Article

PERCEPTION

Does Body Perception Shape Visuospatial Perception?

Perception
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Abstract

How we perceive our body is shaped by sensory experiences with our surrounding environment, as witnessed by poor performance in tasks during which participants judge with their hands crossed the temporal order between two somatosensory stimuli, one applied on each hand. This suggests that somatosensory stimuli are not only processed according to a somatotopic representation but also a spatiotopic representation of the body. We investigated whether the perception of stimuli occurring in external space, such as visual stimuli, can also be influenced by the body posture and somatosensory stimuli. Participants performed temporal order judgements on pairs of visual stimuli, one in each side of space, with their hands uncrossed or crossed. In Experiment 1, participants' hands were placed either near or far from the visual stimuli. In Experiment 2, the visual stimuli were preceded, either by 60 ms or 360 ms, by tactile stimuli applied on the hands placed near the visual stimuli. Manipulating the time interval was intended to activate either a somatotopic or a spatiotopic representation of somatic inputs. We did not obtain any evidence for an influence of body posture on visual temporal order judgment, suggesting that body perception is less relevant for processing extrabody stimuli than the reverse.

Keywords

body, space, multisensory interactions, peripersonal space, temporal order judgments

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Introduction

The way we represent and perceive our body is shaped by our perceptual experience with our surroundings. Indeed, to adequately respond to a somatic stimulus, it is crucial to identify and locate in external space the object in contact with the body (Graziano & Cooke, 2006). It is therefore necessary to remap the location of a somatosensory stimulus from a somatotopic reference frame, that is, a reference frame representing the body surface anatomically, to a spatiotopic frame of reference, which takes into account external space

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as coordinate as well as the relative posture of the body (Brozzoli, Ehrsson, & Farnè, 2014). Spatial remapping of somatosensory stimuli is illustrated by the behavior of patients with cortical lesion, characterized by an impaired perception of tactile stimuli applied on the hand contralateral to the lesion but who improve their performance when that hand is crossed over their body midline, so that it is placed in the ipsilesional side of space (e.g., Smania & Aglioti, 1995). This suggests that the lesion does not only affect the perception of the limb on which the stimuli were applied but also the part of external space occupied by the stimulated limb (see Jacobs, Brozzoli, Hadj-Bouziane, Meunier, & Farnè, 2011). The crossing hand procedure is regularly used to investigate the spatial representation of somatosensory inputs, as it generates a mismatch between somatotopic and spatiotopic reference frames (Holmes & Spence, 2004). In healthy humans, such dissociation can be observed using temporal order judgment (TOJ) tasks with somatosensory stimuli (Heed & Azañón, 2014). For instance, tactile stimuli are delivered in pairs, one applied on each hand, with short interstimulus time intervals, and participants have to judge which of the two stimuli they perceived as having been applied first. In such tasks, participants' performance is usually characterized by the slope of the psychometric function fitting the participants' response probabilities (Heed & Azañón, 2014). The slope defines indeed the precision of the participant's performance (Filbrich, Alamia, Burns, & Legrain, 2017) and can be used to index performance accuracy (Spence & Parise, 2010). Performing somatosensory TOJ with the hands crossed over the body midline has been shown to decrease participants' accuracy, as indexed by flatter slopes of the TOJ psychometric function as compared to TOJ performed in an uncrossed posture (Crollen, Albouy, Lepore, & Collignon, 2017; Crollen, Lazzouni, et al., 2017; De Paepe, Crombez, & Legrain, 2015; Röder, Rösler, & Spence, 2004; Sambo et al., 2013; Shore, Spry, & Spence, 2002; Wada, Yamamoto, & Kitazawa, 2004; Yamamoto & Kitazawa, 2001). This suggests that, when judging temporal order of somatosensory stimuli, participants are influenced by the location of the stimulated hands according to external coordinates, that is, according to the position of the hands. This decrement in performance by changing the hand posture has been interpreted as evidence that somatosensory inputs, initially somatotopically mapped, are recoded according to spatiotopic reference frames (Shore et al., 2002). Such a remapping of somatosensory inputs is hypothesized to be shaped by the development of the visual system (Crollen & Collignon, 2012). For instance, congenitally blind people and very young children are less sensitive to crossed-hand posture when performing TOJ tasks (Crollen et al., 2017; Crollen, Lazzouni, et al., 2017; Pagel, Heed, & Röder, 2009; Röder et al., 2004).

In the present studies, we adopted the opposite reasoning and addressed the question of whether our ability to perceive visual space can be impacted by the perception of our body. First of all, our ability to perceive the location of an external stimulus often relies on using the body as reference (i.e., egocentric reference frame; Vallar & Maravita, 2009). Furthermore, it has also been shown that the perception of the location of visual stimuli might rely on different cognitive processes, depending on their distance from the body (Brozzoli et al., 2014; Graziano & Cooke, 2006), such as, for instance, the largely evidenced dissociation between peripersonal and extrapersonal reference frames, involved in coding position as near versus far from the body, respectively (Brozzoli et al., 2014; Holmes & Spence, 2004; Jacobs et al., 2011). Moreover, pathologies that affect the body structurally (e.g., limb amputation) and functionally (e.g., chronic pain) seem to modify the perception of the visual space around the body (Bultitude, Walker, & Spence, 2017; Filbrich, Alamia, Verfaille, et al., 2017; Makin, Wilf, Schwartz, & Zohary, 2010). In healthy participants, such a hypothesis has been tested using TOJ tasks by asking the participants to judge the temporal order of two lateralized visual stimuli, one located close to either hand. Participants were required to place their hands either in an uncrossed or in a crossed posture. In a first series of experiments, Yamamoto and Kitazawa (2001) did not evidence any change during visual TOJ as a function of body posture. Conversely, Shore et al. (2002) observed a slight but significant, effect of hand posture on visual TOJ, leaving this issue unsolved. In the present studies, we addressed this question by testing in a first experiment the impact of body posture on the TOJ of visual stimuli presented close to the body, as in previous studies (Shore et al., 2002; Yamamoto & Kitazawa, 2001). However, conversely to previous studies, we also added a control condition, during which the participants' hands were placed out of their view at a certain distance from the visual stimuli. This procedure was aimed to test the influence of spatial proximity of body limbs on the perceptual judgments of visual stimuli. Furthermore, we used an adaptive method that allows adapting the temporal delays that are used to characterize TOJ parameters individually to each participant (Filbrich, Alamia, Burns, et al., 2017). It was expected that, if body posture influences visual TOJ sensitivity, this would only be observed when visual stimuli were presented close to the hands.

In a second experiment, we tested the influence of tactile stimuli applied on the uncrossed versus crossed hands on the visual TOJ. Indeed, it could be argued that the absence of significant effects in previous experiments might be related to the fact that the sole manipulation of body posture is insufficient to affect the perception of visual space. Therefore, in the second experiment, we tried to boost the contribution of a certain body awareness and perception to the task by applying tactile stimuli on the participants' hands. The pairs of visual stimuli were therefore preceded by tactile stimuli by one of the two time intervals, either 60 ms or 360 ms before the first stimulus of the visual pairs. These two time intervals were chosen based on a study of Azañón and Soto-Faraco (2008a) who investigated the time course of somatosensory remapping. In that study, participants placed their hands crossed on a table and were asked to react as fast as possible to a target light that was briefly presented in one of two positions on either the left hand (placed in the right side of space) or the right hand (placed in the left side of space). Visual target stimuli were preceded, by various time intervals, by a tactile stimulus applied on one of the hands. They observed that visual reaction times were modulated by the tactile stimulus according to an anatomical reference frame around 60-ms time intervals but according to a spatial reference frame starting from the 160-ms time interval onward. In other words, a tactile stimulus applied on the left hand facilitated reaction times to right-sided visual stimuli (i.e., presented near the left hand in right space, where the left hand currently resides) at longer time intervals, whereas at shorter time intervals, it facilitated reaction times to left-sided visual stimuli (i.e., presented near the right hand in left space, where the left hand usually resides; see also Azañón, Camacho, & Soto-Faraco, 2010; Azañón & Soto-Faraco, 2008b). These data suggest that somatosensory inputs initially activate somatotopic representations of the body (*which is the stimulated hand?*) which are later remapped according to a space-based (*where is the stimulated hand?*) reference frame. The same reasoning was followed in present studies, but, conversely to Azañón and Soto-Faraco (2008a) who used unilateral tactile cues to bias perceptual performance, we focused on participant's sensitivity to perform TOJ on visual stimuli while adapting different hand postures without biasing their perception toward one side of visual space. Therefore, two tactile stimuli were applied simultaneously on either hand before the presentation of each pair of visual stimuli. Indeed, previous experiments have shown that, during TOJ, unilateral cues can induce cross-modal shift of attention toward one of the two targets of the stimulation pairs. Such an effect is indexed by a displacement of the point of subjective simultaneity (PSS), derived from the threshold of the TOJ psychometric function (see Filbrich, Alamia, Blandiaux, Burns, & Legrain, 2017;

Filbrich, Alamia, Burns, et al., 2017; Filbrich, Halicka, Alamia, & Legrain, 2018; McDonald, Teder-Sälejärvi, Di Russo, & Hillyard, 2005). In other words, using bilateral stimuli, we tried to keep the PSS equitably balanced between the two sides of space. In addition, it cannot be guaranteed that slope measures of TOJ functions are not affected by PSS shift, at least when testing TOJ with an adaptive procedure (see procedure below; see Heed & Azañón, 2014 for a diverging opinion with constant stimulation procedures). Based on Azañón and Soto-Faraco's findings, we hypothesized that when visual stimuli shortly followed tactile stimuli by 60 ms, the space-based representation of the visual stimuli would conflict with the anatomical representation of the hands triggered by the presentation of the bilateral tactile stimuli, especially in the crossed-hand position in which the spatial correspondence between visual stimuli and the hands is mismatching (e.g., left visual stimuli near the right hand). Conversely, since at a later latency, the spatial coding of tactile stimuli should be remapped according to a space-based reference frame, the spatial correspondence of the visual stimuli and the hand should not be mismatching anymore, even in the crossed-hand posture (e.g., left visual stimuli are near the left-sided hand). Therefore, we expected that visual TOJ performance should be affected by the crossed-hand posture only when visual stimuli followed the tactile stimuli by 60 ms and not by a longer time interval.

Experiment 1

Methods

Participants. Twenty participants took part in Experiment 1 (12 women, 23.1 years of mean age [±2.23 *SD*] ranging from 20 to 27 years, all but 2 right handed according to the Flinders Handedness survey (Nicholls, Thomas, Loetscher, & Grimshaw, 2013). The number of participants was chosen based on previous studies that demonstrated effects of hand posture on TOJ performance (e.g., De Paepe et al., 2015; Yamamoto & Kitazawa, 2001). All participants had normal or corrected-to-normal vision and did not present any neurological, psychiatric, or chronic pain problem as well as any upper-limb trauma. Psychotropic drugs were not allowed. The experimental procedure was approved by the local ethics committee in agreement with the Declaration of Helsinki, and all participants signed a consent form prior to the experimental session. Participants received financial compensation.

Stimuli and materials. Visual stimuli were presented by means of two white light-emitting diodes (LED, 17 lm luminous flux, 6.40 cd luminous intensity, and 120° diffusion angle [GM5BW97330A, Sharp Corporation, Japan]), perceived by the participants as brief flashes. A third yellow LED (min. 0.7 cd luminous intensity at 20 mA, 120° diffusion angle [GM5BW97330A, Sharp Corporation]) was used as fixation point. LEDs were powered by means of an electrical pulse stimulator (Master-8, A.M.P.I., Israel)

Procedure. Participants were sitting in a dimly illuminated room with their arms positioned on a table, palms down. Their heads were stabilized with a chin rest placed ~10 cm from the trunk. The two white LEDs were fixed on the table, ~40 cm away from the trunk and with a distance of ~30 cm between them. The yellow fixation LED was placed at a distance of ~65 cm in front of the body midline equidistantly from the two white LEDs. Participants' hands were positioned according to four conditions. In the first two conditions, each hand was placed next to one of the two white LEDs, with a maximum distance of 1 cm between the LED and the metacarpophalangeal joint of the index finger, either in an uncrossed or a

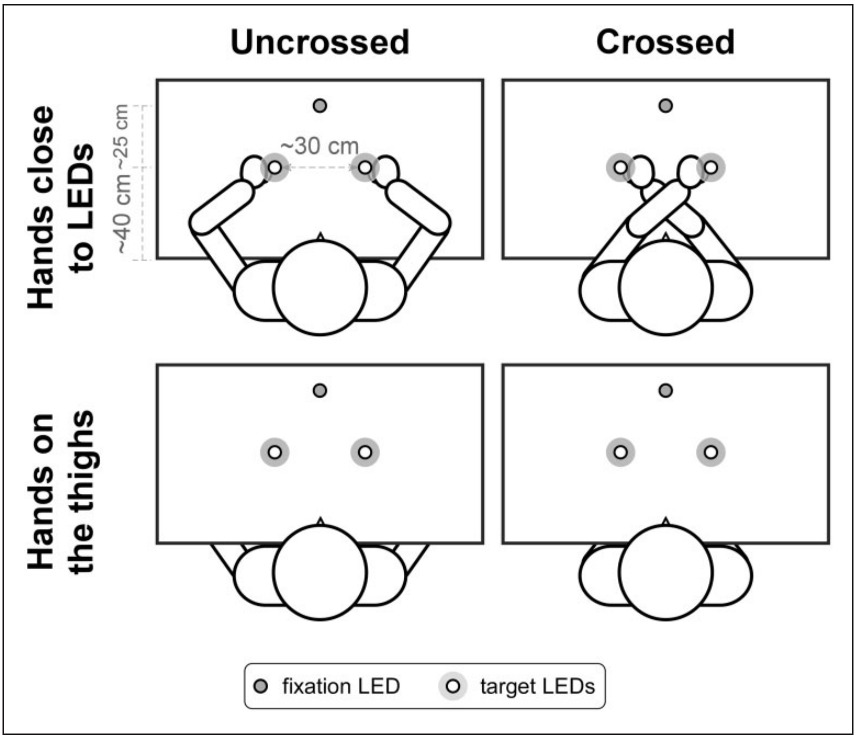

Figure 1. Design of Experiment 1. Participants performed a temporal order judgment task on pairs of visual stimuli presented by means of two white light-emitting diodes (LEDs) placed ~40 cm from the participants' trunk, equidistantly from the yellow fixation LED placed ~65 cm from the participants' trunk. They were asked to place their hands either close to the target LEDs or on their thighs. The task was performed with the hands uncrossed or crossed over their body midline.

crossed posture. In the two other conditions, the hands were placed on the participant's thighs either in an uncrossed or a crossed posture (i.e., in the latter condition the left hand was placed on the right thigh and vice versa; Figure 1). A trial started with the illumination of the fixation point. After 500 ms, the pair of visual stimuli of 5-ms duration each was presented with 20 possible time intervals (i.e., stimulus onset asynchronies [SOAs]) between them: ±200, ±145, ±90, ±75, ±60, ±45, ±30, ±15, ±10, and ±5 ms (negative values indicate that the left LED was illuminated first). Participants were instructed to keep their gaze at the fixation point during the whole trial and to respond verbally which of the two visual stimuli they perceived as occurring first in half of the blocks or which stimulus was perceived as second in the other half (by answering "left" or "right"). The participant's response was encoded by the experimenter. No specific instruction was given regarding response speed. As soon as the response was encoded, illumination of the fixation point was switched off and the next trial started 2,000 ms later. No feedback regarding the accuracy of participants' responses was given. The experiment was composed of eight blocks resulting from the combination of the position of the hands (close to the LEDs vs. on the thighs), their posture (uncrossed vs. crossed), and the response modality ("which is first" vs. "which is second"). The order of the blocks was pseudorandomized, excepting for the position of the hands: Half of the participants started the experiment with the hands on the table, the other half started with the hands on the thighs. Each block consisted of 40 trials and the presented

SOAs (of the 20 possible SOAs) were determined online for each trial according to the adaptive PSI procedure (Kontsevich & Tyler, 1999), that is, based on participants' performance on all previous trials (implemented through the Palamedes Toolbox, www.palamedestoolbox.org; see Filbrich, Alamia, Burns, et al., 2017 for details).

Measures. Data were fitted with a logistic function, that is, $f(x) = 1/(1 + \exp(-\beta(x - \alpha)))$, which was estimated using the adaptive PSI method (Kontsevich & Tyler, 1999), as in previous experiments (see Filbrich, Alamia, Burns, et al., 2017). The α and the β of the logistic function were used to derive the PSS and the slope, respectively. The PSS is defined as the amount of time one stimulus has to precede or follow the other in order for the two stimuli to be perceived as occurring simultaneously (Spence, Shore, & Klein, 2001). This measure corresponds indeed to the SOA at which the two visual stimuli are perceived as occurring first equally often (i.e., the 0.5 criterion on the ordinate) and is used to characterize perceptual biases to the advantage of one of the two stimuli of the pairs (De Paepe et al., 2015; Filbrich, Alamia, Burns, et al., 2017; Spence & Parise, 2010). The slope, generally used to derive the just noticeable difference in classic TOJ studies (Heed & Azañón, 2014), describes the noisiness of the participant's performance, that is, the precision or the variability of the participant's responses during the experiment (Kingdom & Prins, 2010). The mode of the absolute SOA values actually used during the adaptation within each condition was also measured. This third variable indexes the discrimination capacity of the participants, since the smaller the mode, the shorter the SOAs needed to correctly discriminate the temporal order. Although the PSS was not of primary importance with regard to the present hypotheses, these values were still analyzed in order to control for any potential perceptual biases induced during the experiment (Filbrich, Alamia, Burns, et al., 2017; Filbrich, Torta, Vanderclausen, Azañón, & Legrain, 2016) that could influence the measures of interest, that is, the slope and the mode.

Analyses. PSS values of each condition were compared to 0 by means of one-sample *t* tests. Differences between conditions were tested for PSS, slope, and mode values each, using an analysis of variance (ANOVA) with hand position (close to LEDs vs. on the thighs) and hand posture (uncrossed vs. crossed) as within-participant factors (as response modality was used to control for potential response and decisional bias, see Filbrich et al., 2016), data from this variable were merged). Data are expressed in terms of perceiving the left-sided stimuli as first presented. Significance level was set at $p \leq .05$. In addition, Bayesian repeated measures ANOVA (JASP [Version 0.8.1.1], JASP Team, 2017) were performed to quantify the evidence for the alternative hypothesis (i.e., difference in slope and mode measures of visual TOJ between the two hand postures) as compared to the null hypothesis (no difference between the hand postures). Since we had no a priori knowledge as to the effect size we could expect, the default priors implemented in JASP were used. Our interpretations of the obtained evidence for the alternative hypothesis as compared to the null hypothesis (Bayes factor, BF_{10}) were based on the classification scheme proposed by Lee and Wagenmakers (2013; see also Wagenmakers et al., in press), which considers a BF_{10} of 3 to 10 as moderate evidence for the alternative hypothesis and a BF_{10} of .10 to .33 as moderate evidence for the null hypothesis.

Results

Results are illustrated in Figure 2. None of the *t* tests revealed any significant difference in the PSS values from 0 (all $t \leq 1.35$, all $p \geq .19$), suggesting an absence of lateralized bias in all

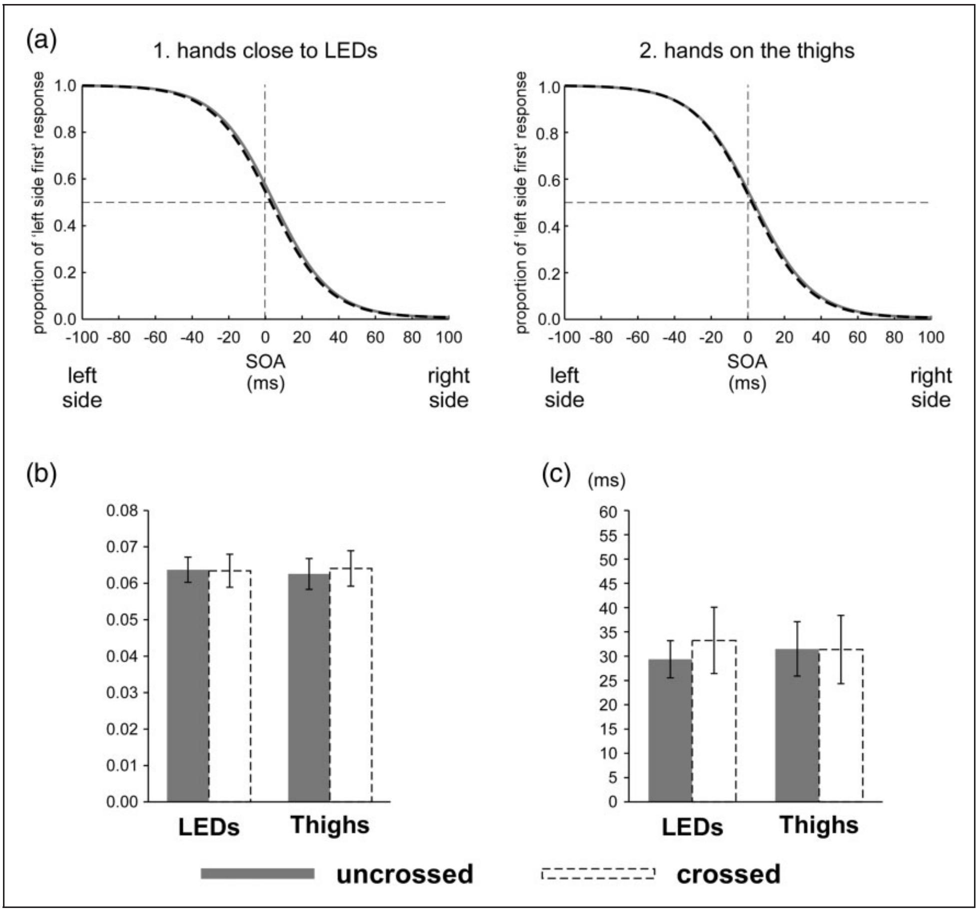

Figure 2. Results of Experiment 1. Data were averaged across all participants according to the position of the hands (close to the LEDs vs. on the thighs) and their posture (uncrossed, solid gray lines vs. crossed, dotted black lines). (a) Fitted logistic function of the participants' responses. The *x*-axis represents different hypothetical stimulus onset asynchronies (SOAs) between the two visual stimuli: Negative values indicate that the visual stimulus occurring in the left side of space was presented first, while positive values indicate that the visual stimulus occurring in the right side of space was presented first. The *y*-axis represents the proportion of trials in which the participants perceived the visual stimulus presented in the left side of space as occurring first. (b) Values of the slope of the fitted functions. (c) Values of the mode of the SOAs presented during the adaptive procedure. Error bars represent the 95% confidence intervals adapted according to Cousineau (2005). LED = light-emitting diode.

conditions. The ANOVA did not show any significant effect of the hand posture, for the PSS, $F(1, 19) = 0.06$, $p = .811$, $\eta^2_p = .003$; for the slope, $F(1, 19) = 0.06$, $p = .814$, $\eta^2_p = .003$; and for the mode of the SOAs, $F(1, 19) = 0.41$, $p = .531$, $\eta^2_p = .021$. No significant results were also observed for the effect of the hand position, PSS: $F(1, 19) = 0.52$, $p = .482$, $\eta^2_p = .026$; slope: $F(1, 19) = 0.01$, $p = .915$, $\eta^2_p = .001$; and mode: $F(1, 19) < 0.01$, $p = .970$, $\eta^2_p < .001$, and the interaction between the two factors, PSS: $F(1, 19) = 0.40$, $p = .538$, $\eta^2_p = .020$; slope: $F(1, 19) = 0.20$, $p = .662$, $\eta^2_p = .010$; and mode: $F(1, 19) = 0.31$, $p = .587$, $\eta^2_p = .016$. The Bayesian analyses of the slope and mode values supported these results showing moderate evidence supporting the null hypothesis, for the main effect of posture (slope: $BF_{10} = .231$, error = 1.006%; mode: $BF_{10} = .265$, error = 1.152%), for the effect of hand position (slope: $BF_{10} = .233$, error = 1.172%; mode: $BF_{10} = .226$, error = 0.964%), and for the interaction between the two factors, with a minor exception for the mode (slope: $BF_{10} = .298$, error = 0.777%; mode: $BF_{10} = .371$, error = 1.969%).

Experiment 2

Methods

Participants. Twenty participants took part in Experiment 2 (14 women, 21.6 years of mean age [±1.59 *SD*] ranging from 19 to 25, all but 4 right handed according to the Flinders Handedness survey, Nicholls et al., 2013). The recruitment procedure and inclusion/exclusion criteria were the same as for Experiment 1. In addition, the use of pain killers such as paracetamol and nonsteroidal anti-inflammatory drugs was not allowed within the 12 hr before the experiment.

Stimuli and materials. Visual stimuli and the experimental setting were exactly the same as for Experiment 1, excepting that participants held a vibrotactile transducer (TL-002-14 R Haptuator, Tactile Labs, Canada) between the thumb and forefinger of each hand. Vibrotactile stimuli were driven through standard audio amplifiers, and their duration was 10 ms at 440 Hz. If necessary, the intensity was adapted individually in order to be matched between the two hands. The procedure was also similar to Experiment 1, excepting that only hand posture (uncrossed vs. crossed) was manipulated, and not the position of the hands. The hands were placed on the table, so that each LED was seen between the thumb and forefinger (see Figure 3). A trial started with the illumination of the fixation point. After 500 ms, the tactile stimuli were applied on both hands simultaneously. The pairs of visual stimuli (using the same possible SOAs as in Experiment 1) followed the tactile stimuli after one of two interstimulus time intervals (ISI): 60 ms vs. 360 ms between the tactile stimuli and the first visual stimulus of the target pair.

Measures and analyses. Measures and analyses were the same as for Experiment 1, excepting that ANOVAs were performed using hand posture (uncrossed vs. crossed) and ISI (60 ms vs. 360 ms) as within-participant factors.

Results

Results are illustrated in Figure 4. None of the *t* tests revealed any significant difference in the PSS values from 0 (all $t \leq 1.47$, all $p \geq 0.16$), suggesting an absence of lateralized bias in all conditions. The ANOVA did not show any significant effect of the hand posture, for the PSS, $F(1, 19) = 2.05$, $p = .168$, $\eta^2_p = .097$; for the slope, $F(1, 19) = 0.12$, $p = .732$, $\eta^2_p = .006$; and for the mode of the SOAs, $F(1, 19) = 0.13$, $p = .726$, $\eta^2_p = .007$. No significant results were also observed for the effect of the ISI, PSS: $F(1, 19) = 0.15$, $p = .702$, $\eta^2_p = .008$; slope: $F(1, 19) = 2.36$, $p = .141$, $\eta^2_p = .111$; and mode: $F(1, 19) = 2.83$, $p = .109$, $\eta^2_p = .130$, and the interaction between the two factors, PSS: $F(1, 19) = 0.42$, $p = .527$, $\eta^2_p = .021$; slope: $F(1, 19) = 0.26$, $p = .616$, $\eta^2_p = .013$; and mode: $F(1, 19) < 0.01$, $p = .944$, $\eta^2_p < .001$. The Bayesian analysis of the slope and mode values revealed moderate evidence supporting the null hypothesis, for the main effect of hand posture (slope: $BF_{10} = .247$, error = 1.545%; mode: $BF_{10} = .247$, error = 3.131%) and for the interaction with ISI (slope: $BF_{10} = .360$, error = 3.168%; mode: $BF_{10} = .292$, error = 0.784%), with a minor exception for the slope value of the interaction. Results are inconclusive for the main effect of ISI (slope: $BF_{10} = .498$, error = 1.074%; mode: $BF_{10} = .622$, error = 6.006%), neither clearly

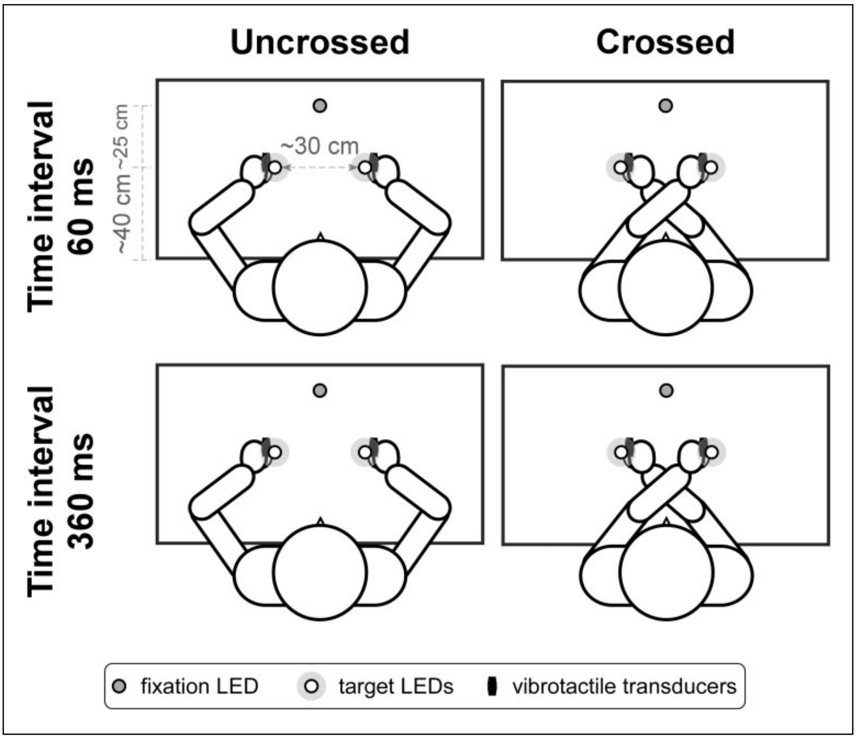

Figure 3. Design of Experiment 2. The setup was similar to Experiment 1, excepting that participants' hands were always placed close to the target LEDs and that they hold two vibrotactile transducers between the thumb and the index finger of each hand. Tactile stimuli were delivered through the transducers either 60 ms or 360 ms before the first visual stimuli of each pair. The task was performed with the hands uncrossed or crossed. LED = light-emitting diode.

supporting the null nor the alternative hypothesis but testing the sole main effect of this factor was beyond the scope of the present study.

Discussion

The present studies were aimed at testing the influence of the body on perceiving extrabody, that is, visual, stimuli. To this aim, we used a TOJ task performed on visual stimuli, one presented near each hand. Two postures were used: the hands were either placed in an uncrossed posture or were crossed over the body midline. This latter condition is regularly used to generate a conflict between the anatomical and the spatial representations of the body (Jacobs et al., 2011; Smania & Aglioti, 1995) as witnessed by changes in the slope of the TOJ psychometric functions in the absence of perceptual bias (Crollen et al., 2017; Crollen, Lazzouni, et al., 2017; De Paepe et al., 2015; Heed & Azañón, 2014; Röder et al., 2004; Sambo et al., 2013; Shore et al., 2002; Yamamoto & Kitazawa, 2001). In Experiment 1, we tested the effect of body posture on visual TOJ without applying any somatosensory stimuli. No significant impact of body posture on visual TOJ performance was revealed, no matter the proximity between the body and the visual stimuli. This was witnessed by both slope and mode values. This latter index was used to evaluate how SOAs were adapted individually during the task. There was an absence of

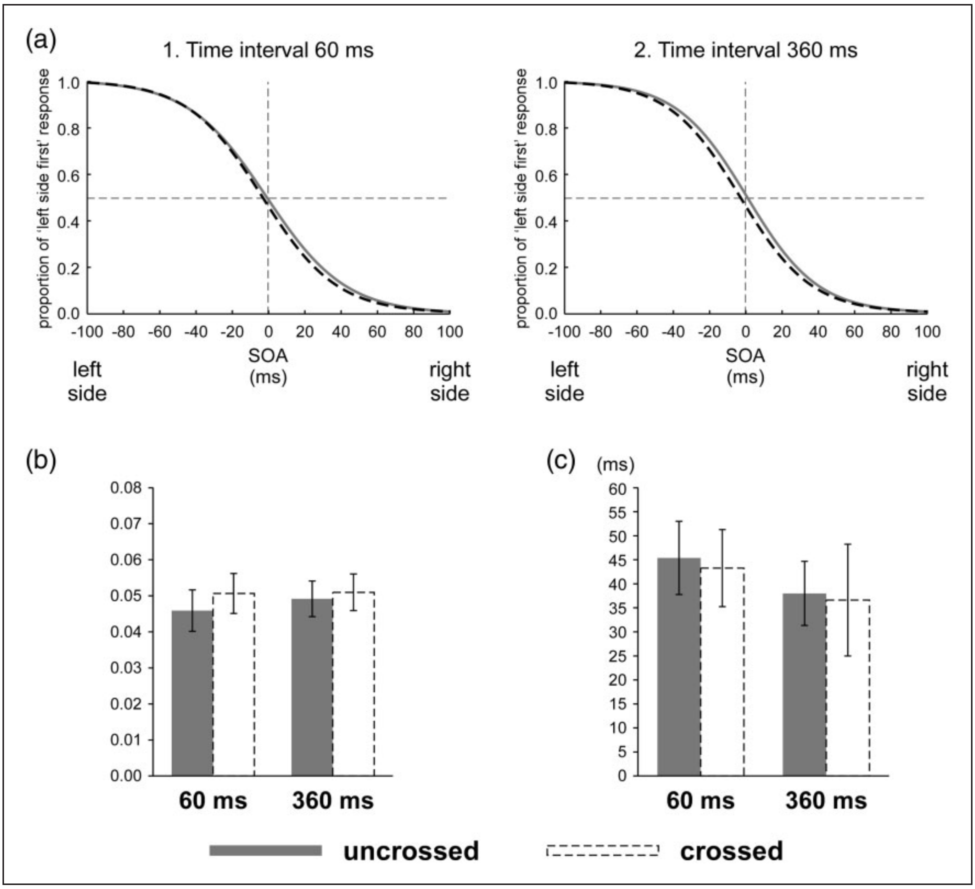

Figure 4. Results of Experiment 2. Data were averaged across all participants according to the time intervals between the tactile stimuli and the first visual stimulus of the pair (60 ms vs. 360 ms) and the hand posture (uncrossed, solid gray lines vs. crossed, dotted black lines). (a) Fitted logistic function of the participants' responses. The *x*-axis represents different hypothetical stimulus onset asynchronies (SOAs) between the two visual stimuli: Negative values indicate that the visual stimulus occurring in the left side of space was presented first, while positive values indicate that the visual stimulus occurring in the right side of space was presented first. The *y*-axis represents the proportion of trials in which the participants perceived the visual stimulus presented in the left side of space as occurring first. (b) Values of the slope of the fitted functions. (c) Values of the mode of the SOAs presented during the adaptive procedure. Error bars represent the 95% confidence intervals adapted according to Cousineau (2005). SOA = stimulus onset asynchronies.

significant difference across conditions, suggesting that the discrimination capacity (i.e., the necessary time interval to correctly discriminate temporal order) of the participants is similar between the two hand postures. In Experiment 2, somatic, that is, tactile, stimuli preceded the visual stimuli according to two time delays, 60 ms versus 360 ms. These two delays were chosen in order to activate somatotopic versus spatiotopic representations of the body, respectively. Indeed, based on the data of Azañón and Soto-Faraco (2008a), we hypothesized that, for the crossed-hand posture, when presented shortly (i.e., 60 ms) after the application of the tactile stimuli, visual stimuli, activating a space-based reference, would occur during the activation of a somatotopic reference frame (which would *boost* a certain body awareness and perception), thus creating a conflict. On the contrary, at the later delay (i.e., 360 ms), the visual stimuli would occur after the somatosensory remapping to a space-based reference for tactile stimuli. Conversely to our hypothesis, no effect of changes in hand posture on visual TOJ parameters was observed, even in the condition with a short time delay. Indeed, because somatosensory inputs are thought to be automatically remapped according to a spatiotopic frame of reference, at a long delay, the positions of the stimulated limbs should be correctly aligned with those of the visual stimuli, and, accordingly, are not expected to affect visual TOJs. Conversely, at a shorter delay when the remapping process can be considered as still ongoing, the anatomical representation of the tactile stimuli mismatches the spatial representation of the visual stimuli when the hands are crossed: The left hand is near the right visual stimulus and vice versa. Despite such a misalignment, no significant effect of hand crossing was observed on visual TOJ with the short time delay. Two possible explanations could be considered with regard to this finding. First, it could be that spatial remapping of somatosensory stimuli is completed at an earlier latency than the one estimated by Azañón and Soto-Faraco (Azañón et al., 2010; Azañón & Soto-Faraco, 2008a, 2008b). These authors hypothesized that somatosensory remapping occurs when neural inputs are sent from the primary (SI) to the secondary (SII) somatosensory area and other associative areas such as the parietal cortex. Accordingly, the same authors also showed that crossing the hands can affect the magnitude of the somatosensory scalp–recorded event-related potentials (ERPs) at a latency not earlier than 70 ms (Soto-Faraco & Azañón, 2013). However, electrophysiological studies that used intracortical recording in humans revealed responses to medial nerve stimulation recorded in SII before 60 ms, sometimes at a latency as early as 30 ms (Barba, Frot, & Mauguière, 2002; Frot & Mauguière, 1999). It would thus be interesting to replicate the study of Azañón and Soto-Faraco (2008a) by combining both reaction time and ERP measures in the same design to finely track the time course of the neurophysiological mechanisms underlying somatosensory remapping. To our knowledge, only one study has used ERPs with a similar design (Kennet, Eimer, Spence, & Driver, 2001), but the shortest time interval between the tactile and the visual stimuli used in that study was 160 ms. The second interpretation could be that, while an external spatial representation is able to come into conflict with an anatomical representation of the body, the reverse is not necessarily true. It has been widely demonstrated that the way we perceive somatic stimuli applied the body is shaped by our sensory experience with external stimuli, especially visual stimuli (Crollen & Collignon, 2012). Accordingly, decreased performance during TOJ on somatosensory stimuli as reflected by the effects on the slope is interpreted as the fact that participants do not only rely on identifying which limb is actually stimulated but also on localizing the stimulated limb in external space. The ability to use both anatomical and spatiotopic frames of reference to code somatic stimuli illustrates the double function of the somatosensory systems. These systems are indeed involved in informing the brain about the state of the body (interoception) and about external objects in contact with the body (exteroception). Change in performance during somatosensory TOJ reflects this ability to locate somatic inputs according to two frames of reference. More particularly, the impact of crossing the hands on the slope of the fitted psychometric function illustrates the confusion between anatomical and spatiotopic reference frames when they are mismatching. Conversely, as the visual system is mainly aimed to provide information about the world around us, the influence of anatomical representations on visual perception could be considered as less relevant. Yet it should be noted that this does not imply that somatic sensations would not be able to affect visuospatial perception. As stressed in the Introduction section, the present studies focused on studying the ability to process stimuli in one spatial dimension (e.g., visual space close to the body) when two spatial representations are conflicting (e.g., somatotopic vs. spatiotopic). In TOJ tasks, such a conflict has been indexed by the slope of the psychometric functions. TOJ performance can, however, also be evaluated by means of the PSS, that is, the threshold of the psychometric function, indexing perceptual biases to the advantage of one of the two stimuli. It has indeed been shown that somatosensory stimuli applied on one hand at a time (i.e., unilaterally) can bias the perception of visual stimuli to the advantage of the visual stimulus presented in the side of space congruent with the stimulated body limb (Filbrich, Alamia, Blandiaux, et al., 2017; Filbrich, Alamia, Burns, et al., 2017; Filbrich et al., 2018; Vanderclausen, Filbrich, Alamia, & Legrain, 2017). These findings corroborate those obtained by Azañón and Soto-Faraco (; Azañón et al., 2010; Azañón & Soto-Faraco, 2008a, 2008b) and Kennett et al. (2001) with unilateral cross-modal cueing tasks. Therefore, it seems that, while somatosensory stimuli can bias the perception of visual stimuli to the advantage of the ipsilateral ones, they do not necessarily affect the spatial frame of reference used to process visual stimuli.

This latter interpretation could be considered in the context of studying individuals who are particularly concerned about somatic information, such as chronic pain patients who are thought to give attentional priority to somatosensory stimuli (Van Damme, Legrain, Vogt, & Crombez, 2010). It could be hypothesized that chronic pain patients could have difficulties to inhibit an involvement of somatotopic reference frames when judging the temporal order of extrasomatic stimuli. Using TOJ tasks, two very recent studies investigated visuospatial abilities of patients suffering from complex regional pain syndrome (CRPS; Bultitude et al., 2017; Filbrich, Alamia, Verfaille, et al., 2017). CRPS is a chronic pain syndrome associating pain, vegetative, trophic, and motor symptoms in one limb. Filbrich, Alamia, Verfaille, et al. (2017) and Bultitude et al. (2017) demonstrated that CRPS patients are also characterized by cognitive deficits affecting the perception of visual stimuli occurring in the side of space corresponding to the pathological side of the patients' body, as reflected by the perceptual biases revealed by PSS measures. In addition, Bultitude et al. (2017) showed that crossing the hands and placing them close to the target visual stimuli impacted the slope measure of visual judgments. Surprisingly, this was shown at the level of the group of participants that also included healthy volunteers. Nevertheless, the sensitivity of the TOJ-related slope measures to changes in body posture seems to index the ability to resolve conflicts between different concurrent spatial frames of reference to map somatic and possibly also extrasomatic sensory stimuli. This ability might be shaped by sensory experience, especially in clinical stiuations affecting particular sensory modalities. Regarding the impact of the body and somatosensory stimulation on visual TOJs and visual perception, in general, future studies should thus take into account or manipulate the relative relevance of somatic information for the participants (see, for instance, Van Damme et al., 2010).

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References

Azañón, E., Camacho, K., & Soto-Faraco, S. (2010). Tactile remapping beyond space. *European Journal of Neuroscience*, *31*, 1858–1867.

Azañón, E., & Soto-Faraco, S. (2008a). Changing reference frames during the encoding of tactile events. *Current Biololgy*, *18*, 1044–1049.

Azañón, E., & Soto-Faraco, S. (2008b). Spatial remapping of tactile events. *Communicative and Integrative Biology*, *1*, 45–46.

Barba, C., Frot, M., & Mauguière, F. (2002). Early secondary somatosensory area (SII) SEPs. Data from intracerebral recording in humans. *Clinical Neurophysiology*, *113*, 1778–1786.

Brozzoli, C., Ehrsson, H. H., & Farnè, A. (2014). Multisensory representation of the space near the had: From perception to action and interindividual interactions. *The Neuroscientist*, *20*, 122–135.

Bultitude, J., Walker, I., & Spence, C. (2017). Space-based bias of covert visual attention in complex regional pain syndrome. *Brain*, *9*, 2306–2321.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simple solution to Loftus ans Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*, 45–45.

Crollen, V., Albouy, G., Lepore, F., & Collignon, O. (2017). How visual experience impacts the internal and external spatial mapping of sensorimotor functions. *Scientific Reports*, *7*, 1022.

Crollen, V., & Collignon, O. (2012). Embodied space in early blind individuals. *Frontiers in Psychology*, *3*, 272.

Crollen, V., Lazzouni, L., Rezk, M., Bellemare, A., Lepore, F., & Collignon, O. (2017). Visual experience shapes the neural networks remapping touch into external space. *The Journal of Neuroscience*, *37*, 10097–10103.

De Paepe, A. L., Crombez, G., & Legrain, V. (2015). From a somatotopic to a spatiotopic frame of reference for the localization of nociceptive stimuli. *PLoS One*, *10*, e0137120.

Filbrich, L., Alamia, A., Blandiaux, S., Burns, S., & Legrain, V. (2017). Shaping visual space perception through bodilty sensations: Testing the impact of nociceptive stimuli on visual perception in peripersonal space with temporal order judgments. *PLoS One*, *12*, e0182634.

Filbrich, L., Alamia, A., Burns, S., & Legrain, V. (2017). Orienting attention in visual space by nociceptive stimuli: Investigation with a temporal order judgment task based on the adaptive PSI method. *Experimental Brain Research*, *235*, 2069–2079.

Filbrich, L., Alamia, A., Verfaille, C., Berquin, A., Barbier, O., Libouton, X., ... Legrain, V. (2017). Biased visuospatial perception complex regional pain syndrome. *Scientific Reports*, *7*, 9712.

Filbrich, L., Halicka, M., Alamia, A., & Legrain, V. (2018). Investigating the spatial characteristics of the crossmodal interaction between nociception and vision using gaze direction. *Consciousness and Cognition*, *57*, 106–115.

Filbrich, L., Torta, D. M., Vanderclausen, C., Azañón, E., & Legrain, V. (2016). Using temporal order judgments to investigate attention bias toward pain and threat-related information. Methodological and theoretical issues. *Consciousness and Cognition*, *41*, 135–138.

Frot, M., & Mauguière, F. (1999). Timing and spatial distribution of somatosensory responses recorded in the upper bank of the sylvian fissure (SII area) in humans. *Cerebral Cortex*, *9*, 854–863.

Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personnal space, and defensive behavior. *Neuropsychologia*, *44*, 845–859.

Heed, T., & Azañón, E. (2014). Using time to investigate space: A review of tactile temporal order judgments as a window onto spatial processing in touch. *Frontiers in Psychology*, *5*, 76.

Holmes, N. P., & Spence, C. (2004). The body schema and multisensory representation(s) of peripersonal space. *Cognitive Processing*, *5*, 94–105.

Jacobs, S., Brozzoli, C., Hadj-Bouziane, F., Meunier, M., & Farnè, A. (2011). Studying multisensory processing and its role in the representation of space though pathological and physiological crossmodal extinction. *Frontiers in Psychology*, *2*, 89.

JASP (Version 0.8.1.1) [Computer software]. Amsterdam: JASP Team 2017.

Kennett, S., Eimer, M., Spence, C., & Driver, J. (2001). Tactile-visual links in exogenous spatial attention under different postures: Convergent evidence from psychophysics and ERPs. *Journal of Cognitive Neuroscience*, *13*, 462–478.

Kingdom, F. A. A., & Prins, N. (2010). *Psychophysics—A practical introduction*. London, England: Elsevier Academic Press.

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research*, *39*, 2729–2737.

Lee, M. D., & Wagenmakers, E. J. (2013). *Bayesian cognitive modeling: A practical course*. Cambridge, England: Cambridge University Press.

Makin, T. R., Wilf, M., Schwartz, I., & Zohary, E. (2010). Amputees ''neglect'' the space near their missing hand. *Psychological Science*, *21*, 55–57.

McDonald, J. J., Teder-Sälejärvi, W. A., Di Russo, F., & Hillyard, S. A. (2005). Neural basis of auditory-induced shift of visual time-order perception. *Nature Neuroscience*, *8*, 1197–1202.

Nicholls, M. E., Thomas, N. A., Loetscher, T., & Grimshaw, G. M. (2013). The Flinders Handedness survey (FLANDERS): A brief measure of skilled hand preference. *Cortex*, *49*, 2914–2926.

Pagel, B., Heed, T., & Röder, B. (2009). Change of reference frame for tactile localization during child development. *Developmental Science*, *12*, 929–937.

Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Current Biology*, *14*, 121–124.

Sambo, C. F., Torta, D. M., Galace, A., Liang, M., Moseley, G. L., & Iannetti, G. D. (2013). The temporal order judgment of tactile and nociceptive stimuli is impaired by crossing the hands over body midline. *Pain*, *154*, 242–247.

Shore, D. I., Spry, E., & Spence, C. (2002). Confusing the mind by crossing the hands. *Cognitive Brain Research*, *14*, 153–163.

Smania, N., & Aglioti, S. (1995). Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology*, *45*, 1725–1730.

Soto-Faraco, S., & Azañón, E. (2013). Electrophysiological correlates of tactile remapping. *Neuropyschologia*, *51*, 1584–1594.

Spence, C., & Parise, C. (2010). Prior-entry: A review. *Consciousness and Cognition*, *19*, 364–379.

Spence, C., Shore, D. I., & Klein, R. M. (2001). Multisensory prior entry. *Journal of Experimental Psychololgy: General*, *130*, 799–832.

Vallar, M. S. A., & Maravita, A. (2009). Personal and extrapersonal spatial percpetion. In G. G. Bernston, & J. T. Cacioppo (Eds.), *Handbook of neuroscience for the behavioral sciences* (pp. 322–336). Hoboken, NJ: Wiley.

Van Damme, S., Legrain, V., Vogt, J., & Crombez, G. (2010). Keeping pain in mind: A motivational account of attention to pain. *Neuroscience and Biobehavioral Reviews*, *34*, 204–213.

Vanderclausen, C., Filbrich, L., Alamia, A., & Legrain, V. (2017). Investigating peri-limb interaction between nociception and vision using spatial depth. *Neuroscience Letters*, *654*, 111–116.

Wada, M., Yamamoto, S., & Kitazawa, S. (2004). Effects of handedness on tactile temporal order judgement. *Neuropsychologia*, *42*, 1887–1895.

Wagenmakers E. J., Love, J, Marsman, M., Jamil, T., Ly, A., Verhagen, J., . . . Morey, R. D. (in press). Bayesian inference for psychology. Part II: Example applications with JASP. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-017-1323-7

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, *4*, 759–765.