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Investigating the Inhibition of the Return of Attention in the Tactile Domain

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Abstract

Purpose: The time-course needed to elicit tactile inhibition of return (IOR) has not been well-defined due to the paucity of research in this area especially studies investigating spatial discrimination. Reportedly tactile IOR uses higher-order mental representations to orient attention spatially yet the properties of low-level dermatomal maps may better account for how IOR orients tactile attention in space although its contribution is unclear. The present study sought to establish a time-course that evokes IOR in a unimodal tactile spatial discrimination task and decouples the contribution of the dermatome from higher-order representations. **Methods:** Two conditions containing distinct tactile cue-target paradigms designed to tap into either the whole finger representation (Finger trial) and its response gradient or the dermatomal representation (Location trial) were applied to the index and middle finger-tips of both hands of 17 participants. Targets appeared at a cued or uncued finger following an inter-stimulus interval (ISI; 150, 600, or 1200 ms) for Finger trials and they appeared at cued or uncued locations after an ISI within a single finger-tip for Location trials. **Results:** At ISIs of 1200 ms IOR and facilitation of response times (RTs) were elicited for cued and uncued homologous Finger trials respectively. As ISIs increased, RTs for uncued homologous and adjacent Finger trials linearly decreased and increased respectively. Thus, Finger trial type trends exhibited a non-linear response gradient but they were not different from those of Location trials, specifically cued and uncued Location trials mirrored cued and uncued homologous Finger trials. While no facilitation and IOR occurred between Location trials, cued and uncued trials showed trends typical of IOR. **Conclusion:** We showed that tactile IOR can be elicited in a unimodal spatial discrimination task and that tactile spatial attention, oriented via IOR, is likely driven by low-level dermatomal maps.

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Attention is a highly adaptive cognitive and behavioural mechanism, which contributes greatly to the survival of complex and simple organisms alike (Koch & Tsuchya, 2007; Treisman, 1969). These attentional processes enable predation and self-preservation through the involuntary orienting of an organism's attention toward an unexpected stimulus at that peripheral spatial location (Klein, 2000). Relatedly, Posner (1980) had postulated that attention can be overtly or covertly oriented to certain locations in space, facilitating target detection and discrimination. As such, the orienting of attention in space, though limited, is an innovative method to decipher the cognitive and neural underpinnings of attention. Interestingly, Posner and Cohen (1984) had shown that certain cases of attentional orienting elicited an inhibitory effect, termed Inhibition of Return (IOR). IOR is an attentional phenomenon where the orienting of attention back to a previously attended location is inhibited and responding is thus delayed. Consequently, IOR has been studied across sensory modalities in an attempt to understand how attention is oriented and whether attention is oriented the same way across modalities (Klein, 2000; Spence, Lloyd, McGlone, Nicholls, & Driver, 2000a; Spence, Pavani, & Driver, 2000b). Most of this research has largely focused on eliciting IOR in the visual and auditory domains, whereas there is a paucity of studies investigating IOR in the tactile domain remain (Roder, Spence, & Rosler, 2002). The purpose of this study is to investigate the induction of faciliatory and IOR effects in the tactile modality by uncovering a definite time-course in which IOR is reliably produced. Surprisingly, there is little information on a time-course that consistently produces both facilitation and IOR in the tactile domain. Furthermore, previous research has observed tactile IOR between limbs (i.e., hands) and within the limb (i.e., between fingers and shoulders) but not among distinct spatial locations within a singular digit. Thus, current literature

does not address whether tactile IOR is modulated by distinct spatial locations subserved by the relevant mechanoreceptors at the level of the dermatome or if tactile stimulation primes the whole finger by way of activating the higher-order cortical representation of the finger itself. Consequently, the present study seeks to identify a specific time-course that will elicit tactile IOR, while also decoupling the contribution of lower-level dermatomal representation from the higher-order whole finger cortical somatotopic representation with respect to IOR.

Orienting of Attention

The term orienting refers to the concept of aligning attention with either the source of a sensory stimulus (overt) or an inner semantic structure (covert) and is likened to a cognitive orienting reflex (Posner, 1980; Klein, 2000). Attention being oriented to a given location does not necessitate the overt perception of that stimulus, however once the stimulus is detected the attendee can become aware of the stimulus, and provide a response (Posner, 1980). As such orienting attention to a spatial location should enhance processing at that location (Posner, 1980). Posner (1980) suggested that processing sensory stimuli effectively requires selective shifts in spatial attention, which as mentioned earlier could be oriented in two ways: exogenously and endogenously. Exogenous attention is stimulus driven, where attention is oriented automatically to a specific location following the onset of a rapid salient stimulus. Endogenous attention, however, is task driven, in that attention is voluntarily oriented to a specific location. The Posner task, which will be described below (see *Inhibition of return* section), has been used to study both forms of attention with respect to the facilitation of stimulus processing by virtue of prompted attentional orienting (Posner, 1980; Spence, Lloyd, McGlone, Nicholls, & Driver, 2000b; Klein, 2000). Accordingly, these studies suggest that exogenous and endogenous

attention are two exclusively distinct mechanisms (Cohen, Bolanowsky, & Verillo, 2005; Klein, 2000; Jones & Forester, 2014). However, exogenous and endogenous attention may likely reflect different expressions of the same neural substrate (Jones & Forester, 2012, 2014). Specifically, with regard to tactile IOR, it would seem that endogenous- and exogenous-cueing produce disparate effects, such that endogenous cueing has not been confirmed to elicit an IOR effect or facilitation, while exogenously cued IOR and facilitation has been established with varying degrees (Cohen et al., 2005; Lloyd, Bolanowski, Howard, & McGlone, 1999). Interestingly, behavioural and somatosensory ERP data indicates that endogenous attention and IOR do not emerge from the same attentional mechanism. It was shown that IOR is not moderated by endogenous attention since the trend of fast then slowed responding at previously attended locations was not seen. The exogenous attentional orienting system, however, shares similar ERP components with IOR and subserves the effect indicative of IOR (Jones & Forester, 2012, 2014). Therefore, it would appear that endogenous attention, exogenous attention, and IOR are separate mechanisms of attentional orienting, nevertheless IOR and exogenous attention seem to be interrelated, in that IOR is obtained through exogenous but not endogenous cuing (Cohen et al., 2005; Jones & Forester, 2014). As a result, the current study will be investigating IOR by means of exogenously orienting attention.

Inhibition of Return

Posner and Cohen (1984) were the first to report inhibited responding to targets presented at previously attended spatial locations through pre-emptively signaling attention to orient to those locations. This seminal experiment consisted of three squares positioned adjacent to one another. Trials began with participants fixating on a cross situated in the central box, next the

border of one of the peripherally located boxes would illuminate, reflexively orienting the participants' attention there. After a variable delay, the border of another peripheral box would illuminate at which point participants were required to respond speedily upon detecting the illuminated box (Posner & Cohen, 1984). The initial peripheral illumination served as a cue which would either predict or would not predict the appearance of the subsequent peripheral illumination or target at that location (Posner & Cohen, 1984). The predictive cue termed the valid cue, occurred 80% of the time, whereas, the non-predictive cue termed the invalid cue, occurred 20% of the time (Posner & Cohen, 1984). The variable delay between the presentation of the cue and the target, called an inter-stimulus interval (ISI), lasted between zero and 500 ms. This is a cue-target paradigm which has been subsequently branded as the Posner task and is instrumental in studying attentional processes. As speculated by Posner (1980) valid cues enabled fast RTs through the facilitation of attentional processing, in contrast to the comparatively slow RTs obtained through invalidly cued trials. This faciliatory effect became more pronounced with longer ISIs, where RTs decreased linearly with increasing ISI durations ranging from zero up to 200 ms (Posner & Cohen, 1984; Klein, 2000). Interestingly, the faciliatory effect of RTs at validly cued locations as a function of increasing ISIs, was faciliatory to a point, where ISIs of 300 ms and above showed the inverse to occur, such that RTs increased linearly with increasing ISIs. Therefore, short ISIs (zero to 200 ms) facilitated attentional processing while longer ISIs (300 ms and up) seems to inhibit attentional processing (Posner, Rafal, Choate, & Vaughan, 1985). More surprisingly it was observed that RTs for invalid trials decreased linearly along with increasing ISIs. However, RTs for invalid trials became significantly faster than RTs for valid trials at ISIs of 300 ms and above (Posner & Cohen, 1984; Posner et al., 1985). This cross-over-point between facilitation and inhibition for valid trials and

the faciliatory effects observed for invalid trials occurred between 200-300 ms (Klein, 2000). Posner and Cohen (1984) postulated that this effect is the product of an evolutionarily conserved attentional mechanism they termed inhibition of return. So, when attention is oriented to a cued location it remains at that location for a period of time, when the target is presented during that period processing is facilitated and RTs are decreased, as seen in short ISI trials (Posner, 1980; Posner & Cohen, 1984; Klein, 2000). However, if a sufficient amount of time passes between the cue and the target, the location is seen as task-irrelevant and attention disengages and is oriented elsewhere in search of the target (Posner & Cohen, 1984; Klein, 2000). Therefore, when the target appears at the cued location after attention has shifted to look for the target at a different location, it must then be re-oriented back to the cued location. Therefore, the return of attention to and the subsequent processing at a previously attended location are inhibited, resulting in the slowed RTs for valid trials observed at long ISIs (Posner & Cohen, 1984). Furthermore, this attentional orienting mechanism of IOR accounts for the faciliatory effect observed at long ISIs in invalid trials. Facilitation occurs at these longer ISIs through the same process that produces inhibition in valid trials, which is the disengaging of attention to search for the target at a different location. Accordingly, once the target is presented there is no need for attention to disengage from a previous location, and so attention is rapidly oriented to the target's location, thereby facilitating processing of the target (Klein, 2000). Taken together, IOR is an attentional mechanism yielding a biphasic effect of facilitating and inhibiting of attentional processing (Posner & Cohen, 1984; Klein, 2000). Consequently, peripheral stimuli, by virtue of IOR, could either orient and facilitate or inhibit attentional processing at that previously attended location (Posner & Cohen, 1984). IOR is an evolutionarily conserved attentional mechanism that biases attention toward novelty, facilitating exploration by way of reflexively orienting attention away

from an already explored location toward new locations (Klein, 2000). As such it is a mechanism with incredible utility for survival, whether it be for the detection of predators or the foraging of food, the bias of attention toward novelty assists in facilitating the detection and discrimination between friend, foe, or food (Klein, 2000).

Exogenous Posner tasks have been applied to the visual and auditory domain reliably producing the biphasic response of facilitation and the subsequent inhibition of RTs at short and long ISIs respectively (Posner et al., 1984; Spence & Driver, 1998). In addition, this effect has been observed cross-modally between cues and targets presented in different sensory domains and locations (Spence et al., 2000b). As such, the vast number of studies on IOR in the auditory domain and particularly the visual domain have established a time-course which reliably produces the biphasic effect of IOR (Klein, 2000; Spence & Driver, 1998, Spence et al. 2000b). The tactile domain on the other hand has been the focus of much less research with respect to producing the stereotypical IOR effect and establishing a definite time-course by which it is evoked, and it is this scarcity and ambiguity that this study seeks to resolve.

Tactile Inhibition of Return

The orienting of attention by way of cueing and the ensuing facilitation of attentional processing has been observed to carry over into the tactile domain, although the evocation and elucidation of tactile IOR along with the identification of a consistent time-course in unimodal spatial discrimination tasks remains to be seen (Cohen et al., 2005; Miles, Poliakoff, & Brown, 2008). Many studies have however, observed either facilitation or inhibition of attentional processing in tactile detection studies though none have produced both in a single study. A study by Cohen et al. (2005) used a spatial detection task to compare endogenous and exogenous

attention with respect to IOR. They applied vibrotactile stimulation on the left and right palmar surfaces with the cue and target separated by five ISIs (500, 1000, 2000, 3500, and 6000 ms). It was found that among exogenous trials there was an increase in RTs for valid but not invalid trials at longer ISIs of 1000 ms. However, they did not observe the facilitation of RTs during short ISIs in valid compared to invalid trials. Additionally, there was no indication of inhibited responding for the endogenous condition. Contrastingly, Spence and McGlone (2001) observed facilitation of targets at cued cutaneous locations in an exogenous spatial discrimination task. Their task involved vibrotactile stimulation in which subjects received simultaneous cues to the index finger and thumb on one hand for 20 ms. The target was a single vibration presented equiprobably on the finger or thumb of either hand following an ISI of either 200, 300, or 400 ms. Subjects were required to discriminate between so-called elevation by responding "up" when target stimulation was on the index finger and "down" when it was on the thumb irrespective of the cued hand. Spence and McGlone (2001) found that cueing a particular hand (by stimulating both the index finger and thumb of that hand simultaneously) facilitated responding to targets on the congruent hand regardless of being "up" – index finger or "down" - thumb at all ISIs. This provided the first instance of peripheral cuing facilitating tactile attention. In an attempt to resolve these disparate findings Miles et al. (2008) argued that cueing the finger and thumb may promote land-marking making spatial discrimination easier. Meanwhile, they asserted that the delayed responding found by Cohen et al. (2005) suggests that this effect may be due to a differing spatial attentional system involving somatic locations instead of environmental coordinates. Accordingly, Miles et al. (2008) used a non-spatial tactile discrimination task wherein a non-predictive white noise cue of high or low frequency was presented to a variable finger for 10 ms followed by an ISI of either 150, 350, 550, or 1000 ms, next, a high or low

frequency of equal probability was presented to the same or different finger as the cue. Discriminating between frequencies at the same finger compared to different fingers was facilitated during ISIs of 150 ms and inhibited during ISIs of 1000 ms. This study provides the first indication of both facilitation and inhibition within a single non-spatial tactile discrimination task. In sum, no definite time-course which produces a biphasic effect of facilitation and inhibition has been unearthed within unimodal tactile spatial discriminations tasks. Although, the aforementioned studies provide intimations about the ISI range within which IOR can be produced. Additionally, the spatial discrimination and detection tasks discussed here may likely utilize differing frames of reference to orient attention, which may contribute to the disparate findings of either facilitation or inhibition due to the location and method of stimulation (Roder, Spence, & Rosler, 2002). Such that discriminating the stimulation of the hands versus the fingers posit inherent differences with respect to the incongruous sensitivity between them, making it difficult to extend the findings from one study to the other (Johansson & Vallbo, 1979). Further the attentional systems within which they are configured may diverge, as limbs can move freely in space, and information about their spatial position and posture is determined in part by integrating visual and proprioceptive feedback, as seen in the rubber hand illusion (Lakatos & Shepard, 1997; di Pelligrino & Ladavas, 1998; Botvinick & Cohen 1998). Meanwhile the fingers are fixed to the hand and do not move through space in the same manner, and instead attending to the fingers may likely correspond to a different attentional referencing system that exists within the hand (Anderson, Snyder, Bradley, & Xing, 1997). This is further supported by the observation of finger agnosia patients who cannot differentiate between fingers but can do so for other body parts, indicating a separate mental representation for the fingers than the hand (Haggard & Wolpert, 2005). Therefore, to identify a definite time-course that produces IOR in a

tactile spatial discrimination task, the attentional orienting system employed must be consistent, and thus it is necessary to determine how attention operates at different levels in the tactile domain.

Tactile Attention

Attention connotes the necessity of a mechanism that routes information into awareness and biases attended priorities against others, it is not however, sensory specific (Posner, 1980). The observation of the biphasic cueing effect of IOR at the visual, auditory, cross-modal, and tactile (to a degree as noted above) modalities suggests that spatial attention in different sensory systems seems to indicate that it is subserved by a common attentional mechanism (Driver & Spence, 1994). These attentional mechanisms are postulated to be mediated by the superior colliculus as it responds to multimodal stimuli (Driver & Spence, 1994; Stein, Jiang, & Stanford, 2004; Sapir et al., 1999; Posner et al., 1984; Meredith & Stein, 1986; Drager & Hubel, 1976; Wallace, Meredith, & Stein, 1992, 1993). Further, it has been shown that IOR is spared in Parkinsonian patients with frontal and parietal cortical lesions, while it is abolished in progressive supranuclear palsy patients which are characterized by midbrain lesions. It has been posited that high-level cortical mechanisms may be critical for the orienting of attention, whereas more primitive low-level systems seem to control biasing towards novelty, which is characteristic of IOR (Posner et al., 1985). Interestingly, tactile attention seems to operate according to a different reference frame arrangement compared to the visual and auditory domains with respect to spatial referencing. Visual and auditory exogenous stimuli use an allocentric reference frame, which utilizes environmental spatial coordinates rather than tonotopic or retinotopic maps (Klein, 2000). However, visual IOR has been shown to use an

occulocentric attentional reference frame when eye-movement responding is required and uses an allocentric one when manual key press responses are required (Abrahams & Pratt, 2000). Similarly, tactile attention seems to be oriented according to both somatotopic and allocentric reference frames.

A study by di Pellegrino and Ladavas (1998) examined the effect of visuo-tactile stimulation of the right (ipsilesional) and left (contralesional) hands of an extinction patient with right fronto-central brain damage. They found that when a tactile stimulus was presented to the obscured left hand and a visual stimulus was presented to the unobscured right hand on the third digit simultaneously, the result was complete left hand tactile extinction. Extinction was not present when the visual stimulus was far from the ipsilesional hand, such as when the right hand was behind the patients back and the visual stimulus remained in the same location or when the visual stimulus was high above the hand. Although, when the right and left hands were crossed and simultaneous visual and tactile stimulation were presented to the hands respectively, complete left hand tactile extinction was seen. This effect is explained through the bimodal neurons found in the premotor cortex, which have receptive fields attached to certain body parts, such that these neurons have tactile receptive fields on the hand and visual receptive fields near the hand. Thus, visual stimulation near the hand taps into the receptive field of the hand, activating the corresponding perceptual representation of the hand (di Pellegrino & Ladavas, 1998). In turn, the effect of extinction seen in both regular and crossed-hand posturing provides evidence for tactile attention operating according to a somatotopic attentional reference system. Contrastingly, a study by Lakatos and Shepard (1997) asked participants to detect and respond to a pneumatic stimulation at a distinct location on their body after attending to a previous somatic location. They found that participants' response times increased as a function of distance from

the previously attended body site, but according to the allocentric rather than the somatotopic distance. These results suggest that tactile stimuli like the other modalities uses an allocentric reference frame. As such it would seem that tactile attention can be oriented with respect to two different frames of reference akin to IOR in the visual modality, which may depend on the task and whether a limb is attended to (allocentric) or a finger is attended to (somatotopic). Additionally, unlike IOR in the visual modality, where attentional systems are task dependent, it seems that in the tactile domain the somatotopic reference frame is activated first, followed by the allocentric attentional frame (Driver & Spence, 1998). A study by Roder et al. (2002) sought to differentiate between somatotopic and allocentric reference frames in an exogenous tactile orienting detection task indexed by tactile IOR. In the first experiment a tactile cue-target detection paradigm was delivered variably on one of the distal index or middle fingers on both hands, with ISIs of either 500 or 1000 ms separating the cue and the target. They found that RTs for target detection were slowed significantly at ISIs of 1000 ms for targets presented to the cued finger and hand compared to when it was on the uncued finger on the same hand, and the whole uncued hand. The magnitude of the tactile IOR effect was most prevalent when the target was presented to the cued rather than the uncued finger on the same hand, expressing that intra-hemespheric IOR effects are larger than inter-hemespheric effects for tactile IOR (Tassinari & Campara, 1996). This suggests that the contralateral hemisphere shows a more robust IOR effect than the ipsilateral hemisphere, suggesting that orienting works differently for different body locations in the same hemisphere than between hemispheres. Thus, Roder et al.'s (2002) findings suggest there is a gradient of tactile IOR similar to that of the visual domain, where target regions in close proximity to cued locations have a greater IOR response than targets distant from the cued location (Berlucchi, Tassinari, Marzi, & Stefano, 1989; Posner et al., 1980). Roder

et al. (2002) conducted a second experiment to clarify whether the gradient of IOR is driven by allocentric referencing – i.e., the magnitude of IOR is due to the cue-target locations being far/close to one another in physical space - or by somatotopic referencing – i.e., the magnitude of IOR is due to the cue-target locations being far/close to one another in cortical space. They used the same cue-target procedure but manipulated the postural positioning of both hands. In the first (non-interleaved) condition the right index and middle fingers were situated farther from the body than the left index and middle finger, such that the right index finger was positioned between the left middle and ring fingers. The second (interleaved) condition, the index and middle fingers of the two hands were interleaved, such that the right index finger was closer and positioned between the left index and middle fingers. Taken together, if the gradient of tactile IOR is determined by a somatotopic reference frame then there should be no difference in the magnitude of tactile IOR between conditions. They found that there was no significant difference between conditions. In both the non- and interleaved finger conditions RTs for detection were longest when the target was presented to the cued finger on the cued hand at a 1000 ms ISI. Interestingly, RTs were somewhat longer for targets presented to the uncued finger on the cued hand compared to the uncued hand at an ISI of 1000 ms. These findings suggest that the gradient of tactile IOR is driven by somatotopic rather than allocentric distances. It can be seen that close somatotopic relationships i.e., between adjacent fingers such as the index and middle fingers, produce greater IOR effects rather than somatotopically distant regions i.e., between non-adjacent fingers such as the index and little fingers. Thus, while exogenous orienting of tactile attention is observed to follow the posturing of one's limbs through physical space as Lakatos and Shepard (1997) found, IOR which is an inter-dependent mechanism of exogenous attentional orienting mechanism, does not (Roder et al., 2002; Jones & Forster, 2014). More complicatedly,

Roder et al.'s (2002) findings show that IOR was present for both the cued and uncued finger on the same hand (though larger in magnitude for the cued finger), while the uncued hand showed facilitated responding to target presentations on both fingers thereby indicating that the whole hand behaves as a cued location even though a specified finger on the hand was cued. This suggests that IOR (to varying degrees) is observed at all fingers on the cued hand, compared to the enhanced responding seen at all fingers for the uncued hand. Thus, IOR is observed both at the whole limb and on digits within the limb according to their respective somatotopic distance. Furthermore, given that IOR appears to be location specific, it stands to reason that IOR can be extended to occur between distinct locations within the finger, however the somatotopic organization within the finger itself is not as well-defined as the whole limb or finger. Yet, tactile IOR has been observed for the detection of targets on the posterior shoulder at the same cued location within the shoulder along with facilitation of uncued target location within the shoulder as well (Tassinari & Campara, 1996). The shoulder like the whole hand or finger has a distinct somatotopic representation associated with it, but the somatotopy of locations within the shoulder itself is crude and seemingly not as discrete. Nonetheless attention can be oriented within somatotopically discrete regions, thereby increasing the complexity of the somatotopic referencing system by which attention in general and IOR specifically is oriented. In turn, understanding the somatotopic organization with particular emphasis on the whole finger and the functional connectivity between and within somatic locations is paramount to understanding the attentional frame that IOR follows.

Somatotopic representations of the hand and fingers

The primary somatosensory cortex since its original *in vivo* mapping by Penfield and Boldrey (1937) has proved substantially more complex than containing a single somatosensory homunculus. There appears to be multiple representations of the human body within the primary somatosensory cortex (S1) (Kaas, Nelson, Sur, & Merzenich, 1979) such that stimulation of the same somatic region activates neurons in different single-cell recording sites in S1 (Powell & Mountcastle, 1959). A single-cell recording study by Kaas et al. (1979) conducted on New World monkeys showed that the four cytoarchitectonically distinct Brodmann's areas in S1 – 3a, 3b, 1, and 2 – include four separate somatic representations, unlike the continuous distorted 'homunculus' representation (Penfield & Boldrey, 1937). The subregions span across the rostro-caudal dimension of the mediolateral S1, where subregions 3b and 1 are mirror reversals of 1 and 2, reversing at subregion 1's boarder. This is not dissimilar from the reversal and retracing of retinal positions found in the visual cortex (Tootell, Tsao, & Vanduffel, 2003). Further, it appears that each subregion is selective to the type of stimulation presented and hence the type of receptor being activated. Areas 3b and 1 seem to respond to low-threshold cutaneous stimulation, while 3a and 2 respond to deep tissue stimulation (Kaas et al., 1979). Ultimately, S1 seems to consist of four functionally distinct subregions and at least areas 3b, 1, and 2 contain separate body representations. This finding was supported in humans by Overduin and Servos (2004) in an fMRI study seeking to identify subareas 3b and 1 by computing the somatotopic organization of the thumb, index, and ring fingers against control regions 3a and 4. Pneumatic stimulation applied in a "sliding window" manner moving along the proximal-distal and distal-proximal axes of the thumb, index, and ring fingers. The stimulation elicited functionally distinct and somatotopic cortical activation in areas 3b and 1 compared to control regions with respect to

representation of the digits. The size of the representations decreased from the thumb to the ring finger, being largest for the former and smallest for the latter. Expressly, the representations in area 1 were larger than those found in area 3b, whereas the frequencies of phase bands and voxels in area 3b were unequally related to the stimulation of the index finger and thumb, seemingly due to the differential size of the digits surface. This finding suggests weighted digit representations that are closely tied to the distribution of mechanoreceptors such as Meissner corpuscles and Merkel cell neurite complexes, which may account for the assortment of digit representations observed in areas 3b and 1. Therefore, like in primates there exists multiple representations of the body, which seem to be linked to the type and density of the mechanoreceptors found in that region. A study by Sanchez-Panchuelo, Francis, Bowtell, and Schluppeck (2010) sought to map the organization of the distal phalanx of all five digits in S1 using a 7.0 T fMRI scanner. They applied piezoelectric cutaneous stimulation in a manner similar to that of Overduin and Servos (2004) and found a well-ordered advancement of phase modulation reflecting an ordered somatotopic representation of digits 1-5 (thumb to little finger). Activation was confined to the posterior central sulcus and the crown of the posterior central gyrus, such that the thumb was located inferior and laterally while the remaining digits increased superior and medially. Furthermore, consistent with the findings of Overduin and Servos (2004) the thumb and index finger presented the largest representations in S1 while the little finger was the smallest representation. Showing a decrease in cortical allocation from the thumb to the little finger in a near linear fashion in the operationally identified subarea 3b (the rostral bank of the post central gyrus). The differing representational allocation is likely due to the decrease of both surface area and receptor density from the thumb to the little finger, where greater receptor density is associated with greater sensitivity (Johansson & Vallbo, 1979, 1983). This is

consistent with the original distribution of the sensory homunculus where body regions of greater sensitivity portend greater cortical territory (Penfield & Boldrey, 1937). Additionally, Overduin and Servos (2004) while finding the aforementioned disproportional representation of the thumb and index finger in area 3b, found an equal distribution of the thumb, index, and ring finger representations in area 1. They posit that this is likely due to a bias in early somatosensory processing toward receptor density, support for this stems from the anatomical evidence showing that area 3b (and 3a) is upstream from and sends projections to area 1 (Jones & Friedman, 1982). Taken together, the somatotopic organization of the digits in area 3b are ordered orthogonally, inferio-superiorly, and latero-medially from the thumb to the little finger respectively, with the cortical representation being proportional to the receptor density corresponding to each digit. This is further exemplified in a fMRI study by Sanchez-Panchuelo et al. (2012) which sought to parse out the within-digit somatotopic representation across Brodmann's areas (3a, 3b, 1, and 2) in S1 using a 7.0 T scanner, which has been shown in single cell-recordings in primates to a degree (Kaas et al., 1979). A previous study on finger-tip somatotopy (Sanchez-Panchuelo et al., 2010) informed the region of interest (ROI) employed to investigate the within-finger mapping of the left index finger. A vibrotactile traveling wave administered to the left index finger moving along the proximal-distal and vice versa axes, stimulated the interdigital pad (palmar region under the digit), base (proximal), middle, and tip (distal) of the finger. Using multivariate pattern analysis (MVPA) on the spatial pattern of responses across voxels in the ROI, allowed for the categorization of responses to distinct stimulation sites. Thus, the discrimination between different stimulus locations along the index finger to be assessed with some degree of accuracy. The observed activation was highly specific to the cortical representations of the index finger in S1, correlating highly with subregions 3a, 3b, 1, and 2. This revealed a mirror reversal of

somatotopic maps in the anterior-posterior direction as predicted by primate studies, whose configuration revealed site-specific activation of four such adjacent maps within the somatotopic representation of the index finger in S1. The anterior most mirror reversal was at the distal phalanx (tip) - at the boarder of 3a/3b, then posteriorly at the proximal phalanx (base) - at the border of 3b/1, and then another reversal at the distal phalanx - at the border of 2/1. The mirrored reversals found by Sanchez-Panchuelo et al. (2012) are identical to those found in primate studies, as such it would stand to reason that these four parallel map reversals likely reflect the four cytoarchetectonically distinct Brodmann's areas, implying four distinct somatotopic representations. Furthermore, consistent with the findings of Overduin and Servos (2004; 2008) and Sanchez-Panchuelo (2010), activation within the finger representation is biased toward the tip stimulation, this representational weighting as mentioned, is due to the higher density of cutaneous receptors found in the distal phalanx compared to the remainder of the whole digit (Johansson & Vallbo, 1979). The small receptive fields of these cutaneous receptors may likely account for the cortical magnification of the finger-tip in area 3b (Pons, Wall, Garraghty, Cusick, & Kaas, 1987). Moreover, the locus of stimulation within the index finger could be decoupled from the activation of the whole finger representation in S1, inferring the existence of a more detailed internal map of the finger. This deeper mapping could deliver information about distinct sites of cutaneous stimulation within each digit, subserving the varying degrees of spatial acuity in the tactile domain (Johansson & Vallbo, 1979). Consequently, in both primate and in non-invasive human studies there are four distinct mirror reversal maps corresponding to specific cytoarchitectonically discrete cortical regions, whose somatic representation reflect both the density and type of mechanoreceptor (Kaas et al., 1979; Sanchez-Panchuelo et al., 2010; Sanchez-Panchuelo et al., 2012; Overduin & Servos, 2004; Johansson & Vallbo, 1979). Wherein,

each subregion is receptive to their preferred type of receptor (with some overlap as will be shown). Such that area 3a – represents muscles sense in terms of position and movement, area 3b – represents slow and rapidly adapting cutaneous receptors, area 1 – represents rapidly adapting cutaneous receptors, and area 2 – represents deep pressure and joint sensation (Kaas et al., 1979; Krubitzer, Huffman, Disbrow, & Recanzone, 2004; Paul, Merzenich, & Goodman, 1972; Pons et al., 1978). Therefore, at its core each somatotopic body representation is demarcated by specific cutaneous receptors that are sensitive to particular tactile stimulation, such that activation in S1 seems to be location-specific rather than very somatotopic. This lack of somatotopy is further evidenced in an fMRI study by Besle, Sanchez-Panchuelo, Bowtell, Francis, and Schluppeck (2014) in which brief vibrotactile stimulation was applied to all five finger-tips on the left hand. The subsequent activation showed increasing overlap in finger-tip representations in S1 along the anterior-posterior direction. The anterior regions in S1 (posterior bank of the central sulcus, corresponding with area 3b) showed little overlap, to the extent that activation overlapped with up to three adjacent digits, presenting maximal activation at the finger-tip ROI for the preferred finger-tip (with overlapping activation decreasing with distance from the preferred finger-tip). Further, more posterior regions in S1 (post-central gyrus, corresponding to areas 1 and 2) showed a great amount of overlap, to the degree that ROIs for the preferred finger-tips responded to stimulation of up to five finger-tips. Accordingly, the posterior and to a lesser degree anterior S1 regions, do not seem to be as somatotopically organized at the level of the distal phalanx, which is consistent with the less precise somatotopic maps found in areas 3a and 2 in the primate S1 region (Krubitzer et al., 2004; Pons et al., 1987). The increasing overlap at the level of the finger-tip in S1 along with the cytoarchetectonically distinct subregions that are proportionally and functionally representative of cutaneous receptor type and density, supposes a location-specific

mapping that is not very somatotopic. Taken together, these findings seem to indicate the presence of a comprehensive low-level dermatomal mapping of cutaneous receptors that lies at the heart of the somatotopic organization in S1. Consequently, while IOR does orient itself with respect to a somatotopic reference system, IOR has also been shown to be location-specific both working at the level of the limb and within limb representations (Tipper & Weaver, 1998; Roder et al., 2002; Tassinari & Campara, 1996). Likewise, in Squirrel-monkeys the overlap of finger-tip representations appears to be greatest when the tactile stimulation is administered briefly, though this overlap is less evident when the tactile stimulation presented is prolonged (Simons, Chiu, Favrov, Whistle, & Tommardahl, 2007). Thus, further advancing the case for the location-specific nature of IOR, as IOR is evoked by means of rapidly appearing stimuli likely inducing substantial representational overlap in S1. In sum, it stands to reason that tactile IOR may reflect orienting with respect to a lower-level dermatomal map that informs the multiple representations of sensory homunculus.

Dermatomal somatotopy

The dermatome loosely defined, is a region of skin that is innervated by a corresponding spinal cord segment which is comprised of posterior (dorsal) and anterior (ventral) roots and their ganglia (Lee, McPhee, & Stringer, 2008). The ventral root of the spinal nerve is a tract of efferent nerve fibres that carry motor information from the spinal cord to the muscles. Meanwhile, the dorsal root is a convergence of afferent sensory nerve fibers that carry information from receptors in the skin outside, subcutaneous, and deep tissues inside the body to the posterior section of the spinal cord (Lee et al., 2008; Sharma, Kulkarni, & Gandotra, 2021). There are eight cervical (C), 12 thoracic (T), five lumbar (L), and five sacral (S) spinal nerves

(Patel, 2015). Here we are concerned with the sensory afferent portion of the dermatome, particularly the cervical dermatomal segments of C6 through C8 as they innervate the upper extremities (Patel, 2015). The dermatome is an integral concept in human anatomy with great clinical importance, however there is a great deal of variability in terms of accepted dermatomal mappings stemming from methodological and individual differences (Lee et al., 2008). As a result, Lee et al. (2008) developed an evidence-based dermatome map by aggregating previous mappings (Foerster, 1933; Bumke & Foerster, 1936; Head & Campbell, 1900) and superimposing them on one another, removing inconsistencies in exchange for good evidence found for those segments. Thus, producing the most consistent dermatomal map corresponding to each dorsal spinal root. However, none of these areas are strict autonomous zones of cutaneous sensory innervation, save for the midline, as adjacent dermatomes overlap to different degrees. It is likely that the dermatomal map is indicative of areas with the greatest concentration of cutaneous sensory innervation for that particular dorsal root. In the hand, segments C6 and C7 overlap in the thumb and index finger, while C6, C7, and C8 overlap considerably in supplying the middle finger, however, somatosensory evoked potentials for the middle finger seem to only be extinguished after sectioning the C7 dorsal root (Nemecek, Avellino, Goodkin, Little, & Kliot, 2003). Further, the ring finger looks like it is innervated primarily by C8 with some potential overlap with other segments, while the little finger is supplied by C8 with surprising overlap with T1. Hence, it can be observed that there is substantial overlap between the cervical dermatomes supplying the hand, with no discrete segment innervating one particular region. This overlap in dermatomal segments of the hand is particularly large likely due to the high proportion of intersegmental anastomoses found in 61% of cervical compared to the other dorsal roots of 100 cadavers (Moriishi, Otani, Tanaka, & Inoue, 1989). A recent study by Sharma et al.

(2021) examining intercommunications between adjacent dorsal spinal nerves in 30 cadavers, found that intra-dural intercommunications exist bilaterally at all segments of the spinal cord. However, all intercommunications were restricted to being within adjacent segments only, never extending past the adjacent segment inferiorly or superiorly. Consistent, with previous research the authors found that the prevalence of cervical interneurons was the highest making up 42.8% of interneurons found. Furthermore, within the cervical segments, bilateral interconnections were greatest between C6-C7 (Right: 66.6%, Left: 73.3%) and C7-C8 (Right: 63.3%, Left: 73.3%) with C2-C3 intercommunications being the largest overall (Right: 76.7%, Left: 80%). This accounts both for individual variability in dermatomal segmenting and the stark overlap found across many dorsal roots in general and primarily in the cervical subdivision. To this end an fMRI study by Weber et al. (2020) sought to investigate the spatial distribution of the cervical spinal nerve during tactile stimulation of the non-glabrous skin of the right and left dorsal middle fingers and lateral shoulders. Laterality was seen for both stimulation conditions but was most significant for the dorsal third finger, which exhibited noteworthy, localized activity at the ipsilateral hemicord. However, some contralateral activity was seen as well, which can probably be explained by the presence of interneurons which integrate and modulate neural activity between hemicords (Weber, Chen, Wang, Kahnt, & Parrish, 2016). Moreover, both the lateral shoulders and dorsal middle fingers did not demonstrate a distinct superior-inferior localization of activity to their respective spinal nerve sections. Instead, activity for both stimulation sites were diffused across C5, C6, and C7 spinal cord segments. This finding is likely explained by the increased proportion of intercommunications among these segments leading to activity across multiple dermatomal segments (Moriishi et al., 1989; Sharma et al., 2021). Additionally, there was a greater spatial coverage and magnitude of activation along either hemicord during the

stimulation of the dorsal middle finger compared to stimuli on the lateral shoulders at the group level (Weber et al., 2020). This effect is likely due to the discrepancy in the distribution density of mechanoreceptors between the shoulder and the finger. Evidence for this comes from studies on spatial acuity – the ability to discriminate between two stimulation loci close in space – which have shown that spatial acuity increases as function of the innervation density of the respective tissue (Mancini et al., 2014). As a result, tactile acuity as well as cutaneous receptors differ across somatic regions, however, both increase along a proximal-distal axis in the limbs (Johansson & Vallbo, 1979). Consequently, spatial acuity with respect to tactile stimulation is far greater at the dorsum of the hand than at the shoulder (Mancini et al., 2014) suggesting that stimulating the dorsal middle finger leads to the activation of a greater number of mechanoreceptors compared to lateral shoulder due to the disparity in receptor density and spatial acuity in these regions (Weber et al., 2020). So, recruiting a greater number of mechanoreceptors likely produces a stronger sensory response into the spinal nerve, thereby accounting for the greater strength and spatial extent of the activation across spinal cord segments. Accordingly, the spinal nerves are themselves not discrete somatotopic regions of sensory innervation with much overlap between dermatome segments due to intercommunication between segments and interneuronal influence (Sharma et al., 2021; Weber et al., 2016; Weber et al., 2021). Therefore, it would seem that the variable distribution of mechanoreceptors across the body is an integral feature in localizing and discriminating somatosensory stimulation, to the degree that different somatic regions will produce a differing magnitude of activation at the dorsal root depending on the density of receptors at that region. Taken together, the distribution of mechanoreceptors throughout the body – which is directly related to spatial acuity and the localization of stimuli on the body – may act as a crude lower-level map within a less distinct

dermatomal representation of the body (Weber et al., 2020; Johansson & Vallbo, 1979, 1983; Abraira & Ginty, 2013). Subsequently, it may be within this low-level representation that tactile stimuli are processed and IOR is oriented.

Tactile Receptors and Localized Attention

The tactile sensory system is responsible for allowing the largest organ in the human body – the skin – to interact directly with the outside world (Barnett, 1972). Consequently, the tactile domain is the largest of the sensory systems and is equipped with a vast array of complex and diverse sensory receptors. These receptors promote the sensation of distinct stimuli and the subsequent perception of pain, pressure, vibration, temperature, textural differences, stretching, proprioception, and so on (Gallace & Spence, 2014; Bensmaia & Hollins, 2005). Ensembles of diverse and specialized mechanoreceptors come together to facilitate the perceptive quality of any given tactile sensation (Abraira & Ginty, 2013). Further, the numerosity of receptors in highly sensitive regions is unparalleled as the human hand alone contains an estimated 17,000 mechanoreceptors, potentially overshadowing the eye in terms of processing complexity (Johansson & Vallbo, 1983). In a similar vein, both the human eye and the human hand are instruments with which humans can explore the world around them, facilitated through the fovea in the eye and the finger-tip in the hand as they are densely populated by sensory receptors fostering high levels of acuity for detection and discrimination of stimuli (Posner, 1980; Johansson & Vallbo, 1983). Likewise, in the visual domain where photoreceptors react preferentially to specific wavelengths collaborating with one another to facilitate colour vision, the same is true for the sensory modalities of touch (Abraira & Ginty, 2013; Bensmaia & Hollins, 2005). The dynamic interplay between mechanoreceptors and their respective

mechanoreceptive afferents at the dorsal root gives rise to the exteroceptive, interoceptive, and proprioceptive functions of the somatosensory system, as well as the elicitation of diverse stimulus specific sensations and perceptions (i.e., vibration, indentation, movement, stretch, etc.) (Abraira & Ginty, 2013; Bensmaia & Hollins, 2005; Gallace & Spence, 2014; Weber et al., 2016).

a) Mechanoreceptors and cutaneous end organs

The initial stage of somatosensory perception involves the activation of the primary sensory neurons nested in the dorsal root ganglia and cranial ganglia. Dorsal root ganglian neurons extend peripherally innervating skin at the extremities and penetrate the spinal cord synapsing with neurons in the gray matter and the dorsal column within the spinal cord (Abraira & Ginty, 2013). With respect to the exteroceptive function of the somatosensory system, there are two divisions of mechanoreceptive sensory neurons: low-threshold mechanoreceptors (LTMR) and high-threshold mechanoreceptors (HTMR; Johansson & Vallbo, 1979,1983). LTMRs respond to innocuous mechanical stimulation at a comparatively low intensity i.e., soft touch, while HTMRs respond to harmful mechanical stimulation at higher intensities i.e., hard taps (Johansson & Vallbo, 1979; Abraira & Ginty, 2013). LTMRs are found both in hairy and glabrous (non-hairy) skin, however their associated fibers differ (it should be mentioned that hairy skin and HTMRs will not be discussed as they do not directly relate to the focus of this thesis). In the glabrous skin, LTMRs are primarily characterized by large cell bodies and heavily myelinated Aβ cutaneous sensory neuron processes with decently fast action potential conduction velocities ranging from 16 to 100 m/s. Additionally, there are Aδ cutaneous sensory fibres which are characterized by medium cell bodies and lightly myelinated processes with conduction velocities ranging from 5 to 30 m/s, in contrast C-type sensory neurons are the

smallest and most plentiful characterized by unmyelinated axons and the slowest conduction velocities ranging from .2 to 2 m/s (Abraira & Ginty, 2013). A further subdivision of LTMRs is found in the differing adaptation properties with respect to sustained mechanical stimuli – being either rapidly adapting (RA) type I and II (RAI and RAII respectively) or slowly adapting (SA) type I and II (SAI and SAII respectively) (Johansson & Vallbo, 1979, 1983). RA units respond only when a mechanical stimulus is applied and when it is removed, while SA units display a sustained rate of irregular firing that is maintained throughout the duration of skin indentation, increasing linearly with the depth of the indentation (Johansson & Vallbo, 1979, 1983). Additionally, LTMR subtypes are characterized by their association with specific cutaneous end organs that selectively respond to particular mechanical stimulation (Johansson & Vallbo, 1983; Abraira & Ginty, 2013). Four types of these mechanoreceptor end organs can be found in the glabrous skin: Pacinian corpuscles, Ruffini endings, Meissner corpuscles, and Merkel discs (Johansson & Vallbo, 1979; Abraira & Ginty, 2013; Gallace & Spence, 2014). The SAI-LTMRs have small well-defined receptive fields, with Merkel cell neurite complex end organs that are enriched at highly sensitive areas of the skin (Abraira & Ginty, 2013). These afferent units densely innervate the skin with the greatest density observed at the finger-tips then decreasing drastically toward the wrist. SAI-LTMRs respond maximally to points, edges, corners, and curves of objects indenting the skin (Johansson & Vallbo, 1983; Vega-Bermudez & Johnson, 1999). Additionally, SAI units are very sensitive to both the position and velocity of a cutaneous stimulus (Johansson & Vallbo, 1983). Taken together, the density of Merkel cell neurite complexes and SAI-LTMRs along with their innervation patterns permit the capacity for the extraordinary ability of tactile discrimination, spatial acuity, and the resolution of local details in humans (Vega-Bermudez & Johnson, 1999). The SAII-LTMRs however, are far less sensitive

than SAI-LTMRs, with wide and not well-defined receptive fields that are uniformly distributed across the skin, they transmit information about skin stretch and changes in hand and finger shape, with end organs likely being the Ruffini corpuscles (Johansson & Vallbo, 1983; Johnson, 2001; Abraira & Ginty, 2013). With respect to the rapidly adapting units, RAI-LTMRs have small well-defined receptive fields that terminate onto the Meissner corpuscle end organs which innervate the skin more densely than but at the same density gradient (decreasing from the finger-tip to the wrist) as the SAI afferent units (Johnson, 2001; Johansson & Vallbo, 1983). The function of RAI afferent units is the detection and scaling of low frequency vibration (1-10Hz) i.e., the sensation of tapping, though they seemingly possess attributes specialized for controlled grip as they are sensitive to object slip (Abraira & Ginty, 2013; Johnson, 2001). Both SAI- and RAI-LTMRs respectively display particular conduction velocities within the Aβ fiber range, suggesting that these two afferent units complement one another in order to discriminate among varying tactile stimuli with respect to type and location (Abraira & Ginty, 2013). To the extent that signals from SAI and RAI afferent units identify the location of edge lines on the skin, suggestive of a mechanism that processes and enriches spatial contrast and the awareness of edges at the afferent unit level (Johansson & Vallbo, 1983). This complementary relationship is akin to that of the scotopic and photopic systems in the visual domain where RAI units are similar to rods which are highly sensitive at the expense of limiting spatial acuity and dynamic range, and SAI units are comparable to the cones in being less sensitive for the benefit of having superior spatial resolution and the ability to function over a wider dynamic range (Johnson, 2001). Unlike the RAI afferent units, the RAII-LTMRs are exceptionally sensitive to high frequency vibrations, with lower amplitude thresholds due to the physiological properties of the Pacinian corpuscle end organs (Johansson & Vallbo, 1979, 1983; Abraira & Ginty, 2013). The

receptive fields of the Pacinian corpuscle are exceptionally large, encompassing whole fingers and often the entire hand, while they are extremely sensitive and can respond to motion on the skin in the nanometer range although Pacinian corpuscles afferents cannot discern between objects with any degree of spatial acuity (Johnson, 2001; Abraira & Ginty, 2013; Johansson & Vallbo, 1983). This may be why Miles et al. (2008) were able to evoke a biphasic IOR effect through the use of different vibrotactile stimulation frequencies, while other uses of vibrotactile stimulation in varying spatial discrimination tasks failed to produce this effect (Cohen et al. 2005; Spence & McGlone, 2001). Therefore, the type of stimulation employed likely impacts the reliable elicitation of IOR with respect to spatial discrimination. By the same token, stimulation of the palm, shoulder, and finger-tip all recruit differing densities of mechanoreceptive afferent units amounting to varying capacities for spatial acuity and tactile discrimination (Weber et al., 2020; Johansson & Vallbo, 1979, 1983). The finger-tip which has the highest such spatial acuity and tactile discrimination has been observed as a fundamental and primary device in tactile exploration, the whole finger and hand are auxiliary components to the finger-tip assisting in object manipulation for the purposes of tactile discrimination (Johansson & Vallbo, 1983; Lederman & Klatsky, 1987). The ease of localizing tactile stimuli depends on the type and the density of mechanoreceptor units stimulated due to their differing innervation patterns, conduction velocities, and strength of input (Abraira & Ginty, 2013). This suggests that tactile IOR may be oriented according to a lower-level dermatomal mapping of cutaneous receptors, particularly through the integration of differing innervation and response patterns of SAI- and RAI-LTMR afferents at the subcortical dorsal horn level (Abraira et al., 2017; Johansson & Vallbo, 1983).

b) Organization and information processing within the dorsal horn of the spinal cord

Cutaneous sensory perception begins by processing the distinct ensemble activations of sensory subtypes that are somatotopically arranged according to LTMR inputs at the dorsal horn (Li et al., 2011). The direct pathway transmitting and processing light touch information begins with direct LTMR projections through the dorsal columns onto the brainstem dorsal column nuclei - nucleus gracilis and cuneatis. These nuclei project the input forward to the thalamus through the medial lemniscus, where thalmocortical projections carry the information to S1 (Mountcastle, 1957). However, evidence suggests that processing of LTMR afferent inputs occurs much earlier potentially within the spinal cord dorsal horn, similar to the pre-cortical visual processing that has been observed within the retina (Li et al., 2011; Masland, 2012). A study by Li et al. (2011) used molecular-genetic labeling and somatotopic retrograde tracing in mice to illustrate the organization of central and peripheral axonal terminations of physiologically dissimilar LTMR subunits mediating touch. It was shown that complex tactile stimuli are differentiated, represented, integrated, and processed via the collective and distinct activations of the three functionally different hair follicle types and their respective conduction velocities at the dorsal horn. They postulate that the integration of the relative spatial distribution and unique morphologies of hair follicles, a combination of associated LTMR endings, and the conduction velocities, spike train patterns, and adaptation features of each hair follicle LTMR type leads to the intricate qualities of touch projected to the CNS. Consequently, the near infinite number of potential combinations provides the somatosensory systems with an exceptional collection of potential LTMR activation groupings to encode and define a specific tactile stimulation. The projections of varying fibres that innervate common external LTMR units orient themselves in a columnar manner that is somatotopically arranged in the spinal cord dorsal horn.

It may be there that the locus of integration and processing of cutaneous information begins prior to its ascent to the CNS. Supporting this notion is that only a subset of LTMRs extend to the dorsal column nucleus, whereas all LTMR axonal branches terminate in the dorsal root (Brown, 1981).

The dorsal spinal cord can be divided into cytoarchitectonically distinct Rexed lamina within the dorsal-ventral plane. Lamina I and II, characterized by thinly myelinated fibers, make up the outer lamina of the dorsal horn, while III through VI, are characterized by much larger cell bodies and comprise the remainder of laminar segments (Li et al., 2011; Abraira & Ginty, 2013). The termination of LTMR arborizations can be found within their functionally associated laminar sections, with C fibres (innervating hairy skin) and Aβ fibres innervating the outer and deeper layers of the dorsal horn lamina respectively (Li et al., 2011; Abraira & Ginty, 2013). Thus, the morphological and anatomical organization of the spinal cord displays the necessary translation of receptive fields for the processing of tactile information carried from the skin through organized inputs of unique LTMR subtypes into a somatotopic columnar arrangement within the dorsal horn (Abraira & Ginty, 2013). Additionally, within the discrete somatotopic columnar distribution, LTMR afferent units converge onto iterative components indicative of an early stage in somatosensory processing (Abraira & Ginty, 2013). Output neurons from the dorsal horn carrying information regarding light touch to the brain suggests functional differences between laminar sections. Innocuous touch information flows from III to VI through ventrally directed interneurons with outputs from these laminae processed within both the post-synaptic dorsal column (PSDC) neurons and the spinocervical tract (SCT) neurons. Originating in overlapping segments of the deep lamina (specifically lamina IV) these outputs along with the direct pathway, carry innocuous tactile information to the brain (Brown, 1981; Abraira & Ginty,

2013; Li et al., 2011). A majority of neurons in the dorsal horn are locally projecting interneurons, which have been well documented at outer lamina layers I and II, and are functionally related to pain, temperature, and itch perception (Abraira & Ginty, 2013). However, much less is known about deep dorsal horn lamina layers III-V. It is speculated that LTMRs that are sensitive to innocuous touch synapse onto interneurons located in laminae IIi, III, and, IV, where ascending indirect PSDC pathways carry processed and perceptually germane innocuous tactile information from the dorsal horn to the cortex (Koch, Acton, & Goulding, 2018; Abraira et al., 2017).

Abraira et al. (2017) identified genes expressed within select LTMR-receptive zone (RZ, found beneath lamina IIi and terminating in lamina IV) neuronal subtypes in the dorsal horn of the spinal cord, to elucidate its organizational logic and the role it plays in processing light touch and tactile perception. It was observed that the LTMR-RZ displays elaborate neuronal and synaptic sophistication, which is integral for sensorimotor gating and the perception of touch (Abraira & Ginty, 2013; Brown, 1981; Bourane et al., 2015). This suggests that the dorsal horn contains a highly integrative paradigm of innocuous touch, driven by LTMR subtype activity from the skin and descending modulatory contributions from the cortex that converge onto LTMR-RZ interneuron subtypes. Each LTMR-RZ interneuron subunit acts as a functionally selective integrator/processor for specific tactile modalities and cortically descending inputs in order to synchronize the impulse patterns of ascending LTMR-RZ projection neurons that subserve the percept of touch. The genetic labeling identified 11 locally projecting LTMR-RZ interneuron subtypes (seven excitatory ~70% and five inhibitory ~30%) which accounts for the majority of neurons in this region, while less than 2% are PSDC projection neurons. This supports the notion that processing, and integration occur within the LTMR-RZ. Further, laminar

positioning does not reflect the way in which LTMR-RZ units receive inputs directly from the large number of LTMRs. Instead, the LTMR-RZ interneuron subunits receive a distinct combination of LTMR inputs, which in turn influence their output by way of being weighted by the combined inputs from those different modalities. This is due to the diverse properties of LTMR subtypes, which differ according to action potential velocities, tuning properties, size of receptive fields, and adaptation properties (Johansson & Vallbo, 1979, 1983; Abraira et al., 2017). Thus, by virtue of the great variety of inputs, LTMR-RZ interneuron outputs can mirror a countless number of LTMR activities, accounting in part, for the perception of the incredible sensational diversity of innocuous touch. Moreover, it is theorized that the integrative processing in the LTMR-RZ is facilitated by parallel LTMR processing modules, which is underscored by the finding that individual LTMR subtypes separate to synapse directly onto several postsynaptic LTMR-RZ interneuron types (Abraira et al., 2017). Additionally, the excitatory wiring scheme for each LTMR-RZ interneuron type is made up by a small fraction of inputs from individual LTMR subtypes. This diffuse input distribution dispensed across the LTMR-RZ illustrates a synaptic architecture characteristic of parallel LTMR input modules. Such parallel channels are further exemplified by a high degree of network interconnectivity, which is observed in LTMR-RZ where most of the synapses formed by its interneuron are found within it and most of the excitatory inputs onto the 11 LTMR-RZ interneurons begin within the spinal cord. The parallel processing of LTMR inputs provides a substrate for integration, plasticity, and context-specific output (Abraira et al., 2017). While sensory integration and processing occur among LTMR input and LTMR-RZ interneuron output, the excitatory synaptic input from corticospinal neurons implies another property of the LTMR-RZ. Excitatory synaptic input from corticospinal neurons broadly and directly involves each LTMR-RZ interneuron, the incidence of these cortical inputs

into LTMR-RZ region specifically, indicates that the LTMR-RZ is a locus for somatosensory modulation during conscious tactile exploration (Abraira et al., 2017; Abraira & Ginty, 2013). Further, the even distribution of cortical inputs across all interneuron subtypes posits that cortical activity can impact the signal strength of all innocuous touch circuit modules, as evidenced through the evocation of dorsal root potentials produced by stimulating S1 in cats (Andersen, Eccles, & Sears, 1962). The corticospinal projections can thus modulate signal strength via interneurons that form axoaxonic inhibitory synapses at LTMR terminals. Subsequently, descending cortical inputs to LTMR-RZ parallels LTMR inputs with respect to the wide assortment of LTMR-RZ interneuron targets and number of synapses. Taken together, the LTMR-RZ may act as a hub for facilitating the modulation of signal strength during active tactile exploration compared to passive touch. Abraira et al. (2017) posit that LTMR-RZ interneurons obtain inputs from the cortex and LTMRs in order to sensitize/desensitize tactile pathways in a manner that is modality-specific and somatotopically arranged, enabling the differential processing of tactile inputs through tactile exploration and passive touch. Finally, the perception of touch largely depends on the LTMR inputs onto the LTMR-RZ interneurons and the resultant neurons carrying output to the brain (Abraira & Ginty, 2013; Abraira et al., 2017). This has been observed in a texture-specific novel object recognition task where control mice prefer novel over familiar textured objects thereby displaying the capacity for tactile discrimination. However, mice with silenced $CCK^{iresCre}$ – or $Ror^{iresCre}$– labelled interneuron lineages did not display novelty seeking, indicating an inability to discriminate between tactually different objects. The modality specific effect the genetic silencing of the interneurons was evidenced by the comparable ability of both mice in discriminating between visually distinct objects -- equally preferring novel objects in a visual form of the same task. Thus, excitatory and inhibitory

LTMR-RZ interneuron subtypes are necessary for texture discrimination and are invaluable for innocuous touch perception. Moreover, the PSDC neuronal pathway is the chief most output neuronal population of the LTMR-RZ, which receives direct inputs from Aβ RA-LTMR and indirect inputs from LTMR-RZ interneurons which are synaptically associated with all LTMR subtypes and cortical neurons. As a result, it is evident that processing of subsequent perception of innocuous touch information is initiated in the LTMR-RZ and is then output to the brain along postsynaptic ascending pathways. In sum, the processing and subsequent perception of touch information leading to the capacity for tactile discrimination necessitates the integration of the myriad LTMR afferent inputs from the skin together with descending modulatory inputs from the cortex where they converge onto LTMR-RZ neuronal networks. As such the LTMR-RZ evidently plays a substantial role in somatosensory processing by integrating the sensory inputs and activity of ascending touch pathways subserving tactile perception, via a complex neuronal and synaptic network that arguably outshines the retina.

c) Tactile IOR is driven by a dorsal horn spinal cord schema

The combination of the diverse array of mechanoreceptors with respect to their preferred stimuli, distribution across the skin, adaptation properties, and conduction velocities provide incredibly distinct inputs onto the interneurons in the spinal cord dorsal root (Abraira & Ginty, 2013). It thus appears that the localization and discrimination of tactile stimulation depends on these inputs and the interneuron processing that occurs within the spinal cord in a parallel manner. Further, the dorsal horn contains cortical inputs that appear to modulate tactile exploration and passive touch, and interneuron subtypes that are responsible for tactile discrimination (Johansson & Vallbo, 1979, 1983; Johnson, 2000; Abraira et al., 2017). Taken together, it appears that the dermatome with specific emphasis on mechanoreceptive units is a

good candidate for a referencing system within which tactile IOR works. This is because the cortical and dermatomal representation of stimulated somatic locations greatly overlap with adjacent somatotopic and dermatomal representations such that the activation of distinctly stimulated locations are distributed across adjacent cortical and dermatomal representations making it difficult to hone in on the particular preferred site of stimulation and disassociating it from non-preferred sites (Weber et al., 2020; Besle et al., 2014; Sharma et al., 2021). In turn the aforementioned mechanisms are likely a good substrate for the integration of inputs from mechanoreceptive units onto the interneurons in the spinal cord dorsal root allowing for the localization of stimulation at discrete locations within the overlapping representations (Abraira et al., 2017). Evidence for this is the observation that the centers of greatest activation within the overlapping dermatomal and somatotopic maps index the location of stimulation (Weber et al., 2020; Besle et al., 2014). The interneurons in the spinal cord are likely responsible for the distribution of activity, however, the differing types and innervation patterns of mechanoreceptive units in the skin lead to differing strengths of activation representative of the stimulated region (Weber et al., 2020; Besle et al., 2014; Johansson & Vallbo, 1983). In turn, it may be this pattern of activity and innervation in the dorsal root that tactile attention is oriented to, as supported by the role they play in facilitating spatial discrimination and acuity (Johansson & Vallbo, 1983; Abraira & Ginty, 2013; Bensmaia & Hollins, 2005; Gallace & Spence, 2014). Further, being that IOR is a reflexive low-level cognitive mechanism that biases attention toward novelty in order to facilitate searching, the modulatory property of cortical inputs may act to facilitate this mechanism as it is implicated in tactile exploration (Klein, 2000; Abraira et al., 2017). This is further exemplified by the observance of interneuron subtypes that are implicated in tactile discrimination prompting mice to explore novel tactile objects rather than familiar ones

(Abraira et al., 2017). In consequence, it is probable that these features come together to facilitate tactile IOR, such that attention is oriented by virtue of the combinatory properties of mechanoreceptive units and their interneuronal connections in the dorsal horn wherein cortical inputs modulating exploration and interneurons implicated in tactile discrimination may work to bias attention toward different populations in the dorsal horn. Finally, this model can account for tactile IOR found in non-spatial tactile discrimination tasks using differing vibrotactile frequency stimulations and tactile detection tasks. This is because the modulatory property of the dorsal horn biases attention to novel cell populations during exploration which are the product of a combination of inputs rather than being strictly somatotopic (Miles et al., 2008; Roder et al., 2002; Cohen et al., 2005; Spence & McGlone, 2001; Tassinari & Campara, 1996; Abraira & Ginty, 2013; Abraira et al., 2017; Johansson & Vallbo, 1979, 1983). Hence, it stands to reason that if tactile IOR functions by biasing attention toward novel cell populations, whose combined input and interneuronal connections colours the type of tactile information to be processed, then it is likely that this mechanism can elicit IOR in a tactile spatial discrimination task by the same token. Ultimately, there is substantial reason to believe that tactile IOR is oriented with respect to a lower-level dermatomal referencing system underlying the location and stimulation specific nature of tactile IOR. Thus, it is necessary to parcel out the contribution of the dermatome from the higher-order representation of the finger with respect to IOR.

Current Study

The current study seeks to investigate a time-course that will reliably produce the biphasic effect of IOR characterized by enhanced and slowed responding to targets presented at a previously attended location within a single unimodal spatial tactile discrimination task, as none

have yet to do so. Furthermore, the complexity of attentional referencing systems with respect to governing tactile attention at the level of the whole limb, finger, and discretely stimulated locations within them suggests the presence of another attentional schema at the dermatome. As such, this study seeks to decouple the contribution of the low-level dermatomal organization from the higher-order whole finger cortical representation. To investigate the time-course of tactile IOR with respect to spatial discrimination a cue-target paradigm, canonically used to elicit IOR, was adapted to the tactile domain. We used a time-course intimated at by previous studies (Miles et al., 2008; Roder et al., 2002; Cohen et al., 2005; Spence & McGlone, 2001; Tassinari & Campara, 1996; Jones & Forster, 2014) of tactile IOR shown to enhance and inhibit responding using ISIs of 150, 600, and 1200 ms. The cue and target were delivered to the distal phalanx of the index and middle fingers of the right and left hand through indenting stimuli via piezoelectric braille devices, where the target was presented to the same or a different finger as the cue. It is hypothesized that cued fingers will facilitate responding to targets at that finger, compared to uncued fingers at an ISI of 150 ms. Whereas, at an ISI of 1200 ms responding to targets on the cued finger will be slower compared to targets at uncued fingers. Additionally, it is suspected that after the optimal ISI of 600 ms ISIs there will be the cross-over point from facilitation to inhibition, such that facilitation should be maximal for cued fingers. Hence, RTs for cued fingers should decrease from 150 to 600 ms and increase from 600 to 1200 ms, while RTs for uncued fingers should decrease from 150 through to 1200 ms. In order to determine whether the dermatome contributes to tactile IOR, we utilize the same cue-target procedure and time-course, however, rather than stimulating the whole pad of the distal phalanx we stimulated distinct points within a given finger-tip. Thus, the cue and target were always within the same finger-tip but their locations on the finger-tip varied. It was hypothesized that if the dermatome does contribute

to tactile IOR as an attentional referencing system, then there should be no difference between the fingers and locations within the finger-tip in terms of IOR effects such that the same trends of enhanced and slowed responding for cued and uncued fingers should be observed for distinct locations within the finger-tip. Lastly, we assessed the gradient of IOR for the fingers in order to parse out the effect of the somatotopic reference system, such that somotatopically proximal digits to a location exhibiting IOR will also express IOR but to lesser extent, while distant somatotopic digits from the inhibited zone will show faciliatory responding.

If our time-course evokes facilitation and IOR then there will be a main effect of ISI and an interaction between validity and ISI for both Finger and Location trials respectively. Additionally, if Finger and Location trials share an attentional reference frame then there should be no main effect of condition, when comparing response time trends between Finger and Location trials for valid and invalid trials separately.

Methods

Participants

Participants were 17 right-handed undergraduate students from Wilfrid Laurier University, recruited using the Psychology Research Experience Program (PREP). Participants recruited through PREP were awarded class credit for participation in the study commensurate to the duration of the experiment. Participants whose accuracy was below 70% were removed from analysis, three were removed because of accuracy scores below 70% (see Table 1, Appendix). All participants gave written and informed consent prior to the start of the experiment.

Apparatus and Stimuli

Tactile stimuli were presented using four piezoelectric braille devices (*Metec*, Stuttgart, Germany) to the distal phalanx of the both the right and left index and middle fingers. The device contains a 4 x 2 matrix of plastic pins (eight pins in total) and would systematically raise a given pin in the matrix causing a sensation of pressure on a specified finger-tip (see figures 1,2, and 3). Each cell was exactly the same with the dimensions being 12.4 mm in length and 6.42 mm in width and each pin on the matrix was separated equidistantly at a distance of 2.5 mm from each other rising at a height of .7 mm with a force of 17 cN. The SAI and RAI receptor density, evenly spaced within the finger-tip is 1.3 mm and .9 mm, respectively, from center-to-center of the receptive field, with minimal thresholds respectively, being less than 15 m for indentation and between 1-10 Hz for tapping (Johansson & Vallbo, 1983; Abraira & Ginty, 2013). The spatial resolution for SAI is up to .5 mm for individual afferents (Abraira & Ginty, 2013). Taken together the stimuli and apparatus used here both fit within the distal pad of the finger and provides indentation stimulations sufficiently distant and deep to exceed the psychophysical threshold for detecting and discriminating pointed cutaneous stimuli. The tactile stimuli were presented to two possible locations on the finger-tip, either top left or bottom left in the 'Location' trial (see Figure 2a, b). In the 'Finger' trial the tactile stimuli were presented to both the top and bottom left portions of the finger-tip(s) simultaneously (see Figure 3a, b). Participants RTs were captured vocally using a *Chronos* multifunctional serial response device (Psychology Software Tools Inc., Sharpsburg, PA, USA). While accuracy of response "same" or "different" was recoded manually while participants responded verbally into the *Chronos* multifunctional serial response device. The study was designed and run using E-Prime 2.0 Professional (Psychology Software Tools Inc., Sharpsburg, PA, USA) which controlled the

Chronos multifunctional serial response device and the *Metec* braille cell device. The study was run on a Dell PC (Windows 7), participants used an Apple iPod Nano with Bose noise cancelling earphones to listen to pink noise during the experimental trials to block out any potential auditory cuing from the tactile stimuli and a black box was placed over both the apparatus and their hands which obscured participants' hands from their view (see figure 4). These measures were instituted to specifically isolate the tactile stimulation.

Procedure

The present study used a cue-target paradigm where a cuing stimulus would be presented initially followed by a variable ISI of 150, 600, or 1200 ms and then subsequently followed by the target stimulus. The participants' task was to respond vocally and as fast as possible whether the target was in the same location or a different location than the cue. There were 12 blocks: six involved Location trials, containing 60 trials in each and six involved Finger trials, containing 62 trials in each block adding up to 732 trials in each session in a within-subjects repeated-measures design: 2 (Trial type: Finger, Location) x 2 (Validity: valid, invalid) x 3(ISI: 150, 600, 1200 ms).

Location trials were presented to a single digit randomly selected from either the left and right index and middle fingers. In this trial type the cue stimulated a distinct location on the distal phalanx on which the target was presented to either the same location in valid trials or a different location in invalid trials following a variable ISI (see Figure 1a, b). Finger trials followed the same cue-target paradigm except the whole finger was cued using two simultaneous pin presentations rather than one, additionally, the target was presented to either the same finger on the same hand (SFSH) in the valid trials or a different finger in the invalid trials following a variable ISI (see Figure 2a, b). The invalid Finger trials however, consisted of three types of

invalid trials meant to account for variation in RT and assess the gradient of response due to the somatotopic functional connectivity between each digit (Roder et al., 2002; Besle et al., 2014). The invalid trials were titled Same-Finger-Different-Hand (SFDH) where the target was presented to the same finger as the cue on the opposite hand (i.e., left index finger to right index finger); Different-Finger-Same-Hand (DFSH) where the target was presented to a different finger than the cue on the same hand (i.e., left index to left middle); and Different-Finger-Different-Hand (DFDH) where the target was presented to a different finger than the cue on the opposing hand (i.e., left index to right middle). Cumulatively these trial types create the invalid level in the Finger trial condition. Location and Finger trials never occurred in the same block. Thus, six different types of trials were used: Location trials which involved valid and invalid cue-target trials, and Finger trials involving valid (SFSH) and invalid (SFDH, DFSH, and DFDH) cue-target trials. The distribution of valid to invalid trails in both the Location and Finger trials consisted of 80% valid trials and 20% invalid trials, mimicking the distribution used in the original Posner task. There were 60 invalid trials and 300 valid trials in the Location trial condition (see Table 2, Appendix) and there were 70 invalid trials and 302 valid trials in the Finger condition (see Table 3, Appendix). All trials in each block were randomized through E-Prime 2.0 Professional (Psychology Software Tools Inc., Sharpsburg, PA, USA) randomizer. Each trial type had 3 levels of ISI: 150, 600, or 1200 ms. These ISIs were spread out evenly across all trial types. However, it must be mentioned that due to coding errors two invalid Finger trial types were not used in the experiment and as a result four invalid Finger trials had a greater number of trials than desired due to the error (see Table 2, Appendix). The coding errors are not suspected to cause an issue in analysis as each invalid finger trial has a parallel trial, such that a cue-target trial exists for cuing the left index to presenting the target at the right index and vice

versa. The order of cue-target stimulation does not influence RT and therefore the data produced is valid (Roder et al., 2002).

The participants began the experiment with a 10-trial practice session for both the Finger and Location condition, which was not analyzed in order to familiarize them with the task of differentiating the tactile stimuli and to orient them with the experiment. Participants were told the study investigated tactile perception in humans and were instructed to respond "same" or "different" according to the cue-target stimuli felt, as quickly as possible into the microphone. Trials would begin with participants saying a word of their choosing into the microphone to prompt the trials to begin. At the start of each trial all eight pins on each finger would rise for 50 ms to both indicate the start of the trial and act as a central fixation cue to un-bias all the fingers from any previous stimulation that may have caused attention or any cross-activation (Besle et al., 2014) to linger at a location from a previous trial. After the central fixation cue was presented a delay of 250 ms occurred prior to the cuing stimulus in order for participants to be ready and not confuse it with the central fixation cue. Next the cue would appear, followed by a variable ISI and then the target, after which participants discriminated between the stimuli as rapidly as possible and state whether they were the same or different. The trial would end only once the participant responded into the microphone which would trigger the next trial. This paradigm was the same for both Location and Finger trials. There was no sensory stimulus used in the experiment other than the tactile stimulation and pink noise that blocked out the sound of the pins popping up. Each block took approximately 10 minutes to complete depending on the rapidity of participants' responses. Participants went through six blocks (three Location and three Finger blocks) per session over two sessions (60 minutes per session). At the end of each two-

part session participants were told the true nature of the study. Concealment was used here so that participants would not fall prey to demand characteristics.

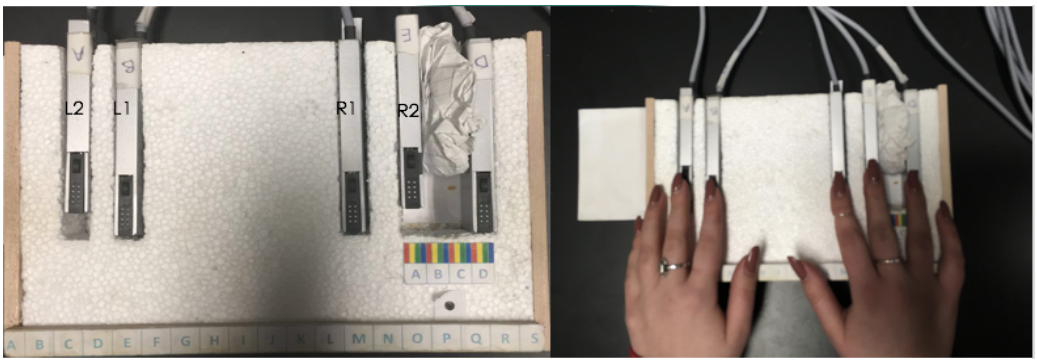


Figure 1: Apparatus and hand positioning. (left) *Metec* piezoelectric refreshable braille device, devices labelled L1, L2, R1 and R2 were used. (right) Participants' hand positioning on the apparatus.

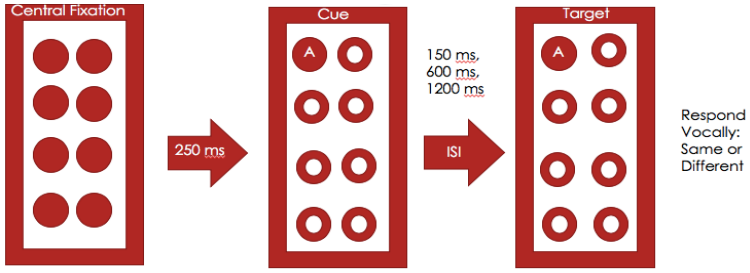
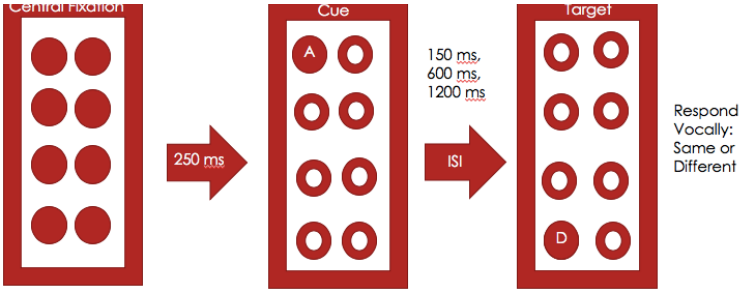


Figure 2: 4 x 2 grid on a piezoelectric braille device during Location trials. (a) Sequence of tactile stimuli for valid location trials, cuing location A and presenting the stimuli at target A after the ISI, on a single digit.



(b) Sequence of tactile stimuli during invalid Location trials, cuing location A and presenting the stimuli to location D after the ISI, on a single digit.

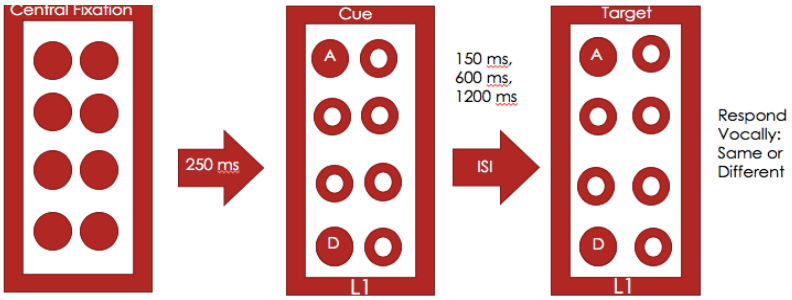
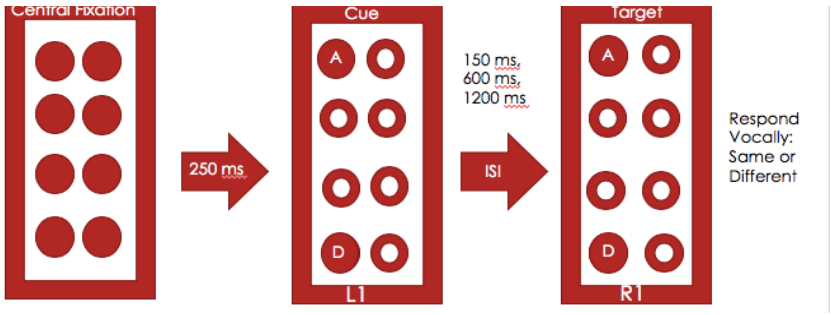


Figure 3: 4 x 2 grid on a piezoelectric braille device during Finger trials. (a) Sequence of tactile stimuli during valid Finger trials, cuing finger L1 with pins A and D and presenting those stimuli to the same finger after the ISI.



(b) Sequence of tactile stimuli during invalid Finger trials, cuing finger L1 with pins A and D and presenting those stimuli to finger R1 after an ISI.

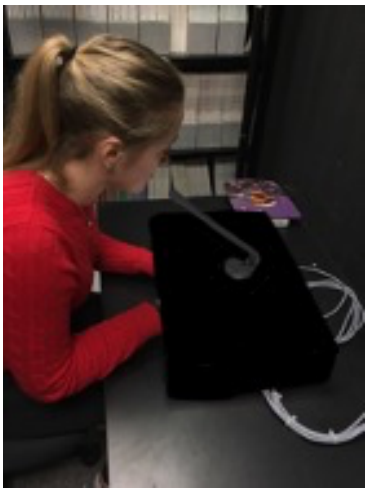


Figure 4: Set up during experiment

Data analysis

RTs were measured for ISIs in valid and invalid trial types in each condition (Location and Finger) and for each Finger trial type separately. Outliers were determined using the interquartile range (IQR) rule, where IQR was determined by subtracting the first quartile (Q_1) from the third quartile (Q_3; IQR = $Q_3 - Q_1$). The value of the lower limit was determined by subtracting 1.5 x IQR from Q_1, while the value of the upper limit was determined by adding 1.5 x IQR to Q_3 so any score exceeding the upper/lower limit of its respective distribution was considered an outlier and removed. This was done for each unique trial type and ISI in both conditions individually, thereby outliers were determined with respect to the distribution of scores for all participants within a given trial type, calculated for each level of ISI for valid and invalid Location and valid (SFSH) and invalid (SFDH, DFSH, and DFDH) Finger conditions across all participants (i.e., any extreme score from all scores for SFSH trials at an ISI of 150 ms exceeding its respective upper/lower limit). Data were organized using Excel 2013 and analyzed using SPSS 25. A 2 (Type: Location; Finger) x 2 (Validity: valid; invalid) x 3 (ISI: 150, 600, 1200 ms) repeated measures multifactorial ANOVA was used to analyze the effect of ISIs on the participants' RTs in discriminating between stimuli for valid and invalid trials across conditions. In order to account for differences between Location and Finger trial with respect to gradient, the invalid Finger factor was deconstructed into its components (SFDH, DFSH, and DFDH). Thus, a 2 (Validity: valid; SFSH) x (ISI: 150, 600, 1200 ms) repeated measures factorial ANOVA was run comparing effect of ISI on RT across valid Location trials and valid Finger trials (SFSH) and another 4 (Validity: invalid; SFDH; DFSH; DFDH) x 3 (ISI: 150, 600, 1200 ms) repeated measures factorial ANOVA was conducted to explore the effect of ISIs on RTs between invalid Location trials and invalid Finger trials. Next, a 2 (Validity: valid; invalid) x 3 (ISI: 150, 600,

1200 ms) repeated measures ANOVA was run on Location trials to examine the effect of ISI on RTs across trial types. Further, a 2 (Validity: valid; invalid) x 3 (ISI: 150, 600, 1200 ms) and a 4 (Validity: SFSH, SFDH, DFSH, DFDH) x 3 (ISI: 150, 600, 1200) repeated measures ANOVA was conducted for Finger trials to investigate the effect of ISIs on RTs between trial types (see Tables 4 and 5, Appendix for mean RTs for participant in each condition). In order to reveal what was driving the interaction for the latter ANOVA four one-way repeated measures ANOVAs were run for SFSH, SFDH, DFSH, and DFDH across ISIs. Further, nine post-hoc pairwise t-tests were run to interpret what may be influencing any interaction found in the one-way ANOVAs. Additionally, Bonferroni simple effects and simple contrast analyses were conducted to unpack the interactions in the repeated measures ANOVA analyses where applicable. In order to assess the gradient of IOR response three 2 (Finger: Same vs Different) x 2 (Hand: Same vs Different) repeated measures ANOVAs were conducted for each ISI level, along with Bonferroni simple effects and simple contrasts in order to unpack interactions where applicable.

Results

Comparing Location and Finger trials

A three-way (Type x Validity x ISI) repeated measures multifactorial ANOVA was conducted for RT. Mauchley's test of sphericity was not violated for any factor showing that the assumption of sphericity was not violated for all main effects and interactions, as such sphericity was assumed for each effect. There was a significant main effect of ISI, $F(2,32) = 7.73$, $p = .002$, however, there was no significant effect of Type and Validity. There was a significant

interaction between Type and ISI, $F(2,32) = 8.44$, $p = .001$, and between Validity and ISI, $F(2,32) = 9.36$, $p = .001$ (see Figure 5).

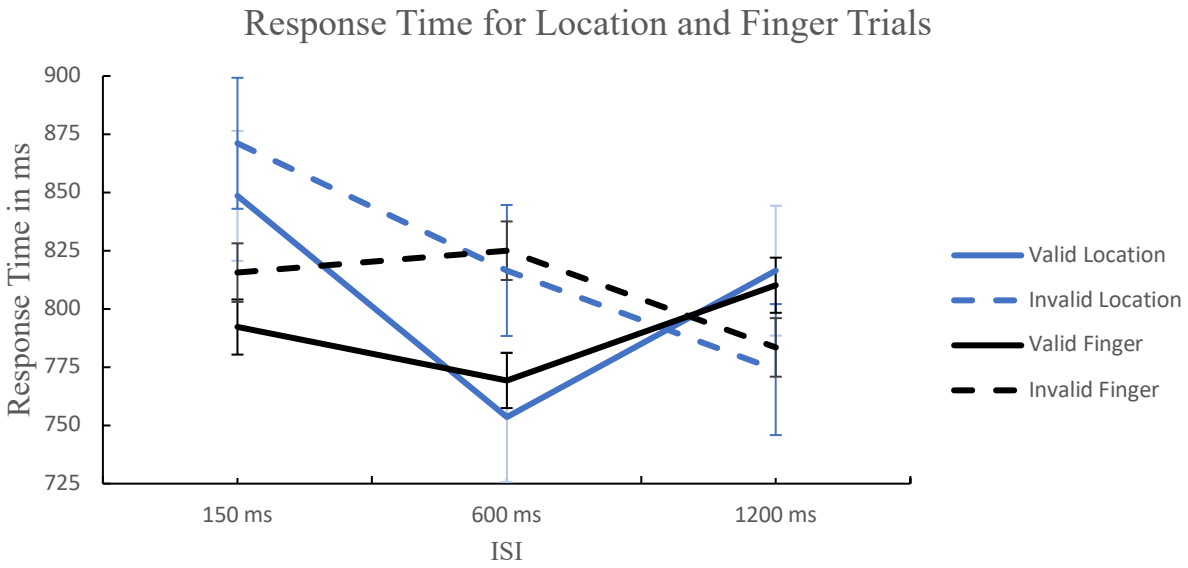


Figure 5. A Comparison of Mean RTs Between Location and Finger Trials Across ISIs and Trial Types. Error bars represent standard error. Y-axis and data points all coded in milliseconds (ms), x-axis are the ISIs.

A two-way (Validity x ISI) repeated measures factorial ANOVA conducted for RTs across ISIs for valid Location and Finger (SFSH) trials. Mauchly's test of sphericity for all factors and interactions was not violated, therefore sphericity was assumed. There was a significant main effect of ISI, $F(2,32) = 10.63$, $p < .001$, on RT. There was a significant interaction between Validity and ISI, $F(2,32) = 4.30$, $p = .022$ (see Figure 6). To understand the nature of the interaction a simple effects analysis was conducted revealing a significant simple effect of ISI for valid Location trials, $F(2,15) = 7.98$, $p = .004$, but was not significant for valid Finger trials, collapsed across ISIs. A simple contrast analysis showed that RTs for valid Location trials were significantly slower at ISIs of 150 ms than 600 ms, $p = .005$, and were

significantly faster for ISIs of 600 ms compared to 1200 ms, $p = .012$ (see Table 4 and 5, Appendix). There was no significant simple effect of Validity for all levels of ISI.

A two-way (Validity x ISI) repeated measures factorial ANOVA was conducted for RTs across invalid trial types and ISIs for Finger (SFDH, DFSH, and DFDH) and Location trials and did not violate Mauchly's test of sphericity for the factors of Validity and ISI, as such sphericity was assumed for these factors. However, Mauchly's test of sphericity was violated for the interaction between ISI and Validity, and the Greenhouse-Geisser correction was used. There were no significant main effects on RT for Validity. However, there was a significant main effect of ISI, $F(2,32) = 3.35$, $p = .048$, and a significant interaction between Validity and ISI, $F(2.51,40.18) = 3.67$, $p = .026$ (see Figure 7). To understand the nature of the interaction a simple effects analysis was conducted and uncovered a simple effect of ISI for invalid Location trials, $F(2,15) = 15.67$, $p < .001$, and invalid Finger trials: SFDH, $F(2,15) = 8.61$, $p = .003$, and DFSH, $F(2,15) = 4.43$, $p = .031$. However, the simple effect of ISI for the invalid Finger trial DFDH was not significant. Similarly, significant simple effects of Validity were observed for ISIs of 150 ms, $F(2,14) = 8.12$, $p = .002$, and 600 ms, $F(2,14) = 8.68$, $p = .002$, collapsed across invalid trial types. A simple contrasts analysis showed that RTs at an ISI of 150 ms for invalid Location trials were significantly slower than DFSH trials, $p = .001$. Additionally, RTs at ISIs of 1200 ms for invalid Location trials were significantly faster than DFSH, $p = .043$, [(shown in gradient and location) and RTs for SFDH trials were significantly faster than DFSH trials at 1200 ms, $p < .001$, no other simple contrasts were significant. Furthermore, a simple contrast analysis showed that RTs for invalid Location trials were significantly faster at 1200 than 150 ms, $p < .001$, RTs for SFDH were significantly slower at 150 compared to 1200 ms, $p = .012$, and faster for 1200 over 600 ms, $p = .035$. Conversely, RTs for DFSH trials were fastest at 150

compared to 1200 ms, $p = .025$, no other simple contrasts were significant] (see Table 4, 6, and 7, Appendix).

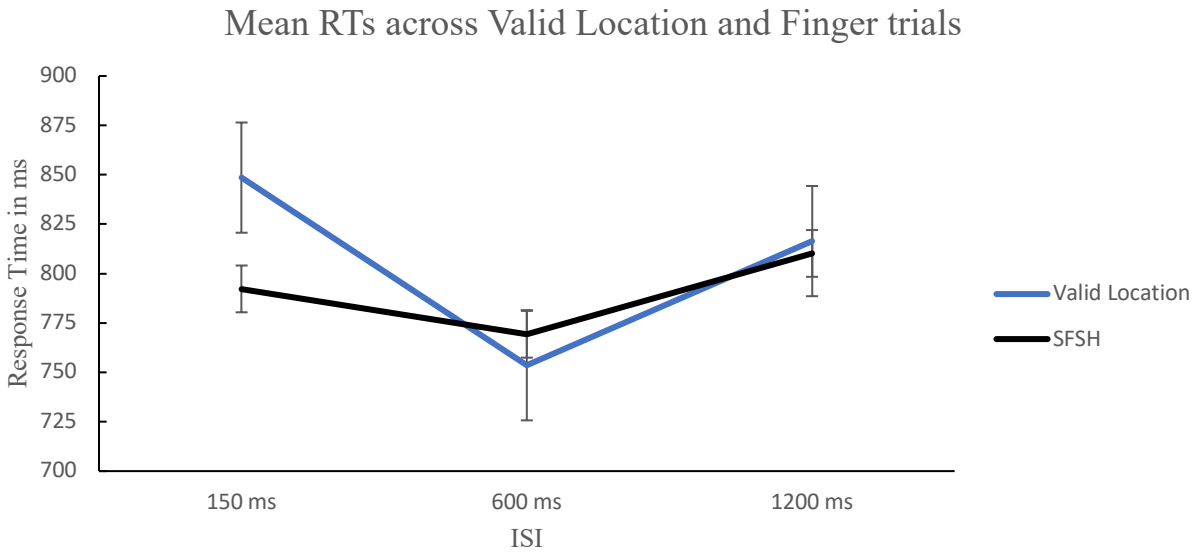


Figure 6. Mean RTs across Valid Location and Finger Trials Across ISIs. Error bars signify standard error. Y-axis and data points all coded in milliseconds (ms), x-axis are the ISIs.

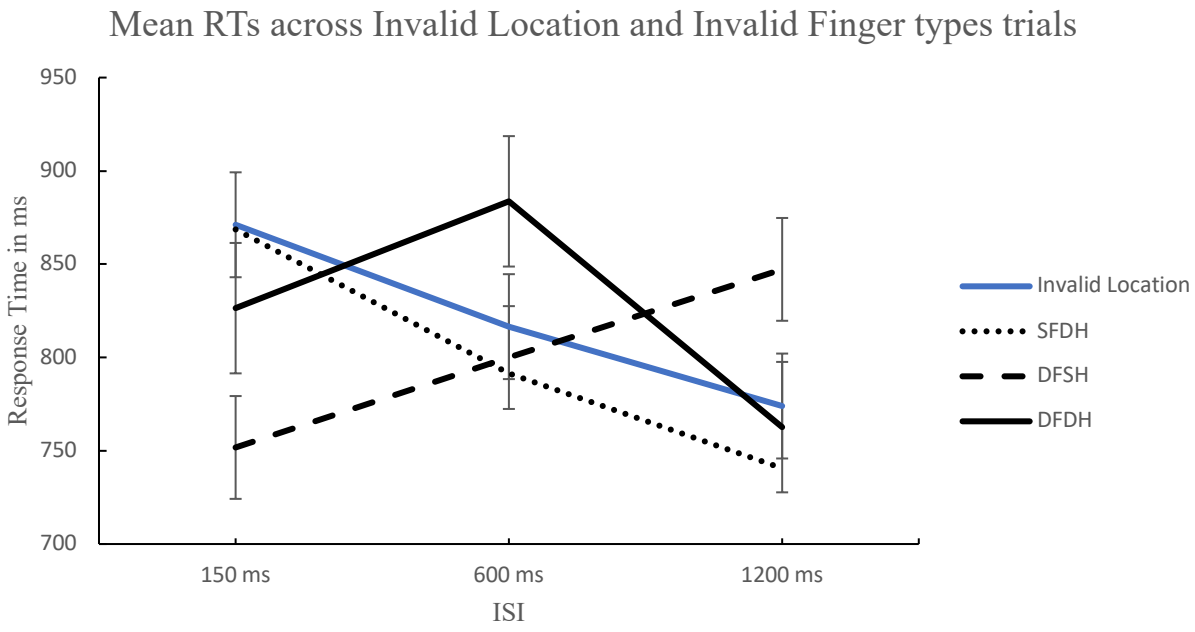


Figure 7. Mean RTs for invalid Location and invalid Finger Type Trials Across ISIs and Trial Types. Error bars represent standard error. Y-axis and data points all coded in milliseconds (ms), x-axis are the ISIs.

Location trials

A two-way (Validity x ISI) repeated measures one-way ANOVA conducted for RTs across Location trial types did not violate Mauchly's test of sphericity and as such sphericity was assumed. There was a significant main effect of ISI, $F(2,32) = 16.34$, $p < .001$ and interaction between Validity and ISI, $F(2,32) = 5.46$, $p = .009$ (see Figure 5). There was significant simple effect for valid Location trials, $F(2,15) = 7.10$, $p = .004$, and invalid Location trials, $F(2,15) = 15.67$, $p < .001$, for RTs collapsed across ISI. A simple contrasts analysis showed that RTs for valid Location trials were significantly slower at 150 compared to 600 ms, $p = .005$, and were significantly faster at 600 than 1200 ms, $p = .012$. Likewise, invalid Location trials were significantly slower at 150 than 1200 ms, $p < .001$, no other simple contrasts or effects were significant (see Table 4, Appendix).

Finger trials

A two-way (Validity x ISI) repeated measures ANOVA conducted for RTs across Finger trial types did not violate Mauchly's test of sphericity and as such sphericity was assumed. There was a significant interaction between Validity and ISI, $F(2,32) = 4.26$, $p = .023$ (see Figure 5). There was no significant simple effects or contrasts (see Table 5, Appendix).

In order to further elucidate the Finger trials a two-way (Validity x ISI) repeated measures ANOVA was run with invalid Finger trials deconstructed into: SFDH, DFSH, and

DFDH. Mauchly's test of sphericity was violated for Validity and the interaction between ISI and Validity as a result the Greenhouse-Geisser correction was used for these factors and sphericity was assumed for ISI. There was a significant interaction between ISI and Validity, $F(2.35, 37.62) = 3.81$, $p = .025$, no other effects were found to be significant (see Figure 5 and 6, Table 6 and 7, Appendix).

To unpack the above interaction four one-way repeated measures ANOVAs were run for each level of the Finger trials.

The first one-way ANOVA was conducted for RTs at SFSH across ISIs, which did not violate Mauchly's test of sphericity and as such sphericity was assumed. There was a significant main effect of SFSH, $F(2,32) = 4.17$, $p = .025$, (see Figure 7 and 8) the effect was uncovered by a paired samples t-test, $t(16) = -2.44$, $p = .027$, such that at 1200 ms RT was significant slower than at 600 ms for SFSH (see Table 6, Appendix).

The second one-way ANOVA was conducted for RTs at SFDH across ISIs, where Mauchly's test of sphericity was violated, prompting the Greenhouse-Geisser correction to be used. There was a significant main effect of SFDH, $F(1.30,20.80) = 7.21$, $p = .009$ (see Figure 7 and 8), which was revealed by paired samples t-tests. There was a significant difference between RTs at 150 and 1200 ms, $t(16) = 3.36$, $p = .004$, and RTs at 600 and 1200 ms, $t(16) = 2.85$, $p = .012$, for SFDH, such that RTs at 1200 ms were significantly faster than at 150 and 600 ms (see Table 6, Appendix).

The third one-way ANOVA was conducted for RTs at DFSH across ISIs and did not violate Mauchly's test of sphericity, as such sphericity was assumed. There was a significant main effect of DFSH, $F(2,32) = 4.52$, $p = .019$ (see Figure 7 and 8), and it was exposed by paired samples t-tests, showing there was a significant difference between 150 and 1200 ms, $t(16) = -$

3.01, $p = .008$. Thus, RTs at 1200 ms were significantly slower than at 150 ms at DFSH (see Table 7, Appendix).

The final one-way ANOVA was conducted for RTs at DFDH across ISIs and did not violate Mauchly's test of sphericity, as such sphericity was assumed. However, there was no significant main effect found (see Figure 7, 8, and Table 7, Appendix).

Gradient of response for IOR

A two-way (Finger x Hand) repeated measures ANOVA conducted for RTs between Finger and Hand types at an ISI of 150 ms, did not violate Mauchly's test of sphericity and as such sphericity was assumed. There was a significant main effect of Finger $F(1,16) = 6.95$, $p = .018$, such that there was a significant difference between same and different fingers across hands. No other main effects or interactions were significant (see Figure 8). There was no significant simple effects or contrasts (see Table 6 and 7, Appendix).

A second two-way (Finger x Hand) repeated measures ANOVA conducted for RTs between Finger and Hand types at 600 ms, did not violate Mauchly's test of sphericity and as such sphericity was assumed. There were no significant main effects or interactions found (see Figure 8 see Table 6 and 7, Appendix).

A third two-way (Finger x Hand) repeated measures ANOVA conducted for RTs between Finger and Hand types at an ISI of 1200 ms, did not violate Mauchly's test of sphericity and as such sphericity was assumed. There was a significant main effect of Hand $F(1,16) = 6.80$, $p = .019$, such that there was a significant difference between same and different hand across fingers. No other main effects or interactions were found (see Figure 8). There was a significant simple effect of Hand $F(1,16) = 8.67$, $p = .010$ for RTs collapsed across fingers. A simple

contrast analysis showed that RTs for the same hand were significantly longer than RTs for different hands at the same finger at an ISI of 1200 ms, $p = .010$ (see Table 6 and 7, Appendix).

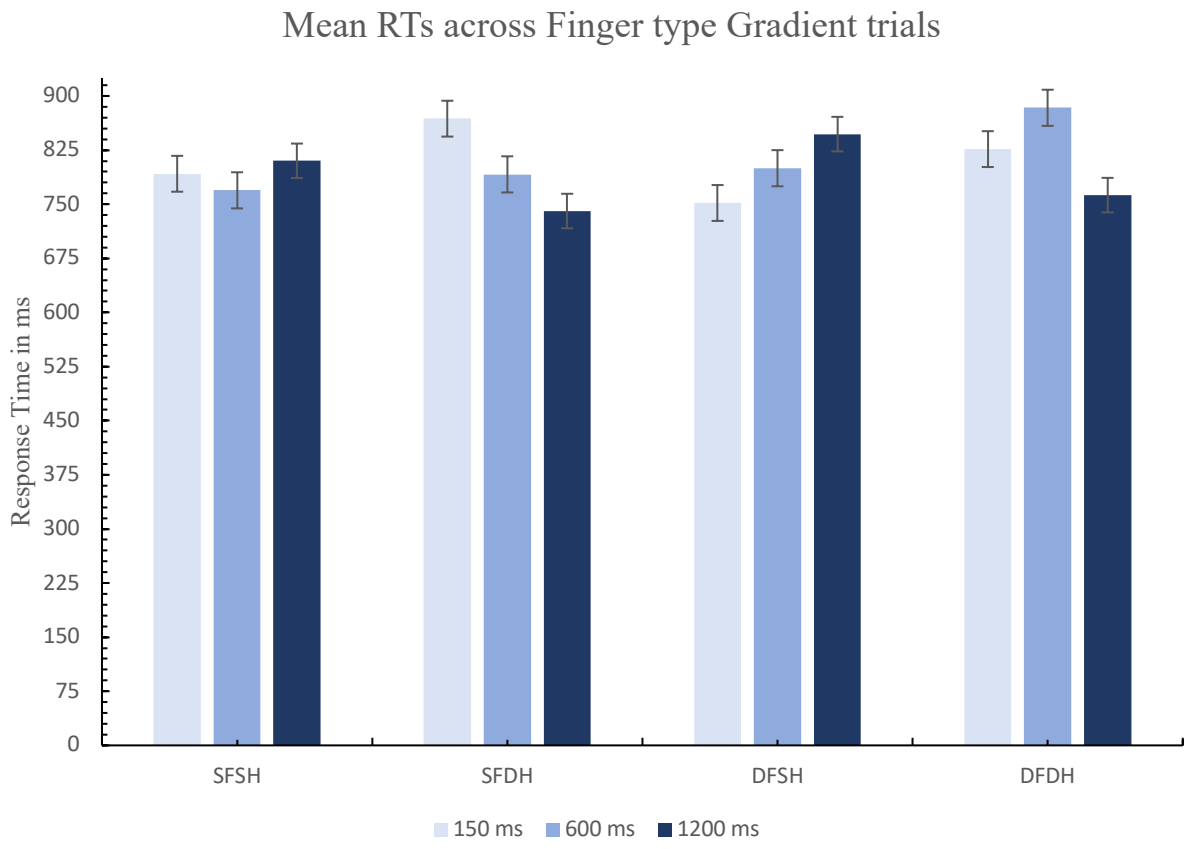


Figure 8. Mean RTs for Finger Type Trials for the Gradient of IOR Across ISIs. Error bars represent standard error. Y-axis and data points all coded in milliseconds (ms), x-axis are Finger trial types. Each ISI is represented by a bar as indicated by the legend.

Discussion

The goal of the current study is two-fold, (1) to demonstrate a time-course that reliably evokes IOR in a single unimodal tactile spatial discrimination task, while also (2) decoupling the contribution of the dermatome from the whole finger somatotopic representation. We studied this by employing a tactile cue-target paradigm with pre-determined ISIs (150, 600, and 1200 ms) to

both the whole finger and to distinct locations within the finger-tip, having participants make speeded discrimination responses as to the spatial correspondence of the cue and target. Our first hypothesis was partially supported, as we successfully elicit IOR at long ISIs (1200 ms) for cued relative to uncued homologous finger targets. Additionally, our results show a trend of increasingly facilitatory RTs as a function of rising ISIs for the latter trial type. We did not observe enhanced RTs for cued relative to any uncued finger target trial at short ISIs. Although, mean RTs for cued finger targets were seemingly faster than for uncued homologous finger targets (See Figure 8 and Tables 6 and 7) which approached significance, but was not statistically significant. This non-significant difference is likely due to the small sample size (N = 17) used in our study. The second hypothesis was also partly supported, as our findings did not show a statistically significant difference between RT trends observed for valid and invalid Location trials, though their mean RTs and trends were in line with our prediction and did come close to being significant (See Figure 5 and Table 5). It is likely that this too is due to the small sample size used in our study, since valid Location trials did show the canonical biphasic effect of quicker then slower mean RTs at short-intermediate (150 and 600 ms) and long (1200 ms) ISIs respectively, relative to invalid Location trials. In fact, when comparing valid Location trial RTs at each ISI, we found that RTs are significantly faster at intermediate compared to short ISIs and significantly slower at long versus intermediate ISIs. Meanwhile, when examining RT differences for invalid Location trials at each ISI, we discover that RTs are slowest at short ISIs and become faster as ISIs grow longer. These observations corroborate part of our hypothesis, displaying a biphasic and increasingly enhanced trend of responding which respectively parallel the trends displayed for cued and uncued homologous finger target trials as predicted. Together these findings provide evidence of a time-course that evokes tactile IOR along with the

prototypical trends associated with it in a unimodal spatial discrimination task. While the juxtaposition of Finger and Location trials reveals an analogous trend of responding, which is suggestive of a shared mental representation which presumably is endowed by a subcortical low-level dermatomal organization.

Subcortical differences underlying tactile detection and discrimination

Interestingly, unlike the gradient of response shown by Roder et al. (2002), where the magnitude of IOR decreases linearly according to the increasing somatotopic distance of the target from the cue, our data show a non-linear response gradient (See Figure 8). This is surprising because if attentional orienting at the finger level follows a somatotopically driven gradient then enhanced and IOR responding at short and long ISIs separately should be maximal at cued finger targets and then decrease in magnitude as the somatotopic distance of the target from the cued finger increases. Further, this seems to be a supramodal property of exogenous attentional mechanisms, as consonant gradients are demonstrated with respect to an allocentric attentional frame in both the visual and auditory domain (Posner, 1980; Klein, 2000; Maylor & Hockey, 1985; Teder-Salejarvi, & Hillyard, 1998). However, our results show that RTs are fastest for finger targets adjacent to the cued finger relative to targets on the uncued homologous finger to the cue at short ISIs. In contrast, cued finger targets are not faster than any invalid finger trial at short ISIs, a visual examination of mean RTs shows they are faster at finger targets adjacent to the cue than for cued finger targets (though this is not a statistically significant difference). Our results demonstrate both IOR for cued finger targets and inhibited responding for finger targets adjacent to the cue in contrast to the enhanced responding at uncued homologous finger targets to the cue at long ISIs. However, this effect of inhibited responding

for adjacent finger targets to the cue is shown to produce slower mean RTs than for cued finger targets. Additionally, uncued contralateral heterologous finger targets display a non-significant trend of inhibition and facilitation (an inverse reflection of the cued finger target trend) which differs from the trend shown by uncued homologous finger target trials. As such our data do not seem to follow a pattern representative of a gradient afforded by a somatotopic attentional reference frame. It may be that the use of spatial discrimination rather than tactile detection (seen in Roder et al., 2002) in our study is responsible for the observed pattern of responding. According to Lupianez, Milan, Tornay, Madrid, and Tudela (1997) discrimination tasks necessitate substantially longer ISIs to enable the facilitation and inhibition of processing to occur. This suggests that the task (i.e., detection or discrimination) influences the rate at which attention is engaged and subsequently disengaged from a specific location (Klein, 2000). As a result, discrimination tasks require more than merely orienting and detecting a target but involves a distinct perceptual awareness, by way of auxiliary processing, to distinguish the degree of correspondence of the cue and the target. Consequently, it takes considerably longer for attention to disengage from an attended location due to the perceptual difficulty of discrimination tasks compared to detection tasks (Lupianez et al., 1997; Klein, 2000). Remarkably, due to the disparate levels of processing commanded by discrimination and detection tasks, different afferent pathways carry different task related inputs arriving at the dorsal horn then to the brainstem, midbrain, and finally to higher-order sensory cortices.

Vierck Jr. (1974) elucidated this divergence with respect to task-related afferent pathways by examining the differential impairment of tactile movement detection and discrimination after sectioning the spinal cord dorsal column in Macaca speciosa monkeys. In the first experiment (detection paradigm) the animals were trained to push a manipulandum on the right when static

brush stimulation was felt on the skin and push the left one when dynamic brush stimulation (proximally moving) was felt on the skin. After sectioning the spinal cord dorsal column, minor deficits in accuracy were observed but ipsilateral tactile movement detection was preserved, as animals correctly chose the right or left manipulandum corresponding to either static or dynamic brush stimulation. In the second experiment, the authors assessed the capacity for tactile movement discrimination, the animals were trained to push a left door when the brush stimulation moved proximally on the skin and push a right door when the brush stimulation moved distally on the skin. Following dorsal column sectioning the animals produced an odd lasting inability to discriminate the direction of the tactile stimulus motion. In both experiments the same stimulus object was used, exciting the same receptors, but movement detection was not deficient after sectioning the ipsilateral dorsal column, however, discriminating between movements was shown to be significantly impaired. Taken together, it appears that the dorsal column is fundamental in discriminating movement direction, though not all information necessary for tactile movement discrimination is carried by it, such that other redundant tracts carry supplementary tactile information necessary for discrimination such as the detection of dynamic or static tactile stimuli.

Based on Vierck Jr.'s (1974) study, it is likely that tasks involving the crude detection of tactile stimuli largely utilize pathways in the ventrolateral funiculus, like the spinothalamic and spinocervicothalamic (SCT) tracts. This pathway is a likely candidate since it has been shown to be responsible for transmitting crude touch (non-discriminative touch where individuals perceive tactile stimulation but cannot localize it) and pressure information to supraspinal segments (Sengul & Watson, 2015; Gallace & Spence, 2014). Unlike the more direct spinothalamic tract, which decussates in the dorsal horn ascending contralaterally and mainly projecting to the

ventoroposteriolateral (VPL) and lateromedial nuclei of the thalamus, the SCT is less direct (Sengul & Watson, 2015; Gallace & Spence, 2014; Abraira et al., 2013; Brown, 1981). Axons from sensory neurons entering the dorsal root ganglia synapse on second-order neurons in laminae III-V of the dorsal horn, making up the SCT which ascends ipsilaterally projecting to the lateral cervical nuclei (LCN), then decussates to join the medial lemniscus pathway terminating onto the VPL (Sengul & Watson, 2015; Abraira et al., 2013). Meanwhile, tasks employing tactile discrimination appear to be conveyed by the dorsal column pathway which is comprised of a direct dorsal column (DDC) and an indirect post-synaptic dorsal column (PSDC) pathway (Sengul & Watson, 2015). That is because both the DDC and PSDC have been shown to carry tactile information, discriminatory touch, vibration, position sense, movement sense, conscious proprioception, innocuous mechanical, and noxious peripheral stimuli to the dorsal column nuclei (DCN; Sengul & Watson, 2015; Abraira et al., 2013; Gallace & Spence, 2014). The DDC is comprised of the gracile fasciculus (GF) – carrying tactile information from the lower body below T6 - and the cuneate fasciculus (CF) – carrying tactile information from the upper body above T6 - to the cuneate and gracile nuclei which form the DCN. After which, the DDC decussates joining the medial lemniscus (comprising the dorsal column medial lemniscus pathway (DCML)) to terminate onto the contralateral VPL (Sengul & Watson, 2015; Loutit, Vickery, & Potas, 2021). However, the PSDC, like the SCT, differs from the DDC as axons from sensory afferents entering the dorsal root ganglia synapse on second-order neurons in laminae III-VII and X of the dorsal horn, projecting onto the DCN and then decussating to connect with the medial lemniscus and terminate onto the VPL (Sengul & Watson, 2015; Loutit et al., 2021). The path taken to the DCN by the afferent fibres is determined by the modality of the afferents which coexists with the somatotopic organization of the receptive fields i.e., whether on the

upper or lower part of the body (Sengul & Watson, 2015; Loutit et al., 2021). This type of synchronous arrangement between modal and somatotopic organization is also witnessed, to a lesser degree, in SCT fibres projecting to the LCN. The organization of cells of origin of the SCT show a greater representation of the digits and palm, suggesting it is significantly less precise in accurately conveying spatial tactile information than the DCML (Hirata & Pubols Jr., 1989; Simone & Pubols Jr., 1991). In this manner the afferents ascending the spinal cord dorsal column pathways (DCs), and the SCT to a lesser extent, are organized to coexist with respect to modality, conduction velocities, adaptation properties, and somatotopic topography (Abraira et al., 2013; Abraira et al., 2017; Hirata & Publos Jr., 1989; Vierck Jr., 1974; Loutit et al., 2020). The modality-based fiber sorting is analogous to the modal organization extant in the DCN, thalamus, and somatosensory cortex (Kaas et al, 1979; Loutit et al., 2021; Hirata & Pubols Jr., 1989). This cataloguing of outputs indicates that afferent inputs entering the dorsal root ganglion are processed and integrated pre-cortically within the spinal cord dorsal horn. Processed output is then likely transmitted largely by the second-order neurons of the PSDC and SCT to the DCN and LCN respectively, and then further upstream to the VPL (Abraira et al., 2013; Abraira et al., 2017; Loutit et al., 2021; Sengul & Watson, 2015). However, the differences observed in the LCN relative to the DCN exhibit properties necessary for their corresponding roles in crude detection and place specific discrimination of tactile stimulation (Simone & Pubols Jr., 1991; Loutit et al., 2021; Downie, Ferrington, Sorkin, & Willis Jr., 1988). The LCN contains exceptionally large receptive fields (RF), much larger than the respective RFs in both the VPL and SCT which are thus not suitable for conveying precise information regarding the exact locus of a tactile stimulation. Furthermore, the somatotopic organization of the LCN is rudimentary, being substantially less precise in both somatotopy and RF segregation than the DCN, displaying

converging RFs from both the glabrous and hairy skin of a stimulated somatic region (Simone & Pubols Jr., 1991). In this respect, it is apparent that crude detection is likely facilitated by the properties of the SCT-LCN-VLP pathway, permitting the recognition of a tactile stimulus along with its approximate location on the body, without conferring any specific information on the submodality and the exact location of the stimulus (Simone & Pubols Jr., 1991). In contrast, the DCN is well suited to enable discriminative properties of touch, as the gracile and cuneate nuclei receive distinct input corresponding to the upper and lower body regions (Loutit et al., 2021). Further, these nuclei contain heterogenous cell populations, densities, RF sizes, response modalities and projection targets. What is more, they are divided rostro-caudally into three parts for a more precise somatotopic organization. These being the rostral zone – which houses large RFs on the proximal and axial body, the middle part – containing three subregions: i) the cluster zone – very somatotopic with small RFs targeting distal forelimbs (i.e., digits and toes) specialized for precise discriminative touch; ii) a shell region – larger RFs (than rostral or caudal zones) on the proximal body responding to proprioceptive and tactile stimuli; iii) the ventral zone – homologous cell populations responding to proprioceptive input; and the caudal zone – very large RFs from the whole body with poorly defined somatotopy and a large ratio of cells responding to Pacinian like input (Loutit et al., 2021; Sengul & Watson, 2015; Abraira et al., 2017; Simone & Pubols Jr., 1991). The cluster and shell regions of the DCN and caudal DCN zones are governed by tactile-related information processing and transmission, while the rostral DCN zones process both tactile- and proprioception-related information. The cluster regions particularly are responsible for spatially precise discriminative touch information from the distal limbs and contains the largest representation of the glabrous skin, a skin region well suited for environmental exploration. The rostral, caudal, and shell regions, on the other hand, are

designated for processing less spatially precise and multimodal information (Loutit et al., 2021; Abraira & Ginty, 2013). Thus, it is evident as Mountcastle and colleagues (Rose & Mountcastle, 1959; Poggio & Mountcastle, 1963) suggested that the DCML pathway plays a unique and specialized role in both place specificity and precise discriminative touch (Loutit et al., 2021; Abraira et al., 2013; Sengul & Watson, 2015; Gallace & Spence, 2014; Simone & Pubols Jr., 1991; Vierck Jr. 1974).

Taken together, utilizing spatial discrimination rather than detection, as in the current study, inherently produces differences by virtue of the distinct pathways required to accomplish either task. Moreover, while endogenous attention is a high-level cognitive feat, IOR however, is a primitive low-level cognitive reflex shown to be produced by the superior colliculus and is not abolished through either endogenously orienting attention to remain at a cued location or via cortical lesions (Posner et al., 1985; Klein, 2000). Being that IOR is a low-level attentional orienting mechanism, it stands to reason that it is mechanised by virtue of an equally primitive representation. In this respect, it is likely that early processing among the rudimentary mechanisms outlined above are responsible for enabling exogenous tactile IOR and the pattern of responding observed in the current study. Additionally, according to this line of thought we suspect that the somatotopic gradient of IOR demonstrated previously is the result of the suggested early processing in conjunction with the functional properties of the hand and fingers rather than a higher-order somatotopic representation as proposed by the authors (Roder et al., 2002; Besle et al., 2014). This is furthered by the observation that sensory dermatomal maps are preserved up to the level of the medulla oblangata, as infarcts in the medial lemniscus lumbar representation presents sensory deficits localized to the respective contralateral dermatomal segment (Lee, Kim, Song, & Roh, 2001). Consequently, our pattern of results, and likely the

results of other tactile IOR studies, are derived from low-level sensory dermatome representations and subcortical processing as will be explored at length (Roder et al., 2002; Cohen et al., 2005; Spence & McGlone, 2001; Poliakoff et al., 2008).

Hierarchical mental representations foster pre-conscious and conscious somatosensory attentional orienting behaviors subserving IOR

Previous studies have shown that crossing one's hands leads to a deficit in correctly discriminating the stimulated hand due to the automatic updating of each hand in the body schema to its new spatial location (Spence & McGlone, 2001; Haggard, Kitadono, Press, & Taylor-Clarke, 2006; Lakatos & Shepard, 1997; di Pelligrino & Ladavas, 1998; Botvinick & Cohen, 1998). However, the updating of finger location in external space is not seen when the fingers are crossed over each other as indicated by Aristotle's Illusion, such that when two crossed fingers hold a single object between them it is perceived as feeling two objects, because the lateral surface of the fingers are felt in the natural position they would maintain in an uncrossed posture (Haggard et al., 2006; Benedetti, 1985). A study by Haggard et al. (2006) showed that stimulating a given finger while vertically interleaving the fingers of the right and left hands (like the posture used in Roder et al.'s (2002) study) at the midline, impaired the identification of the hand belonging to the stimulated finger (i.e., identifying right hand if a finger on it was stimulated). However, identifying the stimulated finger was not impaired in this posture. When the hands were not interleaved and positioned one on top of the other (i.e., pinky on top of thumb/index), hand identification is near normal. Meanwhile, the ability to detect the stimulation was unimpaired in either posture. The authors suggest that these results indicate that hand identification is a hierarchical process, where initially a stimulus on the finger is detected,

then the stimulated finger representation is identified (i.e., index finger), and finally the finger is identified as belonging to the corresponding hand (i.e., right index finger). To investigate if the finger representation does influence hand identification, the authors had participants interleave their fingers in an inverse manner (back of one hand faces the palm of the other) so that the unstimulated homologous finger is far from the stimulated one. They found that, although impairments in hand identification are still present, impairments are significantly less marked than when the homologous fingers are proximal to each other. Thus, the deficit in hand identification seems to arise from the interference associated with the proximity of untouched fingers with the touched finger, specifically, when the latter is near the untouched homologous finger. This indicates the existence of separate mental representations for the hand and the fingers, which seems superfluous, however, hand identification is aligned with its location in egocentric space while fingers are not. This suggests that hand identification automatically involves a process that assigns a stimulated finger to the respective hand by combining tactile input with representation of external space to determine which finger belongs to which hand. In turn, seeing as the identification of a finger does not directly indicate which hand it belongs to, an intermediate process is posited to underly the assignment of the stimulated finger to its particular hand. Accordingly, stimulating one finger seemingly activates a bilateral representation of that finger (i.e., a right and left index finger representation) which is not yet been associated with a specific hand. Further evidence for this comes from the Japanese Illusion where individuals lift the wrong finger than instructed when it is close to the homologous finger (Haggard et al., 2006; Klein & Schilder, 1929). Seemingly, the bilateral finger representation originates subcortically at lower processing levels, possibly in the spinal cord dorsal horn, seeing as higher-order finger representations in the cortex are lateralized. Recent fMRI studies in

support of this assertion, exhibit ipsilateral and contralateral activity within respective spinal cord dorsal horn segments upon stimulating the middle finger of one hand. The bilateral activation is explained through by the presence of interneurons that modulate and integrate neuronal activity between hemicords (Weber et al., 2020; Weber et al., 2016).

It stands to reason that tactile attentional reference frames are arranged in a hierarchical manner such that the allocentric/egocentric spatial representation is a high-level cognitive property owing to the convergence of multisensory information and multimodal input from lower tier mental representations (Haggard et al., 2006; Nixon, Burbaud, & Passingham, 1992). The somatotopic representation, being hierarchically below the allocentric representation, supplies it with the necessary somatic and tactile information to form the complex representation of the body in external space, nevertheless the somatotopic representation, though less multifaceted, is a higher-level cognitive function as well. Seemingly, it too supplies the appropriate somatosensory information by means of subcortically processed tactile input giving rise to a pre-cognitive low-level dermatomal representation. In this hierarchical succession each representation encapsulates the information afforded by the preceding one, thereby, incorporating and combining greater amounts of sensory information at each level (Haggard & Wolpert, 2005). To this end, the recruitment of a single or multiple attentional reference frame(s), is contingent on the respective cognitive demands required by a given task or sensorimotor function, a phenomenon that has been shown in previous visual IOR tasks (Abrams & Pratt, 2000; Posner et al., 1985). Therein all tactile tasks regardless of complexity, must initially engage the low-level dermatomal representation as a fundamental building block by which to construct higher-order spatial representations. In this respect we suggest that tactile

attention oriented by means of this lower-level system effectively enables the perception and necessary reaction to expected or unexpected incoming stimuli.

Paillard, Michel, and Stelmach (1983) demonstrated a case where a woman with a left parietal area lesion producing symptoms of incomplete right-sided hemianopia, hemianacusia of the right ear, and right-sided hemianesthesia, was able to correctly point to the location of an indenting stimuli on the deafferented hand with the normal hand above chance. The patient was unable to detect strong static pressure stimulation on the deafferented arm from the finger-tip to the elbow. However, when blind folded and asked to point to one of 18 different stimulation points on the palmar surface of the normal and deafferented hand with the deafferented and the normal hand respectively, the patient exhibited the ability to localize stimuli on the affected hand well above chance. Remarkably, she did not respond during catch trials where no stimulus was presented to the deafferented hand, indicating that all the responses made were triggered by the stimulations presented to the numb hand. Interestingly, the patient had no phenomenological awareness of the stimulation, though she did express that while she could not feel anything she felt an understanding of where to point to. Surprisingly, the patient reacted positively to varied moving stimuli on the deafferented hand, being able to judge corresponding direction and speed of each stimulus correctly. Considering the patient could phenomenologically detect and discriminate tactile movement but not static stimuli is expressive of separate systems for mapping and transmitting static and dynamic tactile information, as mentioned above (Vierck Jr., 1974; Paul et al., 1972). The authors coined this phenomenon to be a tactile analog of blind sight, due to the functional dissociation between localization and identification which is characteristic of blind sight patients. Paillard et al. (1983), suggest that the effect is likely the result of subcortical processing mechanisms in concert with the multi-channeling of sensory information

innervating the sensory and motor needs of these intact functional systems. Relatedly, studies observing finger agnosia patients who can detect tactile stimuli (i.e., pressure sensitivity and spatial acuity) but are deficient when naming or pointing to an illustration of the stimulated finger, present a similar subcortical preservation of the finger representation akin to observation in blind touch patients (Anema et al., 2008; Paillard et al., 1983). That is, though finger agnosia patients cannot explicitly name or choose the correct finger illustration, they are able to correctly point to the stimulated finger with the non-stimulated hand. This preserved ability presumably involves a sensorimotor representation of the fingers that is not consciously available and is computed via skin location coordinates independent of the elaborate cognitive processing that is necessary for finger identification (Anema et al., 2008). These findings indicate that the implicitly conserved functions of blind touch and finger agnosia patients are subserved by low-level representations of somatosensory information processed subcortically (Djikerman & de Haan, 2007; Paillard et al., 1983).

The presence of an implicit somatosensory representation is an incredibly adaptive apparatus for the reflexive orienting of attention to regions receiving unexpected stimulation on the body. This can be better understood by looking at how multisensory attention is oriented. In general, the natural environment is much noisier than lab settings as they restrict the sensory stimulation received to the modality or function of interest (Gallace & Spence, 2014). However, in normal settings events occurring in space afford myriad multisensory cues, such as seeing and feeling an insect landing on one's forearm or seeing and hearing a predator moving toward oneself. This being the case it is conceivable that IOR and low-level attentional orienting as a whole are not limited to a single sensory modality, but instead are adapted for the real time attendance and reaction toward multisensorial events in the world. The integration of these

multisensory cues is cultivated by the superior colliculus (SC) which receives converging multisensory input and is implicated in localizing, orienting, and attending to visual, auditory, and tactile stimuli (Meredith & Stein, 1986, 1996; Wallace, Wilkinson, & Stein, 1996; Drager & Hubel, 1976; Wallace, Meredith, & Stein, 1992). It is particularly apt for this role as the converging multisensory input is received by modality specific laminar layers, all of which are topographically mapped to coincide with one another by conforming to a retinotopic spatial representation. The superficial layers are dominated by visual input while the deep intermediate and lowest layers respectively receive auditory and somatosensory input. Both deep layers contain unimodal and multimodal neurons which equally respond to broad sensory stimuli preferred by the corresponding layer while the latter responds to additional input from a separate sensory modality (usually vision in humans and primates). Remarkably, these neurons, by virtue of their proximity and their positioning within the layer, have RFs for both unimodal and multimodal stimuli that are coded in good spatial registry with one another. This feature of deep layer SC neurons allows for the combination of coincident multisensory stimuli emerging from the same location via aligned individual sensory RFs, interact to amplify the salience of the event and respond effectively by initiating the coordination of motor responses toward or away from the attended location (Meredith & Stein, 1986, 1996; Wallace et al., 1996). Importantly, both multisensory stimuli must originate at the same locus to fall within each other's RF to interact and enhance responding of the neuron. Adaptively, it enables the enhancement of modest unimodal stimuli that would evoke weak activity on its own, and possibly go undetected, when combined with input from a different sensory cue derived from the same location and likely the same event (Stein, Meredith, Huneycutt, & McDade, 1989; Wallace et al., 1996; Meredith & Stein, 1986, 1996). Interestingly, temporal registry is also a significant determinant of

enhancement. Reportedly, two multisensory stimuli from the same location arriving successively to their RFs in a multimodal neuron, are only enhanced if their respective peak discharge periods overlap (Wallace et al., 1996; Meredith, Nemitz, & Stein, 1987). Contrastingly, if the multisensory stimuli are temporally or spatially distant from one another, their interaction serves to either depress activity or no interaction is seen at all (Wallace et al., 1996; Meredith et al., 1987; Meredith & Stein, 1986). Interestingly, the response properties of unimodal neurons do not change in either case of response enhancement or depression and neither unimodal nor multimodal neurons have particularly selective stimulus parameters. Instead, SC neurons respond to the locus of multisensory stimulation and not the specific constraints of the stimuli, which is evident by the analogous response qualities for optimal and suboptimal stimuli (Wallace et al., 1996). Moreover, enhancement of multimodal neuronal responding is not observed when the stimuli are strong, indicating that multisensory integration in deep SC layers is functionally related to spatial attention and not multisensory perception. Since, strong stimuli evoking equally strong activity do not need the combinatory influence of another sensory stimulus to increase its salience as it is already prominent (Meredith & Stein, 1986, 1996). Therefore, it appears that deep SC layers serves to reflexively orient attention to rapidly detect and respond to stimuli at a given location irrespective optimality (Wallace et al., 1996; Krauzlis, Lovejoy, & Zenon, 2013). These multisensory properties of the deep layers in the SC closely aligns with the characteristics that are required by a supposed neural substrate for IOR. Relatedly, studies using cross-modal cue-target stimuli show that any cross-modal cue-target pairing (i.e., visual-tactile, tactile-auditory, etc.) elicit inhibited target detection at previously cued locations after long ISIs of 950-1250 ms (Spence et al., 2000). Additionally, the authors also showed that IOR is evoked using strictly unimodal cue-target stimuli for all three modalities using the same ISIs. Together these

findings implicate the SC as a probable candidate underlying IOR and spatial attention more generally. Notably, the SC is a particularly low-level structure which seems to work independently from higher-level cortical systems, seeing as cortical lesions affecting stimulus perception do not impair reflexive attentional orienting or IOR, while SC lesions do (Posner et al., 1985; Wallace et al., 1993, 1994; Krauzlis et al., 2013). Thus, while cortical inputs to the SC are necessary for processes leading to complex processes of perception and cognition, the SC itself seems to depend on lower-order sensory representational processes. Specifically, for rapid somatosensory attentional orienting it likely relies on its inherent representation as well as input coming from the DCN, by way of the lemniscal adjunct channel, and the dorsal horn spinal cord circuits (Loutit et al., 2021; Krauzlis et al., 2013; Abraira et al., 2017). Consequently, it is conceivable that the somatosensory representations within the SC and those extant further downstream projecting to it, enable the ability for blind touch and finger agnosia patients to implicitly point to the loci of tactile stimulation on their impaired body regions (Anema et al., 2008; Paillard et al., 1983). This is further supported as the SC sends outputs to sensorimotor regions in the brainstem and spinal cord and likely receives multimodal somatosensory information from the DCN to direct attention and trigger motor responses to them (Loutit et al., 2021; Krauzlis et al., 2013).

Collectively, a low-level sensory dermatomal representation is shown to persist up to the medulla oblangata, and these crude somatosensory representations are recruited to heuristically orient attention to a stimulated somatic area enabling rapid responding upon detection (Lee et al., 2001; Anema et al., 2008; Paillard et al., 1983; Krauzlis et al., 2013; Loutit et al., 2021). Accordingly, seeing as the SC employs low-level sensory representations for pre-cognitive attentional orienting and is heavily implicated as the key structure behind IOR, it is unlikely that

the mental representation engaged emerges from higher-order cognitive processes. Therefore, the pattern of responding in our study arises from a low-level dermatomal representation crudely mapping stimuli coordinates on the skin and thus should not reflect a somatotopic response gradient (Haggard & Wolpert, 2005; Roder et al., 2002). We suspect that our findings reflect the representation formed via the integration and processing of tactile information by cellular populations within the dorsal horn, and further upstream in the DCN. These regions present the capacity to represent both the modality and location of a stimulus presented to the skin and is likely the representation used by a pre-cognitive reflexive spatial attentional mechanism like IOR (Abraira & Ginty, 2013; Abraira et al., 2017; Loutit et al., 2021; Weber et al., 2016; Weber et al., 2020; Paillard et al., 1983; Gallace & Spence, 2014).

Tactile spatial discrimination and detection are subserved by common low-level representations

The influence of a low-level shared finger representation is evident in our results. Notably, the observation of enhanced responding for uncued homologous finger targets which increases linearly as a function of increasing ISIs, a trend that is not observed for uncued finger targets involving adjacent fingers. Meanwhile, on the opposite hand IOR and inhibition responses are evident at the cued finger and uncued adjacent finger respectively (See Figure 8). These behavioural results implicate the effect of a shared representation for both the cued and the uncued homologous fingers. That is, the cue initially primes the shared representation, once sufficient information is delivered, the cued hand is lateralized, and attention shifts to it. However, after a significant amount of time passes and no stimulus is felt (~1000 ms; Meredith et al., 1987) activity at that RF location in the SC is depressed, shifting attention to the opposite

uncued location via the mutual representation. Neurophysiological evidence for the existence of a mechanism supporting a subcortical shared representation arises from DCN circuits within the midbrain, cerebellum, and thalamic nuclei. As discussed above, dorsal pathways carry cutaneous and proprioceptive information from sensory afferents entering the dorsal horn upstream to the DCN either directly or indirectly through primary and secondary afferents respectively (Sengul & Watson, 2015; Loutit et al., 2021; Abraira & Ginty 2013). The DCN-complex (complex is added to include X, Z, extracuneate, and median accessory nuclei) plays a complicated role in processing, integrating, and distributing discriminative touch, multimodal, and proprioceptive somatosensory afferent information it receives to a diverse array of targets (Loutit et al., 2021; Abraira & Ginty, 2013). In particular the projections sent directly from the DCN and indirectly through cerebellar and midbrain structures to the inferior olive (IO) may be well suited to underly the theorized shared representation (Loutit et al., 2021). The IO is a structure found in the superior medulla that is suggested to send error signals to the cerebellum serving to lessen mismatch between sensory input matching the body's current position and the relevant targets movement/position (Paul & Das, 2019; Loutit et al., 2021). The IO receives efferent projections from the SC, pretectum, and the pontine-cerebellar-red nuclei pathway as well as, afferent excitatory contralateral and inhibitory bilateral input from the spinal-CuC and the CuR of the DCN, respectively (see section on *subcortical differences underlying tactile detection and discrimination* for DCN and spinal cord tract abbreviations, structures, and functions; Loutit et al., 2021; Meredith & Stein, 1986). Information provided by the CuR projection inhibits activity bilaterally in the IO, however, when combined with excitatory input transmitted contralaterally via spinal-CuC, activation is observed in the IO (Loutit et al., 2021; Paul & Das, 2019). Contralateral spinal-CuC input to the IO works in tandem with indirect excitatory input to the IO

from the DCN-pontine-cerebellar-red nucleus pathway, where the pontine nuclei receives input from the rostral (only Gr), cluster, and caudal DCN regions (Geborek, Jorntell, & Bengtsson, 2013; Loutit et al., 2021). The bilateral input to IO carries information about the trunk and forelimbs, indicating that signals sent along these projections to IO express the detection of stimulation on either region irrespective of their lateral position. While the contralateral projections carrying information regarding the transitional forelimb (inclusive of the hand, wrist, and upper forelimb), distal forelimb, trunk, and shoulder regions to the IO, function to both lateralize activity to the appropriate side and provide more precise spatial coordinates about the locus of stimulation on the upper body (Loutit et al., 2021; Paul & Das, 2019; Geborek et al., 2013). In turn, this mechanism follows the theoretical sequence proposed by Haggard et al. (2006) and is a potential neural substrate subserving both the shared representation and the intermediate processes of lateralizing stimuli to a given hand. Furthermore, IO input from the indirect pontine-cerebellar-red nucleus pathway carries more spatially precise information regarding discriminative touch from the CuM cluster region, along with input from the CuR and CuC. The cluster region contains the smallest RFs of the three Cu-DCN and distinct clusters representing each digit and palmar segment which are primarily innervated by glabrous skin afferents (Loutit et al., 2021) as such, it is apparent that a shared representation is likely to exist. Although the intermediate process lateralizing activity to the appropriate side of the representation might not be constrained by higher-order finger identification. Instead, this process is likely driven by distinct spatial coordinates provided by low-level representations in the caudal and cluster Cu regions (Loutit et al., 2021). This is supported by the finding that neglect and extinction patients can implicitly process but not explicitly report tactile stimuli applied to the deficient contralateral side of their body (Gallace & Spence, 2014; di Pellegrino &

Ladavas, 1998; Aglioti, Smania, Moro, & Peru, 1998). Moreover, finger agnosia patients do not show deficits in haptic recognition of objects which require the combination of cutaneous and proprioceptive information from and about each finger and can point to the stimulated somatic region involving their agnosic limb above chance (Anema, Overvliet, Smeets, Brenner, & Dijkerman, 2011). Further, a symptom of finger agnosia is left-right disorientation where the execution of explicit requests like touching the left ear with the right hand are significantly impaired, nonetheless, patients can differentiate between left- and right-sided stimulation (Anema et al., 2008; Anema et al., 2011). Thus, the higher-order somatotopic and allocentric representations which required integrated multimodal and multisensory information to form the phenomenal percept that is absent in neglect, extinction, and finger agnosia patients, are not necessary for less cognitively involved tasks. In turn, the intermediate process necessary for lateralizing activity to the appropriate side and the location on that side, is determined by representations within rostral, caudal, and cluster Cu regions. Consequently, given that IOR is an adaptive exogenously driven attentional reflex, the stimuli used need not be complex to spatially reorient attention back to them. This is likely due to the broad response properties of RFs in the SC along with IO projections, allowing attention to be oriented by salient stimuli irrespective of a coherent perception of the stimulus and its respective location (Meredith & Stein, 1986; Wallace et al., 1996). This circuit is closely associated with tectal structures that are supposed to underly IOR and as such it is likely that the representation used by reflexive exogenous attentional orienting and IOR mechanisms to localize peripheral stimuli on the body. Such tectal structure (the SC, intercollicular region (ICo), and inferior colliculus (IC), and pretectal regions) receive analogous inputs from the DCN which then project to the IO (Loutit et al., 2021). It may be the case that such connections help to bias attention away from the previously attended limb

to the unstimulated prospective limb via their mutual representation thereby enhancing target detection at the latter. Presumably this is also mediated by efferent cortical projections to the SC and ICo, which may provide information about the relevant target and where it may appear. The ICo receives the densest input from both the DCN (excluding the cluster region) and spinal cord, containing information from afferents with small cutaneous RFs on the distal body regions. From here information is sent to the posterior group of the thalamus (Po) and then further upstream to the ventral parietal area (VP), and S1 subregions (3b, 3a, 1, and 2) (Loutit et al., 2021; Berkley, 1980). Both the indirect spinal-DCN-ICo-Po pathway and the direct DCN-Po route comprise the multimodal pathway, as it receives, processes, integrates, and projects information from cutaneous and proprioceptive afferents to their respective cortical areas (Loutit et al., 2021; Berkley, 1980). Importantly, the VP sends dense reciprocal inputs to the Po and the ICo while also sending top-down projections to the SC which is essential for the development and function of multisensory integration (Meredith & Stein, 1986, 1992; Wallace et al. 1992). The VP contains the angular gyrus and superior marginal gyrus, which when lesioned produces deficits resulting in finger agnosia, impaired Theory of Mind (ToM), hemi-spatial neglect, and impaired working memory. Furthermore, the VP shows significant bilateral activation during Posner and odd ball paradigms, specifically for invalid targets and deviant (novel) stimuli respectively, strongly suggesting that this region is involved in the reorienting of attention to locations/stimuli that were not attended to but are nevertheless task related (Cabeza, Ciaramelli, & Moscovitch, 2012). Seeing as deficits in ToM, finger agnosia, extinction and neglect patients all share lesions involving the VP to varying degrees, it can be assumed that higher-order allocentric/egocentric and somatotopic representations are formed or exist in this region (Cabeza et al., 2012; Anema et al., 2008; Anema et al., 2011; Gallace & Spence). However, the implicitly conserved abilities

after VP lesioning indicate that reflexive attentional orienting and IOR do not immediately invoke higher-order representations and further do not necessitate an intact VP (Gallace & Spence, 2014; Posner et al., 1985; Cabeza et al., 2012). Instead, the indirect multimodal pathway seems to be the likely candidate in driving exogenous attention and IOR, while the reciprocal connections between the VP and the Po/tectum determine the relevance of an incoming stimulus in accordance with the expectations of the task (Cabeza et al., 2012; Loutit et al., 2021). Relatedly, when peripheral stimuli activate a subcortical group of cells with RFs that overlap with cortical RFs, they are excited by corticofugal inputs, this is observed with respect to unimodal cortical RF correspondence in the spinal cord, DCN, tectum, and thalamus (Hirata & Pubols Jr., 1989; Wallace et al., 1993; Loutit et al., 2021). Meanwhile, non-overlapping RFs are simultaneously inhibited, therefore, unimodal cortical inputs to the tectum, spinal cord, and DCN serve to amplify relevant somatosensory stimuli and inhibit irrelevant stimuli during endogenous tactile exploration (Loutit et al., 2021). However, exogenous attention is seemingly a bottom-up process which is not amplified by cortical inputs because either the target stimulus location or its type do not align with the expectations of the task afforded by a preceding cue (Corbetta & Shulman, 2002; Cabeza et al., 2012). Taken together, exogenous orienting of attention and IOR are seemingly more primitive aspects of attention as a whole and are mechanized by representations, structures, and interconnectivity in the midbrain, DCN, and spinal cord.

Collectively, detecting and localizing stimulation with respect to shared representation of the forelimbs, is likely subserved by the IO through inputs from the rostral and caudal cuneate nuclei wherein a bilateral representation is conferred by rostral projections and is subsequently lateralized by the pontine-cerebellar-red nucleus path along with contralateral caudal Cu inputs. In addition to this, the reticular formation (Rt) which receives input from the rostral DCN and

shares reciprocal connections with the SC, sends projections to the pontine nucleus and back to both the rostral DCN and Cu cluster region (Loutit et al., 2021). This circuit is particularly significant as the Rt has been shown to transform spatial information of a target stimulus sent from the SC into temporal signals and send it back to the SC (Cromer & Waitzman, 2006). Thus, input from the SC could excite duration cells in the Rt, which then sends positive recurrent feedback to the SC to maintain excitation of the target location, until it is terminated by inhibition arising from omnipause neurons (Cromer & Waitzman, 2006; Soetedjo, Kandeko, & Fuchs, 2002). Presumably, this SC-Rt-SC circuit signals attention to disengage from a cued location after duration cells in the Rt determine that the location is not task relevant, which then inhibits processing at that location should the target appear there. As a result, efferent projections from the tectum alongside Rt and VP inputs presumably aid the IO by biasing attention toward novelty to enhance the detection of task relevant stimuli on the unstimulated hand. The IO is implicated in sending error signals to the cerebellum to correct for movement incompatible with sensory input, it is likely that the circuits outlined contribute both to this function and exogenous tactile IOR. Specifically, they provide the ability for effective tactile exploration for a spontaneous tactile stimulus that was previously felt on one hand but is no longer present. In this case after enough time passes the Rt signals the SC to disengage from that location to search elsewhere, at which point the SC could similarly alert the IO to inhibit the current flank and shift attention the novel location of the shared representation. In turn the IO could trigger an error signal to be sent to the cerebellum activating and engaging the opposite limb thereby, refining the performance of the search and increasing the likelihood of target detection. Consequently, these circuits contain the necessary characteristics and functional connections that should underly the involuntary mechanisms of exogenous attention and IOR. Together, these provide a

theoretical substrate for the shared representation suggested by Haggard et al. (2006), although, it may be more likely that these shared representations are broadly location specific and are lateralized by input carrying more precise information regarding the position of the stimulation. Moreover, this low-level representation akin to coordinates on the body inform the circuits underlying exogenous attention and IOR, which may better explain the current findings and tactile IOR in general.

The current study observed that IOR is present at long ISIs for both cued and uncued fingers from the same hand relative to the enhanced responding exhibited for uncued homologous finger targets. However, facilitated responses were not seen for adjacent finger targets to the homologous finger. Since the cued and uncued homologous fingers share a representation by virtue of their same location on their respective hands, attention is oriented away from the cued hand to the uncued homologous finger on the opposite hand via their mutual mapping. As a result processing subsequent targets appearing on either finger of the formerly cued hand are inhibited. Meanwhile, enhanced processing is only evident for uncued homologous finger target on the opposite hand because the finger targets adjacent to it do not share a common representational locus. Similarly, Roder et al. (2002) observed IOR for targets on both the cued and uncued fingers of the same hand. Interestingly, at short ISIs the uncued finger targets adjacent to the cued finger are facilitated compared to the uncued homologous finger target, however, cued finger targets do not show this effect contrary to our prediction. Moreover, mean RTs for the cued finger (which are faster than its homologue, though non-significantly) are slower than the adjacent finger target. Speculatively, this can be explained with respect to the ecology of hand usage and tactile exploration which generally do not restrict stimulation to a single finger, since manipulating objects and other daily tasks recruit multiple

digits at a time. In turn, the cued finger orients attention to the cued location on the hand and primes proximal locations as a result. Therefore, stimulation of a single finger presents an increased likelihood that the stimulus will advance to the adjacent finger(s) as per the natural statistics of the hand (Ejaz, Hamada, & Diedrichsen, 2015; Akselrod, Martuzzi, van der Zwaag, Blanke, & Serino, 2021). Consequently, when attention is oriented to the hand by virtue of attending to the cued finger at short intervals, processing of targets appearing on the hand are enhanced if they are at or near the cued finger location(s) (Haggard et al., 2006; Galvez-Garcia, De Haan, Lupianez, & Djikerman, 2011). Recent fMRI studies have shown this distribution of activity to exist. These studies show that when a given finger is stimulated, activation is observed for cortical finger representations near or adjacent to the stimulated finger representation, this representational overlap increases anterior-posteriorly across subregions in S1 (Akselrod et al., 2021; Besle et al., 2014) to the degree that anterior overlap extends up to three fingers while posterior overlap can cover all five digits. Nevertheless, activation is not uniform and decreases in strength with distance from the stimulated finger (Akselrod et al., 2021; Besle et al., 2014). As a result, in our study cueing a finger orients attention to the hand with particular focus on the cued finger location which consequently primes the adjacent finger through functional cross-activation. Accordingly, processing is accelerated fostering enhanced responding upon target delivery. In this respect processing for the whole hand of the cued finger is facilitated to varying degrees. Similar effects were reported by Spence and McGlone (2001), observing enhanced discrimination of targets appearing on either the thumb or index finger after both were cued simultaneously. The thumb and index finger comprise a functional connectivity that is representative of their cooperative use during precision grip and other opposition behaviours supporting the coordinated action required during grip control to adjust one’s grip force in

response to error signals indicating object slip (Napier, 1956; Johnson, 2001; Smith, Gosselin, & Houde, 2002; Overduin & Servos, 2004). Therefore, it is understandable that stimulation applied to the thumb and index finger simultaneously will promote enhanced responding to targets presented to either one (Napier, 1956; Akselrod et al., 2021; Besle et al., 2014). Unsurprisingly then, the mean RTs of the uncued adjacent finger target are faster at short ISIs than for cued finger targets, consistent with the implication of cross-activation from the cued finger priming the one adjacent to it to anticipate an impending stimulation (Ejaz et al., 2015). Therefore, our results indicate that the mutual representation of the homologous finger locations acts as a 'pivot-point' by which attention can shift from one hand to the other. Since attention is already oriented to the common representation it is both logical and less taxing for attention to orient toward novelty in search of the target by way of this pivot-point. It is less costly than moving to a distant bodily representation because shared representation is attended to and disengaging from it to orienting attention to an entirely unrelated representation would require substantially more time and energy. Also, the hands and particularly the fingers are extremities by which humans and other animals with grasping abilities tactually explore their physical environment, as a result it would stand to reason that both hands would be routinely used during tactile exploration (Johansson & Vallbo, 1983, 1979; Loutit et al., 2021; Squeri et al., 2012; Gallace & Spence, 2014). In turn, when searching for a tactile target with one's hand/fingers which was previously detected on one hand/finger, it is most probable that the target will appear on the opposite hand rather than at other bodily locations. This is particularly useful when feeling one's way around in the dark, in that both hands have an equal probability of touching something. In this way if one hand touches something it may be that if it was felt with the index finger and thumb but not the rest, this could be the border of the object which then would suggest that it exists between the

hands and would likely be confirmed by the opposite hand, more specifically by the homologous thumb and index finger. In a similar sense, the star-nosed mole is a creature that depends predominantly on somatosensory input using 11 hypersensitive appendages on its star-like nose to orient in space in this same manner. However, being that it is tactually dominated, its SC is governed by the mechanosensory star, unlike the SC in visual animals which is organized retinotopically, yet comparably it directs saccades of the star-nose tactile fovea in a similar manner to that of the eye (Crish, Comer, Marasaco, & Catania, 2003). The human finger-tip contains the greatest density of afferent units and is generally the preferred site for tactual exploration, in this respect, the finger-tip can act as a tactile fovea facilitating the same spatial orienting abilities as the visual fovea when vision is not a dependable option (Johansson & Vallbo, 1983). As such this postulated system is a logical and cost-effective method to facilitate attentional orienting in search of task relevant stimuli, requiring less cognitive resources and increasing the likelihood of target detection by pivoting along a shared representational locus. Nevertheless, when processing is enhanced for uncued homologous finger targets, finger targets adjacent to it are not. Ostensibly, this is because none of the fingers on the uncued hand were formerly stimulated, so activation would not be distributed to the adjacent finger to the uncued homologous finger as is the case with adjacent target fingers on the cued hand. Additionally, unlike the uncued homologous finger, the contralateral adjacent finger target does not share a representation with the cued finger, making it improbable that attention would shift to its location after long ISIs. This finding conflicts with the observation that both hands are mutually exclusive regions strictly inducing IOR or faciliatory processing, to different degrees within each hand, as reported by Roder et al. (2002). The authors reported that both fingers on the uncued hand exhibited facilitation, while both finger on the uncued hand displayed IOR (Roder et al.,

2002). This difference might be due to the use of detection rather than a discrimination task, as detecting a stimulus on one hand compared to the other necessitates a general attention of the whole hand. Meanwhile, in our study both the hand and the individual fingers belonging to it required attention, a task requirement that commands more precise spatial information. Further, previous studies have shown that IOR and enhanced responding can be elicited at cued and uncued locations respectively within the same palmar surface, highlighting that low-level representations of skin coordinates rather than the higher-order whole limb or finger representation updates exogenous tactile attentional orienting and tactile IOR (Galvez-Garcia et al., 2011). This suggests that the production of IOR between hands and within distinct locations of the same hand is task dependent i.e., since cortical inputs to thalamic nuclei, SC, DCN, and the spinal cord modulate the relevance of a given stimulus and thus the reaction and orienting behaviour to it (Wallace et al., 1992, 1993; Loutit et al., 2021; Abraira & Ginty, 2013; Abraira et al., 2017).

Detection and discrimination of tactile stimuli are carried to the brain by both common and distinct pathways and the perception of either is abolished through distinct cortical lesions, indicating a functional difference in their processing requirements (Vierck Jr., 1974; Anema et al., 2008; Paillard et al, 1983). This distinction is particularly apparent among finger agnosia patients, whose ability to detect but not overtly distinguish the stimulated finger denotes the redundancy of higher-order finger representation when detecting a stimulus presented to the fingers (Anema et al., 2008; Anema et al., 2011). Instead, being that individuating the finger is not especially important in detection tasks, the higher-level somatotopic representation is not recruited and instead tactile information coded on a somatotopic map of the skin is employed (Longo, Azanon, & Haggard, 2010; Anema et al., 2011). This manner of coding somatosensory

information is sufficient to represent the side (right/left), the extremity (upper/lower), the position (proximal/distal), and the modality type (slow/rapid adapting afferents) of the presented stimulation. All this information is adequately processed and integrated within the DCN and earlier in the spinal dorsal horn itself (Loutit et al., 2021; Abraira, 2017). Interestingly, finger agnosia patients perform near normal for the thumb and little finger. Recent studies looking at the palmar and finger representation in S1 show that the thumb and little finger are heavily associated with the palm, such that palmar stimulation produces large cross-activation patterns in the thumb and little finger representations (Akselrod et al., 2021). This supports the notion that in lieu of activating the finger representation, stimuli on the fingers are coded as spatial coordinates that are part of the whole hand representation (Anema et al., 2008; Haggard & Wolpert, 2005; Galvez-Garcia et al., 2011). In this respect, the representation employed depends on the cognitive requirements commanded by the task, such that simple detection and spatial discrimination (i.e., same, or different location) tasks utilize low-level representations while naming a stimulated limb or discriminating between complex tactile objects requires a greater amount of processing and likely will recruit higher-level cognitive representations. This is indicated by the normal performance of finger agnosia patients compared to healthy controls in their ability to discriminate gaps within a continuous raised line and the absence of a line segment among raised line segments by raising the finger under which they feel the gap or the absence of a line segment respectively (Anema et al., 2011). A similar finding is observed for tasks involving the crossing of the middle finger over the index finger at different orientations (0^o [not crossed], 45^o, 90^o, and 135^o) where a reference and target stimulus are applied simultaneously at different orientations (0^o [horizontal position], 45^o, 90^o, and 135^o) to the crossed index and middle fingers respectively. In these tasks patients perform on par with and in

some cases better than controls in determining the orientation of the stimulus relative to the reference stimulus (Anema et al., 2011). In turn, discriminating stimulation points between fingers seems to be a lower-level function, while the representation supporting the individuation of the fingers (i.e., naming the finger), as per the percept of 'finger fusion', suggests that it is rooted in higher processing stages at the cortical level. Consequently, the results from the current study reflect the recruitment of the low-level dermatome representation within the spinal cord dorsal horn and the DCN for exogenous attention and IOR which is supported by the results testing our second hypothesis.

Spinal cord circuitry and DCN cooperatively process and integrate afferent input in parallel

The results obtained when transposing the tactile Posner task to fit within the finger-tip showed that there was no difference between Location trials and Finger trials. Specifically, cued targets on the finger-tip showed similar trends to cued finger targets, while results for uncued target locations on the finger-tip resembled that of the uncued homologous finger target such that valid Location trials showed significant facilitation from short to intermediate ISIs, and IOR at long relative to intermediate ISIs, whereas, invalid Location trials exhibited facilitation at long relative to short ISIs (See Figure 9).

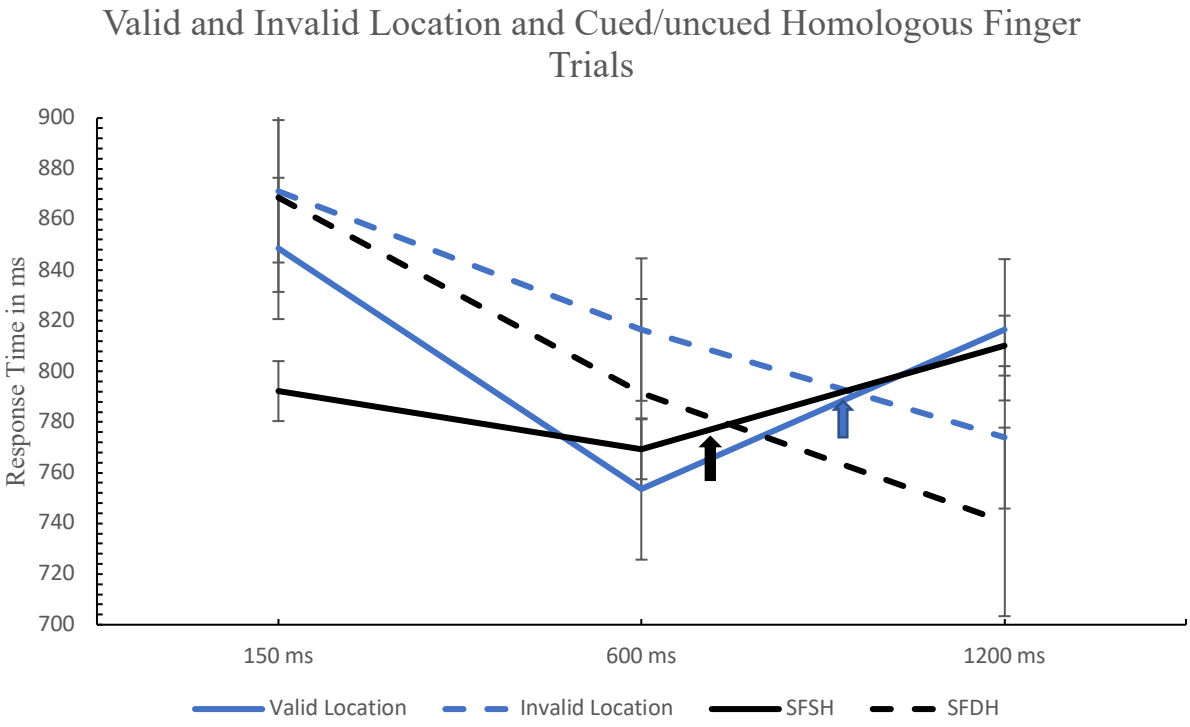


Figure 9. Mean RTs for valid and invalid Location trials compared to valid Finger trials (SFSH) and its uncued finger homologue (SFDH). Y-axis and data points all coded in milliseconds (ms), x-axis are ISIs. Each trial type is indicated by their respective colour/form in the legend. Black Arrow: indicates cross-over point for Finger trials. Blue Arrow: indicates cross-over point for Location trials.

This finding is particularly telling, further expressing that tactile IOR and likely exogenous attention in general, is determined by the dermatome representation using skin coordinates rather than representations indexing the whole finger or limb (Haggard & Wolpert, 2005). However, the difference between invalid and valid Location trials are not statistically significant from each other, although, they did approach significance for intermediate ISIs (p = .06) (See table 4). While it is feasible that increasing the sample size could increase the magnitude of significance for this ISI, it is also likely that cueing effects of facilitation and IOR have longer latencies when applied within the finger-tip. This is supported by findings from a

study by Galvez-Garcia et al. (2011) which investigated the differing mental representations of the finger and the hand by assessing whether the IOR effect elicited within the finger and palm differed from each other.

The within finger condition entailed two possible stimulation points on the volar middle and base pads of a single finger. Below the finger were two more stimulation points on the distal and central side of the palm constituting the within palm condition. As such there were four indentation points arranged in a vertical column ranging from below the distal phalanx to the center of the palm. At long ISI, the detection of intra-finger and intra-palmar cued targets displayed IOR, however, intra-palmar IOR responses were faster than intra-finger IOR. Interestingly, when the cue and target were presented inter-regionally, such that the cue and target were on anatomically different regions (i.e., the palm and the finger), inter-finger and inter-palmer cueing differed substantially. At short ISIs, cued finger targets displayed IOR while cued palmar targets produced facilitated detection relative to when the target was on the opposite anatomical location. However, at long ISIs both cued finger and palmar locations, though faster than the finger trials, produced IOR for target detection. Surprisingly, at IOR producing intervals, when the cue was above the target, responses were significantly faster than when the cue was below the target, and both were significantly faster than when the target and the cue were in the same location. These findings support the idea that the finger and palm utilize different representations while also showing that facilitation increases toward the center of the hand or more broadly moving from distal to proximal locations. This is indicative of the hierarchical and modular nature of somatic representations such that the fingers are part of the hand, the hand is a part of the arm, and so on (Haggard & Wolpert, 2005; Haggard et al., 2006). In this respect, it is understandable that the finger-tip representation should differ from the whole

finger representation in the same modular manner, seeing as a distinct point on the finger-tip must be processed according to its location within the tip, then as a finger-tip belonging to a specific finger of a given hand, and so on. Therefore, while the dermatome is likely responsible for representing both the finger and the finger-tip, according to the case asserted thus far, the finger-tip is a heavily innervated portion of the finger with small RFs relative to those encompassing the whole finger (Loutit et al., 2021; Abraira & Ginty, 2013; Johansson & Vallbo, 1979). In this manner, information integration is associated with the widening of response profiles of neuronal populations in accordance with input arriving from any number of potential sources (Schellekens et al., 2021). As such, it stands to reason that IOR at the finger-tip though driven by the same low-level dermatomal representation as the whole finger necessitates longer latencies. This is evidenced by the cross-over point between facilitation and IOR occurring much later for Location trials than for Finger trials (See Figure 9). Furthermore, while exogenous attention and IOR at the whole finger level is presumably driven by representations in the Cu-DCN along with subcortical circuits in the brain stem and midbrain, they are likely determined by processes within the spinal cord dorsal horn at the level of the finger-tip.

The unique morphological and anatomical organization of LTMR subunit endings in the skin subserves the distinct response properties of the LTMR subtypes for the perception of a given tactile stimulus (i.e., size, shape, texture, vibration, and direction of movement; Abraira & Ginty, 2013; Johansson & Vallbo, 1979, 1983; Gallace & Spence, 2014). However, in contrast to the canonical interpretation of innocuous discriminative touch, processing of the diverse properties of LTMR afferent subunits and their respective end organs does not begin in S1 but occurs in the DCN, as mentioned, and further downstream in the deep dorsal horn of the spinal cord (Loutit et al., 2021; Abraira & Ginty, 2013; Li et al., 2011; Abraira et al., 2017).

Consequently, it is here that we suspect processing and the mechanics of exogenous attention and IOR to subsist for location specific stimulation within the overarching representation of the whole finger in the DCN. Li et al. (2011) showed that while all LTMR axonal branches terminate in the dorsal horn only a small proportion of them ascend directly to the DCN in rats in high somatotopic register, however, the remaining LTMR afferents are arranged in a highly overlapping manner in the dorsal horn lamina comprising the LTMR-RZ (lamina IIi-IV; See *Localized Attention and Tactile Receptors* part *b)*, for abbreviations and review of LTMR-RZ). Nevertheless, the respective position of any LTMR afferent unit's termination in the LTMR-RZ does not inform their relative modality and somatotopy rather the pattern of distinct LTMR afferent subunits along with the interneuronal circuits they terminate onto found in the LTMR-RZ combine to process and integrate such information which is then conveyed through the PSDC originating within the III/IV boundary of the LTMR-RZ (Abraira & Ginty, 2013; Li et al., 2011; Abraira et al., 2017). Within the LTMR-RZ, ~70% of inputs are from sensory neurons and locally projecting interneurons, whereas ~40% are corticospinal projecting neurons. Furthermore, of the neurons intrinsic to the LTMR-RZ ~70% and ~30% are excitatory and inhibitory respectively, with less than 2% of neurons in this region representing supraspinal projections. Thus, given that the majority of LTMR-RZ neurons project locally within the spinal cord and consist of a wide range of morphological and physiological properties this is indicative of a neuronal substrate for innocuous touch processing (Abraira et al., 2017). Of the intrinsic neurons in LTMR-RZ, 11 subtypes are identified, with four being inhibitory and seven being excitatory. When silencing large cohorts of inhibitory and excitatory LTMR-RZ interneurons in mice novelty seeking behaviour supporting the exploration of novel textured objects in control mice was abolished in experimental mice (Abraira et al., 2017). However, novelty seeking

behaviour was not impaired for novel visual objects indicating that the effect is strictly tactile. In turn, these inhibitory and excitatory interneuron subtype ensembles are required for texture discrimination and likely IOR suggesting that the LTMR-RZ is critical for innocuous touch perception. Further, nearly all LTMR-RZ interneuron subunits synapse locally within the LTMR-RZ, where inhibitory subunits make axodendritic synapses to foster feedforward inhibition and a small portion of subunits form axoaxonic synapses to mediate the presynaptic inhibition of primary afferent terminals (Abraira et al., 2017; Todd, 1996). Each of these 11 LTMR-RZ interneuron subtypes gather converging synaptic input from at least two (or more) physiologically distinct LTMR subtypes. Meanwhile, these discrete LTMR subtypes present divergent synaptic connections onto a minimum of four and up to 11 LTMR-RZ interneuron subunits, which also receives input from corticospinal neurons and local spinal cord interneurons. The PSDC mainly receives input from these local LTMR-RZ interneurons, a small amount from Aβ-LTMRs, and even less from corticospinal projections suggesting that the high degree of excitatory local LTMR-RZ inputs onto PSDC neurons which receives distinct LTMR and cortical input influences their output properties. *Ex vivo* recordings of PSDC neurons shows that these neurons possess intricate tuning and RF properties that are distinguishable from any specific LTMR subtype. In fact, PSDC neurons not only receive direct monosynaptic Aβ-LTMR, but also indirect inhibitory and excitatory input from LTMR-RZ interneurons determined by inputs from LTMR subtypes and corticospinal neurons (Abraira et al., 2017; Loutit et al., 2021). Consequently, each LTMR-RZ interneuronal populations acts as a functionally distinct integrator of tactile modalities and efferent cortical inputs, coordinating patterns of ascending LTMR-RZ impulses that underlie the perception of touch (Abraira & Ginty, 2013; Li et al., 2011; Abraira et al., 2017; Loutit et al., 2021).

In this manner, LTMR-RZ output via the PSDC, is the combined weighting of LTMR subtype input that differ with respect to conduction velocities, RF sizes, tuning, and adaptation properties. Because LTMR-RZ interneuron synapses are in the LTMR-RZ and all 11 interneurons receive excitatory input derived from the spinal cord itself expressing a high degree of connectivity within the LTMR-RZ, thus, enabling LTMR input to be computed in parallel. This indicates a cellular and circuit-level substrate for integration and context-specific output. This process could promote the selective gating of certain modalities under specific physiological conditions. Importantly, the broad contribution of excitatory corticospinal neurons directly engaging each LTMR-RZ interneuron, implicates the LTMR-RZ as a locus for somatosensory modulation during active conscious tactile exploration whose broad and relatively even distribution across the LTMR-RZ may likely mediate the signal of all light touch circuit modules. As such, cortical and LTMR input to a given LTMR-RZ interneuron ensemble can either depress or enhance specified tactile pathways of select modalities or in a somatotopically arranged fashion. This in turn allows for the distinctive processing of select task relevant tactile input during tactile exploration and passive touch. Finally, the fact that PSDC neurons receive direct input from Aβ-LTMR and indirect input from LTMR-RZ interneurons, which receive input from at least two LTMR subtypes and cortical neurons and are critical for innocuous touch perception, suggests that processing and integration necessary for perception originates in the LTMR-RZ and is carried to the brain by the PSDC. Taken together, the remarkable properties of the LTMR-RZ suggest it is a likely candidate for facilitating the representational capacity necessary for determining the manner in which exogenous attention and IOR are oriented at significantly low cognitive levels, particularly within the finger-tip.

The cluster regions of the DCN have been shown to send efferent projections through the ipsilateral DC terminating in the ipsilateral dorsal horn laminaes 1, 3, 4, and 5, which coincides with the LTMR-RZ layers (Loutit et al., 2021; Abraira et al., 2017; Abraira & Ginty, 2013). Additionally, cortical projections to the DCN coincide with regions that contain the densest spinal projections, which are likely involved in movement-related touch, active, and passive tactile exploration. These DCN-spinal projecting regions also receive input from the Rt, red nucleus, and tectum which receives direct spinal projections from the dorsal horn that terminate onto the ICo. Further, the DCN-spinal target laminae 3 and 4 contain origin cells for the PSDC, whose neurons share response properties with the DCN but with substantially more discrete RFs, indicative of a DCN-spinal-DCN pathway (Loutit et al., 2021). As such, while dermatomal representations in the DCN likely subserve exogenous attention and IOR at larger areas such as the hand and the finger, reciprocal connections between the DCN and LTMR-RZ as well as integration and processing within the LTMR-RZ itself are doubtlessly responsible for similar functions at more discrete regions such as within the finger-tip. Thus, exploration using the hands and finger simultaneously, such as when navigating in external space or reacting to rapid salient tactile stimulation that requires quick orienting responses (i.e., swatting a mosquito), presumably utilize the wider response profiles of the DCN in conjunction with the various subcortical structures outlined to be involved in exogenous IOR. Meanwhile, when exploring an object, which is largely done through manipulating it with the hand, attention is oriented to the hand containing the to-be explored object through lateralizing mechanisms of the IO. Further, the same cortical and subcortical projections that are necessary for IOR at the hand and limb could also descend via the DCN to the LTMR-RZ to modulate more narrow response profiles required for fine tactile exploration. In this respect, such input would serve to inhibit features of an object

already attended to with respect to the modality invoked by the object, such as texture, indentation, curvature, as well as the distinct locations stimulated by it on the hand. Generally, such exploration would provide information of the finished percept of the tactile object to the DCN and then the cortex. However, when actively exploring the object tactually, more refined response properties are necessary and cannot be represented at the DCN level. This level of recruitment is likely driven by the requirements of the task which via descending cortico-DCN-spinal projections modulate the importance of varying inputs at this level. Since our study separated Finger and Location trials, participants would be aware of whether the task required attendance to the whole finger or individual points within the finger-tip. So, it is reasonable to suggest that Location trials employed LTMR-RZ representations to facilitate attendance necessary for the precise spatial detail required by the discrimination task. Hence, while attention is endogenously brought to the hand manipulating the object, the manner in which information is gathered from the object is ostensibly exogenously driven (Smith et al., 2002). Relatedly, as eye saccades that move through visual space attending to various aspects of the visual scene, the hand works in a similar capacity to collect various aspect of the object of interest. Therefore, IOR is equally important for the processing of tactile information in this way by inhibiting cellular populations within the LTMR-RZ through feedforward inhibition and the mediation of presynaptic inhibition of primary afferent terminals. As a result, such a mechanism would inhibit the processing of previously explored aspects of an object and facilitate the processing of novel portions. So, when a target stimulus appears at a previously explored position, IOR is evidenced. Previous studies have shown this to be the case in the visual domain, where previously attended portions of an object induce IOR even when they are presented in a novel visual position (Tipper & Weaver, 1998; Tipper, Driver, & Weaver, 1991; Klein, 2000; Roder et al., 2002). Given that

IOR is a supramodal attentional mechanism it is understandable that a tactile analog should exist (Spence et al., 2000; Klein, 2000). Accordingly, LTMR-RZ interneuron populations may likely constitute the equivalent of a shared representation which could be supported by the vast interconnectivity of the region, and thereby follow suit with our proposed model of attentional orienting by virtue of these representational pivot points. This is in line with the concept of inhibitory tagging of visual objects suggested by Tipper et al. (1991). Seemingly then, exogenous attention and IOR work in a hierarchical manner with respect to widening response profiles from the LTMR-RZ up to the DCN, recruiting the necessary frame of reference in accordance with the task parameters. In this regard, our findings strongly support the view that tactile IOR, and exogenous attention more generally, are determined by the low-level dermatomal representation. Although, whether it is enabled by early processing properties in the DCN or further downstream within the LTMR-RZ likely depends upon the requirements of the task.

Conclusion, limitations, and future research

The analogous results of the Finger and Location trials support the notion that tactile IOR is mechanized by a common attentional reference frame, notably by the dermatome. The difference in cross-over points speaks to the modular and hierarchical nature of this somatic representational scheme. That is, the response properties of the LTMR-RZ feed into the larger representations of the DCN and as such Location trials confer longer response latencies. Discriminating between fingers works by lateralizing stimulation to the hand and then the RF reflecting the stimulated finger on that hand. Location trials, on the other hand, require this same process along with determining the precise point of stimulation on the respective finger-tip for effective discrimination. Together, we propose that IOR and the reflexive orienting of tactile

exogenous attention on the body, with respect to spatial discrimination, detection, and likely non-spatial discrimination tasks are determined by a low-level dermatomal representation. This is employed to varying degrees according to the demands of the task, where crude detection and discrimination are enabled by processes within the DCN, while more precise tasks, involving finer detail, are fostered by the LTMR-RZ within the dorsal horn spinal cord. As such, IOR is an exploratory mechanism that does not simply aid in predation and self-preservation but is likely an attentional mechanism inherent to the perception of environmental stimuli regardless of sensory modality though, at its core, tactile exogenous attention and IOR seem to be subserved by low-level dermatomal representations. However, while this might be the case for our study where participants cannot see their hands, it may also be that seeing the hands may recruit higher-order representations inherently, as humans are more accustomed to gathering information visually (Gallace & Spence, 2014). In turn, low-level representations may still influence tactile attention, however, they may work in concert with more allocentric representational properties, and thus might be used as a sole referencing system only when other sensory input is scarce or absent. Subsequently, future studies should utilize the current paradigm with conditions where participants are able to view their hands and where they cannot, which would better inform the representational model used for tactile IOR and tactile exogenous attention more generally. Further, Location trials cued the same position on the distal finger-tip with targets appearing at the same position or below it at the proximal portion of the finger-tip, it may be the case that cueing the proximal finger-tip might produce more inhibitory results than cueing the distal portion (see Galvez-Garcia et al., 2011 in *Spinal cord circuitry and DCN cooperatively process and integrate afferent input in parallel*). However, it is unlikely that this would be a significant effect as posited by Galvez-Garcia et al. (2011), as they stimulated the

base and the middle pads of the finger which are mapped by distinct cortical regions in S1 and not distinct regions within a single pad, as in the current study, and does not share such a refined cortical representation (Sanchez-Panchuelo et al., 2012; Overduin & Servos, 2004, 2008). To add, the finger-tip is a region that is densely innervated by LTMR afferents, which decreases toward the palm with a significant decline at the middle and a more gradual decrease from the middle to the base of the finger (Johansson & Vallbo, 1979, 1983). As such it may be that their findings reflect the respective decrease in density of LTMR afferents which feed into larger RFs than the distal portions i.e., the finger-tip (Loutit et al., 2021). Nevertheless, future studies would benefit by having proximal and distal cues on the finger-tip to confirm our findings in addition to increasing the ISIs to account for the increased response latencies posited by such trials. Additionally, incorporating more fingers during whole finger trials would allow for a better understanding of how attention orients between fingers by removing the potential effects of cross-activation by comparing distant fingers such as the index and little finger.

While the current study was conducted with the best practices in mind there remain several limitations. First, the gender of the participants recruited was not accounted for in our study, seeing as previous studies have shown that males have a greater advantage over females in tasks involving response time (Adam et al., 1999) it would have been important to obtain such demographic details. Moreover, RTs seem to be less variable for men than for women as such some variability in our findings may be influenced by differences in gender (Dykiert, Der, Starr, & Deary, 2012). Second, the ages of the participants recruited was not taken, although all participants were undergraduate students it cannot be assumed that all participants were between 18 and 22 (the standard age of undergraduate students) many may be mature students of varying ages. Previous studies have shown that the speed of RT decreases with age suggesting that a

variation in age would likely account for some variation in our RT data (Dykiert et al., 2012). Lastly, there was some degree of variability with respect to how accurate participants were during the discrimination task (See Table 1, Appendix). As such, some participants were extremely accurate while others were just above the cut-off (>70%), suggesting that there may be individual differences with respect to acuity, discrimination ability, or attentional capacity. Therefore, future studies should account for age and gender to minimize the degree of variation inherent in the sample. Additionally, future studies would benefit from measuring participants individual levels of acuity prior to the experiment because lower levels of acuity may increase RTs since the ease of discriminating between tactile stimuli is related to acuity. Thus, participants with lower acuity levels may differ in RTs from participants with higher levels of acuity due to physiological differences confounding RT performance (Johansson & Vallbo, 1979). Furthermore, assessing individual levels of acuity would allow for an investigation of how tactile sensitivity influences tactile exogenous attention and IOR. The same paradigm used in the current study could be employed, however, participants should be grouped according to their respective acuity levels (i.e., high or low). This would be particularly interesting to investigate as Posner and Cohen (1984) showed that increasing or decreasing the magnitude of the cueing stimulus (thus increasing one's sensitivity to the stimulus) in the visual domain had no effect on IOR. As such it would be interesting to see if one's level of tactile sensitivity affects the speed of tactile exogenous attention and the parameters by which tactile IOR is evoked.

The current study showed that IOR is likely driven with respect to the low-level dermatome. However, we noted that the nature of the task employed and thereby the responses required may mediate the recruitment of higher-level representations should the task be more cognitively involved. As such future studies should utilize the same paradigm used in the current

study although with the addition of a new condition. This condition would employ the same cue-target paradigm, but participants would be required to name the target finger which may invoke higher-levels of processing and likely higher-order representations as finger identification is a higher-level function (Anema et al., 2008; Anema et al., 2011). Consequently, findings from such a study would provide insight into whether tactile IOR is always driven by the dermatomal representation regardless of task complexity or if the representational system used for orienting IOR is related to the cognitive involvement of a given task.

In sum, our findings add to the paucity of research in the field of tactile attention and IOR, exhibiting the prototypical trends of IOR both at the level of the whole finger and within a given finger-tip. This suggests that tactile IOR and tactile exogenous attention more broadly are determined with respect to a low-level dermatomal representational referencing system. However, while both the whole finger and the within finger-tip tasks utilize the same representational scheme, the manner of processing likely differs such that tasks requiring more precise spatial or modality-specific detail, like the finger-tip, are likely processed within the dorsal horn spinal cord while more crude parameters, as with the whole finger discrimination, are seemingly processed within the DCN. Importantly, these results convey a modular and hierarchical representational scheme wherein information integration is associated with the widening of response profiles of neuronal populations with respect to incoming somatosensory information and corticospinal projections that modulate exploratory properties with respect to the demands specified by the given context. The proposed model of tactile IOR is consistent with previous findings in the visual and tactile domain further supporting its role as a supramodal attentional mechanism. Lastly, it appears that IOR is a mechanism that not only facilitates

exploratory behaviour responsible for predation and self-preservation but may be an attentional mechanism that supports the conscious perception of the external sensory environment.

References:

Abraira, V. E., & Ginty, D. D. (2013). The sensory neurons of touch. *Neuron*, *79*(4), 618–639.

Abraira, V. E., Kuehn, E. D., Chirila, A. M., Heintz, N., Hughes, D. I., … Ginty, D. D. (2017). The Cellular and Synaptic Architecture of the Mechanosensory Dorsal Horn. *Cell*. *168*(1-2), 295–310

Abrams, R. A., & Pratt, J. (2000). Oculocentric coding of inhibited eye movements to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance*. *26*(2), 776–788

Adam, J. J., Paas, F. G., Buekers, M. J., Wuyts, I. J., Spijkers, W. A., & Wallmeyer, P. (1999). Gender differences in choice reaction time: evidence for differential strategies. *Ergonomics*, *42*(2), 327–335

Aglioti, S., Smania, N., Moro, V., & Peru, A. (1998). Tactile salience influences extinction. *Neurology*. *50*(4), 1010–1014

Andersen, P., Eccles, J. C., & Sears, T. A. (1962). Presynaptic inhibitory actions: Presynaptic inhibitory action of cerebral cortex on the spinal cord. *Nature*. *194*, 740–741

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*. *20*(1), 303–330

Anema, H. A., Kessels, R. P. C., De Haan, E. H. F., Kappelle, L. J., Leijten, F. S., Van Zandvoort, M. J. E., & Dijkerman, H. C. (2008). Differences in finger localisation performance of patients with finger agnosia. *NeuroReport*. *19*(14), 1429–1433

Anema, H. A., Overvliet, K. E., Smeets, J. B. J., Brenner, E., & Dijkerman, H. C. (2011). Integration of tactile input across fingers in a patient with finger agnosia. *Neuropsychologia*. *49*, 138–146

Akselrod, M., Martuzzi, R., van der Zwaag, W., Blanke, O., & Serino, A. (2021). Relation between palm and finger cortical representations in primary somatosensory cortex: A 7T fMRI study. *Human Brain Mapping*. *42*, 2262–2277

Barnett, K. (1972). A theoretical construct of the concepts of touch as they relate to nursing. *Nursing Research*. *21*(2), 102–110

Benedetti, F. (1985). Processing of Tactile Spatial Information With Crossed Fingers. *Journal of Experimental Psychology: Human Perception and Performance*. *11*(4), 517–525

Bensmaïa, S., & Hollins, M. (2005). Pacinian representations of fine surface texture. *Perception and Psychophysics*. *67*(5), 842–854

Berkley, K. J. (1980). Spatial relationships between the terminations of somatic sensory and motor pathways in the rostral brainstem of cats and monkeys. I. Ascending somatic sensory inputs to lateral diencephalon. *Journal of Comparative Neurology*. *220*(2), 229–251

Berlucchi, G., Tassinari, G., Marzi, C. A., & Di Stefano, M. (1989). Spatial distribution of the inhibitory effect of peripheral non-informative cues on simple reaction time to non-fixated visual targets. *Neuropsychologia*. *27*(2), 201–221

Besle, J., Sánchez-Panchuelo, R. M., Bowtell, R., Francis, S., & Schluppeck, D. (2014). Event-related fMRI at 7T reveals overlapping cortical representations for adjacent fingertips in S1 of individual subjects. *Human Brain Mapping*. *35*(5), 2027–2043

Botvinick, M., & Cohen, J. D. (1998). Rubber hand ‘feels’ what eyes see. *Nature*. 391, 756

Bourane, S., Grossmann, K. S., Britz, O., Dalet, A., Del Barrio, M. G., Stam, F. J., … Goulding, M. (2015). Identification of a spinal circuit for light touch and fine motor control. *Cell*. *160*(3), 503–515

Brown, A. G. (1981). *Organization in the Spinal Cord: The Anatomy and Physiology of Identified Neurones*. Springer London. Berlin

Bumke, O.; Foerster, O. (1935). Handbuch Der Neurologie, *The Journal of Nervous and Mental Disease*. *84*(6), 712

Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences*. *16*(6), 338–352

Cohen, J. C., Bolanowski, S. J., & Verrillo, R. T. (2007). A direct comparison of exogenous and endogenous inhibition of return and selective attention mechanisms in the somatosensory system. *Somatosensory & Motor Research*. *22*(4), 269–279

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*. *3*, 201–215

Crish, S. D., Comer, C. M., Marasco, P. D., & Catania, K. C. (2003). Somatosensation in the superior colliculus of the star-nosed mole. *Journal of Comparative Neurology*. *464*, 415–425

Cromer, J. A., & Waitzman, D. M. (2006). Neurones associated with saccade metrics in the monkey central mesencephalic reticular formation. *Journal of Physiology*. *570*(3), 507–523

Dijkerman, H. C., & de Haan, E. H. F. (2007). Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and Brain Sciences*. *30*, 189–239

Downie, J. W., Ferrington, D. G., Sorkin, L. S., & Willes, W. D. (1988). The primate spinocervicothalamic pathway: Responses of cells of the lateral cervical nucleus and spinocervical tract to innocuous and noxious stimuli. *Journal of Neurophysiology*. *59*(3), 861–885

Drager, U. C., & Hubel, D. H. (1976). Topography of visual and somatosensory projections to mouse superior colliculus. *Journal of Neurophysiology*. *39*(1), 91–101

Spence, C. J., & Driver, J. (1994). Covert Spatial Orienting in Audition: Exogenous and Endogenous Mechanisms. *Journal of Experimental Psychology: Human Perception and Performance*. *20*(3), 555–574

Driver, J., & Spence, C. (1998). Cross-modal links in spatial attention. *Philosophical Transactions of the Royal Society B: Biological Sciences*. *353*(1373), 1319–1331

Dykiert, D., Der, G., Starr, J. M., & Deary, I. J.(2012). Sex differences in reaction time mean and intraindividual variability across life the span. *Developmental Psychology. 48*(5), 1262–1276

Ejaz, N., Hamada, M., & Diedrichsen, J. (2015). Hand use predicts the structure of representations in sensorimotor cortex. *Nature Neuroscience*. *18*, 1034–1040

Foerster, O. (1933). The dermatomes in man. *Brain*. *56*(1), 1–39

Gallace, A., Spence, C., (2014). Tactile attention. In *In Touch with the Future*. doi:10.1093

Gálvez-García, G., De Haan, A. M., Lupiañez, J., & Dijkerman, H. C. (2012). An attentional approach to study mental representations of different parts of the hand. *Psychological Research*.*76*, 364–372

Geborek, P., Jörntell, H., & Bengtsson, F. (2012). Stimulation within the cuneate nucleus suppresses synaptic activation of climbing fibers. *Frontiers in Neural Circuits*. *6*(120), 1–9

Haggard, P., Kitadono, K., Press, C., & Taylor-Clarke, M. (2006). The brain's fingers and hands. *Experimental Brain Research*. *172*, 94–102

Haggard, P., & Wolpert, D. M. (2005). Disorders of Body Scheme. In H.J. Freund, M. Jeannerod, M. Hallet, & R. C. Leiguarda (Eds.), Higher-order motor disorders (pp. 261–273). New York: *Oxford University Press*.

Head, H., & Campbell, A. W. (1900). The pathology of herpes zoster and its bearing on sensory localisation. *Brain*. *23*, 353–523

Hirata, H., & Pubols, B. H. (1989). Spinocervical tract neurons responsive to light mechanical stimulation of the raccoon forepaw. *Journal of Neurophysiology*. *61*(1), 138–148

Johansson, R. S., & Vallbo, Å. B. (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *The Journal of Physiology*. *286*, 283–300

Johansson, R. S., & Vallbo, Å. B. (1983). Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neurosciences*. *6*, 27–32

Johnson, K. O. (2001). The roles and functions of cutaneous mechanoreceptors. *Current Opinion in Neurobiology*. *11*(4), 455–461

Jones, A., & Forster, B. (2012). Reflexive attention in touch: An investigation of event related potentials and behavioural responses. *Biological Psychology*. *89*(2), 313–322

Jones, A., & Forster, B. (2014). Neural correlates of endogenous attention, exogenous attention and inhibition of return in touch. *European Journal of Neuroscience*. *40*(2), 2389–2396

Jones, E. G., & Friedman, D. P. (1982). Projection pattern of functional components of thalamic ventrobasal complex on monkey somatosensory cortex. *Journal of Neurophysiology*. *48*(2), 521–544

Kaas, J. H., Nelson, R. J., Sur, M., Lin, C. S., & Merzenich, M. M. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science*. *204*(4392), 521–523

Klein, R. M. (2000). Inhibition of return: review. *Trends in Cognitive Science*. *4*(4), 138–147

Klein, E., & Schilder, P. (1929). The Japanese illusion and the postural model of the body. *Journal of Nervous and Mental Disease*. *70*(3), 241–263

Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. *Trends in Cognitive Sciences*. *11*(1), 16–22

Koch, S. C., Acton, D., & Goulding, M. (2018). Spinal Circuits for Touch, Pain, and Itch. *Annual Review of Physiology*. *80*, 189–217

Krauzlis, R. J., Lovejoy, L. P., & Zénon, A. (2013). Superior colliculus and visual spatial attention. *Annual Review of Neuroscience*. *36*, 165–182

Krubitzer, L., Huffman, K. J., Disbrow, E., & Recanzone, G. (2004). Organization of Area 3a in Macaque Monkeys: Contributions to the Cortical Phenotype. *Journal of Comparative Neurology*. *471*(1), 97–111

Lakatos, S., & Shepard, R. N. (1997). Time-distance relations in shifting attention between locations on one's body. *Perception and Psychophysics*. *59*, 557–566

Lederman, S. J., & Klatzky, R. L. (1987). Hand movements: A window into haptic object recognition. *Cognitive Psychology*. *19*(3), 342–368

Lee, S. H., Kim, D. E., Song, E. C., & Roh, J. K. (2001). Sensory dermatomal representation in the medial lemniscus. *Archives of Neurology*. *58*(4), 649–651

Lee, M. W. L., McPhee, R. W., & Stringer, M. D. (2008). An evidence-based approach to human dermatomes. *Clinical Anatomy*. *21*, 363–737

Li, L., Rutlin, M., Abraira, V. E., Cassidy, C., Kus, L., Gong, S., … Ginty, D. D. (2011). The functional organization of cutaneous low–threshold mechanosensory neurons. *Cell*. *147*, 1615–1627

Lloyd, D. M., Bolanowski, S. J., Howard, L., & McGlone, F. (1999). Mechanisms of attention in touch. *Somatosensory and Motor Research*. *16*(1), 3–10

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*. *48*(3), 655–668

Loutit, A. J., Vickery, R. M., & Potas, J. R. (2021). Functional organization and connectivity of the dorsal column nuclei complex reveals a sensorimotor integration and distribution hub. *Journal of Comparative Neurology*. *529*, 187–220

Lupiáñez, J., Milán, E. G., Tornay, F. J., Madrid, E., & Tudela, P. (1997). Does IOR occur in discrimination tasks? Yes, it does, but later. *Perception and Psychophysics*. *59*(8), 1241–1254

Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C. A., Haggard, P., & Iannetti, G. D. (2014). Whole-body mapping of spatial acuity for pain and touch. *Annals of Neurology*. *75*(6), 917–924

Masland, R. H. (2012). The Neuronal Organization of the Retina. *Neuron*. *76*(2), 266–280

Maylor, E. A., & Hockey, R. (1985). Inhibitory Component of Externally Controlled Covert Orienting in Visual Space. *Journal of Experimental Psychology: Human Perception and Performance*. *11*(6), 777–787

Meredith, M. A., Nemitz, J. W., & Stein, B. E. (1987). Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*. *7*(10), 3215–3229

Meredith, M. A., & Stein, B. E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*. *69*(6), 1797–1809

Meredith, M. A., & Stein, B. E. (1996). Spatial determinants of multisensory integration in cat superior colliculus neurons. *Journal of Neurophysiology*. *75*(5), 1843–1857

Meredith, M. A., Wallace, M. T., & Stein, B. E. (1992). Visual, auditory, and somatosensory convergence in output neurons of the cat superior colliculus: multisensory properties of the tecto-reticulo-spinal projection. *Experimental Brain Research*. *88*, 181–186

Miles, E., Poliakoff, E., & Brown, R. J. (2008). Investigating the time course of tactile reflexive attention using a non-spatial discrimination task. *Acta Psychologica*. *128*, 210–215

Mountcastle, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *Journal of Neurophysiology*. *20*(4), 408–434

Moriishi, J., Otani, K., Tanaka, K., & Inoue, S. -I. (1989). The intersegmental anastomoses between spinal nerve roots. *The Anatomical Record*. *224*(1), 110–116

Napier, J. R. (1956). The prehensile movements of the human hand. *The Journal of Bone and Joint Surgery. British Volume*. *38B*(4), 902–913

Nemecek, A. N., Avellino, A. M., Goodkin, R., Little, J., & Kliot, M. (2003). Mapping dermatomes during selective dorsal rhizotomy: Case report and review of the literature. *Surgical Neurology*. *60*(4), 292–297

Nixon, P. D., Burbaud, P., & Passingham, R. E. (1992). Control of arm movement after bilateral lesions of area 5 in the monkey (Macaca mulatta). *Experimental Brain Research*. *90*(1), 229–232

Overduin, S. A., & Servos, P. (2004). Distributed digit somatotopy in primary somatosensory cortex. *NeuroImage*. *23*, 462–472

Overduin, S. A., & Servos, P. (2008). Symmetric sensorimotor somatotopy. *PLoS ONE*. *3*(1), 1–6

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization Without Content: A Tactile Analogue of 'Blind Sight.' *Archives of Neurology*. *40*(9), 548–551

Patel, S. (2015). Human Dermatomes. In *Nerves and Nerve Injuries*. *Vol. 1*, pp. 477–483

Paul, M. S., & M Das, J. (2019). Neuroanatomy, Superior and Inferior Olivary Nucleus (Superior and Inferior Olivary Complex). *StatPearls*.

Paul, R. L., Merzenich, M., & Goodman, H. (1972). Representation of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in brodmann's areas 3 and 1 of Macaca Mulatta. *Brain Research*. *36*(2), 229–249

Di Pellegrino, G., Ladavas, E., & Farne', A. (1997). Seeing where your hands are [11]. *Nature*. *388*, 730

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*. *60*(4), 389–443

Poggio, G. F., & Mountcastle, V. B. (1963). The functional properties of ventrobasal thalamic neurons studied in unanesthetized monkeys. *Journal of neurophysiology*, 26, 775–806.

Poliakoff, E., O'Boyle, D. J., Moore, A. P., McGlone, F. P., Cody, F. W. J., & Spence, C. (2003). Orienting of attention and Parkinson's disease: Tactile inhibition of return and response inhibition. *Brain*. 126(Pt 9), 2081–2092

Pons, T. P., Wall, J. T., Garraghty, P. E., Cusick, C. G., & Kaas, J. H. (1987). Consistent features of the representation of the hand in area 3b of macaque monkeys. *Somatosensory & Motor Research*. 4(4), 309–331

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*. *32*(1), 3–21

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In *In Attention and Performance Vol. X (Bouma, H. and Bouwhuis, D., eds),*. pp. 531–556 London: Lawrence Erlbaum Associates Ltd.

Posner, M. I., Rafal, R. D., Choate, L. S., & Vaughan, J. (1985). Inhibition of Return: Neural Basis and Function. *Cognitive Neuropsychology*. *2*(3), 211–228

Powell, T. P., & Mountcastle, V. B. (1959). The cytoarchitecture of the postcentral gyrus of the monkey Macaca mulatta. *Bulletin of the Johns Hopkins Hospital*. *105*, 108–131

Pratt, J., Kingstone, A., & Khoe, W. (1997). Inhibition of return in location- And identity-based choice decision tasks. *Perception and Psychophysics*. *59*, 964–971

Röder, B., Spence, C., & Rösler, F. (2002). Assessing the effect of posture change on tactile inhibition-of-return. *Experimental Brain Research*. *143*(4), 453–462

Rose, J. E., & Mountcastle, V. B. (1959). "Touch and kinesthesis," in *Handbook of Physilogy*, ed H. W. Magoun (Washington, DC: American Physiology Society), pp. 387–429

Sanchez-Panchuelo, R. M., Francis, S., Bowtell, R., & Schluppeck, D. (2010). Mapping human somatosensory cortex in individual subjects with 7T functional MRI. *Journal of Neurophysiology*. *103*(5), 2544–2556

Sanchez-Panchuelo, R. M., Besle, J., Beckett, A., Bowtell, R., Schluppeck, D., & Francis, S. (2012). Within-digit functional parcellation of brodmann areas of the human primary somatosensory cortex using functional magnetic resonance imaging at 7 tesla. *Journal of Neuroscience*. *32*(45), 15815–15822

Santangelo, V., & Spence, C. (2008). Is the exogenous orienting of spatial attention truly automatic? Evidence from unimodal and multisensory studies. *Consciousness and Cognition*. *17*(3), 989–1015

Sapir, A., Soroker, N., Berger, A., & Henik, A. (1999). Inhibition of return in spatial attention: Direct evidence for collicular generation. *Nature Neuroscience*. *2*, 1053–1054

Schellekens, W., Thio, M., Badde, S., Winawer, J., Ramsey, N., & Petridou, N. (2021). A touch of hierarchy: population receptive fields reveal fingertip integration in Brodmann areas in human primary somatosensory cortex. *Brain Structure and Function*. *226*, 2099–2112

Sengul, G., & Watson, C. (2015). Ascending and Descending Pathways in the Spinal Cord. In *The Rat Nervous System: Fourth Edition*. pp. 115–130

Sharma, P., Kulkarni, M., & Gandotra, A. (2021). Intra-dural intercommunications between dorsal roots of adjacent spinal nerves and their clinical significance. *Surgical and Radiologic Anatomy*. *43*(9), 1519–1526

Simone, D. A., & Pubols, B. H. (1991). The raccoon lateral cervical nucleus: A single-unit analysis. *Journal of Neurophysiology*. *65*(6), 1411–1421

Simons, S. B., Chiu, J., Favorov, O. V., Whitsel, B. L., & Tommerdahl, M. (2007). Duration-dependent response of SI to vibrotactile stimulation in squirrel monkey. *Journal of Neurophysiology*. *97*(3), 2121–2129

Smith, A. M., Gosselin, G., & Houde, B. (2002). Deployment of fingertip forces in tactile exploration. *Experimental Brain Research*. *147*, 209–218

Soetedjo, R., Kaneko, C. R. S., & Fuchs, A. F. (2002). Evidence that the superior colliculus participates in the feedback control of saccadic eye movements. *Journal of Neurophysiology*. *87*(2), 679–695

Spence, C. (2002). Multisensory attention and tactile information-processing. In *Behavioural Brain Research*. *135*(1-2), 57–64

Spence, C. J., & Driver, J. (1994). Covert Spatial Orienting in Audition: Exogenous and Endogenous Mechanisms. *Journal of Experimental Psychology: Human Perception and Performance*. *20*(3), 555–574

Spence, C., & Driver, J. (1998). Auditory and audiovisual inhibition of return. *Perception and Psychophysics*. *60*, 125–139

Spence, C., Lloyd, D., McGlone, F., Nicholls, M. E. R., & Driver, J. (2000a). Inhibition of return is supramodal: A demostration between all possible pairings of vision, touch, and audition. *Experimental Brain Research*. *134*(1), 42–48

Spence, C., & McGlone, F. P. (2001). Reflexive spatial orienting of tactile attention. *Experimental Brain Research*. *141*(3), 324–330

Spence, C., Pavani, F., & Driver, J. (2000b). Crossmodal links between between vision and touch in covert endogenous spatial attention. *Journal of Experimental Psychology. Human Perception and Performance*. *26*(4), 1298–1319

Squeri, V., Sciutti, A., Gori, M., Masia, L., Sandini, G., & Konczak, J. (2012). Two hands, one perception:How bimanual haptic information is combined by the brain. *Journal of Neurophysiology*. *107*, 544–550

Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multisensory integration: Orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience*. *1*(1), 12–24

Stein, B. E., Jiang, W., & Stanford, T. R. (2004). Multisensory Integration in Single Neurons of the Midbrain. *The Handbook of Multisensory Processes. 15*, 243–264

Tassinari, G., & Campara, D. (1996). Consequences of covert orienting to non-informative stimuli of different modalities: A unitary mechanism? *Neuropsychologia*. *34*(3), 235–245

Teder-Sälejärvi, W. A., & Hillyard, S. A. (1998). The gradient of spatial auditory attention in free field: An event-related potential study. *Perception and Psychophysics*. *60*, 1228–1242

Tipper, S. P., Driver, J., & Weaver, B. (1991). Short Report: Object-centred Inhibition of Return of Visual Attention. *The Quarterly Journal of Experimental Psychology Section A*. *43*(2), 289–298

Tipper, S. P., & Weaver, B. (1998). The medium of attention: Location-based, object-centered, or scene-based? In R. D. Wright (Ed.), *Visual Attention.* pp. 77–107. Oxford University Press.

Todd, A. J. (1996). GABA and glycine in synaptic glomeruli of the rat spinal dorsal horn. *European Journal of Neuroscience*. *8*(12), 2492–2498

Tootell, R. B. H., Tsao, D., & Vanduffel, W. (2003), Neuroimaging weighs in: Humans meet macaques in “primate” visual cortex. *Journal of Neuroscience. 23*(10), 3981–3989

Treisman, A. M. (1969). Strategies and models of selective attention. *Psychological Review*. *76*(3), 282–299

Vega-Bermudez, F., & Johnson, K. O. (1999). SA1 and RA receptive fields, response variability, and population responses mapped with a probe array. *Journal of Neurophysiology*. *81*(6), 2701–2710

Vierck, C. J. (1974). Tactile movement detection and discrimination following dorsal column lesions in monkeys. *Experimental Brain Research*. *20*, 331–346

Wallace, M. T., Meredith, M. A., & Stein, B. E. (1992). Integration of multiple sensory modalities in cat cortex. *Experimental Brain Research*. *91*(3), 484–488

Wallace, M. T., Meredith, M. A., & Stein, B. E. (1993). Converging influences from visual, auditory, and somatosensory cortices onto output neurons of the superior colliculus. *Journal of Neurophysiology*. *69*(6), 1797–1809

Wallace, M. T., & Stein, B. E. (1994). Cross-modal synthesis in the midbrain depends on input from cortex. *Journal of Neurophysiology*. *71*(1), 429–432

Wallace, M. T., Wilkinson, L. K., & Stein, B. E. (1996). Representation and integration of multiple sensory inputs in primate superior colliculus. *Journal of Neurophysiology*. *76*(2), 1246–1266

Weber, K. A., Chen, Y., Wang, X., Kahnt, T., & Parrish, T. B. (2016). Functional magnetic resonance imaging of the cervical spinal cord during thermal stimulation across consecutive runs. *NeuroImage*. *143*, 267–279

Weber, K. A., Chen, Y., Paliwal, M., Law, C. S., Hopkins, B. S., Mackey, S., … Smith, Z. A. (2020). Assessing the spatial distribution of cervical spinal cord activity during tactile stimulation of the upper extremity in humans with functional magnetic resonance imaging. *NeuroImage*. *217*, 1–13

Appendix

Table 1: Accuracy in percent across conditions for each participant

	Accuracy	
Participants	**Location trials**	**Finger trials**
1	79.72%	90.08%
2	82.5%	82.03%
3	85%	82.57%
4	97.22%	87.13%
5	84.44%	74.53%
8	91.68%	83.01%
9	92.78%	82.03%
10	74.17%	79.10%
11	75%	78.55
12	80%	82.31%
13	91.94%	88.74%
14	80%	83.38%
15	92.78%	88.20%
16	88.89%	87.67%
17	90.28%	87.67%
19	76.67%	76.68%
20	84.44%	77.51%

Table 2: Location trial types

Valid			Invalid		
150 ms	**600 ms**	**1200 ms**	**150 ms**	**600 ms**	**1200 ms**
A-A	A-A	A-A	A-D	A-D	A-D
L1	L1	L1	L1	L1	L1
L2	L2	L2	L2	L2	L2
R1	R1	R1	R1	R1	R1
R2	R2	R2	R2	R2	R2

A-A and A-D are valid and invalid locations respectively, L1, L2, R1 and R2 are the left and right index and middle fingers.

Table 3: All Finger trial types

Valid (SFSH)			Invalid					
150 ms	**600 ms**	**1200 ms**	**150 ms**	**Type**	**600 ms**	**Type**	**1200 ms**	**Type**
L1-L2 -	L1-L1	L1-L1	L1-L2 *	DFSH	L1-L2	DFSH	L1-L2	DFSH
L2-L2 +	L2-L2	L2-L2	L1-R1 -	SFDH	L1-R1 +	SFDH	L1-R1	SFDH
R1-R1	R1-R1	R1-R2	L1-R2	DFDH	L1-R2 -	DFDH	L1-R2	DFDH
R2-R2	R2-R2	R2-R2 -	L2-L1 +	DFSH	L2-L1 -	DFSH	L2-L1	DFSH
			L2-R1	DFDH	L2-R1 *	DFDH	L2-R1 -	DFDH
			L2-R2 +	SFSH	L2-R2	SFSH	L2-R2	SFSH
			R1-L1 -	SFDH	R1-L1	SFDH	R1-L1	SFDH
			R1-L2	DFDH	R1-L2 -	DFDH	R1-L2	DFDH
			R1-R2	DFSH	R1-R2	DFSH	R1-R2 -	DFSH
			R2-L1	DFDH	R2-L1 *	DFDH	R2-L1 -	DFDH
			R2-L2	SFDH	R2-L2	SFDH	R2-L2	SFDH
			R2-R1-	DFSH	R2-R1 +	DFSH	R2-R1 +	DFSH

Distribution of Finger trials: valid trials refer to left index finger cued and left index finger target presented (i.e., L1-L1); invalid Finger trials are referring to right index finger cued and left middle finger target presented (i.e. R1-L2). All trials utilize a variable ISI of 150, 600 and 1200 ms. Trials marked by (*) indicate missing trial types due to coding errors (n = 3). Trial marked by (+) indicate trials that are over -represented due to coding errors (n = 5). Trials marked by (-) are trials that are under-represented due to Participant 10's Block 3 being missing or due to coding errors (n = 11).

Table 4: Mean RTs for Location Trials Across Participants

	Valid			Invalid		
Participants	**150 ms**	**600 ms**	**1200 ms**	**150 ms**	**600 ms**	**1200 ms**
1	790.9	897.6	916.8	812.5	867.0	773.6
2	822.3	730.4	805.9	837.3	735.0	651.5
3	901.9	758.2	823.0	1002.6	905.6	877.1
4	917.7	680.3	742.5	864.2	943.0	752.0
5	820.7	636.6	766.3	647.2	691.5	582.3
8	767.2	586.1	713.4	782.1	849.0	764.5
9	871.5	606.0	861.8	877.5	716.0	638.6
10	694.5	634.7	572.8	678.5	598.6	614.5
11	973.9	854.4	862.9	876.8	853.4	787.9
12	641.5	644.8	745.5	888.9	619.0	727.8
13	825.6	715.1	782.6	828.1	856.9	865.6
14	873.3	810.4	838.5	1032.7	923.4	843.0
15	964.1	822.3	763.1	912.3	943.5	812.2
16	670.0	741.8	799.1	830.9	783.9	768.1
17	1041.2	1095.9	1080.4	1079.3	915.3	1031.4
19	1099.9	985.4	1063.4	873.2	841.0	833.8
20	749.2	611.1	741.3	984.9	838.8	833.8

Mean RTs for Location trials across all participants' scores without outliers. All values in milliseconds (ms).

Table 5: Mean Response Times for Finger Trials Across Participants

	Valid			Invalid		
Participants	**150 ms**	**600 ms**	**1200 ms**	**150 ms**	**600 ms**	**1200 ms**
1	791.7	754.9	814.2	711.0	775.9	776.6
2	802.3	787.5	796.8	690.3	765.4	643.4
3	789.4	771.1	836.9	1193.2	1184.9	868.2
4	810.0	733.7	801.5	818.1	696.6	651.4
5	781.3	800.1	811.6	614.5	643.0	666.1
8	782.4	770.5	800.5	780.9	763.3	718.4
9	757.1	772.8	813.2	769.4	828.1	738.4
10	751.7	831.6	666.2	576.7	669.9	686.6
11	791.9	767.8	811.6	931.3	907.3	757.1
12	789.6	803.7	812.9	771.2	761.8	749.3
13	778.8	777.5	813.4	842.5	765.3	809.4
14	899.9	732.6	815.4	875.5	871.9	833.3
15	789.7	767.3	818.7	846.8	1051.3	804.7
16	747.7	741.5	769.6	795.5	696.5	792.0
17	794.6	765.7	856.6	829.5	844.4	934.3
19	857.1	716.9	914.8	988.0	936.5	938.4
20	752.4	782.5	819.0	830.8	863.0	951.8

Mean RTs for Finger trials across all participants' scores without outliers. All Values in milliseconds (ms).

Table 6: Mean Response Times for SFSH and SFDH Trials Across Participants

	SFSH			SFDH		
Participants	**150 ms**	**600 ms**	**1200 ms**	**150 ms**	**600 ms**	**1200 ms**
1	791.7	754.9	814.2	772.9	819.0	839.8
2	802.3	787.5	796.8	701.3	749.6	599.5
3	789.4	771.1	836.9	1500.0	907.5	981.4
4	810.0	733.7	801.5	840.3	674.3	676.0
5	781.3	800.1	811.6	619.9	649.2	574.0
8	782.4	770.5	800.5	829.5	787.7	649.4
9	757.1	772.8	813.2	850.0	733.8	671.8
10	751.7	831.6	666.2	602.6	650.7	657.2
11	791.9	767.8	811.6	1106.0	811.5	683.5
12	789.6	803.7	812.9	736.8	812.7	692.4
13	778.8	777.5	813.4	961.9	735.9	746.6
14	899.9	732.6	815.4	835.9	823.7	826.6
15	789.7	767.3	818.7	913.7	833.4	681.2
16	747.7	741.5	769.6	822.1	762.8	739.5
17	794.6	765.7	856.6	917.8	881.7	895.6
19	857.3	716.9	914.8	959.3	1027.2	891.8
20	752.4	782.5	819.0	796.4	792.6	784.0

Mean RTs for Same-Finger-Same-Hand and Same-Finger-Different-Hand trials across all participants' scores without outliers. All Values in milliseconds (ms).

Table 7: Mean Response Times for DFSH and DFDH Trials Across Participants

	DFSH			DFDH		
Participants	**150 ms**	**600 ms**	**1200 ms**	**150 ms**	**600 ms**	**1200 ms**
1	735.6	712.5	1002.9	624.4	796.1	487.3
2	595.2	768.0	777.3	774.4	778.6	553.4
3	767.0	1158.3	1057.1	1312.6	1488.8	566.0
4	731.7	656.7	697.3	882.3	758.9	580.8
5	511.4	682.6	816.5	712.1	597.1	607.9
8	688.5	810.0	853.2	824.6	692.2	652.5
9	723.0	753.3	862.3	735.3	997.2	681.1
10	492.5	693.8	688.1	634.9	665.2	714.5
11	882.6	822.7	851.0	805.3	1087.6	736.8
12	748.0	755.7	787.4	828.8	717.1	768.0
13	834.2	639.4	889.4	731.0	920.6	792.1
14	855.6	1046.5	845.4	935.1	745.4	827.9
15	832.7	794.9	886.2	794.1	1525.7	846.8
16	797.7	763.7	748.2	766.7	563.0	888.4
17	754.5	802.4	945.5	816.2	848.9	961.9
19	981.4	933.1	874.0	1023.3	849.1	1049.4
20	848.3	805.5	820.7	847.7	990.8	1250.6

Mean RTs for Different-Finger-Same-Hand and Different-Finger-Different-Hand trials across all participants' scores without outliers. All Values in milliseconds (ms).