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Measuring the effects of attention to individual fingertips in somatosensory cortex using ultra-high field (7T) fMRI

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ABSTRACT

Attention to sensory information has been shown to modulate the neuronal processing of that information. For example, visuospatial attention acts by modulating responses at retinotopically appropriate regions of visual cortex (Puckett and DeYoe, 2015; Tootell et al. 1998). Much less, however, is known about the neuronal processing associated with attending to other modalities of sensory information. One reason for this is that visual cortex is relatively large, and therefore easier to access non-invasively in humans using tools such as functional magnetic resonance imaging (fMRI). With high-resolution fMRI, however, it is now possible to access smaller cortical areas such as primary somatosensory cortex (Martuzzi et al., 2014; Sanchez-Panchuelo et al., 2010; Schweisfurth et al. 2014; Schweizer et al. 2008). Here, we combined a novel experimental design and high-resolution fMRI at ultra-high field (7T) to measure the effects of attention to tactile stimulation in primary somatosensory cortex, S1. We find that attention modulates somatotopically appropriate regions of S1, and importantly, that this modulation can be measured at the level of the cortical representation of individual fingertips.

1. Introduction

Attention to incoming sensory information has been shown to modulate neuronal responses and subsequently alter perception of that information and, accordingly, influence behavior (Driver, 2001). To date, the majority of attention research has investigated the processing of visual and auditory information, with a lesser focus on other sensory modalities such as somatosensation. It is clear, however, that people are able to voluntarily direct their attention to a part of their body and that doing so speeds up processing of somatosensory information at that location (Spence and Gallace, 2007). Understanding how attentional processes interact with the cortical processing of sensory information is, thus, central to understanding the neural basis of human somatosensation.

The neuronal processing of tactile information occurs in humans, in large part, in primary somatosensory cortex, S1 (Kandel et al., 2000). Early demonstrations of tactile stimulation eliciting focal neuronal activation within human S1 were performed using Positron Emission Tomography (PET) (Fox et al., 1987; Greenberg et al., 1981). Using fMRI, it became possible to further resolve this activation to individuate the responses to stimulation of individual fingers (Francis et al., 2000; Gelnar et al., 1998; Schweisfurth et al. 2014; Schweizer et al. 2008). More recently, research employing high-resolution fMRI has revealed that human S1 contains multiple orderly somatotopic maps of the fingers, both across digits (Maldjian et al., 1999; Martuzzi et al., 2014; Sanchez-Panchuelo et al., 2010) and within digits (Sanchez-Panchuelo et al., 2012).

Human neuroimaging studies have also investigated the influence of attention in somatosensory cortex finding that attention modulates activity in a number of cortical areas, including early somatosensory cortex (Burton and Sinclair, 2000). For example, using PET it has been shown that attention to tactile information modulates activity in S1 (Meyer et al., 1991; Roland, 1981). Supporting these findings, studies using fMRI have shown that Blood Oxygenation Level Dependent (BOLD) signals elicited in S1 are greater for attended compared to actively ignored (Sterr et al., 2007) or passively experienced (Nelson et al., 2004) tactile stimulation. Although this work has provided clear evidence that attentional modulation occurs at regions of somatotopically organized cortex, these measurements have been rather limited, considering only a single finger, or toe (Johansen-Berg et al., 2000). The limited nature of the measurements in the studies reporting attentional modulation in S1 along with

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the fact that there have been other studies that have failed to demonstrate robust modulation in S1 during active attention to somatosensory information (Backes et al., 2000; Mima et al., 1998) highlight the need for additional investigation.

Here we show that attending to tactile stimulation does indeed modulate somatotopically appropriate regions in S1 and that using high-resolution fMRI allows these effects to be measured at the spatial scale necessary to resolve modulation associated with attending to each individual fingertip. The fact that attention is able to differentially modulate neuronal responses when attending to individual fingertips is in line with known, touch-related behavioral abilities of humans that require individuation of sensory information at each fingertip such as haptic exploration and tactile object recognition (Lederman and Klatzky, 2009). Moreover, the ability to measure this attention-related modulation in awake and behaving humans promises a better understanding of the neural basis of attentional processes and how they influence our perception of somatosensory information.

2. Materials and methods

2.1. Subjects

Six, right-handed subjects (23–31 years, mean 27 years) with no history of neurological or psychiatric diseases completed the experiment. A partial dataset was collected on a seventh subject; however, issues with the MRI scanner prevented collection of half of the functional data as well as the anatomical data. As such, the analysis of this data is only included as supplementary material. The experiment was conducted with the understanding and written consent of each subject and was approved by the local ethics committee in accordance with national guidelines.

2.2. Stimulation and tasks

There were three experimental conditions: sensory, attention, and control. During each, tactile stimulation was delivered via a MR-safe piezoelectric vibrotactile stimulator (www.hybridmojo.com). The device was comprised of 4 units, each capable of delivering vibrotactile stimulation at various frequencies to the pad (i.e. volar surface) of a single fingertip. The stimulation timing and frequency could be controlled independently for each unit.

During the sensory condition (Fig. 1A), 4 fingertips (index, middle, ring, and little) on the right hand were stimulated sequentially using a phase-encoded design (Besle et al., 2013; Engel, 2012) similar to that used for retinotopic mapping of visual cortex (DeYoe et al., 1996; Engel et al., 1994; Sereno et al., 1995). To this end, a single fingertip was passively stimulated (i.e. no task) for 7872 ms before moving to the next. Stimulation began at the first finger (index) and ended with the fourth finger (little), constituting one cycle of stimulation. Stimulation then returned to the first finger to begin another cycle of stimulation. The frequency of vibrotactile stimulation changed every 1968 ms (synced with MRI scanner repetition time), and three different frequencies were used (5, 20, and 100 Hz). The frequency changed randomly among the three frequencies, except that the same frequency could not occur twice in a row at a fingertip. Each run consisted of 5 cycles of stimulation and each cycle was 31.5 s in duration.

During the attention condition (Fig. 1B), attention was swept across the fingertips in a phase-encoded manner under constant sensory stimulation of all four fingertips. Subjects were visually cued to attend to a particular fingertip and report the nature of frequency changes (higher or lower than previous) at that fingertip while ignoring the stimulation at all other fingertips. The task was attentionally demanding, requiring individuation of the vibrotactile stimulation at a single fingertip in the presence of task irrelevant (i.e. distracting) stimulation at the other three fingertips. Each finger was attended for 7872 ms before moving to the next, and after attending to the fourth finger (little), the location of attention returned to the first finger (index). As in the sensory condition, the frequency of stimulation changed randomly every 1968 ms, and the same three frequencies were used. But note that stimulation occurred at

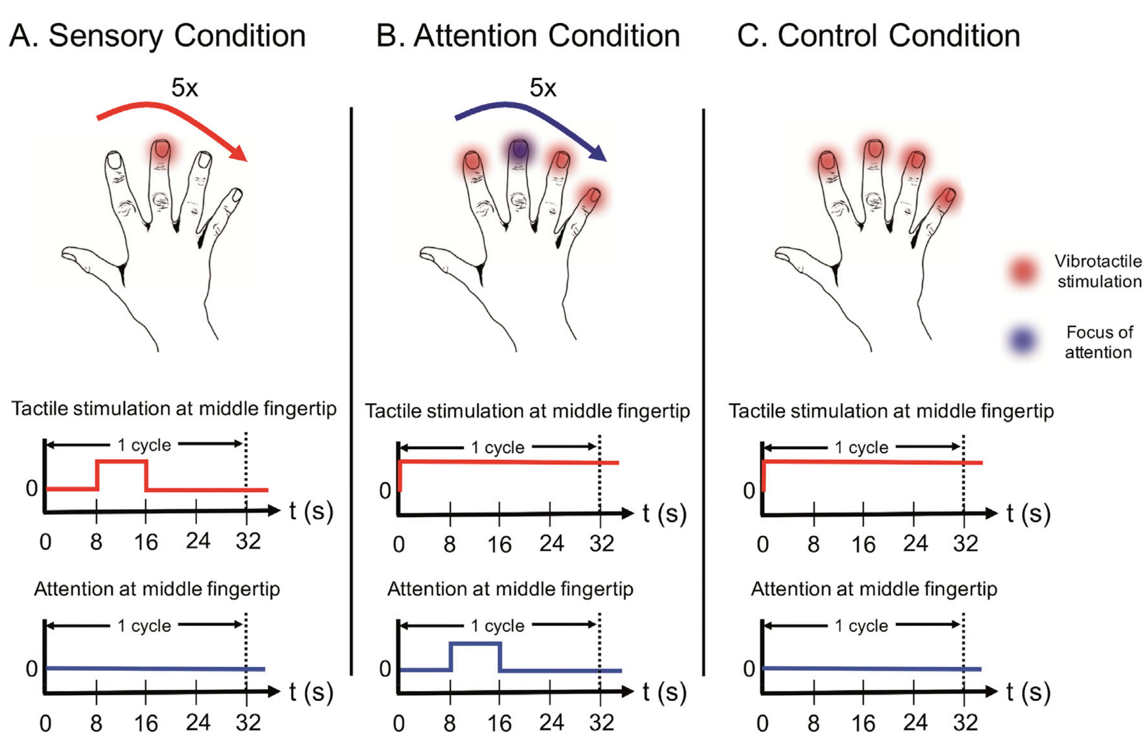

Fig. 1. Experimental design for (A) sensory, (B) attention, and (C) control conditions. Top: (A) During a single cycle, vibrotactile stimulation (red patch) is passively swept across the four fingertips, stimulating only a single finger at a time (middle finger shown here as an example). This is repeated for 5 cycles. (B) During a single cycle, endogenous attention (blue patch) is swept across each fingertip, attending to only a single finger at a time (again, middle finger shown here as an example) during constant sensory stimulation of all fingertips (red patches). This is repeated for 5 cycles. (C) The control condition is identical to the attention condition, except the subject is asked to ignore the sensory stimulation (i.e. no endogenous attention to any fingertip, at any time). Bottom: sensory stimulation and attentional modulation during a single cycle at a single fingertip (middle).