

Neural correlates of tactile perception during pre-, peri-, and post-movement

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Abstract Tactile information is differentially processed over the various phases of goal-directed movements. Here, event-related potentials (ERPs) were used to investigate the neural correlates of tactile and visual information processing during movement. Participants performed goal-directed reaches for an object placed centrally on the table in front of them. Tactile and visual stimulation (100 ms) was presented in separate trials during the different phases of the movement (i.e. preparation, execution, and post-movement). These stimuli were independently delivered to either the moving or resting hand. In a control condition, the participants only performed the movement, while omission (i.e. movement-only) ERPs were recorded. Participants were instructed to ignore the presence or absence of any sensory events and to concentrate solely on the execution of the movement. Enhanced ERPs were observed 80–200 ms after tactile stimulation, as well as 100–250 ms after visual stimulation: These modulations were greatest during the execution of the goal-directed movement, and they were effector based (i.e. significantly more negative for stimuli presented to the moving hand). Furthermore, ERPs revealed enhanced sensory processing during goal-directed movements for visual stimuli as well. Such enhanced processing of both tactile and visual information during the

execution phase suggests that incoming sensory information is continuously monitored for a potential adjustment of the current motor plan. Furthermore, the results reported here also highlight a tight coupling between spatial attention and the execution of motor actions.

Keywords Tactile · Visual · Event-related potentials · Goal-directed movement

Introduction

The importance of perceptual input for the appropriate execution of action (i.e. the perception-to-action link), as well as conversely, of action preparation and execution for the processing of perceptual inputs (i.e. the action-to-perception link), has been studied extensively (James 1890; Jeannerod 1994; Spence 2012).

Convincing evidence for the link from perception to action comes from lesion and inactivation studies. Impaired finger coordination and prehension have been observed when the primary somatosensory finger area of a monkey that had been trained to grasp and lift an object was inactivated, thus underlining the importance of sensory feedback for reach-to-grasp movements (Brochier et al. 1999). In a similar manner, human digital anaesthesia during grasping reveals the importance of cutaneous information in object manipulation tasks (Nowak et al. 2001; Augurelle et al. 2003; Monzée et al. 2003). Importantly, those patients who lacked cutaneous sensation exhibited disturbed control of the grip forces required to manipulate objects (Thonnard et al. 1997; Nowak et al. 2003), as well as deficits in interpreting other people's estimations of weights when they lifted objects (Bosbach et al. 2005).

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With regard to the action-to-perception link, the pre-motor theory of attention underlines the importance of motor planning in the allocation of attention (Rizzolatti et al. 1994). According to this theory, spatial attention leads to enhanced perception (see Rizzolatti and Craighero 2010, for discussion). Experimental evidence in favour of the pre-motor theory of attention comes from those studies that have investigated visual attention during various eye/hand movements. For example, a higher accuracy in discriminating visual targets at the goal of an upcoming saccade (Deubel and Schneider 1996; Baldauf and Deubel 2008; Collins et al. 2010), or the goal of an upcoming reaching movement (Deubel et al. 1998; Baldauf et al. 2006), has been found. Similarly, improved discrimination performance (Rorden et al. 2002) and detection performance for tactile targets presented at the location of an upcoming saccade (Juravle and Deubel 2009) have also been reported. These studies, indicating facilitation of participants' performance in response to sensory stimulation delivered in the motor preparation period, are complemented by the results of ERP studies: Enhanced somatosensory ERPs (e.g. P90 and N140) were described in response to tactile stimuli presented during the preparation of both eye movements (Gherri and Eimer 2008; Gherri and Forster 2012) and finger or arm movements (Eimer et al. 2005; Forster and Eimer 2007; Baldauf and Deubel 2009; Gherri and Eimer 2010).

For example, Gherri and Eimer (2008) used a cueing paradigm in order to examine tactile ERPs by having their participants either prepare a saccade or otherwise covertly direct their attention toward one or the other hand, following the delivery of the cue. For this, they utilized a 'S1–S2 task' with S1 standing for the cue presented at the start of the trial and S2 being the stimulus that the participants needed to make a response to (e.g. a gap/no gap short tactile stimulation). A rather long period of 800 ms between the delivery of S1 and S2 allowed for ERPs to be measured in response to attention orienting or motor preparation processes. The authors found similarly enhanced somatosensory ERPs for both covertly orienting spatial attention and motor preparation, thus suggesting similar underlying processes, as predicted by the pre-motor theory (Rizzolatti et al. 1994; van der Lubbe et al. 2000; Van Der Lubbe et al. 2006; Gherri and Eimer 2008). Other studies from the same authors with similar S1–S2 paradigms have demonstrated related results with various other manual tasks (e.g. finger lifting), as well as for visual information (see Gherri and Eimer 2010). However, here it is important to underline that finger lifting is not a goal-directed movement. At most, it can be considered as a plausible motor equivalent to the propensity to direct attention covertly. Furthermore, although the existing ERP studies provide a comprehensive view for the preparatory phase of

a saccade/finger lifting movement, there has (to the best of our knowledge) been no electrophysiological investigation of other movement periods, such as execution and post-movement.

The forward model of motor control (see Desmurget and Grafton 2000; Wolpert and Flanagan 2009, for reviews) offers a second powerful theoretical stance concerning the action-to-perception link. This model implies an internal representation of the body and environmental signals (i.e. a neural forward model, internal to the central nervous system) that is used to predict the sensory consequences of the outgoing motor command (Wolpert et al. 1995). As such, a forward model describes the causal link between an action and its sensory consequences (Wolpert and Flanagan 2009), based on the current state of the body and a copy of the motor command (i.e. efference copy). The key role of internal models in movement control is to regulate performance by comparing, in real time, the predicted sensory states with the actual sensory states. At the same time, forward models are used *to attenuate* movement-irrelevant sensory information or *to enhance* the sensory information that is essential for movement control. By attenuating the sensory signals resulting from the movement, it has been suggested that such a predictive mechanism serves to enhance the salience of external events, or those that cannot be predicted from the motor command (Bays and Wolpert 2007). This attenuation of what is felt—a phenomenon that has been termed tactile suppression—has been demonstrated for basic active and passive movements of the digits of the hand and forearm (see, for example, Chapman and Beauchamp 2006), as well as for goal-directed arm movements (Gallace et al. 2010; Juravle et al. 2010, 2011).

Therefore, the act of preparing and executing a goal-directed action allows for different predictions to be formulated by the pre-motor theory of attention (Rizzolatti et al. 1994) and the forward model of motor control (Wolpert et al. 1995): While the pre-motor theory predicts perceptual enhancement (driven by an *attentional* mechanism), the forward model predicts perceptual suppression (driven by a *perceptual suppression* mechanism). Although, at first glance, the predictions of these two theories appear to be at odds with one another, the two mechanisms they put forward need not necessarily be exclusive. For example, the forward model would predict enhancement particularly for those sensory stimuli that are rather novel and unexpected, a fact which raises the issue of perceptual relevance for movement (see Juravle et al. 2013). Note that behavioural visual discriminatory performance is enhanced at the expense of tactile information during reach-to-grasp movements (Brozzoli et al. 2009). On the other hand, tactile information can be predicted from self-generated action. If this potentially non-relevant tactile information were prone to sensory attenuation during movement, then we

would hypothesize that visual information (i.e. externally generated and independent of the body/self-image) to be enhanced during self-generated movement. Such a result would support the forward model account. Alternatively, however, if one were to assume that spatial attention ‘travels’ with the effector of the goal-directed movement, then perceptual input—either tactile or visual—should benefit from enhanced processing.

At the same time, the two explanatory theses could be brought together if a different temporal allocation of the two mechanisms during action was assumed. As such, the different mechanisms (attention vs. suppression) could become available, and thus act on the perceptual system, at different points in time during the goal-directed action. In this respect, if attentional facilitation were to be present during the preparatory phase, attenuation would reign over the motor execution period, with facilitation potentially occurring again in the post-movement period.

However, more importantly, the two theoretical accounts would predict opposing outcomes with regard to the perceptual processing at the movement effector (i.e. the moving hand in the present study). In this respect, if we were to consider the effector of the movement as a key delineator between the two contrasting mechanisms, then an attentional shift to the effector of the action would result in enhanced processing of perceptual information at the moving hand. Conversely, the estimates of the internal forward model would instead reflect the diminished processing of the same sensory information at the moving hand.

In the present study, we used the high temporal resolution provided by event-related potentials (ERPs) in order to investigate the neural correlates of tactile perception during the execution of goal-directed movements. The participants performed goal-directed reaches toward a foam object placed centrally on the table in front of them. A tactile-probe paradigm was used to deliver tactile stimulation to the index finger of participants’ moving or resting hands (see Heinze et al. 1990; Mangun and Hillyard 1988, for a similar probe paradigm in the visual domain). In order to investigate whether tactile perception is differently modulated as a function of the movement phase, these tactile probes were delivered at different points in time during the movement: preparation, execution, or post-movement. We were further interested in investigating whether the execution of goal-directed movements specifically affects tactile perception or whether it has a more general influence on perception, possibly relating to spatial attentional orienting. To investigate this hypothesis, visual probes were delivered at the index fingers of both moving and resting effectors during the different phases of the movement.

Methods

Participants

Eighteen participants recruited among the student population of the University of Hamburg took part in this study. The data from two of the participants were excluded from all analyses (see “Data analysis” section). The remaining 16 participants (nine male) had a mean age of 27 years (age range 22–45 years). They were all right-handed, had normal or corrected-to-normal vision, and normal hearing. All of the participants reported normal tactile sensitivity on the hands, as well as no known neurological impairment. The experiment was conducted according to the ethical guidelines of the Declaration of Helsinki (2008). Participants gave their informed consent prior to participating in the study. The preparation, together with the experimental session, lasted approximately 4–4.5 h, and participants were compensated with 8 EUR/h or course credit for taking part in the study.

Apparatus

The participants were seated at a table (70 cm long, 70 cm wide, and 78 cm high) in a dimly lit room. One rectangular piece of foam (52 cm long, 10 cm wide, and 3 cm high) was attached to the table in order for the participants to rest the hand to be moved during the block (*start position*). Another rectangular foam block (15.5 cm long, 4 cm wide, and 4 cm high) was attached centrally on the table at a distance of 32 cm from the start position, directly in front of the participant (*goal object*). Two additional pieces of foam (15 cm long, 12 cm wide, and 2 cm high) were placed on each side of the goal object, to rest the non-moving hand throughout the block (*resting positions*). Tactors (VBW32 skin stimulators, 1.6 × 2.4 cm vibrating surface, Audio-logical Engineering Corp., Somerville, MA, USA) were attached with tape to the ventral part of the fingertips of the index fingers of each of the participant’s hands. LEDs were attached by means of adhesive pastels (UHU-patafix, UHU GmbH, Bühl, Germany) to the nails of each index finger. The tactors and the LEDs were driven by means of custom-built hardware interfaces connected to the main computer running the experiment. For the tracking of the hand movement, infrared markers were attached to each index finger; each marker was positioned on the nail next to the LED and monitored by means of an Optotrak Certus motion tracker (Northern Digital Inc., Waterloo, Canada) with a sampling rate of 150 Hz and a spatial resolution of 0.01 mm. One additional marker, attached centrally on the table, 15 cm away from the goal object, served as an eye-fixation point throughout the trial. Auditory signals were delivered from

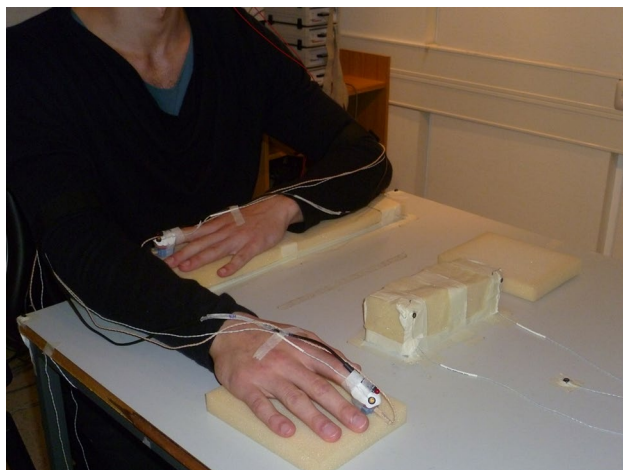


Fig. 1 Experimental set-up. Participant is depicted with his *left hand* at the start position and his *right hand* at the resting position

two loudspeaker cones, placed on a table behind the participants. See Fig. 1 for a depiction of the experimental set-up.

Procedure

Each experimental trial consisted of an outward goal-directed reach-to-grasp movement for the goal object. The participants had to listen out for three auditory signals presented from the two loudspeaker cones placed behind them. Each trial started with a beep (*prepare signal*, 600 Hz, 100 ms), instructing the participants to prepare the movement. After 270 ms, a second higher-pitched auditory signal (*go signal*, 800 Hz, 100 ms) instructed them to initiate their reach towards the goal object. We used the online-monitored spatial Optotrak data to ascertain that the hand was at the expected goal position. A third low-pitched auditory signal (*return signal*, 400 Hz, 100 ms) was delivered 300 ms after the hand had reached the goal object, instructing the participant to return to the start position. The experiment progressed to the next trial following an inter-trial interval of 2000 ms. The coordinates of the moving hand were monitored online throughout the movement phases (start, reach, grasp, and post-grasp), such that if the hand was not at the expected spatial position, the trial was repeated.

For each trial, tactile vibratory probes (250 Hz, 100 ms), visual LED illumination probes (100 ms), or the so-called omission probes (trials where no stimulation was delivered, only the movement was executed) were delivered/recorded. These were randomly distributed throughout the block and participants were told to ignore them and just perform the movement task. For the *moving hand*, visual and tactile probes were presented to the participant's index finger at different points in time, depending on the spatial location

of the hand executing the movement. That is visual/tactile probes were delivered during the *movement preparation* period (i.e. 100 ms before the go signal, when the hand was at the start position). The probes could also arrive during the *movement execution* period (i.e. when the hand was 13 cm (early position), 22 cm (mid-position), or 30 cm (late position) away from the start position). Last, the visual/tactile probes could be delivered in the *post-movement* period 100 ms after the grasp of the goal object. For the *resting hand*, the timing of the visual and tactile probes depended on the spatial location of the hand executing the movement. In particular, probes could be delivered either during the *movement preparation period* (100 ms before the go signal, when the moving hand was at the start position), during the *movement execution* period (22 cm away from the start position), or in the *post-movement* period (100 ms after the grasp of the goal object). The omission probe trials were recorded with the same timing of recording as for the delivery of the tactile probes (preparation, early, mid-, and late execution, and post-movement); note that no sensory stimulation was delivered in the omission trials.

The participants performed a short practice block of ten trials in order to get acquainted to the goal-directed movements to be performed during the experiment. The practice data are not part of the final data analysis.

Design

The experiment comprised 20 blocks of 72 trials each. The moving hand was blocked, so that participants performed ten blocks with the left hand moving, and ten blocks with the right hand moving. All participants started with the left hand moving. Within each block, a fixed number of probes were delivered for each experimental condition: For the *resting hand*, six tactile probes were delivered for each of the preparation, mid-execution, and post-movement periods, amounting to a total of 18 tactile probes per block. The resting hand received visual probes as well; three visual probes were delivered for each of the preparation, mid-execution, and post-movement periods, giving rise to a total of nine visual probes per block of trials. For the *moving hand*, six tactile probes were delivered for each of the preparation and post-movement periods, and four tactile probes for each of the early, mid-, and late execution periods, giving rise to a total of 24 tactile probes. As for the resting hand, the moving hand received three visual probes for each of the preparation, mid-execution, and post-movement periods, amounting to a total of nine visual probes per block.

Furthermore, we additionally recorded omission trials for the preparation, early, mid-, and late execution, as well as the post-movement periods. In total, 12 omission trials were recorded per block for each of the movement periods. Throughout the experiment, participants received 360

tactile probes and 180 visual probes to the resting hand. By contrast, 480 tactile probes and 180 visual probes were delivered at the moving hand. An additional 240 omission probes were also recorded. The experimental conditions were randomized within each block. Participants took short breaks between blocks and a longer break in the middle of the experiment.

Electroencephalographic recording

The EEG was recorded continuously from 74 Ag/AgCl scalp electrodes mounted on an elastic cap with 74 equidistant electrode positions (passive electrodes; cap EC80#, Easycap GmbH, Herrsching, Germany). The signal was referenced online to the left earlobe and re-referenced offline to the right earlobe. The electrode impedances were kept under 5 k Ω . The electrodes were mounted in the cap according to the international 10–10 system (Oostenveld and Praamstra 2001). Vertical eye movements were measured by means of an additional electrode placed under the left eye, with the same reference as the other electrodes. Horizontal eye movements were calculated offline by subtracting the signal recorded at the frontal electrode F10 from that recorded at F9, electrodes positioned in the cap near the outer canthi of the eyes. The electrode signals were amplified using three BrainAmp DC amplifiers with 32 channels each (Brain Products GmbH, Gilching, Germany) and digitally stored using the BrainVision Recorder software (Brain Products GmbH). The analogue EEG signal was sampled at 5000 Hz, filtered online with a band pass of 0.1–250 Hz, and then down-sampled online to 500 Hz to be stored on disc. The signal was filtered offline with a high cut-off at 40 Hz, 12 dB/oct, and a notch filter of 50 Hz.

Data analysis

Behavioural data pre-processing

The behavioural data were inspected to control for trials in which reaction times to initiate the goal-directed movement were slower than 1000 ms and trials in which the total duration of the movement was greater than 2000 ms. These trials were excluded from the final ERP analysis (9 % of all trials).

EEG data pre-processing

EEG data pre-processing was conducted with VisionAnalyzer 2 (Brain Products GmbH). The EEG signal was segmented into epochs of 550-ms duration (from 100 ms pre- to 450 ms post-stimulus). The segmented vertical electro-oculogram data were then submitted to a blink artefact rejection procedure—segments with an absolute voltage

difference between maximum and minimum sample points higher than 60 μ V were removed. Furthermore, a second artefact rejection was conducted on the remaining 74 scalp electrodes to inspect for movement (e.g. horizontal eye movements) and other amplifier artefacts—segments with an absolute voltage difference between maximum and minimum sample points higher than 100 μ V, as well as segments with an activity lower than 0.5 μ V for a period of more than 100 ms, were removed. The remaining data were then averaged by condition and baseline corrected (100 ms pre-stimulus baseline). Participants with more than 33 % of trials per condition rejected were excluded from the final analysis (two participants). The averages [mean amplitudes in (μ V)] for each condition for each participant were exported to MATLAB (MATLAB 2009b, MathWorks, Natick, MA, USA), and the remaining analysis was carried out using this software.

ERP data analysis

The average ERPs for each condition and for each participant were separately calculated for the left and right stimulated sites. The ERPs were then collapsed over the left and right stimulated hands by inverting the electrode configuration of the left stimulated sites and then averaging over both stimulated sites (Heed and Röder 2010). Note that the same remapping procedure was performed separately for the data from the moving and the resting hand. Therefore, in this study, figures are displayed as if stimulation occurred to the right finger only, with ipsilateral activity shown over the right hemisphere and contralateral activity over the left hemisphere. ERPs are plotted with the negative up. Topographic maps were created with EEGLAB (Delorme and Makeig, 2004). Only for visualization purposes, the ERP data in Figs. 2 and 3 were submitted to a low-pass moving average filter with a span of ten data points which was based on a linear regression algorithm set to assign zero weights to the raw data found to be outside ± 6 standard deviations of the mean (Curve Fitting Toolbox, MATLAB 2009b).

Somatosensory ERPs have been shown to be maximal over sites contralateral to the stimulated hand (Röder et al. 1996; Eimer et al. 2005). Following a visual inspection of the data, and in accordance with the previous literature on somatosensory ERPs (Luck 2005), the mean amplitudes of the tactile N140 over the 80–200 ms post-stimulus onset time window were analysed. For the visual N100, we chose, following a visual inspection of our data, a temporal window between 100 and 250 ms post-stimulus onset. The omission probe trials analysis was conducted on the same temporal window as that for the tactile probes (80–200 ms). The somatosensory and visual ERPs were considered for analysis with different temporal windows particularly because of their appearance following the visual inspection,

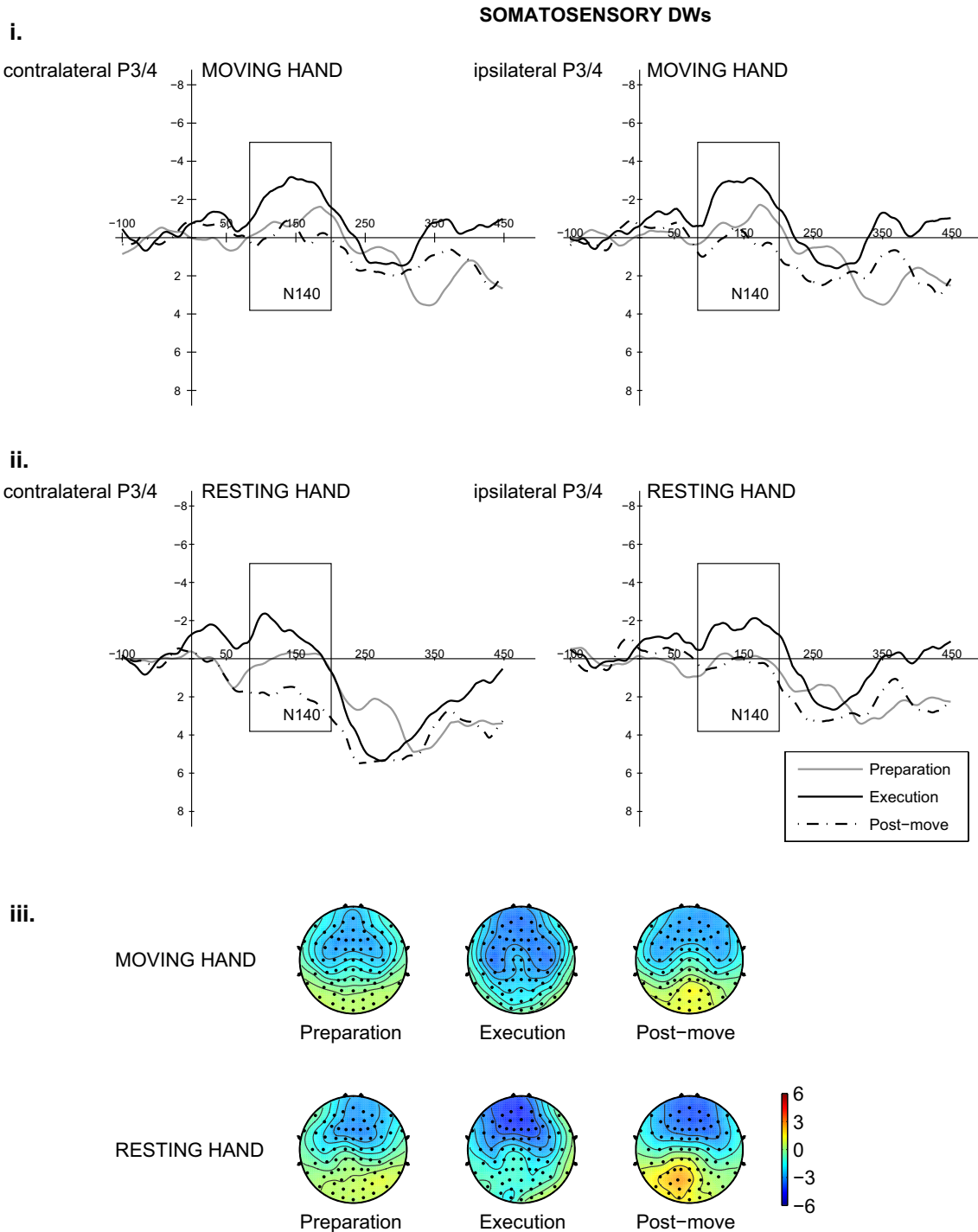


Fig. 2 Somatosensory DWs depicted at the P3/4 electrode pair for the moving hand (**i**) and the resting hand (**ii**); the analysed time period (N140) is enclosed in a rectangle. Time 0 on the abscissa corresponds to the time of tactile stimulus delivery. Note that the electrophysiological activity is displayed as if tactile stimulation was delivered to the right hand only, with ipsilateral activity depicted over the

right hemisphere and contralateral activity over the left hemisphere. DWs are plotted with the negative up. Topographic maps for the N140 (80–200 ms) to tactile stimuli delivered at both moving/resting effectors during the preparation, execution, and post-movement phases are presented in (**iii**)

as well as the different characteristics of sensory information. Note that both the tactile and the visual stimulation in

the present study had a duration of 100 ms, accounting for relatively longer-lasting somatosensory/visual ERPs.

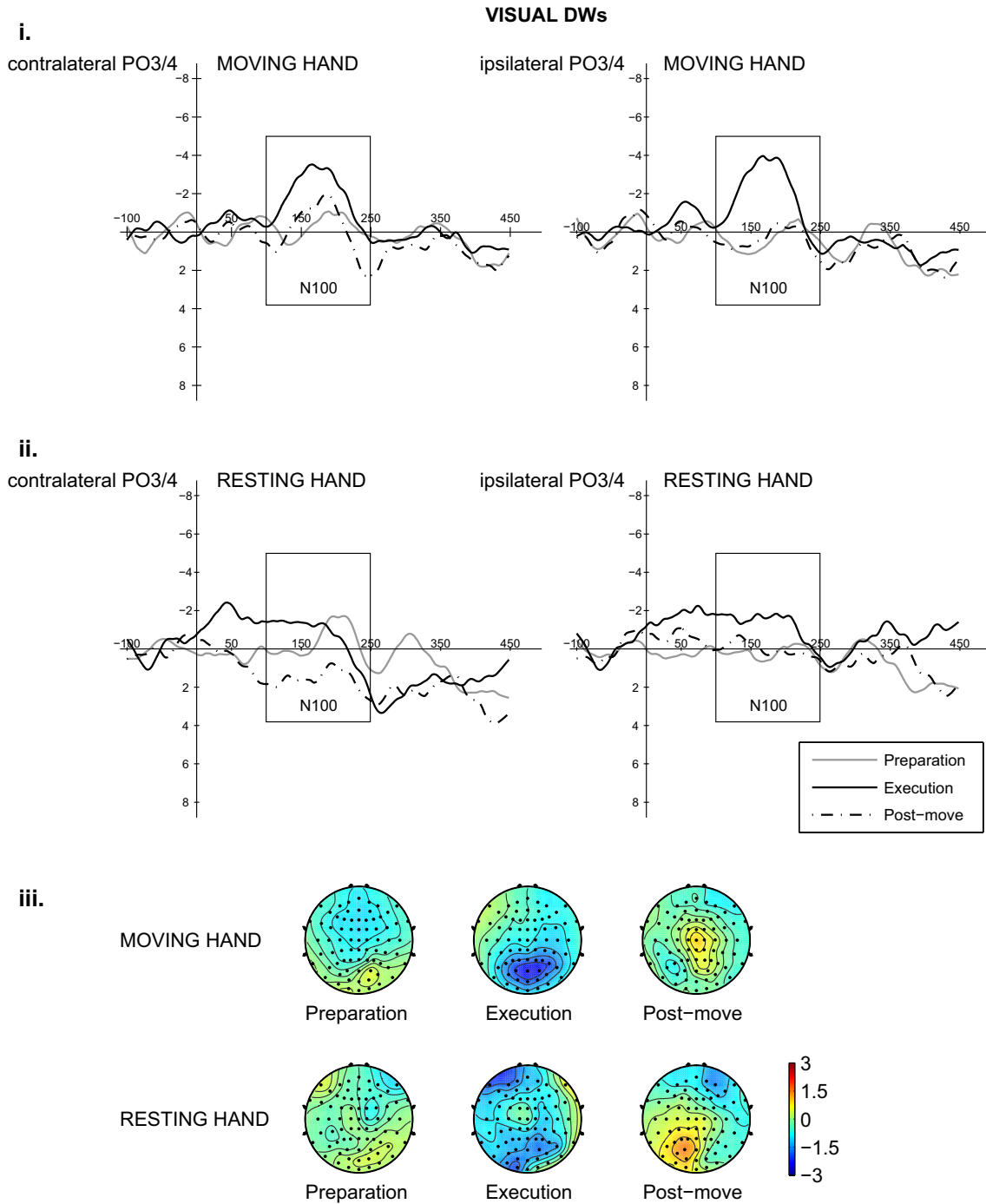


Fig. 3 Visual DWs depicted at the PO3/4 electrode pair for the moving hand (**i**) and the resting hand (**ii**); the analysed time period (N100) is enclosed in a rectangle. Time 0 on the abscissa corresponds to the delivery of the visual stimulus. Note that the electrophysiological activity is displayed as if visual stimulation was delivered to the right hand only, with ipsilateral activity depicted over the right hemisphere

and contralateral activity over the left hemisphere. DWs are plotted with the negative up. Topographic maps for the N100 (100–250 ms) to visual stimulation delivered at both moving/resting effectors during the preparation, execution, and post-movement phases are presented in (**iii**)

The morphology of the ERPs to tactile stimuli is similar to what has been reported previously, comprising a N80 and a N140. Since the first effects for the manipulated

experimental factors (e.g. hand and timing) started 80 ms post-stimulus onset and lasted for approximately 120 ms, we decided to analyse this time epoch, thereby avoiding

multiple testing as well. Note, earlier potentials (i.e. earlier than 50 ms post-stimulus onset) require more stimulus repetitions and a shorter stimulus presentation (Desmedt and Tomberg 1985).

In this ERP pre-processing stage, the activity recorded for the omission trials where only the movement was performed was subtracted from the ERPs in those trials in which participants performed the movement and additionally received a tactile or visual probe; The resulting waves are referred to as somatosensory and visual difference waves (DWs). This procedure eliminates any effect caused by possible movement-related activity, which would differ for the preparation, execution, and post-movement phases. The statistical analysis was conducted on the so-derived somatosensory DWs.

The statistical analysis was carried out over pairs of contralateral/ipsilateral electrodes: frontal-central (FC3/4), central (C3/4), central-parietal (CP3/4), and parietal (P3/4) for somatosensory DWs (see Forster and Eimer 2005, 2007 for a similar selection of electrodes when analysing somatosensory ERPs). The somatosensory DWs were analysed using repeated-measures analyses of variance (ANOVAs) with the factors hand (moving vs. resting), timing (preparation, execution, and post-movement), hemisphere (contralateral vs. ipsilateral), and electrode pair (FC3/4, C3/4, CP3/4, and P3/4). When an interaction proved to be significant, further ANOVAs were conducted that analysed the DWs separately for each factor level of one of the interacting factors. As such, four-way interactions between all experimental factors were split in a first step and the specific location where the effect was arising from was then analysed. For example, if an interaction between the hand that received the stimulation, the timing of stimulus delivery, the hemisphere, and the electrode pair was observed, it was followed up with a separate analysis for each electrode pair with the factors of hand, timing, and hemisphere. Furthermore, significant three-way interactions found in the DWs data were broken down in a hypothesis-driven manner. To continue with the previous example, if a three-way interaction with hemisphere was observed, separate ANOVAs (with the factors hand and timing) were conducted for each hemisphere. Trivial main effects of the topographical factors as hemisphere and electrode pair, as well as interactions between the two, are not reported. Lastly, the two-way interactions that were encountered in the data were followed by post hoc pairwise *t* tests. These subsequent comparisons were conducted using the Sidak adjustment for multiple comparisons; only the tests that survived the comparison are reported. Mauchly's test of sphericity was used to ensure that the data did not violate the sphericity assumption. If the sphericity assumption was violated, then the Huynh–Feldt correction is reported as ϵ throughout the text in order to adjust the degrees of freedom; the corrected

p values are reported. Effect sizes are reported with partial η^2 for the repeated-measures ANOVAs; post hoc *t* tests bear the correlation coefficient *r* as a measure of effect size.

In a subsequent step, a similar statistical analysis as that conducted for somatosensory DWs was performed on the visual DWs data at the occipital pair of electrodes PO3/4 (see, for example, Gherri et al. 2009; Gherri and Eimer 2010; Ley and Röder 2014, for a similar choice of electrodes). This visual DWs analysis accounted for a confound of the design utilized in the present experiment. It is known that the visual ERPs depend on the visual field location of the eliciting visual stimulus (see Luck 2005). The reach-to-grasp movement executed here involved outward extensions of either the right or the left hand. Due to the particular characteristics of the movement, in the preparation period, the visual stimulation was delivered on the (visual) contralateral hemifield for both moving and resting effectors. More exactly, a visual stimulus to the moving left hand would appear to the right of the body midline, whereas when the visual stimulus is delivered to the resting left hand, the stimulus is presented to the left of the body midline. However, in the post-movement period, the visual probe was received in the (visual) contralateral hemifield for the moving hand and the (visual) ipsilateral hemifield for the resting hand. For this reason, the visual DWs analysis involved separate ANOVAs for the resting and moving hand data, with the following factors: timing (motor preparation, execution, post-movement) and electrode (PO3/4).

Results

Here, we report the results for the somatosensory and visual difference waves (DWs, that is, ERPs to tactile or visual stimuli, minus omission ERPs).

Somatosensory DWs analysis at FC3/4, C3/4, CP3/4, and P3/4

Somatosensory DWs together with scalp topographies are presented in Fig. 2. The somatosensory DWs analysis was conducted on the data from both moving and resting hands for the different timings of delivery of the tactile probes, at several pairs of electrodes. Therefore, the main ANOVA had four factors: hand (moving vs. resting), timing (preparation, execution, and post-movement), hemisphere (contralateral vs ipsilateral), and electrode pair (FC3/4, C3/4, CP3/4, and P3/4).

The overall somatosensory DWs analysis revealed main effects of hand [$F(1,15) = 10.98$; $p = .005$; $\eta_p^2 = .423$] and timing [$F(2,30) = 10.53$, $p < .001$; $\eta_p^2 = .413$]. Significant two-way interactions were observed between hand and electrode pair [$F(3,45) = 7.34$; $p = .010$; $\epsilon = .428$;

$\eta_p^2 = .328$] and timing and electrode pair [$F(6,90) = 4.08$; $p = .021$; $\varepsilon = .388$; $\eta_p^2 = .214$]. Furthermore, significant three-way interactions between hand, timing, and hemisphere [$F(2,30) = 4.42$; $p = .021$; $\eta_p^2 = .227$], and between hand, timing, and electrode [$F(6,90) = 11.87$; $p < .001$; $\varepsilon = .428$; $\eta_p^2 = .442$] were found. Lastly, a four-way interaction between hand, timing, hemisphere, and electrode was observed [$F(6,90) = 5.56$, $p = .005$; $\varepsilon = .417$; $\eta_p^2 = .271$]. For each of the electrode pairs (FC3/4, C3/4, CP3/4, and P3/4), we followed up this interaction with repeated-measures ANOVAs with the factors hand, timing, and hemisphere.

At the FC3/4 electrode pair, a significant main effect of timing [$F(2,30) = 5.67$, $p = .008$; $\eta_p^2 = .274$] was observed, with a more negative N140 elicited during movement *execution*, as compared to both *preparation* [$t(15) = 3.05$, $p = .008$, $r = .78$] and *post-movement* periods [$t(15) = -3.28$, $p = .005$, $r = .77$]. The same significant timing main effect was significant at the C3/4 site [$F(2,30) = 7.99$, $p = .002$; $\eta_p^2 = .347$]: The DWs of the *pre-* [$t(15) = 2.87$, $p = .012$, $r = .64$] and the *post-movement* phases [$t(15) = -4.11$, $p = .001$, $r = .70$] were significantly less negative, as compared to DWs of the *peri-movement* phase. At C3/4, a significantly more negative N140 was found for the moving effector, as suggested by a main effect of hand [$F(1,15) = 12.93$, $p = .003$; $\eta_p^2 = .463$].

At the CP3/4 electrode pair, the results revealed significant main effects of hand [$F(1,15) = 22.93$; $p < .001$; $\eta_p^2 = .605$] and timing [$F(2,30) = 10.79$; $p < .001$; $\eta_p^2 = .418$], as well as an interaction between hand, timing, and hemisphere [$F(2,30) = 4.83$; $p = .015$; $\eta_p^2 = .243$]. We followed up on this interaction with separate ANOVAs for each hemisphere with the factors hand and timing; however, no significant interaction was found. Furthermore, for each of the moving and resting effectors, we conducted separate ANOVAs with the factors timing and hemisphere. At the resting hand, a significant interaction between timing and hemisphere was found [$F(2,30) = 3.59$; $p = .040$; $\eta_p^2 = .193$]. This interaction indicated that over the contralateral hemisphere there was a significantly less negative N140 during the *post-movement* period, relative to both *preparation* [$t(15) = -2.84$, $p = .012$, $r = .66$] and *execution* periods [$t(15) = -3.81$, $p = .002$, $r = .62$]. On the other hand, for the ipsilateral hemisphere, we found a significantly less negative N140 over the *preparation* period as compared to the *execution period* [$t(15) = -3.02$, $p = .009$, $r = .63$]. Lastly, separate ANOVAs conducted for each of the movement phases with the factors hand and hemisphere indicated a significant interaction between the two factors over the *post-movement* period [$F(1,15) = 7.02$; $p = .018$; $\eta_p^2 = .319$]. This interaction resulted from a significantly more negative N140 for tactile stimuli at the moving hand

as compared to the resting hand on the contralateral hemisphere [$t(15) = -5.52$, $p < .001$, $r = .82$].

At the P3/4 electrode pair, significant main effects of hand [$F(1,15) = 11.51$; $p = .004$; $\eta_p^2 = .434$] and timing [$F(2,30) = 14.17$; $p < .001$; $\eta_p^2 = .480$] were found, as well as an interaction between timing and hemisphere [$F(2,30) = 5.26$; $p = .011$; $\eta_p^2 = .260$], and between hand, timing, and hemisphere [$F(2,30) = 12.10$; $p < .001$; $\varepsilon = .799$; $\eta_p^2 = .799$]. Separate ANOVAs with the factors hand and timing conducted for each hemifield indicated a significant interaction between the two factors on the contralateral hemisphere [$F(2,30) = 5.36$, $p = .010$; $\eta_p^2 = .263$]. Paired-samples *t* tests revealed that the N140 to tactile stimuli at the resting hand was significantly less negative than the N140 to tactile stimuli at the moving hand over the *post-movement* period [$t(15) = -6.48$; $p < .001$, $r = .78$].

Separate ANOVAs with the factors timing and hemisphere were conducted for each hand. A significant interaction was found between the two factors tested at the resting effector [$F(2,30) = 12.32$, $p = .001$; $\eta_p^2 = .451$], with the resting hand eliciting a significantly less negative N140 during the *post-movement* period, as compared to both the *preparation* [$t(15) = -4.97$; $p < .001$, $r = .66$] and the *execution* periods [$t(15) = -5.05$; $p < .001$, $r = .49$] on the contralateral hemisphere. On the other hand, a significantly more negative N140 was found to tactile stimuli at the resting hand over the ipsilateral hemisphere during movement *execution* as compared to *preparation* [$t(15) = 3.82$, $p = .002$, $r = .54$] and *post-movement* [$t(15) = -3.23$; $p = .006$, $r = .38$]. Lastly, the ANOVAs conducted for each of the movement periods with the factors hand and hemisphere revealed a significant interaction between the two factors over the *post-movement* period [$F(1,15) = 15.23$, $p = .001$; $\eta_p^2 = .504$]. This result was given by the significantly less negative resting hand N140 as compared to the moving hand over the contralateral hemisphere [$t(15) = -6.48$; $p < .001$, $r = .78$].

Summary of results for the somatosensory DWs analysis

The somatosensory DWs analysis conducted for tactile stimuli at the moving and resting effectors found an enhanced N140 for tactile stimuli delivered to the moving, as compared to the resting hand (at C3/4). At more posterior sites (i.e. CP3/4, P3/4), the same effect was lateralized to the contralateral hemisphere. Furthermore, with regard to the timing of the delivery of tactile stimulation, more negative somatosensory DWs were found over the *execution* period, as compared to both the movement *preparation* and *post-movement* periods (at FC3/4 and C3/4 electrodes). With regard to the resting effector, at central-posterior electrodes (CP3/4, P3/4) the timing effect was lateralized: On

the contralateral hemisphere, the *preparation* and *execution* phases of the movement revealed significantly more negative DWs as compared to the *post-movement* period. Over the ipsilateral hemisphere, the DWs of the *execution* phase were more negative, as compared to the *pre-* and the *post-movement* phases.

Visual DWs analysis at PO3/4

The visual DWs analysis was conducted on the visual DWs at PO3/4 separately for the moving and resting hands for the different points in time when the visual probes were delivered (see Fig. 3). The analysis accounted for one confound in the experimental design utilized in this experiment: This confound relates to the fact that in the *post-movement* period, the visual probe was received when the moving hand was located in the (visual) contralateral side, whereas the visual probe was received in the (visual) ipsilateral side at the resting hand. Therefore, at the analysis level, we conducted separate ANOVAs for each of the moving/resting hands, each of these ANOVAs with two factors: timing (*preparation*, *execution*, and *post-movement*) and electrode (PO3 vs. PO4). See “ERP data analysis” section for a more detailed rationale of the analysis.

The analysis of the moving hand visual DWs revealed a main effect of timing [$F(2,30) = 11.60$, $p < .001$; $\eta_p^2 = .436$], with visual DWs significantly more negative in the *execution* period, as compared to the *preparation* [$t(15) = -4.14$, $p = .001$, $r = -.13$] and *post-movement* periods [$t(15) = -3.86$, $p = .002$, $r = -.12$]. The same significant timing effect was observed for the resting hand [$F(2,30) = 3.59$; $p = .040$; $\eta_p^2 = .193$]. Additionally, the analysis of the visual DWs revealed a significant interaction between the two factors of timing and electrode at the resting hand [$F(2,30) = 15.46$; $p < .001$; $\eta_p^2 = .508$]. For the contralateral electrode PO3, a significant main effect of timing was found at the resting hand [$F(2,30) = 5.62$; $p = .008$; $\eta_p^2 = .272$]: The *post-movement* period N100 was significantly less negative as compared to both the *preparation* period N100 [$t(15) = -3.15$, $p = .007$, $r = .40$] and the *execution* period N100 [$t(15) = -2.84$, $p = .012$, $r = -.33$].

Summary of results for the visual DWs analysis

For the moving hand, a bilateral significantly enhanced N100 was found for the motor *execution* period, relative to the *post-movement* and *preparation* periods. At the resting hand, the N100 was significantly less negative in the *post-movement* period, as compared to the N100 in both the movement *preparatory* and *execution* phases. Given that comparable magnitude visual DWs effects are seen for the moving and the resting effectors, it can be concluded

that the findings concerning the visual DWs for the moving hand are not the result of a hemifield change for the visual stimulus, since stimulation was delivered on the ipsilateral side during the movement execution phase. This conclusion is supported by the fact that we find no difference in visual DWs between the movement *preparation* and *execution* phases.

Discussion

The goal of the present study was to use event-related potentials (ERPs) to investigate the neural correlates of tactile and visual processing before, during, and after the execution of goal-directed reach-to-grasp movements. For this purpose, ERPs were recorded in response to tactile and visual probes delivered to the participant's resting and moving hands, during the three temporal phases of the movement: *preparation*, *execution*, and the *post-movement* periods. Additionally, in a control condition, ERPs were recorded while the participants performed the movement, but no sensory stimulation was received during the trial. Therefore, in order to characterize tactile processing (i.e. the facilitatory attentional effect versus the inhibitory suppression effect on tactile processing previously observed at a behavioural level, see “Introduction” section), the analyses performed on the somatosensory and visual ERP data had the goal of distinguishing between the spatial attention versus sensory suppression mechanisms with respect to the different temporal phases of the movement.

Theories of spatial attention predict significantly enhanced somatosensory ERPs for the moving hand, whereas forward models predict attenuation in the processing of somatosensory information at the moving effector instead. In the present experiment, the somatosensory N140 was significantly more negative for the moving hand, as compared to the resting hand. This ERP *enhancement* for the moving hand was particularly evident at central and parietal electrodes, known to be located over somatosensory brain areas. Such a finding provides support for spatial attention accounts, by underlining that it is the moving hand that receives higher attentional prioritization as compared to the resting hand, over the time course of a goal-directed reach-to-grasp movement. Posture was shown to affect the deployment of visual attention in both front and rear the body peripersonal space (see, for example, Eimer et al. 2004; Gillmeister and Forster 2012). It is for this reason that the visual ERPs were considered separately during the analysis at the moving and resting hands.

With regard to the timing of perceptual effects, whereas the forward model predicted a significant attenuation of processing beginning with the *preparatory* phase and extending into the movement *execution* period, the spatial

attention account would, in turn, predict quite the opposite—That is, significantly enhanced processing in the *pre-* and *peri-movement* phases. The results reported here indicated a differential pattern of activity with respect to the timing of tactile stimulation delivery: More exactly, the *execution* phase of the movement was characterized by a significantly more negative somatosensory N140 as compared to both the *preparation* and *post-movement* phases. Enhancements in somatosensory ERPs following stimulation delivered to a resting hand (van Velzen et al. 2002; Forster and Eimer 2007), or in the movement *preparation* period at the movement effector (Eimer et al. 2005; Forster and Eimer 2007; Ghetti et al. 2007), have traditionally been attributed to a neural network responsible for both covert spatial attention shifts, as well as for the programming of corresponding movements (i.e. overt shifts of attention). As an alternative to this (spatial) attentional explanation, this enhancement in activity could result from the peripheral input from the movement being processed at the cortical level during movement *execution*, as opposed to its preparation and initiation (see Urbano et al. 1998). However, note that significantly enhanced ERPs were found for the movement *execution* period even when the movement-only activity (omission trials) was subtracted from the somatosensory ERPs (i.e. in our DWs analyses). Thus, if one were to consider such enhancements in the ERPs as an effect of an attention-directing process, then it would appear as though the *execution* phase of a goal-directed reach-to-grasp movement benefits from the highest attentional prioritization. Interestingly, our results demonstrate the same time course of attentional facilitation throughout the movement *execution* period not only for the movement effector, but importantly for the resting effector as well. Such an outcome could reflect the fact that many of our hand movements are often bimanually coordinated (Kelso et al. 1979) and require the distribution of attention over the two hands. Moreover, it has been demonstrated that our limbs are functionally coupled during reach-to-grasp movements (Jackson et al. 2002). This similar functional involvement of the other hand has been documented in the transcranial magnetic stimulation literature (Chen et al. 2005), as well as in the field of mirror movements in healthy adults (Konagaya et al. 1990; Armatas et al. 1994).

A third prediction of the spatial attention account would be reflected in an enhancement in the processing of both tactile and visual stimulation. By contrast, the forward model prediction would favour an enhancement in processing of only the sensory information which cannot be predicted from the motor command (i.e. visual information). With these predictions in mind, it is interesting that our results indicate that not only tactile, but additionally visual information (i.e. the more negative visual N100) received enhanced consideration during the *execution* phase of a

goal-directed movement. These results thus provide evidence against the modality-based explanation of sensory relevance during movement (Bays and Wolpert 2007) and argue instead in favour of taking spatial attention as the explanatory factor for the change in sensory processing that occurs during the *execution* of goal-directed movements. Support for this explanation comes from the results of a study that differentiated between simple reaching and grasping movements: The processing of visual sensory information was enhanced over the *execution* phase of a grasping movement, as compared to a simple pointing movement (van Elk et al. 2010). The authors concluded that the intention to manipulate/interact with an object determines the enhanced processing during the execution/reaching period of an action of those visual attributes important for the later manipulation.

Finally, even though convincing behavioural evidence for the existence of tactile sensory suppression during movement *execution* has been reported (Gallace et al. 2010; Juravle et al. 2010, 2011, 2013), we did not observe sensory suppression in the present study. Previous studies that have concentrated on earlier somatosensory ERPs than those analysed in the present study (i.e. generated in the first 40 ms post-stimulus onset) have reported an attenuation of early somatosensory ERPs during the *execution* of simple finger movements (Rossini et al. 1999). In a similar manner, in studies examining the sense of agency, suppression of the early auditory N1 deflection has been reported for sounds following as predicted the executed action, as opposed to auditory signals which happened with an unexpected delay (Kühn et al. 2011). Interestingly, the sense of agency seems to result only from self-planned movements, whereas it is not apparent for motor actions triggered by TMS application over the motor cortex (Timm et al. 2014). With regard to the current study, the most sensible explanation for a preferential treatment of incoming sensory information over the movement *execution* period, as observed here is that incoming information could be of use for a potential unexpected adjustment of the current motor plan.

Conclusion

The present study was designed to investigate, at a neural level, the characteristics of tactile and visual processing during the *pre-*, *peri-*, and *post-movement* phases of a goal-directed reach-to-grasp movement. The results suggest that overall the moving effector benefits from enhanced sensory processing, as compared to the resting effector. Moreover, with respect to the timing of the delivery of sensory stimulation, the results reported here indicate that the *execution* period is the processing stage of the movement that receives the highest attentional allocation, as compared

to the *preparatory* and *post-movement* phases. Lastly and most importantly, attention affects the two modalities of touch and vision during the goal-directed reach-to-grasp movement *execution*. The prioritization of sensory information during movement *execution* presumably has the scope of adjusting the ongoing motor plan, in case of an unexpected event.

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