

Opposed optimal strategies of weighting somatosensory inputs for planning reaching movements toward visual and proprioceptive targets

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Submitted 4 December 2013; accepted in final form 11 August 2014

Blouin J, Saradjian AH, Lebar N, Guillaume A, Mouchnino L. Opposed optimal strategies of weighting somatosensory inputs for planning reaching movements toward visual and proprioceptive targets. *J Neurophysiol* 112: 2290–2301, 2014. First published August 13, 2014; doi:10.1152/jn.00857.2013.—Behavioral studies have suggested that the brain uses a visual estimate of the hand to plan reaching movements toward visual targets and somatosensory inputs in the case of somatosensory targets. However, neural correlates for distinct coding of the hand according to the sensory modality of the target have not yet been identified. Here we tested the twofold hypothesis that the somatosensory input from the reaching hand is facilitated and inhibited, respectively, when planning movements toward somatosensory (unseen fingers) or visual targets. The weight of the somatosensory inputs was assessed by measuring the amplitude of the somatosensory evoked potential (SEP) resulting from vibration of the reaching finger during movement planning. The target sensory modality had no significant effect on SEP amplitude. However, Spearman's analyses showed significant correlations between the SEPs and reaching errors. When planning movements toward proprioceptive targets without visual feedback of the reaching hand, participants showing the greater SEPs were those who produced the smaller directional errors. Inversely, participants showing the smaller SEPs when planning movements toward visual targets with visual feedback of the reaching hand were those who produced the smaller directional errors. No significant correlation was found between the SEPs and radial or amplitude errors. Our results indicate that the sensory strategy for planning movements is highly flexible among individuals and also for a given sensory context. Most importantly, they provide neural bases for the suggestion that optimization of movement planning requires the target and the reaching hand to both be represented in the same sensory modality.

somatosensory evoked potential; movement planning; proprioceptive target; movement direction; electroencephalography

REACHING OUR OWN BODY PARTS with the hand is a motor action that we can accomplish as accurately as when reaching for seen objects, even with the eyes closed. In the former case the targets of the reach are defined through somatosensory information (e.g., proprioception), whereas in the latter they are defined through retinal inputs. The neural transformations that convert the spatial coordinates of the target into motor commands therefore depend on the sensory modality of the target.

A prevailing assumption for the control of goal-directed arm movements is that both the target and the reaching hand must be represented in the same sensory map to define the movement vector (Jeannerod 1991; Pouget et al. 2002; Sober and Sabes 2005). In the dark the encoding of the reaching hand relies on somatosensory cues, but in an illuminated environ-

ment visual inputs can also contribute. Therefore, according to the above assumption, the brain would preferably encode the reaching hand within a somatosensory map when planning movements toward proprioceptive targets and within a visual map in the case of visual targets. This idea has received substantial support from behavioral studies in which subjects received true or shifted visual feedback of their reaching finger while planning movement toward either visual or proprioceptive targets (Sarlegna and Sainburg 2007; Sober and Sabes 2005). These studies showed that the false visual feedback of the reaching finger had virtually no effect on movements directed toward proprioceptive targets. This contrasted with the large reaching errors that resulted from the visual shift when subjects reached for visual targets. These results therefore suggest that somatosensory input of the reaching hand has a greater influence when planning movements toward proprioceptive targets while hand visual feedback prevails when reaching for visual targets. Given that somatosensory and visual feedbacks also contribute to control ongoing hand movements (Blouin et al. 1993; Elliott et al. 2010; Reichenbach et al. 2009, 2014; Sarlegna et al. 2003; Saunders and Knill 2003), the sensory modality of the target could similarly modulate the importance of somatosensory and visual inputs of the reaching hand during movement execution.

To date, neural correlates for distinct sensory coding of the hand according to the sensory modality of the target have not yet been uncovered. Differentially weighting somatosensory input when controlling movements toward proprioceptive and visual targets could be part of the neural mechanisms at play. We tested this hypothesis by recording the cortical somatosensory evoked potentials (SEPs, P60-N100 component) following vibratory stimulation of the reaching finger while participants planned movements toward either visual or proprioceptive (unseen fingers of the opposite hand) targets. In light of the capacity of the brain to selectively facilitate or suppress sensory inputs according to task demands (Cybulska-Klosowicz et al. 2011; Legon and Staines 2006; Saradjian et al. 2013), we reasoned that the magnitude of the SEPs should be a key indicator of the weighting of the somatosensory inputs of the reaching hand during the planning stage of the movements. Accordingly, we hypothesized that movement planning in the case of proprioceptive targets would be associated with larger SEPs than when the reaches were directed toward visual targets. This could be achieved by facilitating or inhibiting somatosensory inputs when reaching toward proprioceptive and visual targets, respectively. We also predicted that the SEPs would be greatest when participants reached toward proprioceptive targets without visual feedback of the reaching finger, that is, when the target and the hand can only be

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represented in a somatosensory map to define the movement vector.

The prediction of opposite effects of proprioceptive and visual targets on SEP amplitude was verified for the participants who produced the smallest reaching directional errors. Participants who produced the smallest errors showed larger SEPs when planning movements toward a proprioceptive target without visual feedback of the reaching hand and reduced SEPs when reaching toward a visual target with hand visual feedback. Participants who produced the largest directional errors showed the opposite pattern of results. Our results therefore indicate that increasing and attenuating the weight of somatosensory inputs of the reaching hand are part of the neural processes that allow optimizing movements toward proprioceptive and visual targets, respectively.

MATERIALS AND METHODS

Participants

Ten right-handed healthy paid participants (mean age 26.7 ± 6.6 yr, range 21–38 yr; 5 women and 5 men) took part in this study. The experiment was conducted with the understanding and written consent of each participant, in accordance with the ethical standards of Aix-Marseille University and those set out in the 1964 Declaration of Helsinki. All procedures were accepted by the local ethics committee.

Experimental Protocol

A schematic representation of the experimental setup is presented in Fig. 1. The participants were comfortably seated on a chair in front of a table situated in a dark chamber. In the starting position, the participants' right arm was slightly extended and the index finger was positioned resting above a hole (1-cm diameter) containing a solenoid vibrator. A white light-emitting diode (LED) was positioned 5 cm to the left of starting finger position, and the participants were required to look at this fixating LED throughout the trials and to not perform saccades toward the targets.

The participants' task was to reach with the index finger for targets positioned between the starting position and their body. The movements were essentially performed by small-amplitude elbow joint flexions and arm adductions. Participants were asked to produce relatively fast (mean movement duration = 389 ± 85 ms) and accurate movements without producing corrections when they detected terminal errors. The vibrator underneath the index finger was always activated 100 ms (frequency: 80 Hz, amplitude: 2 mm) after the target presentation (see below) and for a 100-ms duration to stimulate the somatosensory receptors of the reaching index finger and to evoke SEPs. We chose to trigger the vibration 100 ms after target presentation in light of the results of a previous study showing that the earliest significant reach-related activity observable in the frontoparietal areas occurred some 150 ms after target presentation (for both visual and somatosensory targets) (Bernier et al. 2009a). Hence, providing the vibratory stimulus 50 ms before these reach-related activities appeared as a good temporal target window for both target sensory modalities. It is also worth noting that the 100-ms duration of the vibratory stimulus was too short to evoke illusory displacement of the reaching finger. Participants were told that their movement accuracy would be measured and that they did not have to initiate their movements as fast as possible after target presentation or vibration onset (i.e., as in a reaction time task).

Four combinations of target sensory modality (i.e., visual, proprioceptive) and reaching finger visual feedback (i.e., vision, no vision) were carried out in separate blocks of 45 trials. For the visual target modality (Fig. 1A), the participants had to reach for one of three LEDs (3 mm in diameter, 50-ms illumination duration) embedded in the

table surface. These LEDs were located ~ 10 cm from the finger starting position. One of them was located in the participants' medio-sagittal plane and the others $\sim 23^\circ$ on each side of this target. A total of 15 trials were performed for each of the 3 targets. During the trials, the participants rested their left hand on their thigh under the table.

For the proprioceptive target modality (Fig. 1B), the participants positioned their left index, middle, and ring fingers at the same position as the (extinguished) visual targets. The experimental room was illuminated to allow the participants to precisely position their fingers. The tip (nail) of these fingers served as targets. For these trials, we used three cue LEDs to indicate which finger participants had to reach for. These cue LEDs were located just above the fixation LED and were separated by 15 mm. The illumination (50 ms) of the LEDs located to the left (red), central (green), or right (blue) indicated that the ring, middle, and index fingers were the targets, respectively. The reaching finger was vibrated 100 ms after the onset of the cue LED. Because participants could get feedback on movement accuracy by (kinesthetically) sensing the distance between the positions of the reaching and target fingers, we also provided (visual) feedback of the target position in conditions using visual targets by switching the target on for 50 ms at movement offset (finger velocity < 1 cm/s).

For the trials with visual feedback of the initial index finger position, a LED fixed at the tip of the reaching finger was switched on 1.5 s before the target presentation. Providing hand visual feedback prior to the target presumably favored the use of this feedback for planning movement (Desmurget et al. 1997; Prablanc et al. 1979; note that somatosensory input related to the reaching hand is naturally also available prior to target presentation). The finger LED was switched off at movement onset (finger velocity > 1 cm/s). Therefore, for these trials the participants had visual feedback of the reaching finger during movement planning only. Hereafter, the Proprioceptive target/Unseen hand condition and the Visual target/Seen hand condition are referred to as the Full Somatosensory and Full Vision conditions, respectively.

Magnitude of the SEPs, especially when recorded with nonintra-cranial techniques, varies between participants (because of, for instance, impedance, sex, and thickness of the skull; Allison et al. 1984). For this reason, four additional control conditions were performed in order to normalize the amplitude of the SEPs between the participants. In two of these (hereafter called Resting control conditions), the vibratory stimulus was presented but no movement had to be initiated. In these conditions, the 45 vibratory stimulations were interspaced by 2–4 s. The Resting conditions were performed (separately) with and without visual feedback of the right index finger position.

Previous studies have shown modulations in the amplitude of the somatosensory evoked responses during movement preparation (Böcker et al. 1993; Saradjian et al. 2013; Seki and Fetz 2012). To determine whether the expected changes of SEP amplitudes were strictly linked to the planning of motor commands per se (i.e., unspecific sensory modulation) or rather to their fine spatial parameterization, the SEPs obtained in the experimental conditions were also normalized by those obtained in No-Goal control conditions. In these control conditions, participants produced 45 reaching movements without predefined imposed spatial goals (thereby greatly reducing the spatial constraints with respect to the trials using either visual or proprioceptive targets). In these conditions, the middle LED cue appeared for 50 ms. After the cue, the participants had to simply produce hand movements, more or less stereotyped in terms of direction, amplitude, and speed, without attempting to reach a particular spatial goal on the unseen table. These control conditions were also performed separately with visual feedback of the right index finger position (mean movement latency: 384 ± 75 ms, duration: 456 ± 83 ms, amplitude: 18.43 ± 6.22 cm, direction: $-4.84 \pm 1.90^\circ$) and without visual feedback (mean movement latency: 397 ± 80 ms, duration: 460 ± 99 ms, amplitude: 19.31 ± 5.39 cm, direction: $-4.46 \pm 1.81^\circ$). The control conditions without visual feedback of the index finger were used to normalize the SEP recorded in both experimental conditions without index finger visual feedback. The

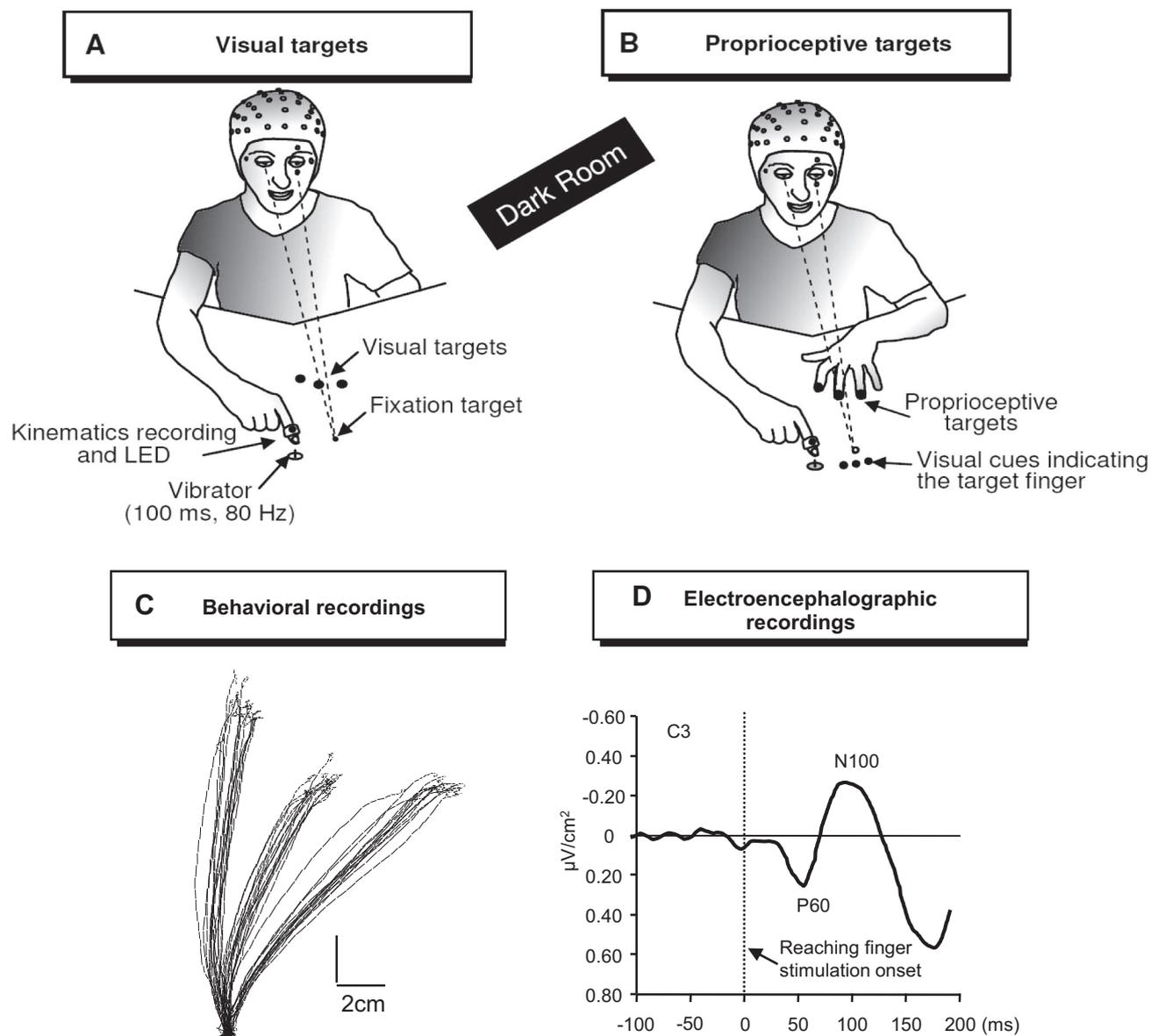


Fig. 1. Schematic representation of the experimental setups and examples of behavioral and electrophysiological recordings. *A*: Visual target condition. Participants reached for 1 of 3 visual targets that illuminated for 50 ms. LED, light-emitting diode. *B*: Proprioceptive target condition. One of the 3 cue LEDs was switched on for 50 ms to indicate whether the tip of the index, middle, or ring finger of the opposite hand served as target. Common to both reaching tasks, 1) participants looked at a fixation LED throughout the trials; 2) an LED positioned on the reaching index finger could provide visual feedback during movement planning; and 3) 100 ms after the target presentation, the index finger of the reaching hand was vibrated for 100 ms. *C*: examples of recorded finger trajectories. *D*: grand average Laplacian trace at electrode C3.

control conditions with visual feedback of the index finger were used to normalize the SEP recorded in conditions that provided this visual feedback. These data normalizations allowed us to wipe out any effects of hand visual stimulation on the SEP (see Cardini et al. 2011) that were not related to sensorimotor transformation (in the case of the Resting control conditions) or to the fine spatial parameterization of the reaches (in the case of the No-Goal control conditions). In addition to enabling SEP comparison between participants, the normalizations therefore allowed better SEP comparison between conditions with and without hand visual feedback.

Each block of trials started ~ 1 min after the light of the experimental room was turned off. In all conditions except the Resting control conditions, the participants informed the experimenter when their reaching index finger was back to the starting position, indicating that they were ready to run a new trial. Because we used a single starting position at a fixed position with respect to

the fixation target, participants had no difficulty in finding the small hole containing the solenoid vibrator (the trials were usually interspaced by ~ 10 s). The ordering of the target selection in the visual and proprioceptive targets conditions was random. The use of three targets in these conditions introduced uncertainty into movement planning and minimized the risk of subjects implementing stereotyped responses. We presented the different experimental conditions in separate blocks because this method proved to be efficient for investigating the existence of an optimal strategy for weighting sensory input according to the sensory context of the motor task. Indeed, changing the sensory context from trial to trial has been found to increase the risk that subjects will adopt a common strategy across the block of trials (Elliott and Allard 1985). The ordering of the 8 types of blocks of 45 trials (total of 360 trials per participant) was counterbalanced across participants (to counteract any effects of condition ordering and fatigue).

Recording Procedures and Data Reduction

Electrophysiological data. Electroencephalographic (EEG) activity was recorded continuously from 64 preamplified Ag-AgCl electrodes (ActiveTwo, Bio-Semi) embedded in an elastic cap in accordance with the extended 10-20 System. Electrooculographic (EOG) activity was recorded bipolarly with surface electrodes placed near both outer canthi and under and above the left orbit. This allowed us to verify that participants complied with the instruction regarding LED fixation (2% of the trials were rejected because of ocular movements). The EEG and EOG signals were digitized online (sampling rate 1,024 Hz, DC 268 Hz, 3 dB/octave) and band-pass filtered off-line (0.1–45 Hz, notch at 50 Hz, 12 dB/octave).

SEPs were obtained by classical mean, which consisted in averaging, for each participant, the EEG data into epochs time-locked to stimulus onset (–200 ms to 500 ms), with the average amplitude of the 200-ms prestimulus epoch serving as baseline. Such averaging is necessary because of the low signal-to-noise ratio of EEG recordings. For both the visual and proprioceptive target conditions, all trials of each target were then collapsed into a single EEG estimate. The monopolar recordings (referenced to the left mastoid) were visually inspected, and epochs presenting artifacts or eye movements were rejected. On average, the number of rejected trials per participant was 5.9, 3.8, 6.1, and 5.6 in the Proprioceptive target/Unseen hand, Proprioceptive target/Seen hand, Visual target/Unseen hand, and Visual target/Seen hand conditions (on average, SEPs comprised 39.7 traces). The fact that the number of rejected trials did not vary greatly between conditions suggests that the signal-to-noise ratio was alike between them, allowing the amplitude of the SEPs to be compared between the different experimental conditions.

We employed current source density (CSD) analyses to sharpen the spatial resolution of the EEG recordings and to obtain a good estimate of their topography (Laplacian transformation; Babiloni et al. 2001). The signal was interpolated with a spherical spline interpolation procedure (Perrin et al. 1987) in order to compute the second-order derivatives in two dimensions of space (order of splines: 3; maximal degree of Legendre polynomials: 10; approximation parameter λ : 1.0×10^{-5}). CSDs are independent of the reference electrode site and are much less affected by far-field generators than monopolar recordings (Manahilov et al. 1992; Nunez et al. 1994). Largely free from artifacts, CSD therefore yields measures that better reflect the underlying cortical activities (Tenke and Kayser 2012). Analyses of the SEPs were performed on CSD data.

Behavioral data. The kinematics of the reaching movements was recorded by tracking the positions of an electromagnetic sensor (Flock of Birds, Ascension, Burlington, VT) fixed on the tip of the index finger at a frequency of 100 Hz.

Measured Variables

Neurophysiological data. SEPs (CSD data) were recorded at electrode C3 (left hemisphere), which overlies the somatosensory area of the right hand (Koessler et al. 2009; Schubert et al. 2008). The first reliable SEP components elicited by the mechanical vibration of the right reaching finger were a positive wave that peaked on average 61 ± 5 ms (P60) after stimulation and a negative wave that peaked on average at 97 ± 8 ms (N100) (see Fig. 1D). These latencies are similar to those reported in studies using finger vibratory stimulation (Eimer et al. 2002; Schubert et al. 2008; Taylor-Clarke et al. 2002). The amplitude of the P60-N100 (i.e., peak to peak, hereafter referred to as the SEP) was expressed as the ratio of the SEP amplitude measured in the Resting and No-Goal control conditions (SEP ratio = SEP experimental conditions/SEP control conditions). The normalizations were performed between the experimental and control conditions having either vision or no vision of the index finger starting position. Because of the inherent exponential nature of a ratio, directly comparing ratios can be misleading. For example, if the SEPs in the

control condition are twice those in the experimental condition, the SEP ratio would equal 0.5, whereas, inversely, if the experimental SEPs are double those of the control, then the ratio becomes 2. To substantially reduce their nonlinearity, the ratios were represented by a \log_2 transformation. For the above example, a ratio of 2 gives a \log_2 value of 1 and the inverse ratio, 0.5, gives a \log_2 value of -1 . On the other hand, similar SEPs between the control and experimental SEPs would be associated with a \log_2 value of 0. \log_2 values were used in the statistical analyses and in Figs. 3 and 4.

Behavioral data. Movement accuracy was assessed by computing the radial error, which was defined as the distance between the target and finger index position at movement offset. The reaching performance was further analyzed by computing the absolute errors in amplitude and in direction. Errors in amplitude were obtained by subtracting the distance reached by the finger at movement offset from the distance of the target from the finger starting position. Errors in direction were obtained by subtracting the angle between the target vector and the movement vector. We also measured hand movement latency, which was defined as the time elapsed between the presentation of the target (or cue target) and movement onset (finger velocity > 1 cm/s) and movement duration (i.e., time elapsed between movement onset and movement offset) (finger velocity < 1 cm/s). Finally, the variability (i.e., standard deviation of the mean) was computed for all these variables.

Statistical Analyses

The behavioral and neurophysiological dependent variables were submitted to separate analyses of variance (ANOVAs). The model was a repeated-measures design with “Target” (visual, proprioceptive) and “Hand feedback” (vision, no vision of the reaching finger) as within-subject factors. This 2×2 factorial design allowed us to compare whether the sensory modality of the target and the availability of visual feedback of the reaching finger had a comparable impact on the amplitude of the SEP and to test for interactions between these factors. We predicted that the SEPs would be greater in the proprioceptive than visual target conditions (i.e., significant main effect of Target) but that the SEPs would be greatest when participants reached toward proprioceptive targets without hand visual feedback (i.e., significant interaction Target \times Hand feedback).

We used nonparametric Spearman’s rank analyses to determine whether the participants’ SEP amplitudes were correlated with their reaching accuracy. The fact that for most behavioral variables and conditions the errors varied across participants (see Fig. 2) provided grounds for exploring the existence of such correlations. The Spearman’s test detects monotonic relationships between variables irrespective of the form of the relationship (e.g., linear, exponential, power, logarithmic). Importantly, the Spearman coefficient is not influenced by the difference between successive data. This analysis is particularly suited to the present study because, due for instance to the complexity of the sensorimotor transformations and to interindividual differences, one may not expect a one-to-one, deterministic relationship between changes of SEPs and changes of performance across participants (as assessed by Pearson’s correlations), even after EEG normalization procedures. The Spearman’s test is most appropriate when the sample sizes are relatively small (Sheskin 2003). In the present study, the Spearman’s analyses consisted in ranking the participants by their performance (separately for each measured variable and for each condition) and then verifying whether there was a correlation between the participants’ rank and the amplitude of their SEPs (also coded in ranked value for each participant). Note that the low signal-to-noise ratio of the EEG recording does not allow one to assess the relationship between SEP amplitude and reaching performance on an individual-trial basis. The statistical threshold was fixed at $P < 0.05$ for all analyses (i.e., ANOVA and Spearman). All dependent variables showed normal distributions (i.e., $P > 0.05$, Shapiro-Wilk tests). The values that accompany the means reported below are SEs.

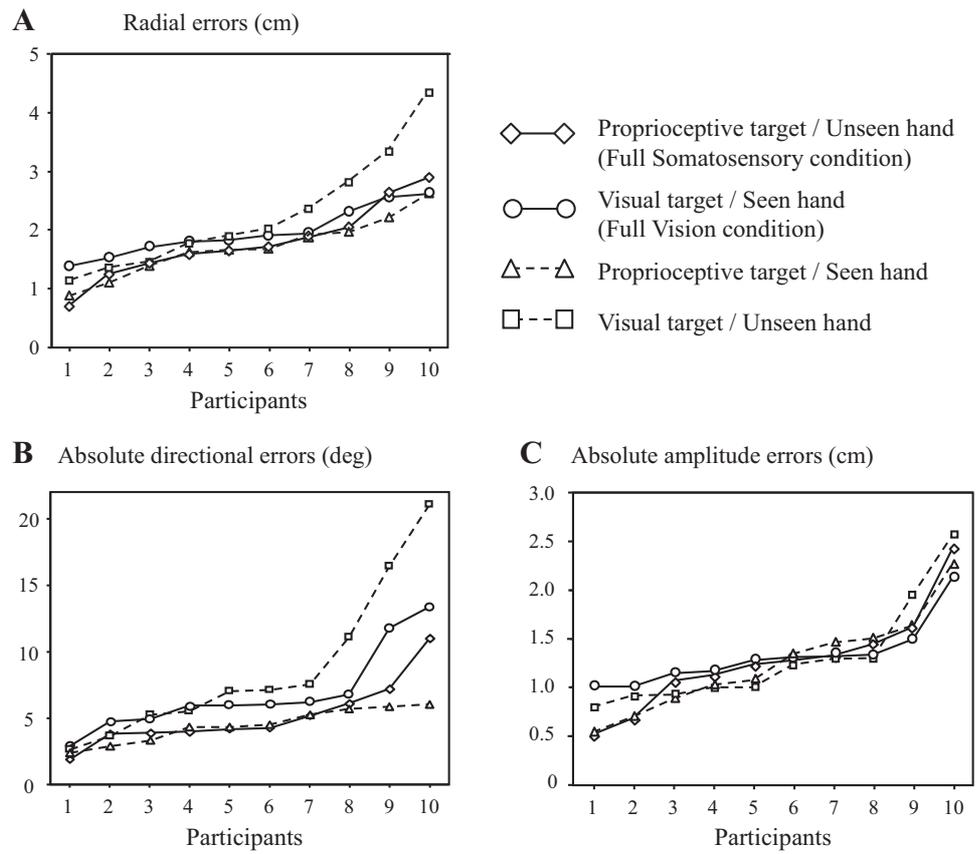


Fig. 2. Mean reaching errors (y-axes) for all participants (x-axes) computed in each target and hand feedback condition. In all graphs, the participants were ranked according to the magnitude of their errors (from smallest to greatest). *A*: radial errors. *B*: absolute directional errors. *C*: absolute amplitude errors.

RESULTS

Behavioral Results

On average, participants initiated their movements 435 ± 122 ms after the target or cue (for the proprioceptive target) presentation (it is worth noting that the participants were expressively told to not react as fast as possible to the target onset). Neither the target sensory modality [$F(1,9) = 2.63$, $P > 0.05$] nor the vision of the index finger [$F(1,9) = 0.11$, $P > 0.05$] had a significant effect on the movement latencies. The fact that the visual and proprioceptive target conditions led to similar latencies indicates that participants had no difficulty in using the visual cues to identify the goal finger in the proprioceptive target tasks and to plan the subsequent movement. On the other hand, considering that reaction times to somatosensory stimulations are ~ 200 ms (Hanson et al. 2009; Yamashiro et al. 2013) and that the vibration stimuli occurred 100 ms after target presentation, the 435-ms measured latencies appear too long for the reaching to have been triggered by the vibration.

Critically, as the reaching finger was always stimulated 100 ms after the target presentation, the absence of significant effect of the target sensory modality and vision of the index finger suggests that the vibration occurred at a similar time of movement planning in all experimental conditions. This is important because the sensitivity to somatosensory stimulations has been shown to fluctuate during movement planning, although to a much lesser extent than during movement execution (Saradjian et al. 2013; Seki and Fetz 2012). Therefore, any difference in SEP amplitude that may be observed between the experimental conditions of the present study could not be

attributed to different timing of the vibratory stimulations with respect to movement planning.

The mean reaching errors computed for all participants and conditions are shown in Fig. 2. In all graphs in Fig. 2, the participants (x-axes) are ranked according to the magnitude of their errors (from smallest to greatest). The errors varied between the participants and increased more or less monotonically between the smallest and greatest errors. This between-subject variation, however, appeared smaller for the absolute directional errors of the visual target/unseen hand condition. The ANOVA revealed that the mean radial error was not significantly affected by the factors Target [$F(1,9) = 4.35$, $P > 0.05$] and Hand feedback [$F(1,9) = 1.37$, $P > 0.05$], the finger end point being on average 1.91 ± 0.69 cm off the target (Fig. 2A). The decomposition of the radial error into directional and amplitude errors led to different results according to the sensory modality of the targets. Indeed, the participants produced smaller directional errors when they reached toward proprioceptive ($4.78 \pm 1.97^\circ$) than toward visual ($7.79 \pm 4.71^\circ$) targets [main Target effect, $F(1,9) = 9.22$, $P = 0.014$] (Fig. 2B). However, the effects of Target [$F(1,9) = 0.59$, $P > 0.05$] and Hand feedback [$F(1,9) = 0.03$, $P > 0.05$] on the amplitude error were not significant (mean 1.28 ± 0.47 cm) (Fig. 2C).

The ANOVAs performed on the variability of the behavioral measurements revealed a significant effect only for the absolute direction errors [$F(1,9) = 7.40$, $P = 0.024$]. The variability in movement direction was smaller for proprioceptive targets (mean = $2.62 \pm 0.73^\circ$) than for visual targets (mean = $3.41 \pm 1.11^\circ$). No significant effect was found for the variability of movement latency (mean = 70 ± 25 ms), radial error

(mean = 0.71 ± 0.14 cm), and absolute amplitude error (mean = 0.63 ± 0.11 cm) (all $P > 0.05$).

Finally, the ANOVA performed on movement duration did not reveal a significant effect of the factors Target [$F(1,9) = 0.15$, $P > 0.05$] and Hand feedback [$F(1,9) = 0.17$, $P > 0.05$]. The interaction Target \times Hand feedback was also not significant [$F(1,9) = 0.42$, $P > 0.05$]. On average, movement duration was 389 ± 85 ms.

Electrophysiological Results

When using group data, the ANOVA did not reveal a significant effect of the sensory modality of the target. This was the case for the SEPs normalized with respect to the Resting condition [$F(1,9) = 1.95$, $P = 0.20$] and the SEPs normalized with respect to the No-Goal condition [$F(1,9) = 1.79$, $P = 0.21$]. Similarly, visual feedback of the reaching finger did not influence the amplitude of the SEPs [$F(1,9) = 0.71$ ($P = 0.42$) and 0.70 ($P = 0.42$) for the Resting and No-Goal normalizations, respectively]. The interaction Target \times Hand feedback was also not significant [$F(1,9) = 1.81$ ($P = 0.21$) and 2.10 ($P = 0.18$) for the Resting and No-Goal normalizations, respectively].

However, a comprehensible pattern of results clearly emerged when submitting the behavioral and electrophysiological data to the Spearman's rank analyses. Indeed, the ampli-

tude of the SEPs strongly correlated with the participants' performance, namely, the directional errors [no significant correlation was found with the other measured variables (absolute or variability) of movement performance, all $P > 0.05$]. Such correlations were first observed when the amplitudes of the SEPs were normalized with respect to the SEPs recorded in the Resting conditions. The amplitude of the SEPs significantly increased as directional accuracy increased when participants planned movements toward proprioceptive targets without vision of the reaching finger (i.e., Full Somatosensory condition) ($r = 0.73$, $P = 0.03$; Fig. 3A). Therefore, the participants showing the greater SEPs were those who produced the smaller directional errors. In contrast, when participants planned movements toward visual targets with visual feedback of the reaching finger (i.e., Full Vision condition), the smaller the SEPs, the smaller the directional errors ($r = -0.84$, $P = 0.01$; Fig. 3B). The Full Somatosensory and Full Vision conditions were the only combinations of Target and Hand feedback factors that showed significant correlations between the amplitude of the SEPs and the participants' performance (see Fig. 3). However, the fact that the mean directional errors hardly varied between participants in the Visual target/Unseen hand condition could explain why the Spearman's rank analyses did not reveal significant corrections in this specific condition.

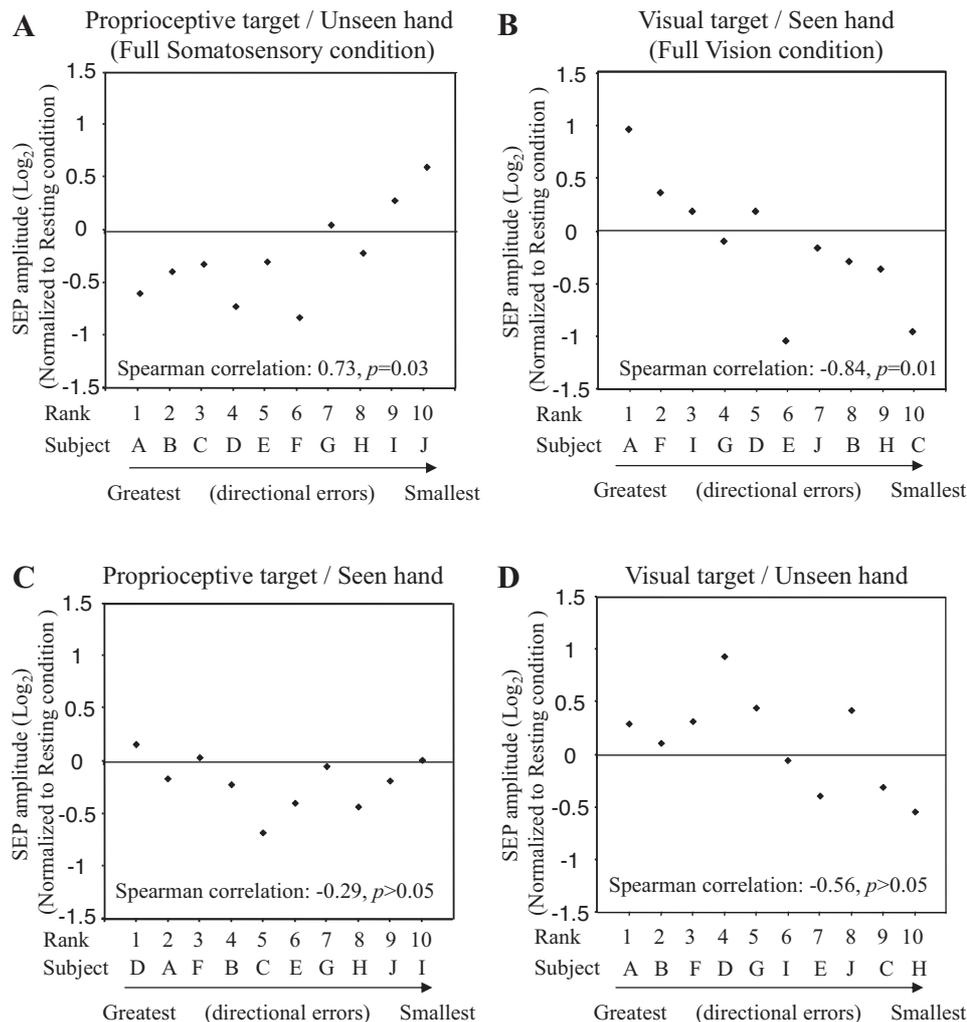


Fig. 3. Amplitude of the P60-N100 (y-axes) of all participants plotted against their performance rank in terms of absolute directional errors (x-axes) in all 4 experimental conditions (A–D). Somatosensory evoked potential (SEP) amplitudes are normalized to the SEP amplitudes recorded in the Resting control condition. Each participant is identified with the same letter in all graphs.

To further test whether the modulations of the SEPs were related to the fine spatial parameterization of the reaches and were not merely linked to the generation of motor actions, we normalized the SEPs with respect to the SEPs recorded in control conditions where participants produced arm movements in darkness without imposed, spatially defined targets (No-Goal conditions). These additional analyses also gave a consistent pattern of results that was similar to that obtained after data normalization with the Resting conditions. The participants who showed the greater SEPs in the Full Somatosensory condition were those who produced the smaller directional errors ($r = 0.76$, $P = 0.02$; Fig. 4A), and participants showing the smaller SEP in the Full Vision condition produced the smaller directional errors ($r = -0.76$, $P = 0.02$, i.e., same statistical results as Full Somatosensory condition expect for the sign of the correlation coefficient; Fig. 4B). Again, the Full Somatosensory and Full Vision conditions were the only conditions that showed significant correlations between SEP amplitude and directional errors (see Fig. 4). Likewise, no significant correlation was found between the amplitude of the SEPs and the other measured reaching performance variables (i.e., radial and amplitude errors, all $P > 0.05$).

As illustrated in Fig. 2, the directional errors varied little between some participants in the Full Somatosensory and Full Vision conditions. To gauge more clearly whether the magni-

tudes of SEPs were related to reaching performance, we performed additional Spearman analyses by assigning the same mean rank to participants showing directional errors smaller than 0.9° . This procedure is used when similar scores are found in a sample, and, in the context of the present study, it can be considered a conservative approach to investigate the relationship between SEPs and reaching performance. Results from these analyses were consistent with those reported above. They revealed significant positive correlations between directional errors and SEP amplitude in the Full Somatosensory condition ($r = 0.61$, $P = 0.05$ and $r = 0.64$, $P = 0.04$ for SEPs normalized to the Resting and No Goal conditions, respectively) and significant negative correlations between these variables in the Full Vision condition ($r = -0.80$, $P = 0.005$ and $r = -0.70$, $P = 0.02$ for SEPs normalized to the Resting and No Goal conditions, respectively).

For both SEP normalizations, the somatosensory input was facilitated in the absence of visual feedback of the hand and target for the participants showing the smallest directional errors (i.e., $\text{SEP}_{\log_2} > 0$; Fig. 3A, Fig. 4A) and inhibited when such visual feedbacks were available (i.e., $\text{SEP}_{\log_2} < 0$; Fig. 3B, Fig. 4B). This can also be seen in Fig. 5, A and B, left, which present, for illustrative purposes, the averaged Laplacian traces recorded for the four participants who showed the smallest directional errors in the Full Somatosensory and Full

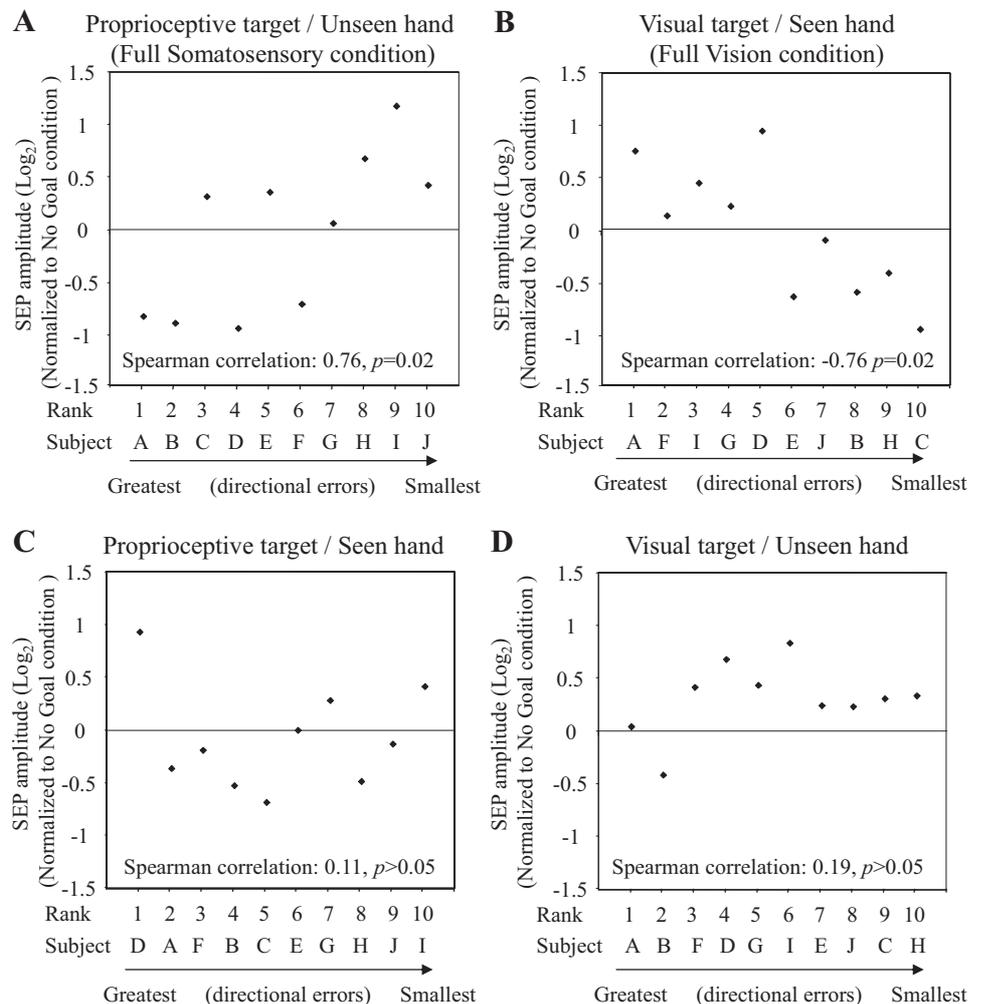


Fig. 4. Amplitude of the P60-N100 (y-axes) of all participants plotted against their performance rank in terms of absolute directional errors (x-axes) in all experimental conditions (A–D). SEP amplitudes are normalized to the SEP amplitudes recorded in the No-Goal control condition. Each participant is identified with the same letter as in Fig. 3.

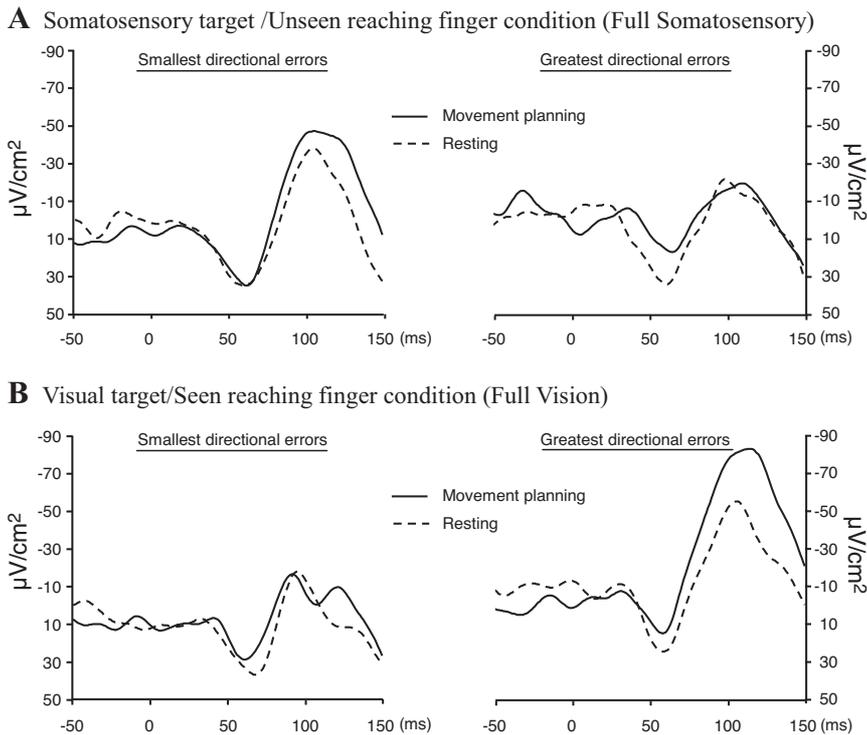


Fig. 5. Average Laplacian traces recorded for the 4 participants who showed the smallest directional errors (*left*) and for the 4 participants who produced the greatest directional errors (*right*). *A*: SEPs recorded when participants either planned reaching movements toward proprioceptive targets without visual feedback of the reaching finger (solid lines) or were resting without hand visual feedback (i.e., baseline control condition; dashed lines). *B*: SEPs recorded when participants either planned reaching movements toward visual targets with visual feedback of the reaching finger (solid lines) or were resting with hand visual feedback (i.e., baseline control condition; dashed lines). In all graphs, 0 indicates the onset of index finger vibration.

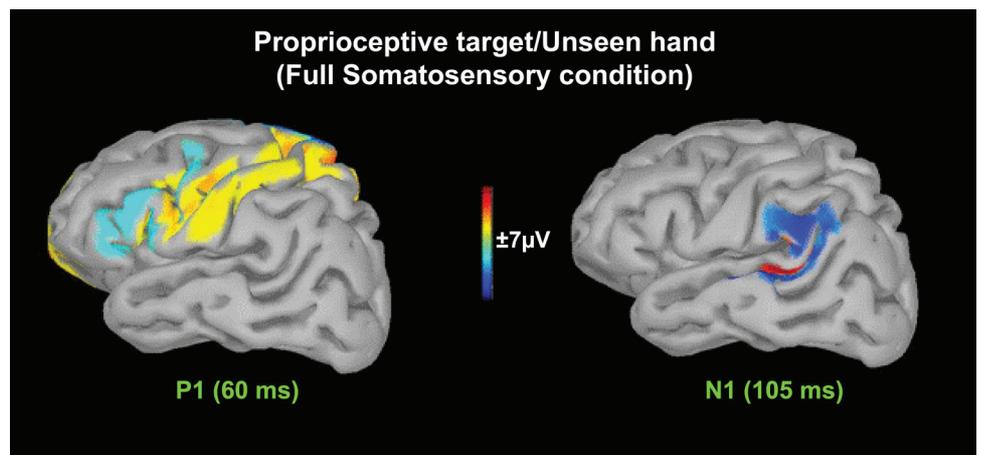
Vision conditions with their respective averaged SEPs computed in the Resting control conditions. The figure also shows that when these participants either planned reaching movements or were simply resting, the SEPs were greater without hand visual feedback than with visual feedback (compare Fig. 5, *A* and *B*, *left*). Diametrically opposed to this, the participants showing the greatest directional errors inhibited the somatosensory input in the Full Somatosensory condition ($\text{SEP log}_2 < 0$; Fig. 3, *A* and *C*) and facilitated this afferent input in the Full Vision condition ($\text{SEP log}_2 > 0$; Fig. 3, *B* and *D*). Such inhibition and facilitation of somatosensory inputs can also be seen on the traces shown in Fig. 5, *A* and *B*, *right*, respectively, which represent the averaged SEPs obtained for the four participants who produced the greatest directional errors. In contrast to those showing the smallest directional errors, these participants had smaller SEPs when hand visual feedback was unavailable (Fig. 5*A*, *right*) than when hand visual feedback was provided (Fig. 5*B*, *right*).

We identified each participant with the same letter in all graphs of Fig. 3 and Fig. 4. Inspecting the rank of the participants in the Full Somatosensory and Full Vision conditions clearly reveals that the participants' rank differed according to the sensory context of the reaching movements. Therefore, participants who showed facilitation of somatosensory input in the Full Somatosensory condition were not necessarily those who inhibited this sensory input in the Full Vision condition. This was confirmed by the Spearman analysis, which did not reveal a significant correlation (either positive or negative) between the participants' rank in the Full Somatosensory and Full Vision conditions ($P > 0.05$).

We used low-resolution brain electromagnetic tomography (LORETA), implemented in Brainstorm software (Tadel et al. 2011, freely available at <http://neuroimage.usc.edu/brainstorm>), to estimate the neural sources of the

SEPs. Because LORETA achieves source reconstruction with high temporal resolution, it allowed us to specifically estimate the generators of the P60 and N100 components. The sources were reconstructed with the waves obtained from the grand average of monopolar recordings of the four participants who showed the smallest directional errors in the Full Somatosensory condition (i.e., participants who generally showed the greatest normalized SEPs; see Fig. 3*A* and Fig. 4*A*). However, because CSD analyses enhance the temporal resolution of the EEG recording compared with monopolar recordings by reducing the spatial overlap between separate sources of activity (Law et al. 1993), the sources were estimated at the latencies of the peaks revealed by the CSD data (electrode C3 as for the analyses of the SEP amplitude). As shown in Fig. 6, LORETA revealed distinct sources for P60 and N100 in the parietal cortex. The peak positivity was associated with a large activity over the lateral postcentral gyrus region, which corresponds to the primary somatosensory area (SI). Note that the LORETA map also revealed simultaneous activity at P60 latency in the precentral gyrus region corresponding to the premotor areas. Premotor activities have also been reported in a previous study in which participants had to reach for proprioceptive targets with the unseen hand (Bernier et al. 2009a). The frontal activities found in the previous and present studies had the same latencies with respect to the time of the target finger identification (~ 150 ms). They may suggest an important contribution of the premotor areas in the integration of target and limb information when reaching for nonvisual somatosensory targets (see Graziano et al. 1994). On the hand, the source identified at N100 latency was more circumscribed to the parietal operculum, known as the secondary somatosensory cortex (SII).

Fig. 6. Topographic maps of voltage distribution [low-resolution brain electromagnetic tomography (LORETA)] computed with the grand average of the waves (monopolar recordings) obtained by the 4 participants who showed the smallest directional errors in the Full Somatosensory condition. The maps are shown at the latency of the peak positivity (i.e., 60 ms, *left*) and at the latency of the peak negativity (i.e., 105 ms, *right*). The scale of the maps was chosen to maximize identification of the sources localized in the postcentral gyrus region, and the sources were given a marked threshold to only show source activity that was 18% (*left*) and 49% (*right*) above minimal activation.



DISCUSSION

Previous studies have shown that the somatosensory estimate of the hand position strongly influences the planning of reaching movements aimed toward somatosensory targets but decreases in importance in the case of visual targets (Sarlegna and Sainburg 2007; Sober and Sabes 2005). Here we provide insights into the neural mechanisms that might explain these observations. Specifically, increased transmission of somatosensory inputs of the reaching hand to the cerebral cortex during movement planning (as evidenced by the greater P60-N100 recorded at electrode C3) was associated with smaller directional errors when movements were directed toward somatosensory targets. We observed this phenomenon when the starting hand position could be estimated through somatosensory inputs only (i.e., Full Somatosensory condition). In contrast, attenuation of somatosensory inputs during movement planning was associated with smaller directional errors in the case of visual targets, but only when participants had visual feedback of their reaching finger (i.e., Full Vision condition). These task-specific modulations of the SEPs persisted after normalization of the EEG recordings with respect to those recorded when participants planned movements without a defined spatial goal in darkness. This provides additional evidence to suggest that the spatial constraints of the task played a major role in the variations of SEP amplitude.

Source localization analyses (LORETA) revealed that the P60 and N100 were generated in SI and SII, respectively. These results are in agreement with a previous simultaneous EEG-fMRI study by Schubert et al. (2008) showing similar distinct generators for these SEP components. Salinas et al. (2000) reported that the activities of a majority of monkeys' SI neurons are phase-locked with the stimulus input and encode the stimulus frequency. Their findings therefore showed that SI activity is strongly linked with the incoming sensory inputs. On the other hand, Salinas et al. (2000) also found that SII neurons modulated their firing rate when the monkeys had to discriminate between two sequential stimuli. Giving the important role of SII for processing task-relevant somatosensory inputs, these results suggest that SII might have accounted for the modulations in the amplitude of the SEPs observed in the present experiment (with respect to SEPs recorded in the baseline control conditions). In this regard, our results are therefore consistent with studies showing enhancement (Saradjian et al. 2013; Staines et al. 2002; Taylor-Clarke et al. 2002) or inhi-

bition (Bernier et al. 2009b) of sensory afferents in the somatosensory cortex according to the task demands.

A pertinent issue to consider is whether the accuracy with which participants determined the position of the targets was linked to the magnitude of the SEPs. This assertion appears very unlikely in the tasks with visual targets but could be envisaged in those with proprioceptive targets. However, the fact that the modulations of afferent inputs are known to be very specific provides elements to rule out this possibility. For instance, the sensory gating observed during digit movements targets only the moving finger and not the other fingers of the same hand (Rushton et al. 1981).

We found that the amplitude of the SEPs correlated with the directional errors but not with errors in movement amplitude. According to the vectorial coding model of the movements, the brain would compute the hand-target vector and then plan the motor commands according to the direction and the amplitude of this vector (Davare et al. 2012; Messier and Kalaska 2000; Rossetti et al. 1995). There is evidence that the amplitude control of rapid reaching movements impairs the online control of movement direction. For instance, corrections of movement direction when a target is displaced after reaching onset are smaller when participants have to stop on the target than when amplitude requirements are relaxed (i.e., reach-and-stop vs. shooting movements; Blouin et al. 1995a, 1995b; Sarlegna and Blouin 2010). Hence, because of the limited capacity for controlling the direction of ongoing movements with amplitude constraints (as those of the present study), the final directional errors appear as good indicators of the precision of the feed-forward planning of movement direction. However, errors in amplitude may not be so informative regarding the quality of the planning of movement amplitude because of the possibility of correcting movement extent in flight (through proprioceptive feedback control; Sainburg et al. 2003; Sarlegna et al. 2006; van Beers et al. 2002). Therefore, the somatosensory inputs of the reaching hand could be beneficial to the planning of both the direction and amplitude of the movement but would be more critical for directional accuracy.

Goal-directed arm movements result from a series of complex processes that allow conversion of the sensory information regarding target location into the limb configuration corresponding to it, and ultimately into the required motor output (Batista et al. 1999; Crawford et al. 2004; Ghilardi et al. 1995). While the reweighting of somatosensory inputs is likely a

factor that can optimize one or more stages of the sensorimotor transformations, it may not be sufficient to completely account for all facets of the studied motor task. For instance, in the present study the (absolute and variable) directional errors were smaller in conditions with proprioceptive targets than in conditions with visual targets. However, the amplitudes of the SEPs were not significantly greater in conditions with proprioceptive targets (Spearman rank's analyses revealed significant correlations between directional accuracy and SEP amplitude). In the proprioceptive target conditions, touching the target hand with the reaching finger might have elicited relevant feedback to improve movement planning (more than the target illumination after movement offset in trials with visual targets), irrespective of the weighting of the somatosensory input during this planning.

Multiple frames of references for planning movements coexist in the cerebral cortex (Battaglia-Mayer et al. 2003; Bernier and Grafton 2010; Buchholz et al. 2013; McGuire and Sabes 2009), but their importance varies according to the sensory modality of the target. Movements toward proprioceptive targets would be encoded in body-centered (somatosensory) reference frames (Bernier and Grafton 2010; Lacquaniti et al. 1995), whereas those directed toward visual targets would involve eye-centered (retinal) reference frames to a greater extent (Batista et al. 1999; Crawford et al. 2004; Medendorp et al. 2005). In this light, one can hypothesize that increasing the weight of somatosensory input in the Full Somatosensory condition compared with the Resting and No-Goal control conditions served as a means for the participants showing the greater directional accuracy to enhance the use of a body-centered reference for planning movements. Conversely, decreasing the weight of this input in the Full Vision condition may have favored the use of an eye-centered frame.

Further studies will be required to specifically test whether changing the weight of somatosensory input influences the frame of reference (e.g., selection, accuracy) in which movement is encoded. Nevertheless, the above hypothesis is consistent with the view that optimization of goal-directed arm movements requires the target and the reaching hand to be represented in a common frame of reference (i.e., either visual or somatosensory) (Pouget et al. 2002; Reichenbach et al. 2009; Sober and Sabes 2005). Direct comparison of the positions of the hand and target in a common frame of reference could reduce probability of errors (e.g., bias, distortion, variability) due to transformations between different frames of reference (McIntyre et al. 2000; Soechting and Flanders 1992). This could be beneficial to both the planning and execution phases of the movement. We performed additional analyses to specifically determine whether the variability of the initial movement direction was smaller in conditions in which both the hand and the target could be encoded in the same sensory modality. The results of a 2 (Hand feedback) \times 2 (Target) ANOVA showed that the variability of hand direction measured 100 ms after movement onset was not significantly different between the experimental conditions ($P > 0.05$, mean = $8.34 \pm 1.85^\circ$). This suggests a similar noise level in the sensory transformations irrespective of the sensory modality of the hand and target coding. However, the transformation of the information related to the hand and target positions in a common frame of reference could also be affected by errors like bias and distortion, for instance (not only variability). In

light of these observations, the fact that the variability of the initial direction was similar across conditions cannot be used to rule out the hypothesis that movement planning and online control are optimized when both the hand and the target can be encoded in a common sensory map.

In the present study, the use of optimal strategies for weighting somatosensory inputs according to the sensory context of the reaching task was only apparent for the participants showing the greater directional accuracy. Indeed, those participants who produced the greater directional errors actually attenuated the somatosensory input when reaching for proprioceptive targets and facilitated this input in the case of visual targets. This suggests that the relation between the sensory context of the reaching and the selection of the frames of reference to plan the movement may be not as univocal as it might previously have been supposed. Moreover, we observed opposite significant correlations between the amplitude of the SEPs and of the directional errors in the Full Somatosensory and Full Vision conditions, while the level of performance varied for most participants between these conditions (i.e., participants did not hold the same rank in Figs. 3 and 4, A and B). Together, these findings are indicative of different capacities for facilitating and inhibiting somatosensory inputs or for selecting the optimal sensory strategy for planning the reaching movements.

The amplitude of the SEPs did not correlate with the participants' performance when the hand and target could not be directly encoded in a common sensory modality. This was also the case when vision of the reaching finger was available while planning movement toward somatosensory targets. In these multisensory contexts, movement planning could underlie more complex sensorimotor transformations that could not be appraised through SEP amplitude measurements. An alternative, but not mutually exclusive, possibility is that different efficient strategies for integrating sensory inputs may coexist when the target and hand positions can be encoded in different sensory modalities. These strategies could vary regarding the respective weights given to visual and somatosensory inputs, yet allowing similar level of accuracy. For instance, in the Proprioceptive target/Seen hand condition, some participants may have used a strategy that consisted of transforming proprioceptive spatial information related to the unseen finger target into an eye-centered (retinal) reference frame common to the seen reaching finger (see Blangero et al. 2007; Buchholz et al. 2013; Darling et al. 2007; Pouget et al. 2002). Such a strategy might have led to inhibition of somatosensory input, as observed in this condition for several participants (see Fig. 3C).

There is growing evidence suggesting that the accuracy and variance (or noise) of sensory inputs influence multisensory integration (Block and Bastian 2011; Ernst and Banks 2002; McGuire and Sabes 2009; Tagliabue and McIntyre 2011; van Beers et al. 2002, 2011). The weight of a given sensory cue would be inversely correlated to the accuracy and variance of the sensory cue (see references cited above for mathematical models of sensory integration based on variance of sensory cues). These properties are considered to be fluctuating, being for instance subject and context dependent (e.g., lighting of the room). Moreover, the importance of sensory cues is also known to be under the influence of cognitive factors such as conscious effort (Block and Bastian 2010). Thus the sensory strategy for planning movements appears highly flexible, even for a given sensory context, and, to some extent, under the

participant's cognitive control. However, the results of the present study suggest that these strategies are not all equal in terms of efficiency, at least in poor and enriched visual contexts. The possibility of using suboptimal sensory weighting strategies may also provide a neural explanation for the large and often poorly understood movement performance interindividual variability that is sometimes reported in research on reaching arm movements (e.g., Coello et al. 2003; van Beers et al. 2004).

ACKNOWLEDGMENTS

We thank Dany Paleressompoule for technical assistance, Franck Buloup for developing the software Docometre used for data acquisition, Marcel Kaszap for developing the software Analyse used for data processing, and Pierre-Michel Bernier and Gerome Manson for helpful comments made on the manuscript.

GRANTS

This study was funded by the Centre National de la Recherche Scientifique (CNRS, program DEFI-SENS).

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: J.B. and L.M. conception and design of research; J.B. and A.H.S. performed experiments; J.B. and N.L. analyzed data; J.B., A.H.S., N.L., A.G., and L.M. interpreted results of experiments; J.B. and N.L. prepared figures; J.B. drafted manuscript; J.B., A.H.S., N.L., A.G., and L.M. edited and revised manuscript; J.B., A.H.S., N.L., A.G., and L.M. approved final version of manuscript.

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