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Dynamic causal modeling suggests serial processing of tactile vibratory stimuli in the human somatosensory cortex—An fMRI study

Christian Kalberlah [a,*], Arno Villringer [a,b,c], Burkhard Pleger [a,b,c]

[a] Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[b] Clinic for Cognitive Neurology, University Hospital Leipzig, Leipzig, Germany
[c] Mind and Brain Institute, Berlin School of Mind and Brain, Humboldt-University, Berlin, Germany

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ABSTRACT

Sensitivity to location and frequency of tactile stimuli is a characterizing feature of human primary (S1), and secondary (S2) somatosensory cortices. Recent evidence suggests that S1 is predominantly receptive to stimulus location, while S2 is attuned to stimulus frequency. Although it is well established in humans that tactile frequency information is relayed serially from S1 to S2, a recent study, using functional magnetic resonance imaging (fMRI) in combination with dynamic causal modeling (DCM), suggested that somatosensory inputs are processed in parallel in S1 *and* S2. In the present fMRI/DCM study, we revisited this controversy and investigated the specialization of the human somatosensory cortical areas with regard to tactile stimulus representations, as well as their effective connectivity. During brain imaging, 14 participants performed a somatosensory discrimination task on vibrotactile stimuli. Importantly, the model space for DCM was chosen to allow for direct inference on the question of interest by systematically varying the information transmission from pure parallel to pure serial implementations. Bayesian model comparison on the level of model families strongly favors a serial, instead of a parallel processing route for tactile stimulus information along the somatosensory pathway. Our fMRI/DCM data thus support previous suggestions of a sequential information transmission from S1 to S2 in humans.

Introduction

The cortical representation of somatosensory stimulus location and frequency has been studied extensively in monkeys (e.g., Friedman et al., 2004; Salinas et al., 2000) and humans (Francis et al., 2000; Gelnar et al., 1998; Jack et al., 1994; Kurth et al., 2000; Maldjian et al., 1999; Nelson and Chen, 2008; Schweizer et al., 2008). However, a deeper understanding of the functional organization of the somatosensory cortices also demands knowledge about the level at which stimulus information enters the somatosensory network, and the exchange of information between the hierarchical stages.

Over the last two decades two contrary somatosensory network theories were debated: the serial and the parallel pathway theory. The parallel pathway theory assumes parallel inputs from the thalamus directly to both human primary somatosensory cortex (S1) *and* human secondary somatosensory cortex (S2), and has been confirmed for non-primate species like the cat and the rabbit, but also for one primate species, namely the marmoset monkey (Rowe et al., 1996). The serial pathway theory assumes that stimulus information is projected from the thalamus to S1 before being relayed to S2. This theory has been well established by anatomic and electrophysiological studies of macaques (Pons et al., 1992). In humans, electrophysiological recordings assessed with M/EEG also favored a serial functional organization which nowadays became the commonly accepted theory (Hu et al., 2012; Inui et al., 2004; Schnitzler et al., 1999).

A more recent technique for the non-invasive investigation of human brain networks is dynamic causal modeling (DCM) based on fMRI data. This method allows estimating and making inferences about the coupling among small numbers of brain areas in a Bayesian framework (Friston et al., 2003). To this end, one standard application of DCM is the characterization of a neuronal system as having a serial or parallel processing system. This is done by using Bayesian model evidence to compare models reflecting serial and parallel pathways (Stephan et al., 2010).

In a recent study Liang et al. (2011) applied DCM to fMRI data and suggested that next to nociceptive, also non-nociceptive somatosensory information is processed in a parallel and not serial fashion which speaks against the well-accepted theory of a serial processing route in the human somatosensory network. In this study, however, the dynamic causal models being compared differed only in the modulatory

Abbreviations: BA, Brodmann area; BMC, Bayesian model comparison; D2, index finger; D5, little finger; DCM, dynamic causal modeling; EP, exceedance probability; GLM, general linear model; S1, human primary somatosensory cortex; S2, human secondary somatosensory cortex; SOA, stimulus-onset asynchrony.

* Corresponding author at: Max Planck Institute for Human Cognitive and Brain Sciences, Postfach 500355, 04303 Leipzig, Germany. Fax: +49 341 99 40 22 21.
E-mail address: kalberlah@cbs.mpg.de (C. Kalberlah).

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influences stimulus information had on the thalamocortical connections. Thus, different cortical entering levels of stimulus information were not systematically investigated.

In the present human fMRI/DCM study, we revisited the controversy on whether somatosensory information in humans is relayed in a serial or parallel fashion by unveiling (1) the specialization of the human somatosensory cortical areas with regard to tactile stimulus representations and (2) their effective connectivity. To this end, we used a pattern discrimination task. During brain imaging, participants discriminated between one of two 4-dot stimulus patterns applied to either the right index finger (D2) or right little finger (D5) at vibrating sinusoids of either 30 or 200 Hz (Fig. 1). Thus, the stimulus pattern was the task feature requiring subjects' attention, while frequency and location were the features of interest. Using this distraction task we aimed to identify differences in cortical functional specialization for the representations of vibrotactile stimulus location and frequency in humans. Next we applied DCM to assess how stimulus information is relayed to the somatosensory areas, S1 and S2, by systematically varying the information transmission from pure parallel to pure serial information transmission and direct comparison on the level of model families in a Bayesian framework (Penny et al., 2010).

Materials and methods

Participants

Fourteen right-handed healthy volunteers (8 males, $M = 27$ years, age range: 23–33 years) participated in the study and gave their written informed consent. The study was approved by the Local Ethical Committee of the Medical Faculty of the University of Leipzig, Germany, and conformed with the Human Subjects Guidelines of the Declaration of Helsinki.

Stimuli and task

Participants were engaged in a pattern discrimination task. On each trial, either D2 or D5 was stimulated by one of two 4-dot

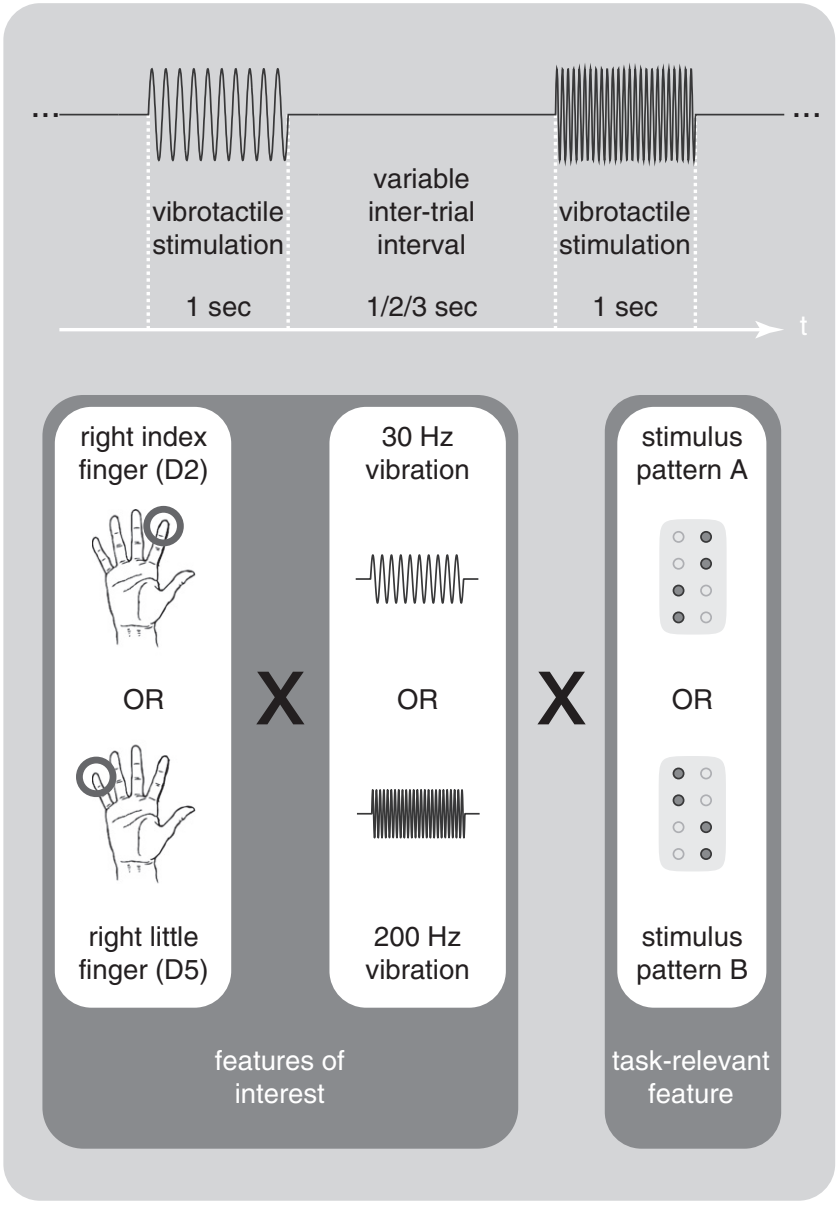

Fig. 1. Sketch of vibrotactile stimulation paradigm. In each trial lasting for 1 s either the right index (D2) or little finger (D5) was stimulated at 30 or 200 Hz by a vibratory pattern A or B. In the fMRI experiment trials were separated by variable inter-trial intervals of 1, 2, or 3 s.