

Frequency tagging of steady-state evoked potentials to explore the crossmodal links in spatial attention between vision and touch

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Abstract

The sustained periodic modulation of a stimulus induces an entrainment of cortical neurons responding to the stimulus, appearing as a steady-state evoked potential (SS-EP) in the EEG frequency spectrum. Here, we used frequency tagging of SS-EPs to study the crossmodal links in spatial attention between touch and vision. We hypothesized that a visual stimulus approaching the left or right hand orients spatial attention toward the approached hand, and thereby enhances the processing of vibrotactile input originating from that hand. Twenty-five subjects took part in the experiment: 16-s trains of vibrotactile stimuli (4.2 and 7.2 Hz) were applied simultaneously to the left and right hand, concomitantly with a punctate visual stimulus blinking at 9.8 Hz. The visual stimulus was approached toward the left or right hand. The hands were either uncrossed (left and right hands to the left and right of the participant) or crossed (left and right hands to the right and left of the participant). The vibrotactile stimuli elicited two distinct SS-EPs with scalp topographies compatible with activity in the contralateral primary somatosensory cortex. The visual stimulus elicited a third SS-EP with a topography compatible with activity in visual areas. When the visual stimulus was over one of the hands, the amplitude of the vibrotactile SS-EP elicited by stimulation of that hand was enhanced, regardless of whether the hands were uncrossed or crossed. This demonstrates a crossmodal effect of spatial attention between vision and touch, integrating proprioceptive and/or visual information to map the position of the limbs in external space.

Descriptors: Electroencephalogram (EEG), Steady-state evoked potentials (SS-EP), Crossmodal, Vision, Vibrotactile

Efficiently interacting with the external world requires the ability to integrate information from multiple sensory systems in order to build a coherent multimodal representation of the body and space surrounding the body.

For example, to assess whether, when, and where an object will make contact with our body, or to grasp an object of interest, somatosensory input provides information regarding physical contact with our body, whereas proprioceptive input provides information regarding the position and movement of our limbs, and visual inputs provide information about the external space prior to any body contact (Macaluso & Maravita, 2010). Temporal and spatial congruence of the inputs related to the object or related to reaching and grasping the object would allow linking together these inputs to form a unified multimodal representation, and has been hypothesized to constitute one of the key means to achieve multisensory

integration. Furthermore, crossmodal links of selective attention, in particular, spatial attention, would allow that the object approaching the body does not only orient attention toward the location of the object in external space, but also toward the body part being approached by the object. Similarly, contact of the object with the body surface would orient attention both toward the stimulated body part and the external space immediately surrounding that body part (Eimer & Driver, 2001; Eimer, van Velzen, & Driver, 2002; Kennett, Eimer, Spence, & Driver, 2001; Spence, Nicholls, Gillespie, & Driver, 1998). In humans, studies on the crossmodal links in attention between vision and touch have shown that attending to visual or tactile stimuli at a given location improves the detection and discrimination of stimuli delivered at that location, regardless of whether they belong to the attended modality (Eimer & Driver, 2001; Eimer et al., 2002; Spence et al., 1998). A central issue about the representation of space across modalities relates to the frame of reference used to encode stimulus location across sensory systems. Within a given sensory modality, the initial encoding of spatial information is thought to be highly modality specific (e.g., the somatotopic encoding of tactile input, the retinotopic encoding of visual input; Sur, Nelson, & Kaas, 1982; Tootell, Silverman, Switkes, & De Valois, 1982). However, as the position of the eyes, head, and body vary continuously in external space, spatial mapping across sensory modalities must take into consideration gaze position and body posture. This remapping must allow, for

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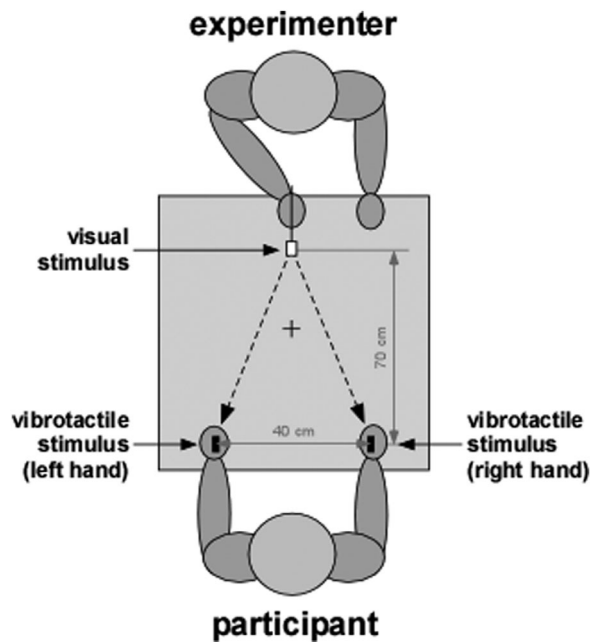


Figure 1. Experimental design. The participant was seated in front of a 75×75 cm wooden table, with the palms of his hands resting symmetrically on the table surface (the distance between the index fingers of the two hands was 40 cm). The experimenter was seated at the opposite side of the table, facing the participant. Trains of vibrotactile (4.2 and 7.2 Hz) and visual stimuli (9.8 Hz) were presented concomitantly. The vibrotactile stimuli were applied to the left and right hand, while the visual stimulus was delivered using a LED placed at the end of a 20-cm motion tracking stylus. A central fixation cross was located in the middle of the table, at an equal distance between the participant and the experimenter. Each trial lasted 16 s. During the first 6 s, the experimenter kept the stylus away from the subject, at an equal distance from the two hands. For the following 2 s, the experimenter moved the visual stimulus close to the dorsum of the left or right hand. The stimulus was then maintained over the left or right hand for 6 s. Finally, during the last 2 s, the experimenter moved the visual stimulus away from the participant, back to its initial position.

example, tactile stimuli delivered to the hand and visual stimuli delivered close to the hand to be colocalized within a frame of reference taking into account the relative position of the limbs in external space. Studies have suggested that this remapping of tactile input in external space can be already achieved 200–360 ms after stimulus onset (Azañón & Soto-Faraco, 2008).

Between vision and touch, it has been hypothesized that cross-modal links could be established through a unified frame of reference of the body space and the external space immediately surrounding the body (Ladavas, di Pellegrino, Farne, & Zeloni, 1998; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). The existence of such a “peripersonal” frame of reference is supported by the identification of bimodal visual-tactile neurons in the putamen, ventral intraparietal area, and ventral premotor cortex of monkeys (Duhamel, Colby, & Goldberg, 1998; Graziano, Hu, & Gross, 1997; Graziano, Yap, & Gross, 1994; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). In particular, Graziano et al. (1997) found visual-tactile neurons in the ventral premotor cortex responding to both tactile and visual stimuli, whose visual receptive fields correspond to the space surrounding the tactile receptive field on the body surface. In humans, there is also evidence suggesting the existence of such an integrated representation of the body and peri-

personal space (Bremmer, Schlack, Duhamel, Graf, & Fink, 2001; Ladavas et al., 1998; Ladavas & Farne, 2004; Macaluso, 2006). In patients with left tactile extinction consecutive to right hemisphere damage, Ladavas et al. (1998) showed that the detection of tactile stimuli delivered to the contralesional hand is impaired by the presentation of visual stimuli near the ipsilesional hand (crossmodal visual-tactile extinction), but not by the presentation of visual stimuli in ipsilesional space far from the hand (i.e., “extrapersonal” space).

The cortical mechanisms underlying the crossmodal interactions between touch and vision have been widely assessed using EEG to measure the ERPs elicited by transient stimuli of different sensory modalities presented either simultaneously (Sambo & Forster, 2009) or in rapid succession (Eimer, 2001; Eimer & Driver, 2001). However, a fundamental limitation of these approaches is the impossibility to efficiently distinguish the responses elicited by each of several stimuli presented close in time, as the elicited responses will necessarily overlap.

For this reason, we aimed to explore the interactions between vision and touch in humans using a different approach, referred to as *frequency tagging* with steady-state evoked potentials (SS-EPs; D. Regan, 1989). SS-EPs reflect the sustained response of neuronal populations entrained by the periodic modulation of a long-lasting stimulus, and appear as a peak in the EEG frequency spectrum at the frequency corresponding to that of the driving stimulus and its harmonics (D. Regan, 1989). Therefore, the cortical activity elicited by simultaneously presented streams of sensory input can be “tagged” using distinct stimulation frequencies (Colon, Nozaradan, Legrain, & Mouraux, 2012; Nozaradan, Peretz, & Mouraux, 2011; Saupe, Schröger, Andersen, & Müller, 2009). Here, we used SS-EPs to examine whether a visual object approaching one hand modulates the processing of somatosensory input simultaneously delivered to the same or the other hand. The visual stimulus consisted of a stylus held by the experimenter and ending with a punctate light source flashing at a first frequency (Figure 1). Concomitantly, vibrotactile stimuli were delivered to the two hands, using two other frequencies. This stimulation set-up was expected to elicit SS-EPs at three distinct sets of frequencies, respectively tagging the cortical activity elicited by visual stimulation, vibrotactile stimulation of the left hand, and vibrotactile stimulation of the right hand.

First, we hypothesized that visual-tactile links in spatial attention would lead to an enhancement of the vibrotactile SS-EPs elicited by stimulation of the hand being approached by the visual stimulus.

Second, we hypothesized that if proprioceptive and visual information are mapped in a common frame of reference integrating the body and nearby space, visual-tactile interactions would be dependent on the actual position of the hands in external space (Eimer, 2001; Kennett et al., 2001). To assess this, participants crossed their hands in half of the trials. If visual-tactile interactions integrate the relative position of the limbs, we expected that visual stimuli approaching one hand would enhance the SS-EPs elicited by stimulation of that hand regardless of its position in the external space. Conversely, if visual-tactile interactions do not account for the relative position of the limbs, we expected that visual stimuli approaching the left or right hand would enhance the SS-EPs elicited by stimulation of the left or right hand regardless of their position.

Finally, it has been suggested that cortical integration of different streams of sensory input can be revealed by the appearance of additional SS-EPs, appearing at nonlinear cross-modulation frequencies corresponding to the sum or differences of the eliciting

frequencies or their harmonics (Giani et al., 2012; M. P. Regan, He, & Regan, 1995). Importantly, our experimental design was very similar to the original experiments of [Graziano et al. \(1997\)](#) performed in monkeys to identify bimodal neurons responding to visual stimuli approaching the location of their tactile receptive fields. In these experiments, the bimodal neurons responded most vigorously when the visual stimuli moved toward the corresponding tactile receptive field. Therefore, our third hypothesis was that if activity of bimodal visual-tactile neurons can be sampled using EEG, this would lead to the appearance of additional SS-EPs at frequencies corresponding to the cross-modulation between the frequency of the visual stimulus and the frequency of the vibrotactile stimulus delivered onto the hand toward which the visual stimulus is approaching.

Method

Participants

Twenty-five healthy volunteers (18 females, aged 20 to 39 years, 24 right-handed) took part in the experiment. All participants had normal or corrected-to-normal vision and no prior history of neurological or psychiatric disorders. Before the experiment, participants were familiarized with the experimental set-up and task, and exposed to a small number of test stimuli. Written informed consent was obtained from all participants, and they were paid for their participation. The study was approved by the local Ethics Committee and conformed to the latest revision of the Declaration of Helsinki.

Vibrotactile Stimulation

Vibrotactile stimuli were generated by a recoil-type vibrotactile transducer driven by a standard audio amplifier (Haptuator, Tactile Labs Inc., Canada) and positioned on the dorsal surface of each hand, between the thumb and the index finger (Figure 1). The vibrotactile stimulus lasted 16 s and consisted of a 240 Hz carrier frequency periodically modulated at 4.2 Hz on one hand and 7.2 Hz on the other hand. For 17 participants, the 4.2 Hz modulation was applied on the left hand and the 7.2 Hz modulation was applied on the right hand. For eight participants, the 4.2 Hz modulation was applied on the right hand and the 7.2 Hz modulation was applied on the left hand. The participants perceived the stimulation trains as a continuous vibration.

Visual Stimulation

Visual stimuli were continuous flashes generated by means of a white LED with a 12 lm luminous flux, a 5.10 cd luminous intensity, and a 120° visual angle (GM5BW97333A, Sharp Corporation, Japan). The LED was placed at the end of a 20-cm motion-tracking stylus (8" Stylus, Fastrak motion scanner, Polhemus, USA). This allowed for monitoring the position of the visual stimulus using a Fastrak electromagnetic motion tracking system (Polhemus). The visual stimuli were delivered as trains lasting 16 s during which the LED was switched on and off with a periodicity of 9.8 Hz. The participants perceived the stimulation trains as a continuous flashing white light. During the stimulation, the stylus was held and displaced manually by the experimenter using his right hand (Figure 1).

Experimental Procedure

The experiment was conducted in a dim and silent room. White noise was presented continuously through headphones, at a comfortable listening level, to mask any sounds produced by the vibrotactile stimulator. During the experiment, the participant was seated in front of a 75 × 75 cm wooden table, with the palm of their hands resting symmetrically on the table surface (Figure 1). The distance between the index fingers of the two hands was 40 cm. The experimenter was seated at the opposite side of the table, facing the participant. During each trial, the participant was asked to maintain his gaze on a central fixation cross marked on the middle of the table, at an equal distance between the participant and the experimenter. The experiment consisted of eight blocks with 10 trials in each block. In half of the blocks, the hands of the participants were positioned in an uncrossed fashion relative to the body midline. In the other half, the hands were crossed relative to the body midline. The order of the blocks was counterbalanced across the participants. Each trial consisted of 16 s of concurrent vibrotactile stimulation of the left hand, vibrotactile stimulation of the right hand, and visual stimulation. For the first 6 s, the experimenter maintained the visual stimulus away from the participant and at his body midline, by holding the stylus such that the flashing LED was located at a distance of 70 cm from the two hands of the participant. For the following 2 s, the experimenter moved the visual stimulus close to the dorsum of the left or right hand. The stimulus was then maintained over the left or right hand for 6 s. Finally, during the last 2 s, the experimenter moved the visual stimulus away from the participant, back to its initial position. To control the timing of these four displacements, the experimenter was helped by the sound of a metronome played through earphones. Furthermore, the actual motion of the visual stimulus was monitored and recorded using the electromagnetic motion tracking system. A 10-s intertrial interval separated the end of each trial from the beginning of the next trial. The entire recording lasted approximately 1 h.

Electrophysiological Recording

The EEG was recorded using 64 Ag-AgCl electrodes placed on the scalp according to the International 10/10 system (Waveguard 64 cap, Cephalon A/S, Denmark). Electrode impedances were kept below 10 kΩ. Ocular movements and eyeblinks were recorded using two pairs of electrodes, the first placed above and below the right eye, the second placed at the external corners of the left and right eyes. Signals were amplified and digitized using an average reference and a sampling rate of 1000 Hz (64-channel high-speed amplifier, Advanced Neuro Technology, The Netherlands).

Analysis of the EEG data was carried out using Letswave 5 (<http://nocions.webnode.com/letswave>; [Mouraux & Iannetti, 2008](#)). The continuous EEG recordings were filtered using a 0.375 Hz high-pass fast Fourier transform (FFT) filter to remove slow drifts in the recorded signals. Nonoverlapping EEG epochs were then obtained by segmenting the recordings from 0 to 16 s relative to the onset of the stimulation trains. Each EEG epoch was demeaned using the time interval ranging from 0 to 16 s. Artifacts due to eyeblinks or eye movements were then removed using a validated method based on an independent component analysis (FastICA algorithm; Hyvarinen & Oja, 2000).

Single-subject average waveforms were then computed by averaging together all trials. The obtained average waveforms were transformed in the frequency domain using a discrete Fourier

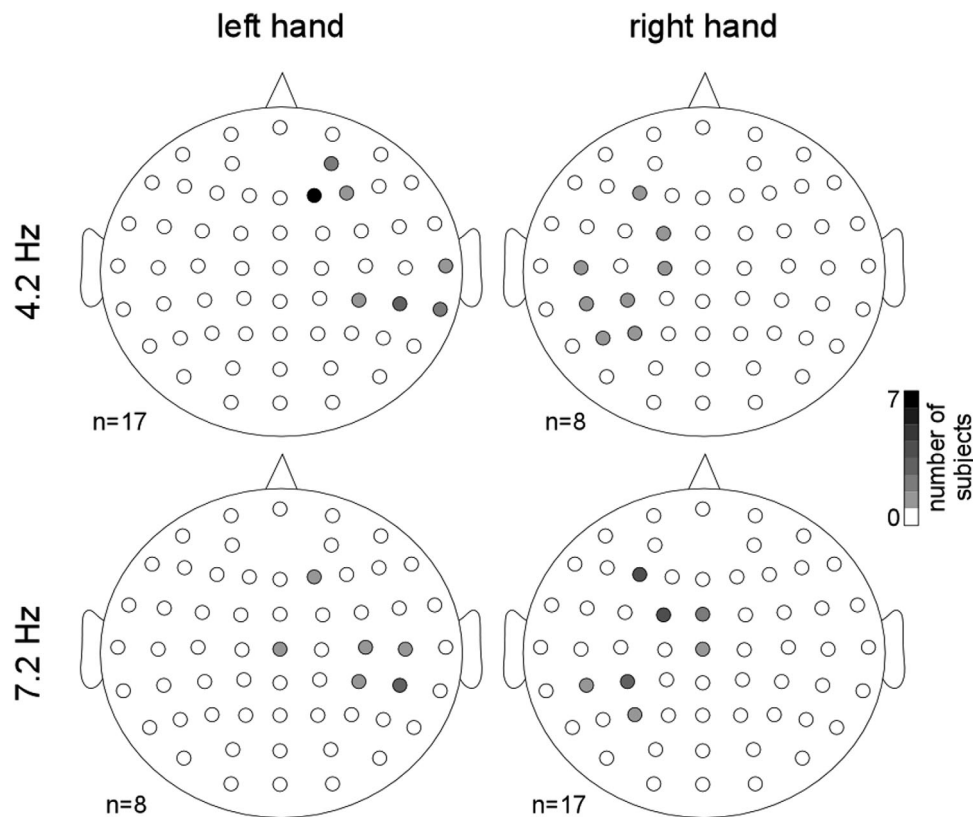


Figure 2. Location of the scalp electrodes displaying the maximal vibrotactile SS-EP amplitude across subjects. The upper panel shows the locations for 4.2 Hz vibrotactile stimulation of the left and right hands. The lower panel shows the locations for 7.2 Hz vibrotactile stimulation of the left and right hands. Note that vibrotactile SS-EPs elicited by stimulation of the left and right hands were predominant over frontal and parietal electrodes contralateral to the side of stimulation.

transform (FFTW; Frigo & Johnson, 1998), yielding an amplitude spectrum (μV) ranging from 0 to 500 Hz (Bach & Meigen, 1999). Within the obtained frequency spectra, the signal amplitude at 4.2 Hz (vibrotactile stimulus), 7.2 Hz (vibrotactile stimulus), and 9.8 Hz (visual stimulus) were measured at each EEG electrode. These measures may be expected to correspond to the sum of the stimulus-evoked steady-state response and unrelated residual background noise. Therefore, to obtain valid estimates of the magnitude of the elicited SS-EPs, the contribution of this residual noise was removed by subtracting, at each electrode and at each frequency bin, the average amplitude of the signal measured at neighboring frequencies ($\pm 0.2\text{--}0.5$ Hz relative to the expected SS-EP frequency; Mouraux et al., 2011). For each SS-EP and for each participant, an electrode of interest was then determined by selecting, within this average spectrum, the electrode exhibiting the maximum amplitude at the corresponding vibrotactile SS-EP frequency (Figure 2). This selection procedure was applied to take into account the across-subject variability of SS-EP scalp topographies. Importantly, because the electrode of interest was determined based on the scalp distribution of the spectrum averaged across all conditions, the procedure did not bias our results toward finding a difference between conditions.

In a second step, the 16-s epochs were segmented relative to each phase of the displacement of the visual stimulus: 0–6 s (corresponding to the 6 s during which the stimulus was maintained away from the participant), 6–8 s (corresponding to the 2 s during which the stimulus was moved toward the target hand), 8–14 s (corresponding to the 6 s during which the stimulus was maintained

close to the target hand), and 14–16 s (corresponding to the 2 s during which the stimulus was moved away from the hand and back to its initial position). Separate average waveforms were then computed for each condition (visual stimulation toward the left vs. right hand; hands crossed vs. uncrossed) and movement phase of the visual stimulus (far, moving toward, close vs. moving away from the target hand). The obtained average waveforms were then transformed in the frequency domain using the same FFTW Fourier transform, and the contribution of residual noise was removed by subtracting the average amplitude of the signal measured at neighboring frequencies (Mouraux et al., 2011). In the absence of a steady-state response, noise-subtracted average signal amplitudes may be expected to tend toward zero. To assess the significance of the responses measured at each frequency and experimental condition, a *t* test against zero was thus used to determine whether the magnitude of the noise-subtracted signal amplitudes were significantly greater than zero (SPSS 18, IBM, USA).

Finally, the amplitude of each SS-EP was assessed for each condition (visual stimulation toward the left vs. right hand; hands crossed vs. uncrossed), movement phase of the visual stimulus (far, moving toward, close vs. moving away from the target hand), using the electrode exhibiting the maximum amplitude across conditions.

Effect of Spatial Congruence on the Magnitude of Vibrotactile SS-EPs

For each trial and each vibrotactile SS-EP, the visual and vibrotactile stimulation could be either spatially congruent (vibrotactile

SS-EP recorded from the hand targeted by the visual stimulus) or spatially incongruent (vibrotactile SS-EP recorded from the hand not targeted by the visual stimulus). The effect of spatial congruence was assessed separately for each movement phase (far, moving toward, close, and moving away from the target hand), using a two-way repeated measures analysis of variance (ANOVA) with the factors spatial congruence (spatially congruent vs. spatially incongruent) and hand position (crossed vs. uncrossed). Effect sizes of ANOVAs were measured with partial eta squared (η_p^2).

Two additional analyses were performed to assess the time course of the effect of the visual stimulus on the magnitude of the vibrotactile SS-EPs. In a first analysis, the 16-s epochs were segmented in eight consecutive epochs of 2 s. The effect of spatial congruence was then assessed in each 2-s epoch using the same two-way repeated measures ANOVA with the factors spatial congruence (spatially congruent vs. spatially incongruent) and hand position (uncrossed vs. crossed). As in the original analysis, SS-EP amplitudes at the electrode exhibiting maximum amplitude across conditions were averaged for 4.2 Hz and 7.2 Hz stimulation. In a second analysis, we used a windowed canonical correlation analysis (CCA; Lin, Zhang, Wu, & Gao, 2007) to assess the magnitude of the two vibrotactile SS-EPs throughout the 16-s epochs. CCA is an alternative method to extract a narrowband frequency component in the EEG (Lin et al., 2007). Instead of measuring the magnitude of a periodic pattern, CCA-based detection methods measure the correlation between the recorded EEG signals and the given stimulation frequencies. For each frequency of interest, it is then possible to obtain a point-by-point estimate of the temporal dynamic of the responses throughout the entire stimulation period (Hakvoort, Reuderink, & Obbink, 2011). Compared to traditional methods based on the Fourier transform, CCA can make full use of the spatial information contained in multichannel EEG recordings to detect steady-state EEG responses. Most importantly, CCA analysis circumvents the problem related to interindividual variations in scalp topography and the selection of electrodes of interest. For each participant, CCA uses an optimal combination of EEG channels to achieve the correlation between EEG signals and stimulation frequencies, thereby improving the signal-to-noise ratio and reducing intersubject variability (Hakvoort et al., 2011). The CCA analysis was used to estimate the correlation coefficients between the EEG signal and each frequency of vibrotactile stimulation (4.2 Hz and 7.2 Hz) during the entire 16 s of stimulation. The CCA was computed using a window length of 4 s and a window step of 0.2 s, and using the signals recorded from the five electrodes exhibiting maximum vibrotactile SS-EP amplitudes across participants (vibrotactile stimulation of the right hand: F3, FC1, CP5, CP3, and P3; vibrotactile stimulation of the left hand: F2, F4, CP6, CP4, and C6). The CCA epochs at 4.2 Hz and 7.2 Hz were then averaged for each participant, yielding four average waveforms (hands crossed vs. uncrossed; spatially congruent vs. incongruent).

Cross-Modulation Frequencies

For each condition, when the visual and the vibrotactile stimulus were spatially congruent, we examined whether SS-EPs appeared at the frequencies corresponding to the cross-modulation between the visual SS-EP (F_{vision} : 9.8 Hz) and the spatially congruent vibrotactile SS-EP (F_{touch} : 4.2 Hz or 7.2 Hz), using the frequency spectra averaged across all scalp channels. Cross-modulation SS-EPs ($F_{cm} = m.F_{vision} \pm n.F_{touch}$) were considered up to the second m and n harmonic. To assess the significance of the signal measured at these frequencies, a t test against zero was used to determine

whether the magnitude of the noise-subtracted signal amplitudes were significantly greater than zero.

Results

Vibrotactile SS-EPs

Vibrotactile stimulation elicited clear SS-EPs in all conditions, and during all phases of the movement of the visual stimulus. Regardless of spatial congruence and hand position, the magnitude of the vibrotactile SS-EPs elicited during the first phase of the trials (far: 0–6 s) was significantly greater as compared to the later close phase of the trial (8–14 s), all $t(24) > 3.055$, all $p < .005$ (Figure 3). This general effect of time could result from some form of response habituation or adaptation (Rossion & Boremanse, 2011), possibly occurring already at the level of peripheral mechanoreceptors (McGlone & Reilly, 2010).

The scalp topographies of the two vibrotactile SS-EPs (4.2 Hz and 7.2 Hz) were maximal over the parietal region contralateral to the stimulated hand (Figure 4). A t test against zero was used to determine whether the amplitudes of the SS-EPs elicited by stimulation of the left and right hand (averaged across all scalp channels) were significantly greater than zero, at each phase of the movement of the visual stimulus (far, moving toward, close, and moving away from the target hand), in each hand position (crossed vs. uncrossed) and for each congruence condition (spatially congruent vs. spatially incongruent). In the first phase (0–6 s: visual stimulus away from the hands), the noise-subtracted frequency amplitude spectra were significantly greater than zero at each frequency in all conditions, 4.2 Hz: all $t(24) > 7.27$; all $p < .001$; 7.2 Hz: all $t(24) > 7.64$; all $p < .001$. During the second phase (6–8 s: visual stimulus moving toward the left or right hand), the noise-subtracted frequency amplitude spectra were also significantly greater than zero at each frequency in all conditions, 4.2 Hz: all $t(24) > 2.93$; all $p < .007$; 7.2 Hz: all $t(24) > 4.53$; all $p < .004$. This was also the case in the third phase (8–14 s: visual stimulus maintained close to the left or right hand), 4.2 Hz: all $t(24) > 5.34$; all $p < .001$; 7.2 Hz: all $t(24) > 6.52$; all $p < .001$. In contrast, in the last phase (14–16 s: visual stimulus moving away from the hand), the noise-subtracted frequency amplitude spectra were significantly greater than zero at 4.2 Hz, all $t(24) > 2.46$; all $p < .02$, but not at 7.2 Hz. At this frequency, the amplitudes of the SS-EPs were significantly greater than zero in the spatially congruent condition, all $t(24) > 2.67$; all $p < .01$, but not in the spatially incongruent condition, all $t(24) < 1.67$; all $p > .11$.

Visual SS-EP

The scalp topography of the visual SS-EP was maximal over occipital regions. The visual stimulation elicited a clear SS-EP at 9.8 Hz in each movement phase (far, moving toward, close, and moving away from the target hand), in each hand position (crossed and uncrossed) and in each congruence condition (spatially congruent vs. spatially incongruent). The noise-subtracted frequency amplitude spectra (averaged across all scalp channels) were significantly greater than zero whatever the condition, all $t(24) > 2.41$; all $p < .02$.

Modulation of Vibrotactile SS-EPs by the Visual Stimulus

A repeated measures ANOVA with the factor spatial congruence (vibrotactile SS-EP recorded from the hand spatially congruent

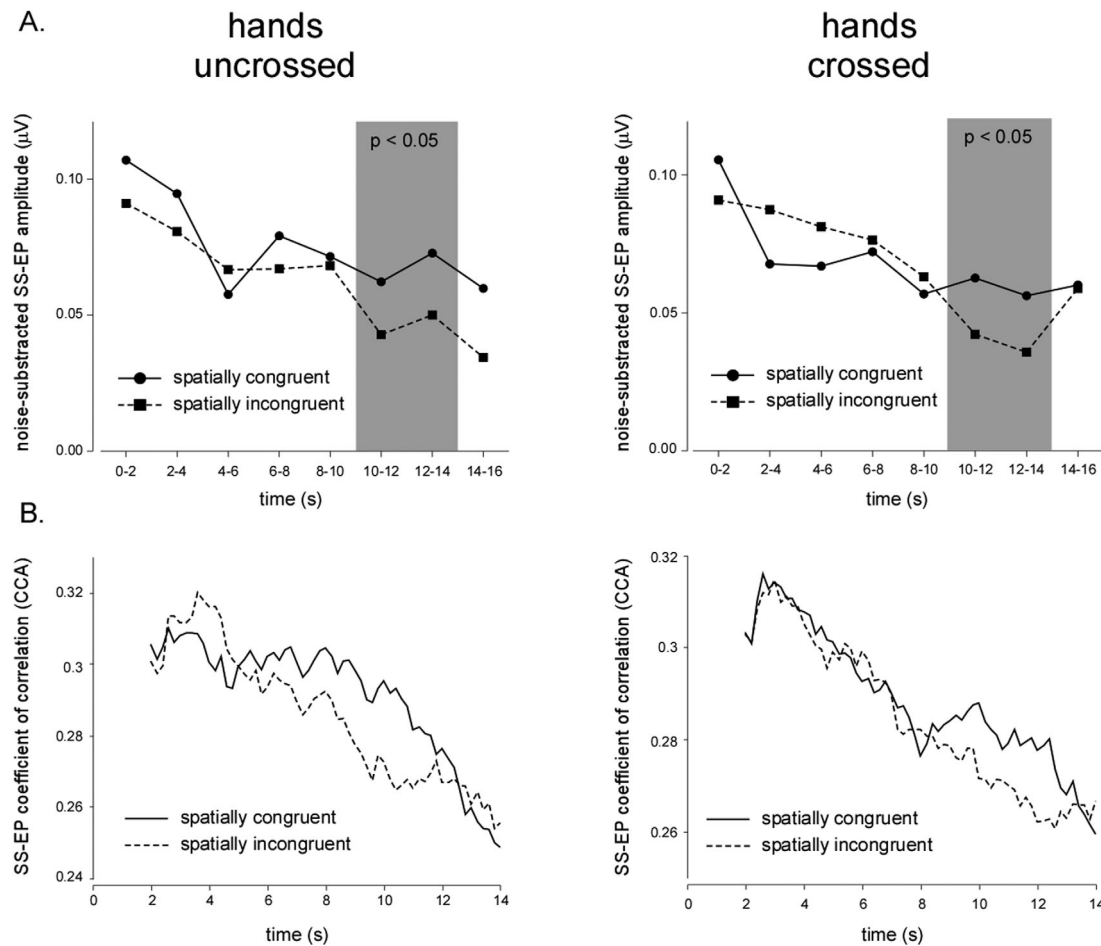


Figure 3. Time course of vibrotactile SS-EP magnitude. The upper panel shows the group level average amplitude of spatially congruent (continuous line) and spatially incongruent (dashed line) vibrotactile SS-EPs (averaged for 4.2 Hz and 7.2 Hz) within consecutive 2 s epochs. The gray bars indicate the time interval during which the magnitude of the spatially congruent vibrotactile SS-EP is significantly greater than the magnitude of the spatially incongruent vibrotactile SS-EP. The lower panel shows the results of the CCA analysis of vibrotactile SS-EPs. The continuous and dashed waveforms correspond to the group level average coefficients of correlation of spatially congruent and spatially incongruent vibrotactile SS-EPs, respectively (averaged for 4.2 and 7.2 Hz). In both analyses, and regardless of the position of the hands, the effect of spatial congruence on the magnitude of the vibrotactile SS-EPs appeared only once the visual stimulus was maintained over the hand, and disappeared as soon as it started moving back towards its initial position.

vs. incongruent relative to the hand targeted by the visual stimulus) and the factor hand position (hands crossed vs. uncrossed) was used to assess the crossmodal effect of the spatial location of the visual stimulus on the magnitude of the vibrotactile SS-EPs obtained in each movement phase (far, moving toward, close, and moving away from the target hand). As expected, in the first phase of the movement (0–6 s: visual stimulus away from the hands), the repeated measures ANOVA revealed no effect of spatial congruence, $F(1,24) = 0.12$, $p = .74$, $\eta_p^2 = .005$, no effect of hand position, $F(1,24) = 0.25$, $p = .63$, $\eta_p^2 = .1$, and no interaction between the two factors, $F(1,24) = 0.44$, $p = .51$, $\eta_p^2 = .02$ (Figure 5 and 6). In the second phase of the movement (6–8 s: visual stimulus moving toward the left or right hand), the repeated measures ANOVA also revealed no effect of spatial congruence, $F(1,24) = 0.57$, $p = .46$, $\eta_p^2 = .02$, no effect of hand position, $F(1,24) = 0.02$, $p = .88$, $\eta_p^2 = .001$, and no interaction between the two factors, $F(1,24) = 0.19$, $p = .66$, $\eta_p^2 = .008$. In contrast, during the third phase of the movement (8–14 s: visual stimulus maintained close to the left or right hand), there was a significant main effect of spatial congruence, $F(1,24) = 12.38$, $p = .002$, $\eta_p^2 = .34$, with no

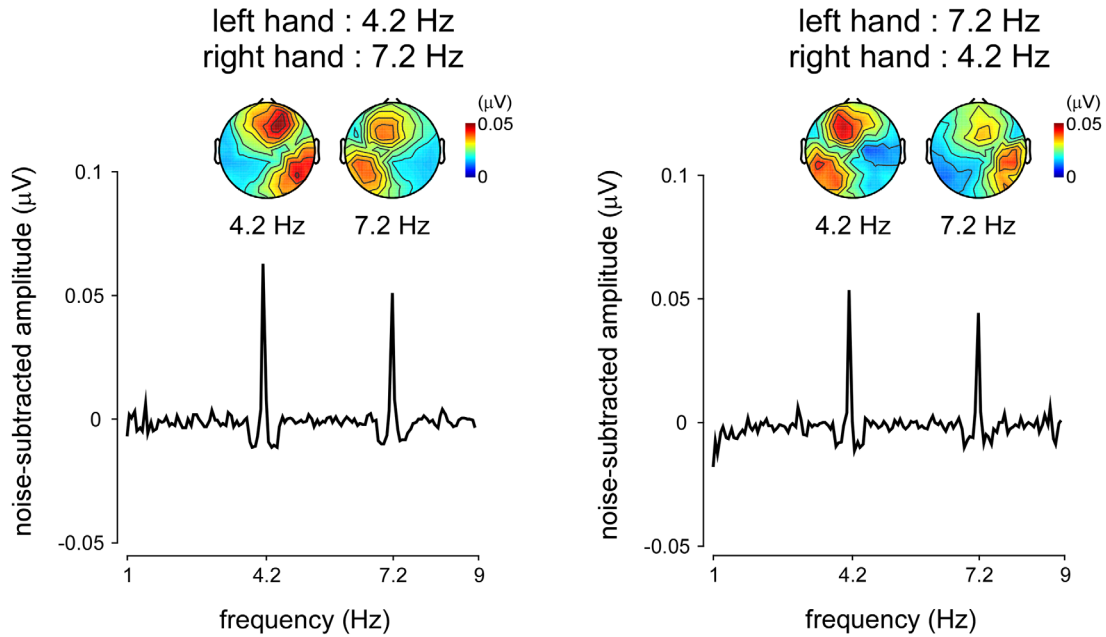
effect of hand position, $F(1,24) = 0.39$, $p = .54$, $\eta_p^2 = .02$, and no interaction between the two factors, $F(1,24) < 0.001$; $p = .99$, $\eta_p^2 < .001$ (Figure 5 and 6). Regardless of whether the hands were uncrossed or crossed, the magnitude of the spatially congruent vibrotactile SS-EPs (uncrossed hands: $0.14 \pm 0.06 \mu\text{V}$ (mean \pm SD); crossed hands: $0.14 \pm 0.04 \mu\text{V}$) was significantly greater than the magnitude of the spatially incongruent vibrotactile SS-EPs (uncrossed hands: $0.12 \pm 0.05 \mu\text{V}$; crossed hands: $0.12 \pm 0.04 \mu\text{V}$). The results are depicted in Figures 5 and 6.

Finally, in the fourth phase of the movement (14–16 s: visual stimulus moving away from the hand), there was no effect of spatial congruence, $F(1,24) = 0.02$, $p = .91$, $\eta_p^2 = .001$, no effect of hand position, $F(1,24) = 0.24$, $p = .63$, $\eta_p^2 = .01$, and no interaction between the two factors, $F(1,24) = 0.08$; $p = .79$, $\eta_p^2 = .003$.

Temporal Dynamics of the Modulation of Vibrotactile SS-EPs by Vision

In the first analysis, the two-way repeated measures ANOVA performed in each 2-s epoch showed a significant effect of spatial

hands uncrossed



hands crossed

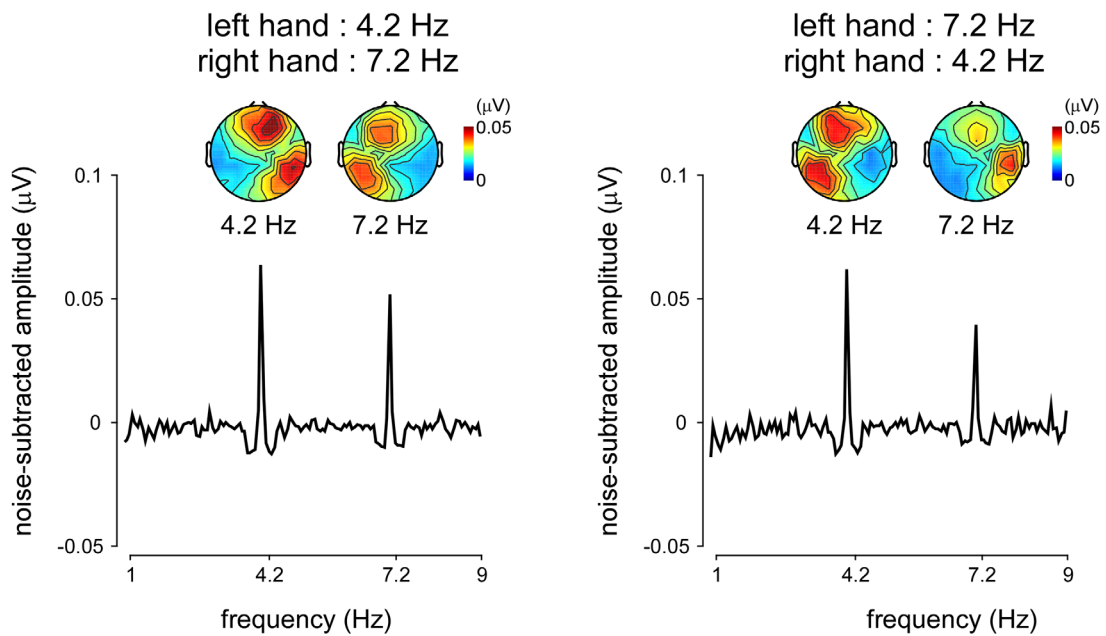


Figure 4. Group-level average vibrotactile SS-EPs elicited by the concomitant stimulation of the left and right hand at 4.2 Hz and 7.2 Hz. The black traces represent the noise-subtracted EEG amplitude spectrum (μV) recorded during the entire 16-s trains of stimulation and averaged across all scalp electrodes, in the uncrossed hands condition (upper) and the crossed hands condition (lower). In all conditions, vibrotactile stimulation elicited a clear peak at 4.2 Hz and 7.2 Hz. The topographical maps represent the scalp topography of the SS-EPs obtained at each of the two frequencies. Note that the SS-EP scalp topographies are maximal over frontal and parietal regions contralateral to the stimulated side.

congruence from 10 s to 12 s and from 12 s to 14 s, regardless of whether the hands were uncrossed or crossed (Table 1). In other words, the effect of the visual stimulus on the magnitude of the vibrotactile SS-EPs appeared only once the visual stimulus had

been maintained over the congruent hand for more or less 2 s, and disappeared as soon as the visual stimulus started moving back to its initial position (Figure 3A). These observations were confirmed by the results of the windowed CCA (Figure 3B).

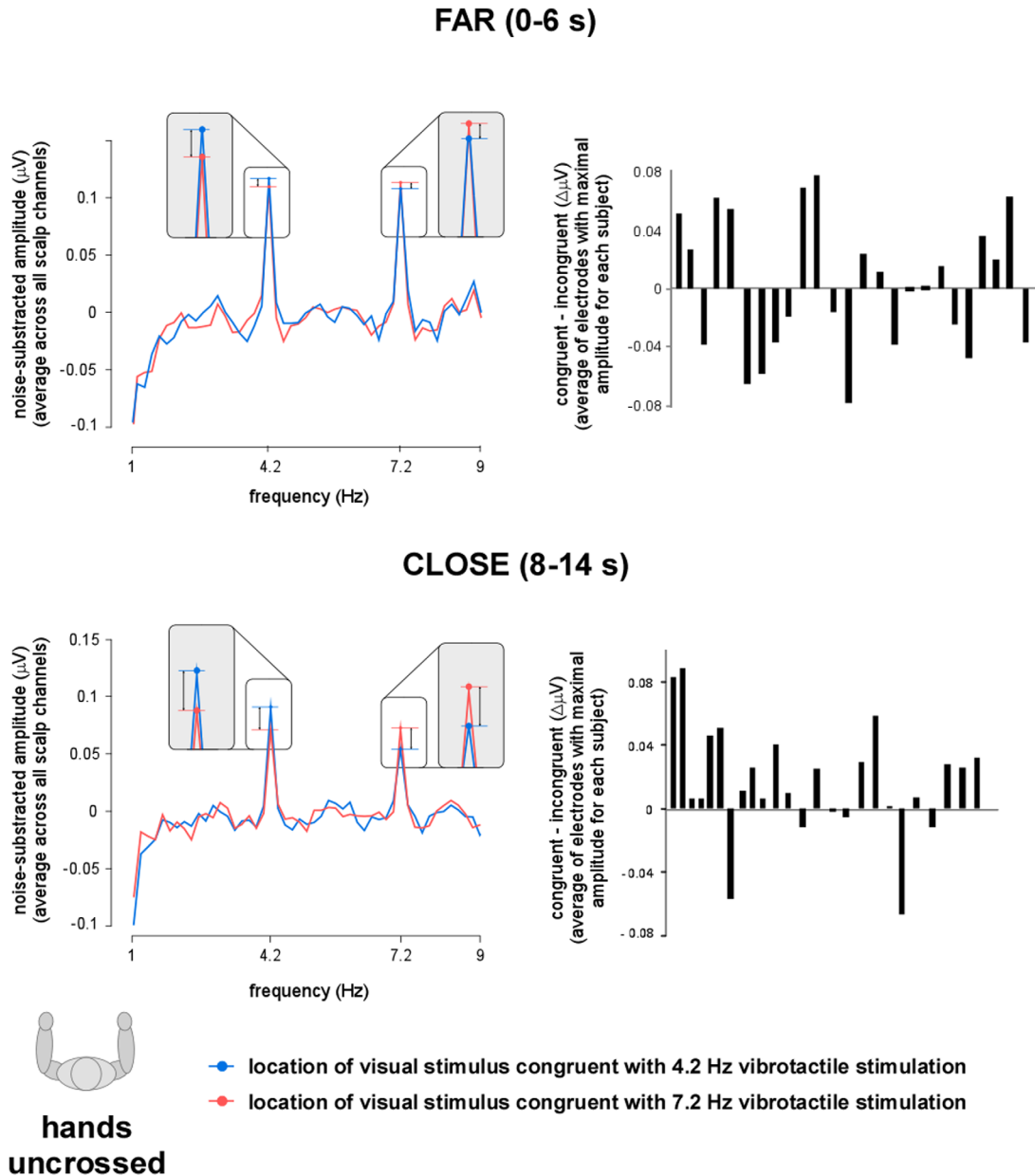


Figure 5. Effect of spatial congruence on the magnitude of vibrotactile SS-EPs elicited in the uncrossed hands condition. The upper graphs show the vibrotactile SS-EPs obtained when the visual stimulus was maintained far from the hands (FAR 0–6 s). The lower graphs show the vibrotactile SS-EPs obtained when the visual stimulus was maintained close to the left or right hand (CLOSE: 8–14 s). The traces represent the group-level average of the noise-subtracted EEG amplitude spectrum (μV) obtained when the location of the visual stimulus was congruent with the location of the 4.2 Hz vibrotactile stimulus (black) or the location of the 7.2 Hz vibrotactile stimulus (gray). The bar graphs represent the single-subject difference in amplitude of the SS-EPs obtained from the spatially congruent vs. incongruent hand. For each subject, the amplitude corresponds to the amplitude of the electrode exhibiting the maximal vibrotactile SS-EP across conditions. Note that when the stylus is maintained close to one of the two hands, vibrotactile stimulation of the spatially congruent hand elicits an SS-EP of greater magnitude than vibrotactile stimulation of the spatially incongruent hand.

Cross-Modulation Frequencies

For each condition, when the visual stimulus and the vibrotactile stimulus were spatially congruent, we examined whether additional SS-EPs appeared at the frequencies corresponding to the cross-modulation between the frequency of visual stimulation (F_{visual} : 9.8 Hz) and the frequency of the spatially congruent vibrotactile SS-EP (F_{touch} : 4.2 Hz or 7.2 Hz). Cross-modulation SS-EPs ($F_{cm} = m.F_{\text{vision}} \pm n.F_{\text{touch}}$) were considered up to the second m and n harmonic. None of the frequencies elicited a significant amplitude greater than zero.

Discussion

In the present study, we explored the crossmodal spatial interactions between vision and touch. Using frequency-tagging of SS-EPs, we isolated the cortical activity elicited by the presentation of vibrotactile stimuli delivered concomitantly to the left and right hand combined with visual stimuli approaching either the left hand or the right hand. Specifically, we tested whether a sustained visual stimulus applied toward one hand in external space enhances the processing of vibrotactile input originating from that hand as compared to the other hand. The effect of the location of the visual

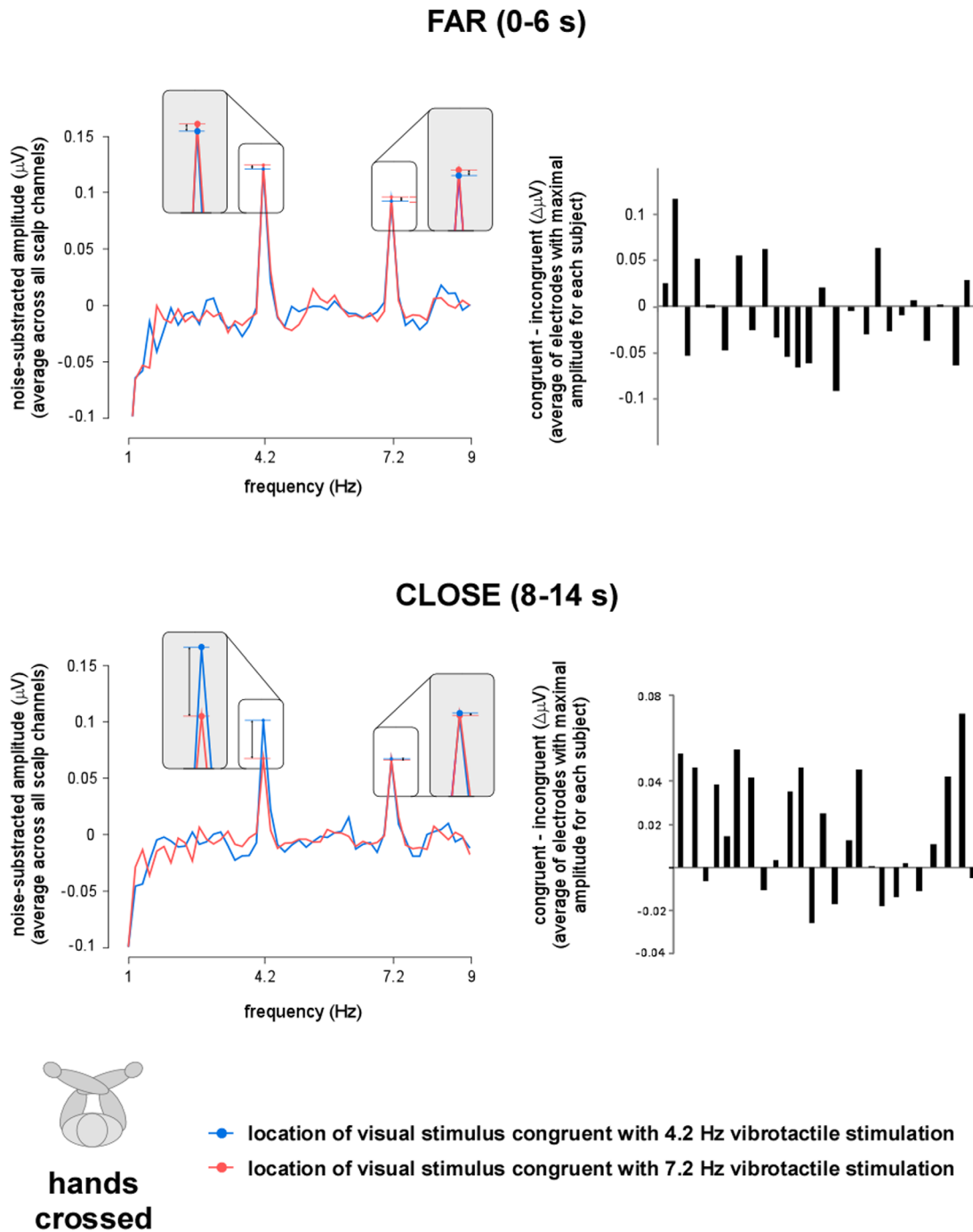


Figure 6. Effect of spatial congruence on the magnitude of vibrotactile SS-EPs elicited in the crossed hands condition. The upper graphs show the vibrotactile SS-EPs obtained when the visual stimulus was maintained far from the hands (FAR 0–6 s). The lower graphs show the vibrotactile SS-EPs obtained when the visual stimulus was maintained close to the left or right hand (CLOSE: 8–14 s). The traces represent the group-level average of the noise-subtracted EEG amplitude spectrum (μV) obtained when the location of the visual stimulus was congruent with the location of the 4.2 Hz vibrotactile stimulus (black) or with the location of the 7.2 Hz vibrotactile stimulus (gray). The bar graphs represent the single-subject difference in amplitude of the SS-EPs obtained from the spatially congruent vs. incongruent hand. For each subject, the amplitude corresponds to the amplitude of the electrode exhibiting the maximal vibrotactile SS-EP across conditions. Note that when the stylus is closed to one of the two hands, vibrotactile stimulation of the spatially congruent hand elicited an SS-EP of greater magnitude than vibrotactile stimulation of the spatially incongruent hand, even though the hands were in a crossed position.

stimulus in external space on the magnitude of the vibrotactile SS-EPs elicited by stimulation of each of the two hands was evaluated by comparing the magnitude of the vibrotactile SS-EPs elicited by tactile stimulation of the hand targeted by the visual stimulus (spatially congruent condition) with the magnitude of the vibrotactile

SS-EPs obtained when the visual stimulus targeted the other hand (spatially incongruent condition). This comparison revealed that the amplitude of the vibrotactile SS-EPs elicited by stimulation of the spatially congruent hand was significantly greater than the amplitude of the vibrotactile SS-EPs obtained when the visual

Table 1. Two-Way Repeated Measures ANOVA of Effect of Visual Stimulus on Magnitude of Vibrotactile SS-EPs

Time	Hand position			Spatial congruence			Interaction		
	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2	<i>F</i>	<i>p</i>	η_p^2
0–2 s	0.003	.95	< .001	1.76	.19	.07	0.001	.97	< .001
2–4 s	0.62	.44	.03	0.07	.79	.003	1.57	.22	.06
4–6 s	0.6	.45	.02	2.09	.16	.08	0.09	.76	.004
6–8 s	0.02	.89	.001	0.19	.66	.008	0.52	.48	.02
8–10 s	0.97	.34	.04	0.08	.78	.003	0.27	.61	.01
10–12 s	< 0.001	.99	< .001	5.14	.03*	.18	0.003	.96	< .001
12–14 s	2.71	.11	.101	4.72	.04*	.16	0.01	0.91	.001
14–16 s	0.72	.41	.03	2.05	.17	.08	3.662	.07	.13

Note. In uncrossed and crossed hand conditions, the two-way repeated measures ANOVA show a significant effect of the visual stimulus on the amplitude of the vibrotactile SS-EPs from 10 s to 12 s and from 12 s to 14 s of the displacement of the visual stimulus.

* $p < .05$.

stimulus targeted the other hand. Interestingly, this difference was significant only when the visual stimulus had been maintained over the congruent hand for more or less 2 s, and disappeared as soon as the visual stimulus started to move back toward its initial position.

Previous studies aiming at exploring the effects of spatial attention have mainly focused on assessing the effect of a cue on the responses elicited by a subsequent task-relevant target. Two kinds of cueing paradigms have most often been used, leading authors to distinguish two types of spatial attention mechanisms: stimulus-driven exogenous attention and expectancy-directed endogenous attention (see Posner & Cohen, 1984, Jones & Forster 2014). Endogenous attention is usually studied by characterizing the effect of cues predicting the most probable location of the upcoming target. In contrast, exogenous attention is usually studied using cues having a spatial location that is not actually predictive of the location of the upcoming target. In the present study, we did not rely on such cueing paradigms. The visual stimulus as well as the tactile stimuli delivered to the two hands were presented concomitantly during the entire duration of the trial. Participants fixated a central cross during the 16 s of stimulation, and the duration of the displacement of the visual stimulus was relatively long (2 s). Because they could covertly see which hand would be reached by the visual stimulus, the observed crossmodal effects of the spatial location of visual input on the processing of tactile input could have resulted from endogenous spatial orienting mechanisms. However, the effect of spatial congruence varied across time, being significant only once the visual stimulus had been maintained over the congruent hand for more or less 2 s, and disappearing as soon as the visual stimulus started moving back to its initial position. This suggests that the observed effect of spatial congruence was related to the actual spatial location of the visual stimulus, and not simply related to a classic cueing of left or right space. Indeed, if the effects had been related to a cueing of left or right space, one might have expected the effects to appear soon after movement onset, and to remain present throughout the entire trial duration. Furthermore, the finding that the effect of spatial congruence was present only when the visual stimulus was maintained close to the hand indicates that this effect of vision on touch is present only when the visual stimulus is located in the peripersonal space of the hand.

The scalp topography of the vibrotactile SS-EPs showed two clear maxima, one over the frontal region, the other over parietal areas contralateral to the stimulated hand. This scalp topography is compatible with a tangential dipole located close to the hand representation within the primary somatosensory cortex (S1; Figure 4; Giabbiconi, Trujillo-Barreto, Gruber, & Müller, 2007; Mouraux et al., 2011; Snyder, 1992). Our results showing that the spatial

location of concurrent visual stimulation can selectively modulate the magnitude of the SS-EPs elicited by spatially congruent vibrotactile input indicate that these crossmodal interactions exert an effect on tactile processing within somatosensory-specific areas.

Because we were unable to monitor eye movements, the occurrence of pursuit eye movements cannot be entirely excluded. However, it seems unlikely that such eye movements could explain our results, as the effect of the visual stimulus on the amplitude of the vibrotactile SS-EPs appeared only 10 s after the onset of stimulation, when the visual stimulus remained stable over the targeted hand.

Our results are in accordance with previous studies demonstrating that SS-EPs can be modulated by spatial attention (Bidet-Caulet et al., 2007; Giabbiconi, Dancer, Zopf, Gruber, & Müller, 2004; Giabbiconi et al., 2007; Morgan, Hansen, & Hillyard, 1996; M. M. Müller et al., 2006; N. Müller, Schlee, Hartmann, Lorenz, & Weisz, 2009). Regarding vibrotaction, these studies showed that selectively attending to one hand leads to a selective increase of the magnitude of the SS-EPs elicited by vibrotactile stimulation of the attended hand, as compared to the magnitude of the SS-EPs concomitantly elicited by vibrotactile stimulation of the unattended hand (Adler, Müller, & Giabbiconi, 2009; Giabbiconi et al., 2004, 2007). Importantly, our study differs from these previous studies by the fact that participants were not asked explicitly to pay attention to the left or right hand, and did not know which hand would be reached by the visual stimulus before the beginning of the trial. Thus, we show that crossmodal effects of the spatial location of visual input on the concurrent processing of a somatosensory input occur even when the visual and tactile inputs are not relevant for behavioral goals, and when attention is not explicitly directed toward a given location.

A large number of studies using predictive lateralized cues have also characterized the effect of unimodal spatial attention within the tactile modality using transient ERPs. In most of these studies, participants were instructed to attend one hand while electrical or mechanical somatosensory stimuli were delivered to the attended and unattended hands. Comparison of the ERPs elicited by stimuli delivered to the attended versus unattended hands showed that the focus of spatial attention can modulate the amplitude of early- and midlatency somatosensory ERPs, in particular, the N80 elicited by stimulation of the attended hand (Eimer & Forster, 2003; Michie, Bearpark, Crawford, & Glue, 1987), P100 (Desmedt & Robertson, 1977; Eimer & Forster, 2003; Josiassen, Shagass, Roemer, Ercegovac, & Straumanis, 1982; Zopf, Giabbiconi, Gruber, & Müller, 2004), and N140 (Desmedt & Robertson, 1977; Eimer & Driver, 2000; Garcia-Larrea, Lukaszewicz, & Mauguier, 1995; Michie et al., 1987; Zopf et al., 2004). Most of these results are thus in line with those of the present experiment demonstrating that the spatial

location of visual input can modulate the responses to spatially congruent tactile input already within somatosensory areas.

Only a few ERP studies have investigated crossmodal effects of spatial attention on tactile processing. Using an endogenous paradigm, Eimer and Driver (2000) found no crossmodal effect on the magnitude of tactile ERPs when a visual stimulus was task relevant and the tactile modality could be entirely ignored. However, in a follow-up experiment where vision was the primary modality but infrequent tactile stimuli required also a response regardless of their spatial location, they found that the spatial location of visual attention exerted a modulation of the late N140 component of somatosensory ERPs. Similarly, Eimer et al. (2002) found no crossmodal attentional effects on the tactile ERPs when audition was task relevant and the tactile modality could be entirely ignored. However, using a sustained attention paradigm, Hotting, Rosler and Roder (2003) found a bidirectional crossmodal interaction between touch and audition. When audition was task relevant, tactile ERPs elicited by stimuli delivered to the attended location showed an enhancement of middle- and late-latency N70–100 and N125–175 components. To our knowledge, no study has yet investigated the crossmodal effects of the spatial location of nonsomatic cues on the processing of tactile stimuli using an exogenous paradigm.

Therefore, whereas ERP studies have shown significant crossmodal effects of visual spatial attention only when the tactile input is at least partly task relevant, and at latencies corresponding to higher-level stages of sensory processing no longer involving the primary somatosensory cortex, the present study shows crossmodal effects on the processing of tactile stimuli with a scalp topography compatible with a modulation of S1.

Most interestingly, our study showed that the visual-tactile effect of spatial congruency was preserved when the hands were crossed relative to the body midline. Visual stimulation delivered close to a given hand enhanced the vibrotactile SS-EP elicited by stimulation of that hand regardless of where the hand was positioned relative to the body midline. This indicates that the crossmodal effects of spatial congruency observed when the hands were uncrossed is not simply due to the fact that, in this condition, spatially congruent visual and tactile inputs primarily project to the same cerebral hemisphere (Kinsbourne, 1970). Indeed, when the hands were crossed, visual stimulation toward a given hand still enhanced the responses to vibrotactile stimulation of that hand. In this condition, spatially congruent tactile and visual inputs no longer project to the same cerebral hemisphere. Therefore, the spatial interactions between vision and touch necessarily take into consideration knowledge of where the hands are located in external space. In addition, the two supplementary analyses indicated that the onset of the effect of spatial congruency was similar with uncrossed and crossed hands (Figure 3). This suggests that the integrative processing of body posture was already achieved and still ongoing at the time when the crossmodal interaction emerged. This is not surprising considering that tactile input can

be expected to be remapped to external space within 200–360 ms after stream onset (Azañón & Soto-Faraco, 2008). Moreover, it has been suggested that integrative processing of body posture is quite stable over time (Azañón, Stenner, Cardini, & Haggard, 2015). Azañón et al. (2015) demonstrated that, when a crossed posture is maintained during a certain time, tactile localization abilities improve rapidly as a function of recent tactile experience, even if previous tactile stimuli are not task relevant. Following this rapid improvement of tactile localization, no further change of performance was observed when participants maintained the crossed posture for at least 15 s without receiving any tactile input.

We could not identify any SS-EPs at frequencies corresponding to the cross-modulation between the frequency of the visual stimulus (9.8 Hz) and the vibrotactile stimulus (4.2 Hz or 7.2 Hz) when the visual and tactile stimuli were spatially congruent. Had they been present, these cross-modulations SS-EPs would have constituted a direct measure of activity generated by neuronal populations onto which spatially congruent vibrotactile and visual inputs converge (Giani et al., 2012; M. P. Regan et al., 1995). Their absence could be related to the fact that participants did not perform a task requiring attention to be focused on the two stimuli. This could have interfered with the multisensory integration of the two inputs into a unified percept. Supporting this view, it has been shown that audiovisual interactions assessed using ERPs depend on whether subjects attend to both sensory modalities (Talsma, Doty, & Woldorff, 2007). However, in a recent study, Giani et al. (2012) recorded SS-EPs to concomitant auditory and visual stimulation, and failed to identify cross-modulation SS-EPs even when participants were actively engaged in a task that required simultaneously attending the two streams of sensory input.

In conclusion, using frequency tagging of SS-EPs, we show that a sustained visual stimulus delivered close to a given body part is able to selectively enhance the concurrent processing of somatosensory input originating from that body part as compared to other body parts, and that this enhancement already involves stages of cortical processing in somatosensory-specific cortical areas. Moreover, we show that this effect was not dependent on the relative position of the limbs in space, and that it was present only when the visual stimulus was maintained close to the congruent hand, disappearing as soon as the visual stimulus started moving back to its initial position. Taken together, this suggests that the observed effects involve a supramodal spatial frame of reference, integrating tactile input and visual input located in peripersonal space, and taking into consideration the relative position of the hands in external space.

Finally, like other previous studies (Giani et al., 2012), we did not identify cross-modulation frequencies between the concurrently presented visual and tactile stimuli. This raises the question of whether multisensory integration processes can actually be tagged using this approach, as only a few studies have shown evidence for the emergence of such cross-modulation SS-EPs across modalities (Nozardan, Zerouali, Peretz, & Mouraux, 2015; M. P. Regan et al., 1995).

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