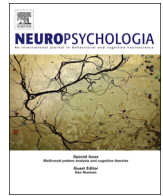




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Relative contributions of visual and auditory spatial representations to tactile localization

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ABSTRACT

Spatial localization of touch is critically dependent upon coordinate transformation between different reference frames, which must ultimately allow for alignment between somatotopic and external representations of space. Although prior work has shown an important role for cues such as body posture in influencing the spatial localization of touch, the relative contributions of the different sensory systems to this process are unknown. In the current study, we had participants perform a tactile temporal order judgment (TOJ) under different body postures and conditions of sensory deprivation. Specifically, participants performed non-speeded judgments about the order of two tactile stimuli presented in rapid succession on their ankles during conditions in which their legs were either uncrossed or crossed (and thus bringing somatotopic and external reference frames into conflict). These judgments were made in the absence of 1) visual, 2) auditory, or 3) combined audio-visual spatial information by blindfolding and/or placing participants in an anechoic chamber. As expected, results revealed that tactile temporal acuity was poorer under crossed than uncrossed leg postures. Intriguingly, results also revealed that auditory and audio-visual deprivation exacerbated the difference in tactile temporal acuity between uncrossed to crossed leg postures, an effect not seen for visual-only deprivation. Furthermore, the effects under combined audio-visual deprivation were greater than those seen for auditory deprivation. Collectively, these results indicate that mechanisms governing the alignment between somatotopic and external reference frames extend beyond those imposed by body posture to include spatial features conveyed by the auditory and visual modalities – with a heavier weighting of auditory than visual spatial information. Thus, sensory modalities conveying exteroceptive spatial information contribute to judgments regarding the localization of touch.

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1. Introduction

The multisensory nature of our external world poses a number of challenges for the central nervous system in decoding the incoming information, including the fact that this information is initially encoded in a variety of reference frames. Visual information is first encoded in a frame of reference tied to the retina (i.e., retinotopic), auditory information in a frame based on the position of the head (i.e., craniotopic), and somatosensory information in a somatotopic reference frame. How these coordinate frameworks interact in order to solve the problem of accurately locating (and

acting upon) a stimulus in space is a question of intensive inquiry.

The example of tactile localization, in particular while using a tactile temporal order (TOJ) task to stimuli delivered on the hands, has received much attention under this framework. The observation that participants' performance in establishing the order with which tactile stimulation is administered – a task seemingly achievable without taking body posture into account – is heavily influenced by proprioceptive information (Yamamoto & Kitazawa 2001a; Shore Spry and Spence, 2002) has resulted in a number of interpretations regarding the solution to the reference frame problem.

Kitazawa and colleagues (Yamamoto and Kitazawa, 2001a; Kitazawa, 2002; Kitazawa et al., 2008) suggest that tactile stimulation is processed in space with the assumption of a 'standard' (i.e., aligned) posture and then projected back onto skin location taking into account body posture. An interesting line of evidence for this

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space-to-body directionality comes from studies describing the path of saccades to single tactile stimuli. When a tactile stimulus is administered to crossed hands, saccades occasionally initiate toward the opposite hand – namely, toward the external space routinely occupied by the stimulated hand – and correct toward the appropriate hand mid-action (Overvliet et al., 2011).

Similarly, Shore and colleagues (Shore et al., 2002; Cadieux et al., 2010) postulate that a tactile stimulus is initially represented according to its somatotopic location on the skin and only after it is remapped onto external coordinates. In a crossed hand condition, the decreased performance in tactile TOJ is presumed to be a result of a misalignment between the somatotopic and external spatiotopic coordinate frames. Lastly, Heed, Badde, and colleagues (Heed et al., 2015; Badde et al., 2014a, 2014b) propose that somatotopic and external spatial reference frames are concurrently active, and that the precise localization of touch in space is determined by integrating across sources of information and according to task demands. Their account posits that information is pooled across different reference frames (with varying weights) and that TOJ crossing effects reflect this (uneven) integration of spatial information once the remapping between frames of reference is complete. Noteworthy, hence, is that, although somewhat different in their implementation, all theoretical accounts posit a transformation process from one reference frame to another (Heed and Azañón, 2014) implying a space-to/from-body remapping process (e.g., Yamamoto and Kitazawa 2001a; Shore et al., 2002). Thus, in addition to scrutinizing the bodily aspects that govern tactile localization (i.e., posture, features of the particular body part being stimulated), delineating what features of a particular spatial representation, or even simply what spatial representations at all (i.e., auditory, visual, both) are implicated in the process of localizing touch *in space* is a fundamental question that remains to be answered.

Whereas the impact of body position on tactile localization has been well studied, less work has focused on the exteroceptive senses and the role that the spatial representation(s) constructed from these senses play in tactile localization. Intriguingly, whereas the crossed hands effect occurs in sighted individuals in the absence of visual information congenitally blind participants are unaffected by crossing the hands (Röder et al., 2004). Additionally, individuals who turn blind later in life performed just as the sighted. Further, crossing effects are weaker, albeit present, when hands are crossed behind the back in sighted individuals (Kóbor et al., 2006). These results suggest that whereas visual experience drives the establishment of a crossing effect, the sustained presence of vision is not required for it to be demonstrated. Virtually unknown is the role of the auditory system, as well as how multisensory audiovisual spatial representations mediate this effect. In the current study we sought to examine the role of auditory, visual and combined audiovisual spatial representations on tactile TOJ performance for both uncrossed (i.e., aligned somatotopic and external reference frames) and crossed (i.e., misaligned somatotopic and external reference frame) leg conditions, by examining performance in the absence of auditory, visual and combined audiovisual spatial information. This was achieved by placing participants in an anechoic chamber (auditory absent), blindfolding them (vision absent), or placing them in an anechoic chamber while blindfolded (audiovisual absent). Prior studies (e.g., Yamamoto and Kitazawa, 2001) have masked task-relevant sounds due to tactile stimulation using white noise. We consider our use of the anechoic environment to be comparable, **but not identical**, to the use of white noise in that both mask spatially informative sounds. These two conditions do differ in that white noise masks all sounds, including those that are self-generated, whereas the anechoic chamber maintains self-generated sounds, sounds that have been shown to be important in the maintenance of an

implicit body-representation and tactile perception (Tajadura-Jiménez et al., 2012).

2. Materials and methods

2.1. Participants

A total of forty-eight participants took part in this study (20 females, mean age = 19.43 ± 1.1 , $n_{\text{auditory}} = 17$, $n_{\text{visual}} = 15$, $n_{\text{audiovisual}} = 16$). All participants reported normal touch and hearing, and had normal or corrected-to-normal visual acuity. No participant had a history of either psychiatric or neurological condition. All participants gave their informed consent to take part of this study. The protocols were approved by Vanderbilt University Medical Center's Institutional Review Board.

2.2. Materials and apparatus

Tactile stimulation consisted of 10 ms of vibrotactile stimulation delivered on the ankles (medial malleolus) by means of a Pico Vibe Vibrator Motor (9mm diameter, 25 mm length, 230 Hz, 4 g amplitude) driven at 3.3 V by an Arduino™ microcontroller (<http://arduino.cc>; Arduino Mega 2560, 16 MHz). Experimental protocols were carried out by in-house software (ExpyVR, <http://Inco.epfl.ch/expyvr>) at 100 Hz. Tactile stimulation was applied on the ankles in order to minimize a putative auditory occurrence as a consequence to mechanical tactile stimulation (see Schicke and Röder, 2006, for a previous account of a tactile TOJ on foot). Further, in order to rule out the possibility that vibrotactile stimulation produced an auditory signal that participants were capable of employing during tactile temporal order judgments we ran a control experiment in which an independent group of 14 participants judged the temporal order of tactile stimulation that was not given to the subjects, but rather to the experimenter. We opted for this control experiment, as opposed to, say, performing tactile TOJ with electrical stimulation or simply detaching the vibrotactile stimulators from the participant (but not placing them on the experimenter), as this condition most closely matched the putative auditory signal delivered to participants during vibrotactile stimulation in the experimental conditions (see below). The experimenter placed his legs as to mimic the relative ear-leg location of the participant's legs in the main experiment, and participants were asked to make their temporal order judgment based not on vibrotactile stimulation, but on the auditory stimulation associated with this vibrotactile stimulation. Only the legs uncrossed, and not crossed, condition was tested, as these conditions are unchanged vis-à-vis the participants when vibrotactile stimulation is given to the experimenter and not to the subject. The rest of procedures followed as for the main experiment (see below). Results indicated no effect of SOA ($p = 0.388$) – that is, performance did not increase with longer auditory SOAs as would be expected if participants made use of this information in determining temporal order – thus ruling out the possibility that auditory information from vibrotactile stimulation played considerable role in tactile TOJ.

Deprivation of visual spatial information was accomplished by blindfolding participants for 15 min prior the tactile temporal order judgment (TOJ) task, as well as during the protocol itself. Similarly, reduced far auditory spatial information was accomplished by placing participants in an anechoic chamber (ambient noise = 15 dB(A)) 15 min prior to and during the experiment. Far environmental audiovisual spatial information was reduced by combining the two aforementioned approaches.

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