

**Measuring the sensitivity of tactile temporal order judgments in sighted
and blind participants using the adaptive *psi* method**

Camille Vanderclausen ^{1,2}^{\$}, Lieve Filbrich ^{1,2}, Anne De Volder ^{1,2} & Valéry Legrain ^{1,2,3}

¹Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium

²Psychological Sciences Research Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium

³Louvain Bionics, Université catholique de Louvain, Louvain-la-Neuve, Belgium

^{\$} Corresponding author: Camille Vanderclausen, Institute of Neuroscience, Université catholique de Louvain, Avenue Mounier 53, boîte COSY B1.53.04, 1200 Brussels, Belgium.

E-mail: camille.vanderclausen@uclouvain.be

Keywords: Temporal order judgment, adaptive *psi* method, spatial representation, early blindness, touch.

20 **Abstract**

21 Spatial locations of somatosensory stimuli are coded according to somatotopic (anatomical
22 distribution of the sensory receptors on the skin surface) and spatiotopic (position of the body
23 parts in external space) reference frames. This was mostly evidenced by means of temporal
24 order judgment (TOJ) tasks in which participants discriminate the temporal order of two tactile
25 stimuli, one applied on each hand. Because crossing the hands generates a conflict between
26 anatomical and spatial responses, TOJ performance is decreased in such posture, except for
27 congenitally blind people, suggesting a role of visual experience in somatosensory perception.
28 In previous TOJ studies, stimuli were generally presented using the method of constant stimuli,
29 i.e. the repetition of a predefined sample of stimulus-onset asynchronies (SOA) separating the
30 two stimuli. This method has the disadvantage that a large number of trials is needed to obtain
31 reliable data when aiming at dissociating performances of groups characterized by different
32 cognitive abilities. Indeed, each SOA among a large variety of different SOAs should be
33 presented the same number of times irrespective of the participant's performance. This
34 study aimed to replicate previous tactile TOJ data in sighted and blind participants with the
35 adaptive *psi* method in order to validate a novel method that adapts the presented SOA
36 according to the participant's performance. This allows to precisely estimate
37 the temporal sensitivity of each participant while the presented stimuli are adapted to the
38 participant's individual discrimination threshold. We successfully replicated previous findings
39 in both sighted and blind participants, corroborating previous data using a more suitable
40 psychophysical tool.

41

1. Introduction

Localizing somatosensory stimuli on the body is an important process as it allows to adapt our behavior and interact with the objects that are in contact with the body. At the same time, our body is constantly moving in space, adopting various postures as a function of the ongoing action. Therefore, to be able to adequately adapt our behavior to a somatosensory stimulus applied on a given part of the body at a specific time, it is also crucial to take into account the current position of this stimulated body part in external space. This would allow, for instance, to derive the location of the object in contact with the body in external space and to efficiently orient a behavioral response towards this object. Accordingly, the ability to locate somatosensory stimuli on the body relies on different coordinate systems. Several studies have indeed demonstrated that somatosensory stimuli are not only mapped according to somatotopic frames of reference, but are also remapped according to spatiotopic frames of reference. Whereas somatotopic frames of reference correspond to anatomical representations that are derived from the ordered projection of the receptor fields to spatially segregated groups of neurons in the primary somatosensory cortex (Penfield & Boldrey, 1937), spatiotopic reference frames take the position of the stimulated limb in external space into account (Azañón & Soto-Faraco, 2008; Driver & Spence, 1998; Graziano, Hu, & Gross, 1997; Shore, Spry, & Spence, 2002; Smania & Aglioti, 1995; Yamamoto & Kitazawa, 2001).

This spatiotopic remapping of somatosensory inputs has been evidenced for both innocuous tactile and nociceptive stimuli, among other tasks, by means of temporal order judgement (TOJ) tasks (e.g. Crollen, Albouy, Lepore, & Collignon, 2017; De Paepe, Crombez, & Legrain, 2015; Heed & Azañón, 2014; Heed, Backhaus, & Röder, 2012; Kobor, Furedi, Kovacs, Spence, & Vidnyanszky, 2006; Pagel, Heed, & Röder, 2009; Röder, Rösler, & Spence, 2004; Sambo et al., 2013; Shore et al., 2002; Vanderclausen, Bourgois, De Volder, & Legrain, 2020;

66 Vanderclausen, Manfron, De Volder, & Legrain, 2020; Yamamoto & Kitazawa, 2001). In a
 67 typical TOJ task, participants are presented with two successive stimuli, applied on two body
 68 parts, separated by various time intervals between their respective stimulation onsets (i.e. SOA
 69 for stimulus onset asynchrony). Most often, two somatosensory stimuli are applied, one on each
 70 hand, and the participants report which of the two stimuli **they** perceived as having been
 71 presented first, i.e. **they judge** their order of appearance (e.g. Sambo et al., 2013; Shore et al.,
 72 2002; Yamamoto & Kitazawa, 2001). Crucially, in order to dissociate the somatotopic and
 73 spatiotopic frames of reference, the task is usually performed while the participants adopt
 74 different body postures, i.e. with the arms either placed in an uncrossed, canonical, posture or
 75 crossed over the body midline. The crossed posture is intended to create a mismatch between
 76 the somatotopic and spatiotopic representations, given that the left hand is placed in the right
 77 side of space and vice versa. **Therefore, it enables to dissociate between both types of**
 78 **representations. Indeed, a change in TOJ performance in the crossed as compared to the**
 79 **uncrossed posture** is indicative of the activation of spatiotopic representations, **since this**
 80 **indicates that the position of the stimulated hands in external space is taken into account during**
 81 **TOJ tasks** (Heed & Azañón, 2014). One parameter **that is often used to reflect** the participants'
 82 performance during TOJ tasks is the just-noticeable difference (JND), which characterizes the
 83 minimal amount of time needed for a participant to discriminate the temporal order between
 84 the two stimuli at a specified level of performance, e.g. **to obtain** a certain percentage of correct
 85 responses (Spence & Parise, 2010). JND values are derived from the slope of the psychometric
 86 function used to fit **the participants' judgments** (see Heed & Azañón, 2014 for a review). In
 87 other studies, participants' performance **is** simply measured by **reporting the proportion of**
 88 **errors** (Badde, Roder, & Heed, 2019; Cadieux, Barnett-Cowan, & Shore, 2010; Maij, Seegelke,
 89 Medendorp, & Heed, 2020). Previous TOJ studies have repeatedly shown that crossing the
 90 hands decreases **the** participants' performance, suggesting that they need more time to

discriminate the temporal order of the two somatosensory stimuli when they are applied on crossed as compared to uncrossed hands (e.g. Sambo et al., 2013; Shore et al., 2002; Yamamoto & Kitazawa, 2001). This decrease in performance during the crossed hands posture can be evidenced by a flattening of the slope of the psychometric function used to fit the data in this condition. This effect has been explained by a confusion about the stimulus location that would result from the conflict between the misaligned somatotopic and spatiotopic reference frames when the hands are crossed. The presence of such conflict would in turn indicate that spatiotopic coordinates of the stimuli are automatically taken into account, even though they are actually irrelevant for the task, i.e. participants were instructed to report on which hand they perceived the first stimulus of the pair (Heed & Azañón, 2014). It is worth noting that the ability to automatically remap somatosensory stimuli according to spatiotopic representations is hypothesized to be shaped by early visual experience, since crossing the hands does not affect the performance of newborns (Begum Ali, Spence, & Bremner, 2015; Bremner, Holmes, & Spence, 2008; Bremner, Mareschal, Lloyd-Fox, & Spence, 2008) and of adults with congenital visual deprivation (Crollen et al., 2017; Röder et al., 2004; Vanderclausen, Bourgois, et al., 2020).

Importantly, most of these findings have been evidenced with TOJ tasks during which stimuli were presented by means of the method of constant stimuli (Crollen et al., 2017; Kobor et al., 2006; Röder et al., 2004; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Accordingly, a sample of SOAs was selected and randomly presented to the participants a fixed number of times. In other words, all possible SOAs have to be tested extensively in order to estimate the parameters reflecting the participants' performance in the TOJ task. While the method of constant stimuli has the advantage that participants cannot predict what stimulus level (i.e. SOA) will be tested at each trial, its main disadvantage is that a large number of stimulus levels must be tested to correctly estimate the parameters of interest (i.e. each SOA of the sample must

116 be repeated several times in each of the experimental conditions). As a consequence, the number
 117 of trials **can** be considerably high when several conditions are interweaved (i.e. usually around
 118 400 trials in total when only two conditions are tested (Crollen et al. 2017; Crollen, Spruyt,
 119 Mahau, Bottini, & Collignon, 2019; Röder et al., 2004; Shore et al., 2002), but up to 1600 trials
 120 in, for instance, the study of Kobor and collaborators (2006) in which both hand posture and
 121 the hand position were manipulated). This can either lead to extremely long experiment
 122 durations, or, in order to avoid such unreasonably long durations, to limiting the number of
 123 stimulus levels (i.e. SOAs) that can be tested (e.g. Crollen et al., 2017; De Paepe et al., 2015;
 124 Heed et al., 2012; Kobor et al., 2006; Sambo et al., 2013; Yamamoto & Kitazawa, 2001).
 125 Indeed, long experiment duration **can potentially result** in performance **degradation unrelated**
 126 **to the experimental manipulation** (e.g. due to fatigue) or loss of data (see e.g. De Paepe et al.,
 127 2015). Conversely, testing fewer trials in order to preserve a reasonable **experiment** duration
 128 can reduce the quality of the estimation of the psychometric function and its derived parameters
 129 of interest. An additional problem arising from this method is related to the comparison of
 130 conditions that actually require different stimulus levels in order to be performed **correctly**, or
 131 to the comparison of groups of participants that differ in terms of their respective ability to
 132 perform the task. For instance, with the hands uncrossed, healthy participants are usually able
 133 to correctly judge **the temporal order between** two tactile stimuli at very short SOAs (i.e. from
 134 ~30 to ~75 ms ; e.g. Yamamoto & Kitazawa, 2001). However, when crossing the hands, some
 135 participants invert their judgements at longer SOAs (i.e. between ~100 and ~300 ms), while
 136 again correctly judging the temporal order at very long SOAs (i.e. over ~500 ms) (Yamamoto
 137 & Kitazawa, 2001). In other words, a large sample of different SOAs was needed in this study
 138 to cover the participants' performances throughout the two posture conditions. However,
 139 increasing the sample of to-be-tested SOAs in order **to take into account** such task requirements
 140 significantly increases the number of trials, and thereby the experiment duration. Similarly, De

Paepe et al. (2020), who used the method of constant stimuli, reported that chronic pain patients could not correctly perform TOJ tasks with the range of SOAs within which healthy volunteers usually achieve a very satisfactory performance, suggesting that the chosen SOAs were not adapted to the cognitive abilities of both groups of participants. This might in turn lead to floor effects in one of the subgroups, with the risk of masking results of potential interest or uninterpretable data.

One way to circumvent these problems is to present the SOAs by means of an adaptive procedure during which the SOA presented at each trial is selected based on the participant's individual performance on all previous trials. Among the different adaptive methods used for testing temporal discrimination (e.g. Stelmach & Herdman, 1991; Sternberg, Knoll, & Gates, 1971; Zampini, Guest, Shore, & Spence, 2005), somatosensory TOJ tasks have been recently adapted with the *psi* method (Kingdom & Prins, 2010; Kontsevich & Tyler, 1999 ; Vanderclausen, Bourgois, et al., 2020; Vanderclausen, Manfron, et al., 2020). This method relies on a Bayesian framework adopted by the adaptive algorithm. The ultimate goal is to estimate the posterior probability of the parameters of interest without extensively probing all the stimulus levels, i.e. the SOAs. More specifically, the core idea is to minimize the expected entropy of the posterior distribution of the parameters trial by trial, by selecting the most appropriate stimulus level at each trial in a way that the response of the participant provides the most information about the distribution of these parameters. The method offers several advantages. Mainly, it allows adapting the tested stimulus levels to each participant's own performance in each experimental condition. Thus, different populations or experimental conditions between which the performance is known to - or can potentially - differ can be compared while avoiding ceiling or floor effects. In addition, it enables to increase the validity and the reliability of the measures by allowing to test a wide range of different SOAs with a lower number of trials (i.e. without extensively probing all the possible SOAs). This also

minimizes the risk that task-independent factors related to extended experiment duration, such as fatigue or sustained attention difficulties, influence the data. Finally, the *psi* method allows to estimate the two main parameters of interest during the same experimental session, i.e. the slope and the inflection point of the psychometric function fitting the participants' performance, characterizing the judgment sensitivity and the sensory threshold, respectively (Kingdom & Prins, 2010).

The adaptive *psi* method has already been implemented to investigate temporal discrimination of visual (Filbrich, Alamia, Blandiaux, Burns, & Legrain, 2017; Filbrich, Alamia, Burns, & Legrain, 2017; Filbrich, Halicka, Alamia, & Legrain, 2018; Legrain, Manfron, Garcia, & Filbrich, 2018; Manfron, Legrain, & Filbrich, 2020; Vanderclausen, Filbrich, Alamia, & Legrain, 2017), tactile (Filbrich, Alamia, Verfaillie, et al., 2017) and nociceptive stimuli (Vanderclausen, Bourgois, et al., 2020; Vanderclausen, Manfron, et al., 2020), and also between visual and nociceptive stimuli (Manfron, Filbrich, Nijs, Mouraux, & Legrain, 2020). However, for the visual and tactile modalities, the main purpose of these studies was to investigate spatial cognitive biases by means of the point of subjective simultaneity (PSS), characterized by the threshold parameter of the psychometric function. The PSS actually refers to the SOA at which the participants report each of the two stimuli as occurring first equally often (Spence & Parise, 2010). When there is no spatial bias, the magnitude of the PSS should be around 0. In contrast, when the perception of one of the stimuli is prioritized over the other, the PSS corresponds to the amount of time one stimulus has to precede the other in order for both stimuli to be perceived as occurring at the same time. For instance, Filbrich and collaborators, by means of visual TOJ tasks adapted with the *psi* method, succeeded to demonstrate the existence of a privileged interaction between nociceptive and visual stimuli when the visual stimulus occurred in the peripersonal space of the body part on which the nociceptive stimulus was applied (Filbrich, Alamia, Blandiaux, et al., 2017; Filbrich, Alamia,

Burns, et al., 2017; Filbrich et al., 2018; Manfron et al., 2020; Vanderclausen et al., 2017). Regarding the tactile modality, the only study that adapted TOJ tasks with the adaptive *psi* method was conducted in patients suffering from complex regional pain syndrome (CRPS), a chronic pain condition usually affecting one limb, and was mainly aimed at evidencing cognitive spatial biases by means of the PSS (Filbrich et al., 2017). While this study also examined potential differences in performance related to the posture of the hands (i.e. uncrossed vs. crossed) by means of the slope parameter of the psychometric function, the performance of the patients was often too inconsistent (i.e. the estimates did not converge on a stable value) to be able to reliably compare and interpret the slope data between the two hand positions for a same patient.

When addressing the question of the spatiotopic remapping of somatosensory inputs, we are thus specifically interested in estimating the slope parameter of the psychometric function fitting the participants' performance, as it characterizes the participants' sensitivity in the task, i.e. the precision of their performance (Kingdom & Prins, 2010; Kontsevich & Tyler, 1999). Specifically characterizing participants' sensitivity during somatosensory TOJs with the *psi* method has been previously achieved with nociceptive heat stimuli (Vanderclausen, Bourgois, et al., 2020; Vanderclausen, Manfron, et al., 2020). Information about nociceptive vs. innocuous tactile stimuli are transmitted to the brain through distinct pathways (i.e. the extralemniscal vs. the lemniscal pathways, respectively). Moreover, although tactile and nociceptive afferents activate similar brain areas (Legrain, Iannetti, Plaghki & Mouraux, 2011), the spatiotemporal patterns of these cortical activities are not exactly the same for the two somatosensory sub-modalities (e.g. Mouraux et al., 2013; Lenoir, Huang, Vandermeeren, Hatem & Mouraux, 2017; Torta et al., 2013). In addition, spatial representations of somatosensory stimuli are often used to shape motor response to objects in contact with our body (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Given that nociceptive and innocuous tactile stimuli drive different types of

actions (defensive for nociceptive vs. grasping and manipulation for tactile stimuli), it seems therefore important to investigate whether the mechanisms underlying the spatial representations of nociceptive stimuli are similar to those of tactile stimuli. In our previous studies we compared the performances of early blind and normally sighted individuals during TOJs on stimuli that specifically and selectively activate skin nociceptors, by using the adaptive *psi* method. Our results corroborated the findings of previous tactile TOJ studies that used the method of constant stimuli: the performance of normally sighted participants, when judging the temporal order of nociceptive stimuli, was decreased in the crossed as compared to the uncrossed hands posture, whereas the posture of the hands did not affect the performance of early blind participants (at least when they responded according to which hand they felt as first stimulated; see Vanderclausen, Manfron et al., 2020). This suggests that somatosensory information about the skin surface is mapped according to similar mechanisms whatever the pathways through which these somatosensory inputs are conveyed. These results also confirmed that mapping processes of nociceptive stimuli are shaped by early visual experience.

However, the *psi* method has never been adapted for TOJ tasks involving innocuous mechanical tactile stimuli which specifically aim at studying the spatiotopic remapping of touch in early blind and normally sighted participants. The main goal of the present studies was therefore to investigate the impact of body posture on early blind and normally sighted participants' sensitivity in tactile TOJ tasks by means of the adaptive *psi* method. By doing so, the present experiments aimed at filling the literature gap between studies that explored the influence of visual deprivation on tactile spatial remapping using the method of constant stimuli and those that studied this question in the nociceptive modality using the adaptive *psi* method. In other words, the aim of the present studies was to validate the use of the adaptive *psi* method in the context of tactile TOJ tasks involving early blind as well as normally sighted participants. The objective of Experiment 1 was to calibrate the adaptive *psi* method for TOJ tasks in order

241 to validate its use for the investigation of the spatial representations underlying the perception
242 of tactile inputs. To this aim, young healthy participants were asked to perform a tactile TOJ
243 task in which the SOAs were presented according to the *psi* method with their hands either
244 uncrossed or crossed over the body midline. The objective of Experiment 2 was to test whether
245 we could replicate previous findings showing an automatic remapping of tactile inputs into
246 spatiotopic coordinates in sighted but not in early blind participants, while adapting the task to
247 each group's sensitivity with the adaptive *psi* method. To this aim, early blind and matched
248 normally sighted participants were asked to perform the same task as in Experiment 1.

249

2. Methods

2.1. Participants

Eleven healthy volunteers took part in Experiment 1 (4 women, 24.5 years of mean age ($SD=3.7$, range 20-34 years). One of the participants was left-handed according to the Flinders Handedness Survey (Nicholls, Thomas, Loetscher, & Grimshaw, 2013). Participants had normal or corrected-to-normal vision and did not report any prior history of severe psychiatric, neurological or chronic pain disorder, serious traumatic injury of the upper limbs within the 6 months preceding the experiment, regular use of psychotropic drugs and intake of analgesic drugs (e.g. NSAIDs and paracetamol) within the 12 h preceding the experiment.

Eighteen early blind individuals as well as 21 normally sighted participants took part in Experiment 2. Inclusion/exclusion criteria for sighted participants were the same as those of Experiment 1. Four sighted participants were excluded from Experiment 2 because they couldn't achieve task requirements properly (see paragraph 2.5). The remaining 17 sighted participants had a mean age of 35.82 years ($SD=10.85$, range 20-63 years, 5 women), three of them were left-handed. Inclusion/exclusion criteria were the same for blind participants, except for the sight-related criteria. Early blind participants were recruited according to blindness attributed to peripheral deficits with no additional neurological problem (see Table 1 for a detailed description of the blind participants included in the study). The causes of blindness included Leber congenital amaurosis, retinopathy of prematurity, severe corneal dysplasia, hereditary retinal dysplasia, bilateral retinoblastoma, severe retinal dystrophy (congenital pigmentary retinitis with macular perforation), anterior chamber cleavage syndrome (Peters syndrome), persistent hyperplastic primary vitreous involving both eyes, unspecified genetic eye disorder. They were totally blind or had only rudimentary sensitivity to brightness but no

ability for pattern perception. They were all considered as totally blind since birth. One early blind participant was excluded because of a residual vision of 1/50 of diopter in both eyes. The remaining 17 blind participants had a mean age of 36.12 years ($SD=10.71$, range 18-65 years, 5 women). Two participants were left-handed and one ambidextrous. One early blind participant was epileptic (participant EB7) and was on medication for that reason (Levetiracetam: 1750 mg and Oxcarbazepine: 1500 mg daily). The epileptic focus was located in the left temporo-occipital border of the cortical brain. Nevertheless, this participant was not excluded from the study as there was no evidence of cognitive impairment or somatosensory perception deficit. Another participant (EB1), became completely blind at 3 months of life because of a genetic disease, but was still considered as early blind since his visual acuity was very poor in the first months of life. Most of the early blind participants (14 out of 17 participants) reported playing or having played at least one musical instrument for several years, such as the piano, the guitar, drums, organ, flute, harmonica or accordion. The participants of the sighted group were matched to the blind participants in terms of age, gender and level of education.

Written informed consents were obtained from all participants and all experimental procedures were approved by the local ethics committee and conformed to the Declaration of Helsinki. All participants received financial compensation for their participation.

Participant	Gender - Age	Handedness	Profession / Educational level	Visual Perception	Onset of blindness	Braille	Cane	Other
EB1	M 65	R	College degree	None	<18 months	Yes	Yes	/
EB2	M 49	R	College degree	None	Birth	Yes	Yes	/
EB3	M 31	L	Some college	None	Birth	Yes	Yes	Slight auditory loss
EB4	F 43	L	College degree	None	Birth	Yes	Yes	/
EB5	M 39	R	College degree	None	Birth	Yes	Yes	Torball
EB6	M 39	R	Teacher/ College degree	None	Birth	Yes	Yes+ Dog	Hearing aids
EB7	F 39	R	Interpreter/ College degree	None	Birth	Yes	Yes	/
EB8	M 31	R	Some college without degree	None	Birth	Yes	Yes	/
EB9	F 38	R	Official High School	None	Birth	Yes	Yes	/
EB10	M 36	R	College degree	None	Birth	Yes	Yes+ Dog	/
EB11	F 35	R	Phone sale/ Official High School	None	Birth	Few	Yes+ Dog	/
EB12	M 29	R	College degree	None	Birth	Yes	Yes	Various sport activities
EB13	M 22	R	Some college	None	Birth	Yes	Yes	/
EB14	M 25	A	Official high school	None	Birth	Yes	Yes	ADHD syndrome

EB15	F 38	R	College degree	None	Birth	Yes	Yes	/
EB16	M 37	R	Specialized school until 6 th grade	None	Birth	Yes	Yes	/
EB17	M 18	R	High school (inferior degree)	None	Birth	Few	Yes	/

Table 1. Description of the early blind participants of Experiment 2

***Note:** EB: early blind; Age in years; F= female; M= male; R= right; L= left. As subject EB1 had very poor vision from birth and underwent a bilateral eye enucleation by the age of 18 months, he was considered early blind. Torball is an indoor sport for blind individuals.*

2.2. Stimuli and apparatus

Vibrotactile stimuli were generated by means of two vibrotactile transducers driven by standard audio amplifiers (TL-002-14R Haptuator Redesign, Tactile Labs, Inc., Montreal, Canada). The duration of the vibration was 10 ms and the stimulation was delivered at 440 Hz in order to activate Pacinian mechanoreceptors (Johansson, Landstro, & Lundstro, 1982). Participants held the two vibrotactile transducers slightly above the table, one in each hand, between the thumb and the index finger. Two of the normally sighted participants from Experiment 2 held the transducers between the thumb and the middle finger because of the presence of a minor injury on the tip of the index finger on the day of the experiment. The stimuli were supra-threshold and perceived as clear vibratory sensations by all the participants. The two transducers were held at a distance of ~30 cm between them and a distance of ~30 cm from the edge of the table. All the participants were familiarized with the vibrotactile stimulations and the experimental set-up before starting the experiment. The intensities of the stimulations were matched between both hands and, if necessary, individually adapted so that the perceived intensity and sensation were identical on the left and the right hand for each participant. The intensity had to be slightly adapted for two blind participants (EB7 and EB11) in two out of the four experimental blocks, because the perceived intensity was no longer judged as equivalent between both hands. Vibrotactile stimulations were remotely controlled using Matlab 2014a.

2.3. Procedure

The procedure was exactly the same for both Experiment 1 and Experiment 2. The participants were sitting in a chair in front of a table. Participants' arms were placed in an

uncrossed posture in half of the experimental blocks. In the other half, they crossed their arms over their sagittal body midline. Participants' heads were placed in a chin-rest at an individually adapted level, in order to minimize head movement during the experiment. Noises from experimental devices were covered by means of a white noise played through earphones. The sighted participants were blindfolded with an eye mask.

During each block of stimulation, on each trial, the participants were presented with two vibrotactile stimuli, one on each hand, separated in time by 22 possible stimulus-onset asynchronies (SOA): ± 5 , ± 10 , ± 15 , ± 30 , ± 45 , ± 60 , ± 75 , ± 90 , ± 145 , ± 200 , ± 400 ms. Negative values indicate that the first stimulus of the pair was applied on the left hand, and the second one on the right hand; positive values indicate that the right hand was stimulated first. The SOAs were selected and presented using the adaptive *psi* method (see paragraph 2.4). After each trial the participants reported verbally which of the two hands they perceived as having been stimulated first (in half of the blocks) or as having been stimulated second (in the other half of the blocks), by responding 'left' or 'right'. These two different response conditions were used to minimize the influence of potential response biases (Filbrich, Torta, Vanderclausen, Azañón, & Legrain, 2016; Spence & Parise, 2010). By responding according to the stimulated hand, the participants most likely based their responses on somatotopic representations of the tactile stimuli (a discussion about the importance of task instruction in the context of somatosensory TOJ tasks can be found in Crollen et al., 2019 and Vanderclausen, Manfron, et al., 2020). This response modality was chosen to be in accordance with previous tactile TOJ studies (Crollen et al., 2017; Crollen et al., 2019; Röder et al., 2004). The response was encoded by the experimenter by pressing a key of the keyboard, which triggered the next trial 2000 ms later. Participants were told to be as accurate as possible, but no specific instruction was given regarding response speed. They did not receive any feedback on their task performance.

The experiment started with a practice session of 4 blocks of 10 trials each, composed of one block per condition (hand posture: *uncrossed* vs. *crossed* and response modality: ‘*which is first*’ vs. ‘*which is second*’), with only two SOAs (± 145 , ± 200 ms). In the experimental session per se, participants were presented with 4 blocks of 40 trials each, one per condition. The order of the blocks was counterbalanced across participants **with regard to** the posture (half of the participants started the experiment with their hands uncrossed while the other half started **with** the crossed posture), as well as **in terms of** which of the two arms was crossed over the other (half of the participants **placed** their left arm on the right one and the other half did the reverse). Concerning the response modality, the order of the experimental blocks was randomized within each posture condition. The whole experiment lasted about 30 minutes.

2.4. Measures

For all experimental conditions, the proportion of left stimuli reported as presented first was plotted as a function of SOA. Data were fitted during the experiment, **i.e. online**, with a logistic function, i.e. $f(x) = 1/(1+\exp(-\beta(x-\alpha)))$, from which the parameters of interest (α , the threshold, and β , the slope) were derived (see Filbrich, Alamia, Burns, et al., 2017). The main parameter of interest in the present experiments was the β parameter, characterizing the slope of the logistic function. It describes the noisiness of the participant’s responses, **i.e. their** precision during the experiment (i.e. their sensitivity in the task). **The slope was** thus considered as a measure of the participant’s performance (Kingdom & Prins, 2010). The α parameter **corresponds to** the threshold of the function and refers to the point of subjective simultaneity (**PSS**), which aims at measuring potential perceptual biases. Although our hypotheses were not focused on the α parameter, that parameter was also measured in order to assess the possible presence of biases that could affect the estimation of the slope (see Filbrich, Alamia, Blandiaux, et al., 2017; Filbrich, Alamia, Burns, et al., 2017; Vanderclausen et al., 2017). To estimate the

362 logistic function, the adaptive *psi* method was used (Kontsevich & Tyler, 1999). Hence, the
 363 psychometric curve and its parameters were estimated at each trial, the final parameter
 364 estimates corresponding to the last update computed by the algorithm of the adaptive procedure
 365 (Kingdom & Prins, 2010; Kontsevich & Tyler, 1999). This method has the particularity that it
 366 adapts the experimental procedure and the presented SOA according to the individual
 367 performance on all previous trials in order to target the estimation of both the threshold and the
 368 slope (Kingdom & Prins, 2010). Based on previous trials, it chooses the most informative
 369 condition (i.e. SOA) to estimate the joint distribution of the parameters, which minimizes the
 370 expected entropy, i.e. uncertainty, of the posterior distribution trial by trial. Hence, the
 371 distributions are shaped during the experiment, based on all the previous trials. At each trial,
 372 the *psi* method finds the best-fitting psychometric function to the participant's responses
 373 collected so far (Kingdom & Prins, 2010; Kontsevich & Tyler, 1999). Since this procedure is
 374 based on a Bayesian approach, a prior probability distribution needs to be postulated (Kingdom
 375 & Prins, 2010). We used a prior distribution of 0 ± 20 to estimate the α parameter, since no bias
 376 towards one of the two hands was expected (e.g. Filbrich, Alamia, Blandiaux, et al., 2017;
 377 Filbrich, Alamia, Burns, et al., 2017). Based on pilot experiments performed with healthy
 378 volunteers, 0.06 ± 0.6 was chosen as prior distribution to estimate the β parameter. This range of
 379 values is indeed large enough to take the potential difference of performance between the two
 380 experimental conditions (i.e. postures) as well as possible inter-individual differences **into**
 381 **account**. Prior values were also postulated for the lapse and guess rates. The lapse rate (λ
 382 parameter) is defined as the probability of an incorrect response independently of stimulus
 383 intensity (i.e. SOA), related to vigilance or response errors (e.g. participants answered "left"
 384 but meant "right") **for example**. The guess rate (γ parameter) is defined as the probability of a
 385 correct response when the stimulus is not detected (Kingdom & Prins, 2010; Prins, 2012). The

λ parameter was set to 0.02 and the γ parameter was set to 0 for all conditions, as recommended by Kingdom and Prins (2010).

Since we used an adaptive method, the participants were not all presented with the same sequence of SOAs during the experiment. Therefore, a third, but non-standard, parameter was derived *a posteriori* from the present data: the mode of the presented SOAs. This corresponds to the value of the SOA, among all the possible SOAs, that was the most frequently presented to a given participant during a particular condition of the experiment. A significant difference between the modes of the two experimental conditions would illustrate that the participants needed different ranges of SOAs between the experimental conditions in order to be able to correctly perceive the temporal order between the stimuli with a satisfactory level of performance. In other words, a larger mode value in one condition as compared to the other would indicate that the task was more difficult to perform in this condition as compared to the other. The mode of the presented SOA was used as a complementary index of participants' performance.

2.5. Analyses

Data were excluded from further statistical analyses if the slope of the psychometric function couldn't be reliably estimated during the 40 trials within one condition (i.e. the parameter estimate did not converge on a stable value on the last trials), indexing that their performance was too inconsistent and below chance level. Before statistical analyses, data from the two response modalities ('*which is first*' and '*which is second*') were averaged. In order to examine the presence of possible biases towards one of the two hands, one sample t-tests were performed to compare the PSS values to 0 for each condition of *posture* (i.e. uncrossed vs. crossed) and for each group. The PSS, slope and mode values of Experiment 1 were analyzed

by means of an analysis of variance (ANOVA) for repeated measures with *posture* (i.e. uncrossed vs. crossed) as a within-participant factor. For data from Experiment 2, the same ANOVAs were performed, adding *group* (i.e. blind vs. sighted) as a between-participants factor.

Greenhouse-Geisser corrections of degrees of freedom and contrast analyses were used if necessary. Effect sizes were measured using partial Eta squared for ANOVAs and Cohen's *d* for t-tests. Significance level was set at $p \leq .05$.

3. Results

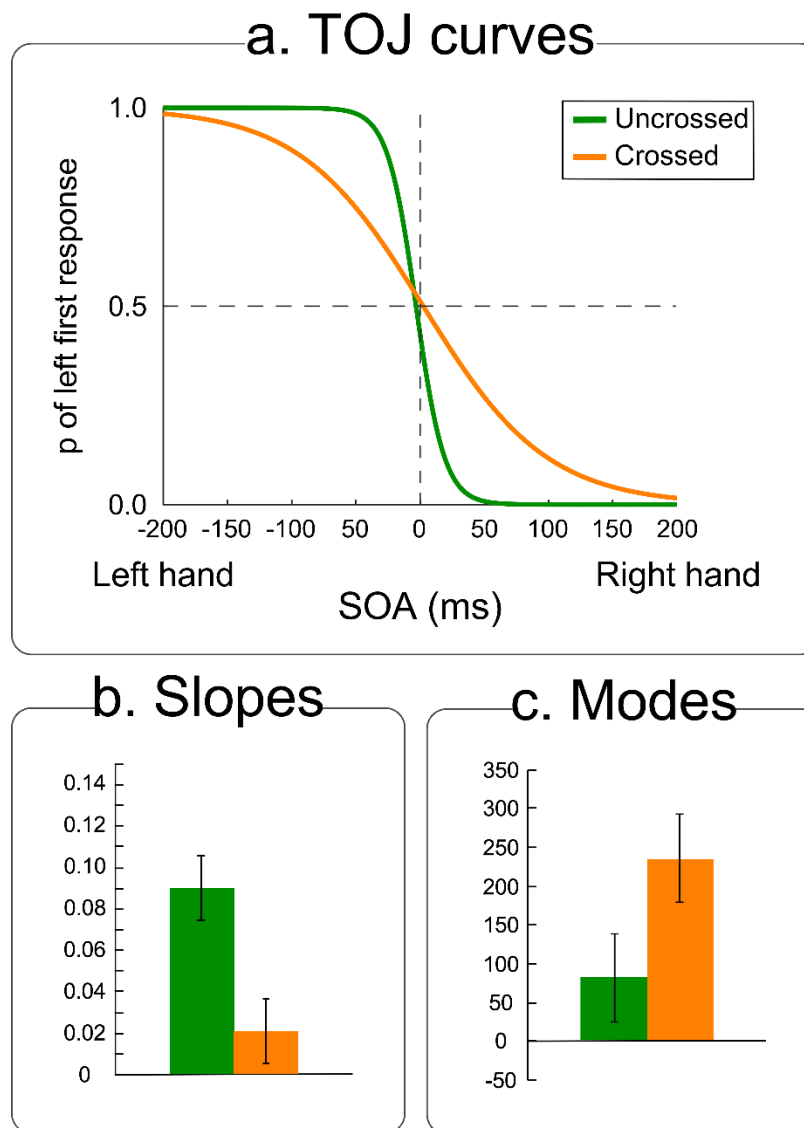
3.1 Experiment 1

The curves of the fitted psychometric functions are illustrated in Figure 1a. The t-tests revealed that none of the PSS values were significantly different from 0 (uncrossed: $t(10)=-1.312$, $p=.219$, $d=.395$; crossed: $t(10)=0.940$, $p=.369$, $d=.283$). The ANOVA didn't reveal any significant effect of the hands' posture on PSS values ($F(1,10)=3.628$, $p=.086$, $\eta^2p=.266$). These results confirm the absence of any spatial bias during the TOJ.

Regarding the slopes, the ANOVA revealed a significant effect of the hands' posture ($F(1,10)=23.669$, $p=.001$, $\eta^2p=.703$). The slope values were significantly smaller when the participants performed the tactile TOJ with the hands in a crossed posture ($M \pm SD = 0.021 \pm 0.016$) as compared to the uncrossed posture ($M \pm SD = 0.090 \pm 0.038$) (Figure 1b).

The same pattern of results was observed for the mode of the presented SOAs as the ANOVA revealed a significant effect of the hands' posture ($F(1,10)=8.937$, $p=.014$, $\eta^2p=.472$). Participants' performances were adapted using greater SOA values when the task was

430 performed with the hands in the crossed posture ($M \pm SD = 245.910 \pm 180.724$) than with the hands
 431 in the uncrossed posture ($M \pm SD = 84.550 \pm 156.100$) (Figure 1c).



432

433 **Figure 1. Tactile temporal order judgments (TOJs) in Experiment 1.** (a) Fitted curves of the
 434 psychometric function from the data of the 11 participants according to the hands posture condition.
 435 The x-axis represents different possible SOAs. A negative value indicates that the left hand was
 436 stimulated first and a positive value indicates that the right hand was stimulated first. The y-axis
 437 represents the proportion of trials in which the tactile stimulus applied on the left hand was perceived
 438 as being presented first. The lines represent the fitted curves for the uncrossed posture condition (green)
 439 and the crossed posture condition (orange), respectively. (b) Mean slope values for each posture

condition. The slope value of the crossed posture condition was significantly lower than the slope value corresponding to the uncrossed posture condition. (c) Mean mode values of the presented SOAs in milliseconds for each posture condition. The averaged mode in the crossed posture condition was significantly higher than the averaged mode value of the uncrossed posture condition. Error bars represent confidence intervals calculated according to Cousineau's method for within-subject designs (Cousineau, 2005).

3.2. Experiment 2

Curves of the fitted psychometric functions are illustrated for the two groups in Figure 2a. None of the t-tests revealed PSS values significantly different from 0 in the sighted group (all $t(16) \leq 1.059$, all $p \geq .305$, all $d = .257$). However, both the PSS values of the uncrossed and crossed posture conditions appeared to significantly differ from 0 in the early blind group (uncrossed: $t(16) = 2.352$, $p = .032$, $d = .570$; crossed: $t(16) = 3.977$, $p = .001$, $d = .964$). This indicates that judgements of the participants in this group were slightly biased towards the left hand. Overall, the stimulus applied on the right hand had to precede the stimulus presented on the left hand by 3.736 ms (SD=6.549) for the uncrossed posture and by 8.496 ms (SD=3.967) for the crossed posture in order for both to be perceived as occurring at the same time. Nevertheless, the ANOVA did not show any significant effect of the posture ($F(1,32) = .386$, $p = .539$, $\eta^2 p = .012$), nor of the group ($F(1, 32) = .630$, $p = .433$, $\eta^2 p = .019$), nor any significant interaction between the two factors ($F(1,32) = 3.961$, $p = .055$, $\eta^2 p = .110$). This suggests that the observed PSS values for the blind participants in the uncrossed and crossed posture conditions were neither significantly different from each other, nor from the ones observed in the sighted participants.

Regarding the slope values, the ANOVA revealed a significant main effect of the posture ($F(1,32) = 12.802$, $p = .001$, $\eta^2 p = .286$) and a significant main effect of the group

($F(1,32)=12.190$, $p<.001$, $\eta^2p=.276$). Importantly, the interaction between the posture and the group factors also reached significance ($F(1,32)=4.166$, $p=.050$, $\eta^2p=.115$). Contrast analyses revealed a significant effect of the posture in the sighted group ($t(16)=3.844$, $p=.001$, $d=.932$), the averaged slope value being larger in the uncrossed ($M\pm SD=0.062\pm 0.039$) as compared to the crossed posture condition ($M\pm SD=0.024\pm 0.017$). In contrast, such difference was not significant in the early blind group ($t(16)=1.126$, $p=.277$, $d=.273$; $M\pm SD$ uncrossed= 0.113 ± 0.080 ; $M\pm SD$ crossed= 0.102 ± 0.071). Additionally, the averaged slope value was significantly greater for the early blind than for the sighted participants for both the uncrossed ($t(32)=2.346$, $p=.025$, $d=.402$) and the crossed posture conditions ($t(32)=4.449$, $p=.000$, $d=.763$) (Figure 2b). Individual slope values are illustrated in Figure 3, showing that a crossing-hand effect on the slope values is almost systematically present in the normally sighted participants of both Experiment 1 and 2, whereas it is much more inconsistent in the blind participants.

Regarding the mode of the presented SOAs, the ANOVA revealed a significant main effect of the hands' posture ($F(1,32)=16.477$, $p<.001$, $\eta^2p=.340$), a significant main effect of the group ($F(1,32)=18.254$, $p<.001$, $\eta^2p=.363$), as well as a significant interaction between the two factors ($F(1,32)=15.198$, $p<.001$, $\eta^2p=.322$). Contrast analyses revealed a significant effect of the posture in the sighted participants ($t(16)=-3.990$, $p=.001$, $d=.968$). On the contrary, such a difference was not significant for the blind participants ($t(16)=-1.083$, $p=.295$, $d=.263$). The sighted participants needed lower SOA values to correctly perform the TOJ task with the hands uncrossed ($M\pm SD=34.120\pm 19.222$) than with the hands crossed ($M\pm SD=208.82\pm 187.471$), whereas the blind participants seemed to need similar SOA values to correctly perform the task in both posture conditions ($M\pm SD$ uncrossed= 17.350 ± 12.884 , $M\pm SD$ crossed= 20.880 ± 14.815). In addition, early blind participants appeared to perform the TOJ task

with smaller SOAs than the sighted, both in the uncrossed ($t(32)=-2.987$, $p=.005$, $d=.512$) and the crossed posture conditions ($t(32)=-4.121$, $p=.001$, $d=.707$).

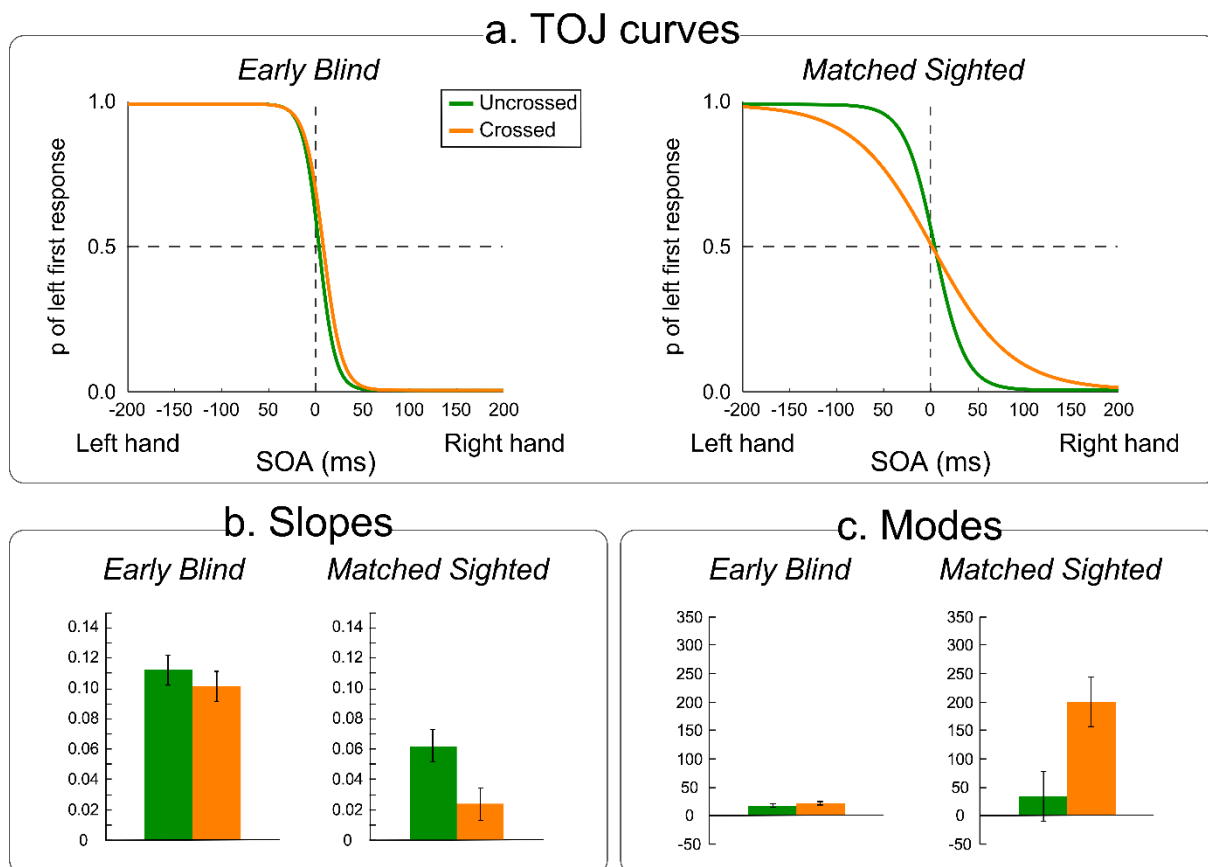


Figure 2. Tactile temporal order judgments (TOJs) in Experiment 2. (a) Fitted curves of the psychometric function from the data of the 17 early blind and the 17 normally sighted participants according to each posture condition. The x-axis represents different possible SOAs. A negative value indicates that the left hand was stimulated first and a positive value that the right hand was stimulated first. The y-axis represents the proportion of trials in which the vibrotactile stimulus applied on the left hand was perceived as being presented first. The lines represent the fitted curves for the uncrossed posture condition (green) and the crossed posture condition (orange) for the early blind group and the normally sighted group, respectively. (b) Mean slope values for each posture condition and according to each group. The slope value of the crossed posture condition was significantly lower than the slope

value of the uncrossed posture condition for the sighted group but not for the blind group. Additionally, the averaged slope value of the early blind group was significantly greater than the averaged slope value of the normally sighted group, regardless of the posture. (c) Averaged mode values of the presented SOAs in milliseconds for each posture condition and each group. The averaged mode in the crossed posture condition was significantly higher than the averaged mode value of the uncrossed posture condition in the normally sighted group but not in the early blind group. In addition, the averaged mode of the presented SOA was smaller in the blind, as compared to the sighted group, irrespective of the posture. Error bars represent confidence intervals calculated according to Cousineau's method for within-subject designs (Cousineau, 2005).

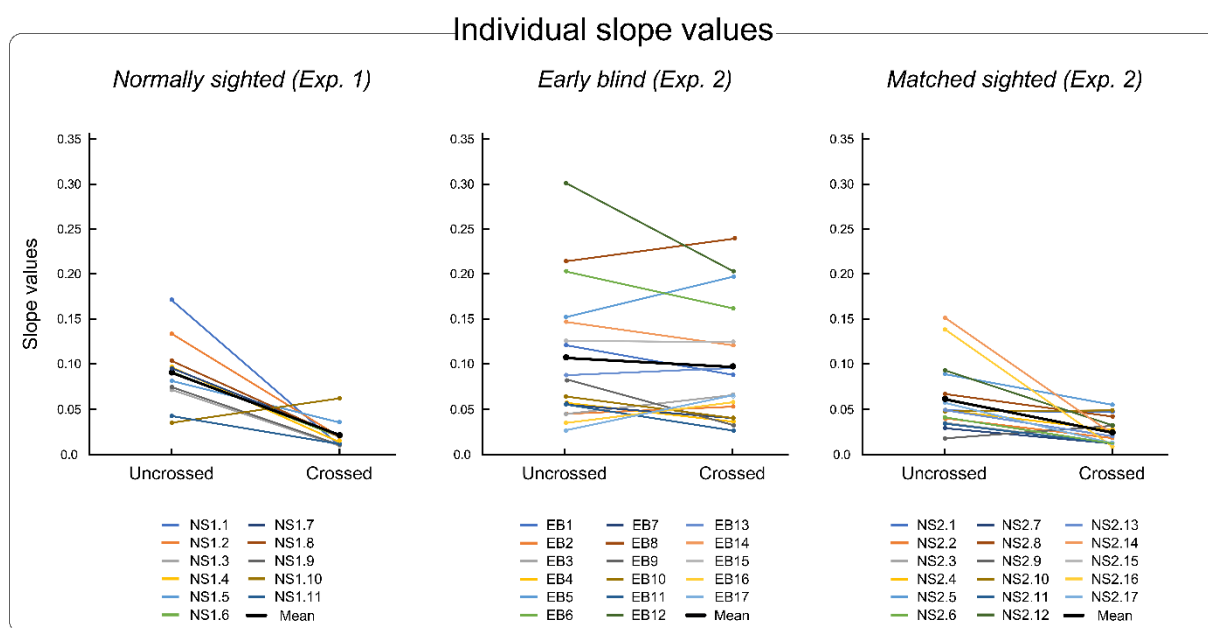


Figure 3. Individual data from experiment 1 and 2. Individual slope values corresponding to the uncrossed and crossed posture conditions for each sighted participant of Experiment 1, as well as each early blind and matched normally sighted participant of Experiment 2. Mean slope values for each experiment and each group are represented in black.

4. Discussion

The present study aimed to investigate the spatial representations underlying the localization of tactile stimuli in both early blind and matched normally sighted participants by using an adaptive psychophysical method, i.e. the *psi* method. Accordingly, the main goal of this study was to validate the use of such an adaptive tool in the context of tactile TOJ tasks by replicating previous findings in early blind and normally sighted participants from tactile TOJ studies based on another method, i.e. the method of constant stimuli. The *psi* method was used to adapt the levels of the stimuli, i.e. the SOA, to each participant's sensitivity during the tactile TOJ task. Indeed, to investigate the spatial frames of reference of touch by means of TOJ tasks with posture manipulation, the majority of previous studies have used the method of constant stimuli, in which each SOA is presented a fixed number of times (e.g. Crollen et al., 2017; Röder et al., 2004; Shore et al., 2002; Yamamoto & Kitazawa, 2001). However, when it comes to comparing different experimental conditions or groups of people between which the performance is expected to vary, i.e. when different ranges of SOA are needed to correctly discriminate the order of the stimuli (De Paepe et al., 2020; Yamamoto & Kitazawa, 2001), the to-be-tested stimulus levels (i.e. the SOAs) should be adaptable to the specific condition or population in order to maximize the accuracy of the parameter estimates while avoiding floor or ceiling effects which could potentially mask an effect of the experimental variable(s). Here, the presented SOAs were adapted by the *psi* procedure according to each participant's performance in each experimental condition. This method allowed us to investigate the spatial representations underlying touch perception with a high level of precision, by comparing performances of early blind and normally sighted participants who judged the temporal order of tactile stimuli at their respective level of sensitivity, without extending the experiment duration by extensively testing all the possible SOAs. To be able to use a wide variety of possible SOAs to increase the accuracy of the parameter estimates without concurrently having

to increase the total number of trials is thus a key advantage of the adaptive procedure. Although other alternative methods to that of constant stimuli, such as comparing the error rate at given SOAs as an estimate of task performance (Bäddé et al., 2019; Cadieux et al., 2010; Maij et al., 2020), also allow in some cases to reduce the total number of trials, they usually also do so by limiting the number of different SOAs that are tested during the experiment. In contrast, the adaptive *psi* method allows to reduce the total number of trials without having to also reduce the number of tested SOAs, which enables to get reliable and accurate estimates of the parameters regarding the performance of the participants while decreasing the risk of fatigability. For instance, Cadieux et al. (2010) used 640 trials to test 8 different SOAs, whereas we used 160 trials to test 22 SOAs. Considering that with a constant stimuli method at least 24 trials are usually used for testing each SOA in each hands posture (e.g. Crollen et al., 2017; 2018; Röder et al. 2004; Shore et al., 2002), testing all our 22 SOAs with this method would have resulted in delivering 528 trials for each posture condition, and 1056 trials in total. Using the adaptive *psi* method is thus particularly advantageous when many experimental conditions have to be tested.

In our first experiment, the results of the tactile TOJ in young normally sighted participants revealed decreased performances in the crossed as compared to the uncrossed posture condition, which is completely in accordance with previous findings that used the method of constant stimuli (e.g. Cadieux et al., 2010; Shore et al., 2002; Wada et al., 2004; Yamamoto & Kitazawa, 2001). Moreover, the adaptive character of the method allowed us to derive a second estimation of the participants' performance, which is the mode of the presented SOA, i.e. the most frequently presented SOA to a given participant in each posture condition during the adaptive procedure. Results indicated that the participants were presented with higher SOA values in the crossed as compared to the uncrossed posture. This indicates that participants needed larger time intervals to correctly judge the order of the two tactile stimuli when their hands were

crossed relative to the canonical uncrossed posture, corroborating the findings on the slope values. From a theoretical point of view, these results emphasize the presence of an automatic spatiotopic remapping of tactile inputs, taking the position of the stimulated limbs in external space into account.

Regarding the second experiment, we found that crossing the hands did not affect the ability of early blind participants to discriminate the temporal order of the two tactile stimuli, while the crossed posture impacted the performance of their matched normally sighted controls, as in the first experiment. This effect was indexed by both the slope and the mode values. Indeed, results for the mode of the SOA values indicated that early blind participants were presented with a similar range of SOA values for both hand postures, whereas normally sighted participants were globally presented with larger SOAs in the crossed as compared to the uncrossed posture. These results are in accordance with previous tactile TOJ studies that used the method of constant stimuli (Crollen et al., 2017; Crollen et al., 2019; Röder et al., 2004). Hence, we successfully replicated the findings of previous research with the use of an adaptive procedure which allows to enhance the accuracy of the parameter estimates by choosing the most appropriate range of stimulus levels according to each participant's sensitivity. While our results with the adaptive *psi* method corroborate those of previous studies using the method of constant stimuli, the present study does nonetheless not allow a direct and quantitative comparison between the results of either method within the same group of participants. Since one of the main advantages of the adaptive *psi* method is to allow testing a broad range of SOAs without increasing experiment duration, running the same experiment with the method of constant stimuli would have resulted in significantly extending the experiment duration and potentially associated detrimental consequences such as fatigue and loss of data.

The present findings can also be related to our other recent TOJ studies with the adaptive *psi* method in which we observed the same pattern of results, but with stimuli specifically and selectively activating cutaneous nociceptive receptors (Vanderclausen, Bourgois, et al., 2020; Vanderclausen, Manfron, et al., 2020). This suggests that the spatial representations of innocuous and noxious somatosensory inputs, transmitted through lemniscal and extral-lemniscal pathways, respectively, involve similar mechanisms.

Our results suggest that the tactile TOJ task adapted with the adaptive *psi* method is a valid and reliable tool to investigate the complexity of spatial representations underlying touch localization, even when a limited number of trials are used. Considering the fact that not all participants were presented with the same SOAs, and, consequently, with the exact same task, one could argue that the data of a given participant cannot be compared to those of the other participants. However, in our opinion, it seems instead even more relevant to be able to compare data from distinct groups of participants or different experimental conditions that are obtained with a task that is adapted to individual performance. Indeed, in this case, the parameters reflect a similar subjective level of difficulty across participants, considering each participant's discrimination threshold of TOJ sensitivity. Notably, the use of the adaptive method allowed us to obtain reliable data, provided by an algorithm that selected within a wide range of different SOAs those that were the most suitable for each participant within each experimental condition. Importantly, the present studies also showed that this could be achieved without extending the experiment duration, and, therefore, by minimizing the risk of increased fatigability in the participants.

It is worth noting that, overall, i.e., regardless of the posture condition, blind participants displayed better performances as compared to their sighted counterparts. This was indicated by higher slope values and smaller discrimination thresholds as reflected by the mode of the

presented SOAs in this group. Hence, the use of the *psi* method allowed to adapt the task to the increased sensitivity of early blind participants, who were globally presented with smaller SOAs throughout the TOJ tasks. Similarly, TOJ tasks were also adapted to the need of larger SOAs in the normally sighted participants, especially in the crossed posture. This indicates that this method allows to adapt a task to each individual's level of performance (i.e. the poorer performance of the sighted in the crossed hands posture as well as the globally better performance of early blind individuals), and that its use could be extended to other situations in which the TOJ performance of the participants may vary. This higher sensitivity of the early blind in tactile TOJ tasks could be explained by increased tactile acuity (e.g. Alary et al., 2008; Goldreich & Kanics, 2003; Legge, Madison, Vaughn, Cheong, & Miller, 2008), and/or enhanced spatial resolution of touch, possibly resulting from a stronger reliance on the sense of touch in this population (Wong, Gnanakumaran, & Goldreich, 2011). Moreover, and quite interestingly, the use of an adaptive method in our experiment allowed to highlight greater inter-individual differences among early blind participants than within the two groups of normally sighted participants (see Figure 3). This higher level of variability regarding the performance of the blind could be due to different levels of expertise in everyday life activities involving the tactile modality (e.g. braille reading) and diversity in the strategies used to compensate for the lack of visual input among the early blind individuals tested in this study.

In conclusion, using a novel paradigm combining tactile TOJ tasks with the adaptive *psi* method, the present study allowed to corroborate previous literature outcomes regarding the spatial remapping of touch in both early blind and normally sighted people, by providing accurate and reliable data while maintaining a reasonably short experiment duration. We therefore encourage future TOJ studies to consider using this method, especially if they aim at either comparing populations that might differ in terms of their respective performance (e.g. patients with specific pathologies) or experimental conditions that can impact the participants'

639 sensitivity differently. The paradigm seems indeed particularly suitable for the investigation of
640 the spatial representations of somatosensory stimuli in these specific situations.

641

642 ***Acknowledgments***

643 C. Vanderclausen, L. Filbrich, A. de Volder and V. Legrain are supported by the Funds for
644 Scientific Research of the French-speaking Community of Belgium (F.R.S.-FNRS). We thank
645 Andrea Alamia (Institut des sciences biologiques (INSB), centre de recherches Cerveau et
646 Cognition (CerCo), Toulouse, France) for his valuable help in originally adapting the Matlab
647 scripts and for his technical support during the experiments.

648 ***Open practices***

649 The datasets generated during and/or analysed during the current study are available in the
650 OSF repository, <https://osf.io/a2g4b/>

651

652 ***Conflict of interest***

653 None.

654

655

References

- Alary, F., Goldstein, R., Duquette, M., Chapman, C. E., Voss, P., & Lepore, F. (2008). Tactile acuity in the blind: a psychophysical study using a two-dimensional angle discrimination task. *Exp Brain Res*, 187(4), 587-594. doi:10.1007/s00221-008-1327-7
- Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. *Curr Biol*, 18(14), 1044-1049. doi:10.1016/j.cub.2008.06.045
- Badde, S., Roder, B., & Heed, T. (2019). Feeling a Touch to the Hand on the Foot. *Curr Biol*, 29(9), 1491-1497 e1494. doi:10.1016/j.cub.2019.02.060
- Begum Ali, J., Spence, C., & Bremner, A. J. (2015). Human infants' ability to perceive touch in external space develops postnatally. *Curr Biol*, 25(20), R978-979. doi:10.1016/j.cub.2015.08.055
- Bremner, A. J., Holmes, N. P., & Spence, C. (2008). Infants lost in (peripersonal) space? *Trends Cogn Sci*, 12(8), 298-305. doi:10.1016/j.tics.2008.05.003
- Bremner, A. J., Mareschal, D., Lloyd-Fox, S., & Spence, C. (2008). Spatial localization of touch in the first year of life: early influence of a visual spatial code and the development of remapping across changes in limb position. *J Exp Psychol Gen*, 137(1), 149-162.
- Cadieux, M. L., Barnett-Cowan, M., & Shore, D. I. (2010). Crossing the hands is more confusing for females than males. *Exp Brain Res*, 204(3), 431-446. doi:10.1007/s00221-010-2268-5
- Cousineau, D. (2005). Confidence intervals in within-subject designs: a simpler solution to Loftus and Masson's method. *Tutor Quant Methods Psychol*, 1(1), 42-45.
- Crollen, V., Albouy, G., Lepore, F., & Collignon, O. (2017). How visual experience impacts the internal and external spatial mapping of sensorimotor functions. *Sci Rep*, 7(1), 1022. doi:10.1038/s41598-017-01158-9
- Crollen, V., Spruyt, S., Mahau, P., Bottini, R., & Collignon, C. (2019). How visual experience and task context modulate the use of internal and external spatial coordinate for perception and action. *J Exp Psychol Hum Percept Perform*. doi:10.1037/xhp0000598
- 10.1037/xhp0000598.supp

- 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*(8), e0137120. doi:10.1371/journal.pone.0137120
- De Paepe, A. L., Legrain, V., Van der Biest, L., Hollevoet, N., Van Tongel, A., De Wilde, L., . . . Crombez, G. (2020). An investigation of perceptual biases in complex regional pain syndrome. *PeerJ*, *8*. doi:10.7717/peerj.8819
- Driver, J., & Spence, C. (1998). Attention and the crossmodal construction of space. *Trends Cogn Sci*, *2*(7), 254-262. doi:10.1016/S1364-6613(98)01188-7
- Filbrich, L., Alamia, A., Blandiaux, S., Burns, S., & Legrain, V. (2017). Shaping visual space perception through bodily sensations: Testing the impact of nociceptive stimuli on visual perception in peripersonal space with temporal order judgments. *PLOS ONE*, *12*(8), e0182634. doi:10.1371/journal.pone.0182634
- 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. *Exp Brain Res*, *235*(7), 2069-2079. doi:10.1007/s00221-017-4951-2
- Filbrich, L., Alamia, A., Verfaillie, C., Berquin, A., Barbier, O., Libouton, X., . . . Legrain, V. (2017). Biased visuospatial perception in complex regional pain syndrome. *Scientific Reports*, *7*(1), 9712. doi:10.1038/s41598-017-10077-8
- 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. doi:<https://doi.org/10.1016/j.concog.2017.11.011>
- 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. *Conscious Cogn*, *41*, 135-138. doi:10.1016/j.concog.2016.02.008
- Goldreich, D., & Kanics, I. M. (2003). Tactile acuity is enhanced in blindness. *The Journal of Neuroscience*, *23*(8), 3439-2445.
- Graziano, M. S. A., Hu, X. T., & Gross, C. G. (1997). Visuospatial Properties of Ventral Premotor Cortex. *J Neurophysiol*, *77*(5), 2268-2292.
- 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. doi:10.3389/fpsyg.2014.00076

- Heed, T., Backhaus, J., & Röder, B. (2012). Integration of hand and finger location in external spatial coordinates for tactile localization. *Journal of Experimental Psychology: Human Perception and Performance*, 38(2), 386-401. doi:10.1037/a0024059
- Johansson, R. S., Landstro, U., & Lundstro, R. (1982). Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements. *Brain research*, 244 (1), 17-25.
- Kingdom, F. A. A., & Prins, N. (2010). *Psychophysics - A practical introduction*. London: Elsevier Academic Press.
- Kobor, I., Furedi, L., Kovacs, G., Spence, C., & Vidnyanszky, Z. (2006). Back-to-front: improved tactile discrimination performance in the space you cannot see. *Neurosci Lett*, 400(1-2), 163-167. doi:10.1016/j.neulet.2006.02.037
- Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Res*, 39, 2729-2737.
- Legge, G. E., Madison, C., Vaughn, B. N., Cheong, A. M., & Miller, J. C. (2008). Retention of high tactile acuity throughout the life span in blindness. *Percept Psychophys*, 70(8), 1471-1488. doi:10.3758/PP.70.8.1471
- Legrain, V., Iannetti, G. D., Plaghki, L., & Mouraux, A. (2011). The pain matrix reloaded. A salience detection system for the body. *Prog. Neurobiol.* 93, 111-124. doi: 10.1016/j.pneurobio.2010.10.005.
- Legrain, V., Manfron, L., Garcia, M., & Filbrich, L. (2018). Does Body Perception Shape Visuospatial Perception? *Perception*, 301006618763269. doi:10.1177/0301006618763269
- Lenoir, C., Huang, G., Vandermeeren, Y., Hatem, S. M., & Mouraux, A. (2017). Human primary somatosensory cortex is differentially involved in vibrotaction and nociception. *J Neurophysiol* 118, 317-330. doi: 10.1152/jn.00615.2016.
- Maij, F., Seegelke, C., Medendorp, W. P., & Heed, T. (2020) External location of touch is constructed post-hoc based on limb choice. *eLife* 9, e57804. doi:10.7554/eLife.57804.
- Manfron, L., Legrain, V., & Filbrich, L. (2020). Seeing or not Seeing Where Your Hands Are. The Influence of Visual Feedback About Hand Position on the Interaction Between Nociceptive and Visual Stimuli. *Multisens Res*, 33, 457-478. doi:10.1163/22134808-20191448

- Mouraux, A., De Paepe, A. L., Marot, E., Plaghki, L., Iannetti, G. D., & Legrain, V. (2013). Unmasking the obligatory components of nociceptive event-related brain potentials. *J Neurophysiol* 110, 2312-2324. doi: 10.1152/jn.00137.2013.
- 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(10), 2914-2926. doi:10.1016/j.cortex.2013.02.002
- Pagel, B., Heed, T., & Röder, B. (2009). Change of reference frame for tactile localization during child development. *Developmental Science*, 12(6), 929-937. doi:10.1111/j.1467-7687.2009.00845.x
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Original articles and clinical cases*, 389-443.
- Prins, N. (2012). The psychometric function: the lapse rate revisited. *J Vis*, 12(6). doi:10.1167/12.6.25
- Rizzolatti, G., Fadiga, L., Fogassi, L., Gallese, V. (1997). The space around us. *Science* 277 :190-191
- Röder, B., Rösler, F., & Spence, C. (2004). Early Vision Impairs Tactile Perception in the Blind. *Current Biology*, 14(2), 121-124. doi:10.1016/j.cub.2003.12.054
- Sambo, C. F., Torta, D. M., Gallace, A., Liang, M., Moseley, G. L., & Iannetti, G. D. (2013). The temporal order judgement of tactile and nociceptive stimuli is impaired by crossing the hands over the body midline. *PAIN*, 154(2), 242-247. doi:10.1016/j.pain.2012.10.010
- Schicke, T., & Roder, B. (2006). Spatial remapping of touch: confusion of perceived stimulus order across hand and foot. *Proc Natl Acad Sci U S A*, 103(31), 11808-11813. doi:10.1073/pnas.0601486103
- Shore, D. I., Spry, E., & Spence, C. (2002). Confusing the mind by crossing the hands. *Cogn Brain Res*, 14, 153-163.
- Smania, N., & Aglioti, S. (1995). Sensory and spatial components of somaesthetic deficits following right brain damage. *Neurology*, 45(9), 1725-1730. doi:10.1212/wnl.45.9.1725
- Spence, C., & Parise, C. (2010). Prior-entry: a review. *Conscious Cogn*, 19(1), 364-379. doi:10.1016/j.concog.2009.12.001

- Stelmach, L. B., & Herdman, C. M. (1991). Directed attention and perception of temporal order. *Journal of Experimental Psychology: Human Perception and Performance*, 17(2), 539-550.
- Sternberg, S., Knoll, R. L., & Gates, B. A. (1971). *Prior entry reexamined: effect of attentional bias on order perception*. Paper presented at the Annual meeting of the Psychonomic society, St-Louis, Missouri.
- Torta, D. M., Legrain, V., Algoet, M., Olivier, E., Duque, J., & Mouraux, A. (2013). Theta burst stimulation applied over primary motor and somatosensory cortices produces analgesia unrelated to the changes in nociceptive event-related potentials. *PLOS ONE*, 8(8), e73263. doi: 10.1371/journal.pone0073263.
- Vanderclausen, C., Filbrich, L., Alamia, A., & Legrain, V. (2017). Investigating peri-limb interaction between nociception and vision using spatial depth. *Neurosci Lett*, 654, 111-116. doi:10.1016/j.neulet.2017.05.060
- Vanderclausen, C., Manfron, L., De Volder, A., & Legrain, V. (2020). The influence of visual experience and cognitive goals on the spatial representations of nociceptive stimuli. *PAIN*, 161, 328-337. doi:10.1097/j.pain.0000000000001721
- Vanderclausen, C., Bourgois, M., De Volder, A., & Legrain, V. (2020). Testing the exteroceptive function of nociception: the role of visual experience in shaping the spatial representations of nociceptive inputs. *Cortex*, 126, 26-38.
- Wada, M., Yamamoto, S., & Kitazawa, S. (2004). Effects of handedness on tactile temporal order judgment. *Neuropsychologia*, 42(14), 1887-1895. doi:10.1016/j.neuropsychologia.2004.05.009
- Wong, M., Gnanakumaran, V., & Goldreich, D. (2011). Tactile Spatial Acuity Enhancement in Blindness: Evidence for Experience-Dependent Mechanisms. *Journal of Neuroscience*, 31(19), 7028-7037. doi:10.1523/jneurosci.6461-10.2011
- Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, 4(7), 759-765.
- Zampini, M., Guest, S., Shore, D. I., & Spence, C. (2005). Audio-visual simultaneity judgments. *Perception & Psychophysics*, 67(3), 531-544.