increasing from preparation to execution and decreasing from execution toward post-movement [$F(1,15) = 18.48$; $p = .001$].

3.2.3.2. Experiment 2b. Numerical values of the thresholds in the five conditions are presented in Table 2. The results show that the timing of tactile stimulation to the LH significantly influenced the threshold data [$F(4,60) = 4.55$; $p = .003$]. Repeated contrasts showed the thresholds to be significantly lower (i.e., better performance was observed) in the preparation period than in the early-execution [$F(1,15) = 13.35$; $p = .002$], mid-execution [$F(1,15) = 5.03$; $p = .04$], or late-execution periods [$F(1,15) = 5.45$; $p = .034$]. Thresholds were significantly lower in the post-movement period as compared to the early-execution period [$F(1,15) = 7.89$; $p = .013$], and marginally, the late-execution period [$F(1,15) = 4.69$; $p = .05$]. Participants were therefore significantly worse at comparing the two tactile pulses when one of them was delivered early during the execution of the movement between the two mice, as compared to the rest conditions

3.2.4. Experiment 2a vs. 2b

3.2.4.1. Movement task. RTs. The raw untransformed threshold data from both Experiments 2a and 2b were tested together with Levene's test for homogeneity of variance which was statistically non-significant for the preparation [$F(1,30) = 2.89$; $p = .099$], early [$F(1,30) = .09$; $p = .757$], mid [$F(1,30) = .02$; $p = .882$], late [$F(1,30) = .23$; $p = .633$], and post-movement [$F(1,30) = .28$; $p = .602$] levels of the experimental factor TIME. Independent *t*-tests showed there was no significant difference in the mean RTs for either the preparation [$t(30) = .14$; $p = .890$], early-execution [$t(30) = .28$; $p = .777$], mid-execution [$t(30) = .22$; $p = .826$], late-execution [$t(30) = -.25$; $p = .806$], or post-movement period [$t(30) = -.16$; $p = .872$].

3.2.4.2. Movement duration. Levene's test for homogeneity of variance was statistically significant for the preparation period [$F(1,30) = 11.67$; $p = .002$]. However, Levene's test was non-significant for the early [$F(1,30) = .35$; $p = .559$], mid [$F(1,30) = 1.68$; $p = .204$], late [$F(1,30) = 1.47$; $p = .234$], and post-movement [$F(1,30) = 3.47$; $p = .072$] levels of the experimental factor TIME. Independent *t*-tests showed there was no significant difference in the mean movement duration of the two hands for either the preparation [$t(17.862) = -.56$; $p = .578$], early-execution [$t(30) = .65$; $p = .519$], mid-execution [$t(30) = .13$; $p = .899$], late-execution [$t(30) = -1.01$; $p = .815$], or post-movement periods [$t(30) = -.24$; $p = .815$].

3.2.4.3. Perceptual task. Levene's test for homogeneity of variance was statistically non-significant for the preparation period [$F(1,30) = .73$; $p = .398$], the early-execution [$F(1,30) = .06$; $p = .808$], mid-execution [$F(1,30) = 2.97$; $p = .095$], late-execution [$F(1,30) = .31$; $p = .583$], and post-movement [$F(1,30) = .29$; $p = .592$] levels of the experimental factor TIME. Independent *t*-test showed there was no significant difference in the mean tactile thresholds for the two hands for either the preparation [$t(30) = -1.42$; $p = .166$], early-execution [$t(30) = -1.37$; $p = .181$], mid-execution [$t(30) = -.58$; $p = .565$], late-execution [$t(30) = -.27$; $p = .789$], or post-movement periods [$t(30) = -1.69$; $p = .100$].

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3.3. Discussion

The movement task in Experiment 2a revealed faster RTs to release the start mouse following the go signal for comparison pulses delivered during the movement preparation period (i.e., with a SOA of 100 ms between the LH and the RH), as compared to the early-execution and post-movement periods. One explanation for this result is an alerting effect resulting from the presentation of the RH vibrotactile pulse, which may have speeded the already prepared goal-directed movement [9].

If Experiment 1 showed a significant improvement in performance in the post-movement period as compared to the preparation period, the same pattern of results was not observed in Experiment 2a. Tactile thresholds for the movement execution periods were significantly increased as compared to motor preparation and post-movement, thus indicating poorer performance for the moving RH as compared to rest conditions. Just as for the RH, the results of Experiment 2b show a sensory suppression-like pattern for the LH. Moreover, when the pattern of performance for the two hands was compared, the RTs, the total movement duration, as well as the thresholds of the LH were not statistically different from those reported for the RH. It therefore appears that sensory suppression is a robust phenomenon equally affecting both moving hands.

One explanation for the significantly decreased thresholds found in the preparation and post-movement periods of both Experiment 2a and 2b involves the notion of attentional facilitation [7,8,21,24,27,39,41]. When we are about to move, we attend to the hand that we are preparing to move, as well as to the hand that grasps the goal object. More specifically, one can argue that this post-movement period is of specific importance for grasping, since the tactile feedback from the object conveys information to us regarding whether we should be making adjustments in our grip force in case, for example, the object slips. On the other hand, it may be that tactile sensitivity was indeed suppressed during movement in both Experiments 1 and 2, but that it returned to a normal state in the post-movement period. To test this hypothesis, we performed a third and final experiment in which the participants sat still and received the standard and comparison tactile pulses separated by a short, medium, or long time interval. If facilitation were to be observed in the post-movement period, then one would expect tactile thresholds to be significantly higher in Experiment 3 as compared to Experiment 2a. However, if the decreased thresholds in Experiment 2a are indicators of the normal tactile perception once a movement has terminated, then we would not expect to find any significant difference between the two experiments.

4. Experiment 3

4.1. Methods

4.1.1. Participants

Sixteen participants (5 male, one left handed) took part in this experiment. They all reported normal touch, as well as normal or corrected to normal vision. They had a mean age of 25 years (age range 20–34 years). Eleven of the participants had already taken part in Experiment 2b. The experiment lasted for approximately 20 min.

The *apparatus*, *design*, and *procedure* were similar to those used in Experiment 2a. However, participants now only performed the *perceptual task*. For this, they were instructed to take a comfortable position on the chair, with their hands on either side of the arm rests. Moreover, they were asked to keep their hands still, to not look at their hands, or touch the arm rests with their hands. Each trial started with an auditory signal (800 Hz, 50 ms) which was followed after a random time interval [200–300 ms] by the delivery of a *standard* tactile pulse (250 Hz, 100 ms) to the participants' LH. After either a short [100 ms], medium [699 ms] or long [1145 ms] time interval, a second *comparison* tactile pulse (250 Hz, 100 ms) was delivered to the participants' RH. The three time intervals correspond to the average LH-RH time difference from Experiment 2a (see Table 1). Given the fact that the LH-RH time difference for the three movement periods (short, medium and long) in Experiment 2a were so close together in time, as well as not statistically different in terms of their tactile thresholds, we used the mid-execution one as the medium time interval in the present experiment. The comparison pulse was followed by another random time interval ([300–400] ms) and the trial finished with an auditory signal (800 Hz, 50 ms) that indicated to participants that they should make a response. The rest of the procedure, as well as the design, were identical to Experiment 2a.

4.1.2. Data analysis

First, a one-way repeated measures ANOVA was conducted on the threshold data with the factor TIME comprising the three levels of LH/RH time difference in stimulation: Short, medium, and long. Second, a repeated measures ANOVA was then conducted on the threshold data, with a within-participants factor TIME (short, medium and long) and a between-participants factor of EXPERIMENT (2a vs. 3). For Experiment 2a, the mid level of factor TIME was taken as the mid-execution period.

4.2. Results

Mean threshold data for the short, medium, and long time periods of Experiment 3 are plotted together with the corresponding time periods of Experiment 2a in Fig. 3b.

4.2.1. Experiment 3

Mauchly's test of sphericity on the threshold data indicated a violation of the sphericity assumption ($\chi^2(2) = 9.50$; $p = .009$). We therefore corrected the degrees of freedom using the Greenhouse–Geisser correction ($\varepsilon = .670$). The results show that the LH/RH time difference in tactile stimulation significantly influenced the threshold data [$F(1.340, 20.099) = 12.93$; $p = .001$]. Repeated contrasts showed thresholds to be significantly higher (i.e., worse performance was observed) in the short period as compared to the medium [$F(1,15) = 8.85$; $p = .009$] and long periods [$F(1,15) = 82.04$; $p < .001$]. There was no significant difference between the medium and long periods [$F(1,15) = 1.852$; $p = .194$]. Participants were therefore significantly worse at comparing the two tactile pulses for a time difference between the two of them as small as 100 ms.

4.2.2. Experiments 2a vs. 3

The raw untransformed threshold data from Experiments 2a and 3 were tested together with Levene's test for homogeneity of variance which was statistically non-significant for the short [$F(1,30) = .006$; $p = .938$], medium [$F(1,30) = 3.75$; $p = .062$] and long [$F(1,30) = 2.25$; $p = .144$] levels of the experimental factor TIME. Independent *t*-tests showed there was no significant difference in the mean tactile thresholds for the two hands for the short [$t(30) = -1.33$; $p = .192$] and long [$t(30) = 1.65$; $p = .109$] periods of the two experiments. A significant difference was observed between the mean thresholds of the medium period of the two experiments [$t(30) = 2.33$; $p = .027$], with significantly decreased thresholds in the medium period of Experiment 3, as compared to the same period of Experiment 2a.

4.3. Discussion

It appears that tactile discrimination performance is significantly impaired while the RH performs a reaching movement between the start and goal computer mice, as compared to the

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RH at rest in the present study. This result provides clear evidence in favour of sensory suppression occurring during goal-directed reaching movements [1,6,51,52]. On the other hand, performance was equally good (comparable) in the early and late time periods of both Experiments 2a and 3, suggesting that tactile perception is in a normal (non-facilitated) state shortly before starting, as well as immediately after finishing a goal-directed reaching movement. However, it has been shown that for very short durations up to 150 ms, a contralateral comparison stimulus will most likely be perceived as having a decreased intensity with respect to the standard stimulus. This 'sensory suppression' in the absence of movement appears when two vibratory stimuli are delivered to different skin locations with a very short time separation between them [50]. Nevertheless, studies involving tactile discrimination [39], as well as tactile detection [24] at the goal location of an upcoming saccade, have demonstrated improved performance for stimuli delivered a long time in advance of the start of the movement to the finger toward which the saccade was about to be directed as compared to another finger. This attentional facilitation effect present for goal-directed eye-movements did not reach significance for the goal-directed reach-to-grasp movements used in the present study, thus suggesting a possible combined effect of visual and tactile attention for the previously found facilitatory effects on tactile perception [17,24,39].

5. General discussion

The three experiments reported in the present study were designed to measure any changes in participants' tactile sensitivity over the course of a goal-directed reach-to-grasp movement. Our hypothesis was that participants' tactile discrimination performance would be facilitated in the motor preparation period, decrease at the start of the movement, over the reach phase, and at the time of grasping the goal object. We hypothesized that performance would return in the post-movement period to a comparable level of performance to that observed in the preparation period. Additionally, no difference in performance between the preparation and post-movement periods was expected. The results reported here demonstrate that *the timing* of the delivery of tactile stimulation constituted a decisive factor that differentially affected tactile sensitivity in the various phases of a goal-directed movement. Depending on the paradigm used, motor preparation has been characterized by *facilitation* in either tactile detection [24] or tactile discrimination [39]. At the start of the movement, *interference* from visual distractors [4], interference from the performance of a secondary task [15], as well as *suppression* of tactile stimuli applied to the moving limb [1,6,51,52] have all been documented. Such suppression effects are present throughout the reach phase and peak at the hand's contact with the goal object (see [1,6]). Shortly after contact–i.e., during the post-movement period–suppression diminishes and gives way to a return to the baseline state of tactile perception. With regard to the present study, tactile thresholds were significantly increased over the start, execution, and grasp periods (Experiment 1), or the early, mid, and late execution phases of the movement (Experiment 2a) indicating a suppression mechanism acting on tactile perception as soon as the hand began its reach-to-grasp toward the goal location. Interestingly, the results of Experiment 2b demonstrated that the RH is not special: That is, the tactile sensitivity of RH reaching was no different from LH reaching. Lastly, when comparing the RH reaching between the two computer mice and the RH at rest receiving passive stimulation (Experiments 2a vs. 3), the suppression thesis was reinforced; however, no attentional facilitation [24,39] was found.

Interestingly, tactile sensitivity in Experiment 1 in the preparation period was significantly lower than in the post-movement period. We were not expecting to see any difference in sensitivity between these two time periods. It seems that visual attention may have interfered with participants' tactile performance during the course of the movement. For example, viewing one's hand has been shown to improve the detection [46] as well as the discrimination [25] of tactile targets, even though vision of the hand was itself non-informative with regards to the task at hand in these studies. Our participants executed a speeded reach-to-grasp movement from the 'start mouse' to the 'goal mouse'. The task instructions given to our participants did not specify any constraints for visual fixation, as we wanted the movement to be executed under the most naturalistic conditions possible (that one can achieve in a constrained laboratory setting). Therefore, it may be that following the instruction to execute the speeded movement from the start mouse to the goal mouse, the participants in Experiment 1 first moved their eyes to the goal location and, at the delivery of the go signal, the hand 'followed' the eyes to the goal mouse. From this point of view, performance in the post-movement period would clearly be facilitated by visual attention with the eyes already 'waiting' at the goal location [34]. Indeed, when participants are asked to execute a hand movement to a peripheral target, it has been shown that their eyes first land at the goal location within 250 ms of the saccade initiation and the hand follows approximately 100 ms later [36], suggesting that the latency of the goal-directed movement was affected by vision of the hand. More importantly, studies that have actively manipulated the time period in which vision is available during the course of a goal-directed movement [2,13,56] have shown that early vision, especially at the beginning of the movement, is decisive in the control of prehension movements. With this mind, as observed in Experiments 2a and 2b, shortening the duration of tactile stimulation resulted in steadier performance and no significant difference between the preparation and post-movement periods. This result implies that vision could indeed have played a role when the hand was at rest. However, it stemmed from the time given to the eyes 'to linger' over the goal location and consequently, to extract discrimination cues [25,46]. Nevertheless, this difference found in Experiment 1 between the preparation and post-movement periods was rendered non-significant in the remaining experiments of the present study. We can therefore conclude that preparation and post-movement periods have comparable tactile sensitivity and the role of vision when comparing the two is, if anything, of little importance.

Some further considerations with regard to the timing of the tactile stimulation have to be taken into account. First, tactile stimulation in the present experiment involved the delivery of a standard pulse to the LH at the beginning of each trial, which was followed at various intervals (see Table 1) by the delivery of the comparison pulse to the RH. Gallace and Spence [14] refer to a 'memory for touch', pointing to the fact that the tactile memory trace should decay rapidly as the time interval between sequential stimulations increases, especially when distractors from the same modality are presented. However, this was not case in the present study; sensitivity was highest at the longest interval. Evidence supporting the lack of involvement of tactile working memory in the performance of the task reported here comes from another study in which the participants were asked to compare vibrotactile stimuli separated by various time intervals ranging from 300 to 1200 ms [19]. The results of this study showed that during this period there was no effect of SOA on participants' discrimination performance. An interesting unexpected effect in Experiment 3 of the present study was to find better tactile discrimination performance for the RH at rest in the medium period as compared to the short time period. If one considers the memory for touch [14], then performance should have shown the opposite pattern: namely, better pattern of results at the shorter time interval to deliver stimulation between the two hands. However, in this case it may be that an attentional mechanism acts on tactile perception,

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facilitating performance at the longer time intervals. Indeed, traditional attentional cuing studies have shown costs of a little over 30 ms on average for contralaterally-cued trials [42]. Moreover, it has been demonstrated that it takes around 250 ms on average to direct tactile attention from the right arm to the left arm [29], which argues in favour of either an attention-directing process [29,42], or a possible contralateral sensory masking process [50], already taking place at the shortest time difference between the delivery of tactile stimulation at the two hands in Experiment 3.

In this context, one has to mention that the comparable thresholds for the 'preparation' and 'post-movement' periods in Experiments 2a and 3 point toward a natural state that encompasses the sensory suppression observed during movement. Surprisingly, the reach-to-grasp movements in the present study did not result in tactile attentional facilitation as previously observed when preparing goal-directed saccades [17,24,39], as well as following simple finger-lifting movements [10,12,24].

Moreover, when comparing tactile sensitivity for reaches performed with either the right or left hand as in Experiments 2a and 2b of the present study, one finds that the two are no different. This effect holds not only for sensitivity, but also for the speed of reaction to the go signal, as well as the movement duration. This result provides evidence that tactile sensation to both hands deteriorates in a similar manner, as soon as one of the hands starts moving.

To continue with other possible interfering factors, even if, as traditionally thought, we tend to rely on vision when performing goal-directed movements in peripersonal space [5,37,43,44], information from the other senses is combined with vision in a statistically optimal fashion in the process of sersorimotor control [11,26]. Another factor contributing to the present data may therefore be proprioception. For example, it has been shown that when moving in depth, hand positions closer to the shoulder are localized in a more precise manner, as compared to more distant positions (see [48]). Moreover, studies that involved the introduction of a perturbation to the visual feedback of the moving hand have pointed toward an important role of proprioception, as well as motion feedback and hand position signals to the on-line control of hand reaching movements [40,49]. In this context, returning briefly to the importance of vision, it is interesting to note that studies using the 'mirror illusion' have reported the visual capture of proprioception when the right hand performs reaching movements behind an occluding panel with visual feedback provided only from the static left hand [22,23].

Other factors, such as the position of the hand at the start of the reach-to grasp movement [20], also appear to influence the grasping kinematics of the right hand with adjustments for specific objects properties being made in the first part of the reach movement. Since the start and end position for the right hand was always the same in the present study, no additional costs in tactile performance can be attributed to the start position. Finally, no differences were found between the grasping patterns of the dominant and non-dominant hand, nor were there any significant differences in grasping kinematics between instructions of normal, slow or deliberately fast movements [18].

To summarize, tactile performance as reported in the present study, may indeed have been influenced primarily by vision, to a lesser extent by proprioception, as well as the starting position of the hand, and the instruction for participants to make a speeded reach-to-grasp movement. Note, however, that everyday naturalistic situations involve the integration of information coming from different senses into a unitary multisensory representation [5,37,43,44].

To conclude, perception and action come together in reach-to-grasp movements, relying on the integration of information from multiple sensory modalities. The present data can therefore support the motor control related suppression with significantly impaired tactile discrimination performance during movement execution [51]. The main cause of the reported decline in performance is most probably the reafferent sensation that results from body movements and exerts a backward masking effect on the incoming sensory information (see [6]). This impairment in performance has been shown to be present throughout the movement period and peaks once contact is made with the goal surface [1]. Once the movement has terminated, performance once again recovers to its previous natural state. This study brings clear behavioral evidence for a different temporal distribution of tactile sensitivity over the various phases of reach-to-grasp movements. As sensory suppression dominates the reach phase and peaks shortly before the grasp of the goal object, we believe the crucial time point in sensory suppression takes place in this gross interval extending from 100 ms before the grasp until approximately 100 ms after the grasp. It would be interesting to conduct an ERP follow-up study of the research outlined here in order to have a clear time separation of the sensory suppression phenomena as reported in the present study.

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