Journal Club

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Tactile Spatiotemporal Perception Is Dependent on Preparatory Alpha Rhythms in the Parieto-occipital Lobe

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Review of Takahashi and Kitazawa

When touch is sequentially applied to crossed hands with only a brief pause between touches, we are often incorrect about which hand was touched first. This crossed-hands deficit is also commonly observed in the schoolyard game in which the fingers are also interlaced. When asked to wiggle a particular finger, the volunteer often wiggles the incorrect finger. One hypothesis is that these crossed-arms effects arise from the integration of sensory information from spatially conflicting reference frames into an external reference frame. It is generally agreed that such a behaviorally relevant external reference frame is required for determining tactile temporal order (Badde and Heed, 2016). For instance, to act on a touch to the body (e.g., to swat a fly that lands on the arm), the sensorimotor system must account for not only the location on the skin, but also the positions of the limbs and body. Thus, the location needs to be brought from skin-based coordinates in the primary somatosensory cortex to external coordinates in higher-order areas (Colby, 1998). Although multiple models of reference frame integration have been proposed (Heed and Azañón, 2014; Badde and Heed, 2016), their neural mechanisms remain an open question.

One method commonly used to examine the remapping of touch location into external coordinates is the temporal order judgment task (TOJ). In this task, participants must report the temporal order of two sequentially presented tactile stimuli, which are typically separated by a variable time interval, the stimulus onset asynchrony (SOA). When responses to touches presented at different stimulus SOAs are plotted by right (or left) first responses, the curve is S-shaped in the arms-uncrossed situation (Fig. 1*a*, blue line). When the arms are crossed, participants typically show reversed judgments at short-to-moderate SOA, leading to an N-shaped response curve (Fig. 1*a*, red line). Previous studies have presented evidence that tactile TOJs are mediated by activity in posterior parietal cortex (e.g., Ritterband-Rosenbaum et al. 2014).

Alpha rhythms (∼8–13 Hz) are generally considered to regulate temporal perception (Milton and Pleydell-Pearce, 2016), but whether they also organize spatiotemporal tactile processing has been unclear. Therefore, Takahashi and Kitazawa (2017) tested whether posterior alpha rhythms influence tactile TOJ in a recent paper in *The Journal of Neuroscience*. The authors initially screened participants to identify "top-reversers," those showing inverted judgment at $>$45% probability with crossed hands at their optimal SOA. In the critical condition, these participants received two touches on their crossed arms at an SOA of -100 or 100 ms. Participants indicated which touch arrived second with a key press using the index finger of that hand. Inverted judgments were observed in 20%–43% of trials at this SOA. In addition, MEG recordings were obtained during a period beginning 1 s and ending 3 s after the first stimulus of every trial. The MEG recordings of the group were subject to independent component analysis, according to their power in the alpha rhythm range. This analysis was performed to identify the cortical regions most important in the early stages of stimulus processing.

The analysis identified five statistically significant components of the alpha rhythm; the major one was located around the posterior parieto-occipital region. Components were also identified in a mid parieto-occipital region, sensorimotor cortex, and primary auditory cortex. Having identified these components at the group level, the independent component analysis was then applied to each participant separately, which again identified the posterior parieto-occipital region. The authors computed the phase of the alpha rhythm every 10 ms from 500 ms before the first stimulus to 500 ms after the first stimulus. They compared the instantaneous phase for each component at each of these times to TOJ success. Critically, when judgments were inverted, the pa-

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rieto-occipital alpha rhythm was in opposite phase during the prestimulus period than when judgments were correct, whereas the phase of the other identified components was independent of TOJ success. Although phase differences between correct and inverted trials were seen in the prestimulus period, the difference was actually maximal at 40 ms after the presentation of the first stimulus.

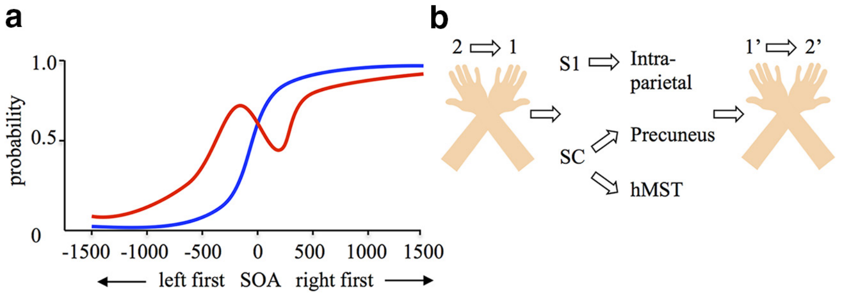

Figure 1. ***a***, Probability of participants reporting "right hand first" in the TOJ task for varying SOAs and arm position: blue line indicates uncrossed; red line indicates crossed. ***b***, When two touches are applied first to the left hand (1) and soon after to the right hand (2), touch locations are rapidly mapped in a skin-based representation in somatosensory cortex (S1) and/or superior colliculus (SC). This mapping is in conflict with intraparietal areas, precuneus, and human MST, which map tactile stimuli in external space. Takahashi and Kitazawa (2017) showed that prestimulus alpha rhythms in the parieto-occipital region could interact with any of these regions to cause inverted judgments (1′ and 2′).

Takahashi and Kitazawa (2017) provided evidence that tactile TOJs are dependent on the phase of the posterior alpha rhythm in the prestimulus period. They identified other alpha rhythm components, but these were not associated with inverted judgments. Furthermore, it was found that the judgments were independent of the amplitude of the five components. Of particular interest was that there were independent mu components in each hemisphere. These mu rhythms have been hypothesized to organize alpha rhythms (Pineda, 2005). Mu rhythm power has also been shown to influence tactile detection threshold (Jones et al. 2010). One possibility is that the effects of the mu rhythm are constrained to primary touch sensation but do not contribute to the spatiotemporal processing required in the TOJ task.

Having established that the parieto-occipital component is implicated in reversals, the authors identified three regions (Fig. 1*B*) where changes in neuronal excitability from the alpha rhythm could influence tactile processing. These were the intraparietal areas, middle temporal and medial superior temporal (MST), and the precuneus. The MST contributes to the processing and representation of tactile apparent motion (Takahashi et al. 2013). The involvement of intraparietal areas and MST is consistent, respectively, with the spatial conflict and motion-projection hypotheses of representing touch in external space. The spatial conflict hypothesis holds that, when the limbs are crossed, there is fast mapping of the signal to a skin-based reference frame in the primary somatosensory cortex followed by slower mapping of the signal into the representation of the arms location in external space from proprioceptive and visual inputs in intraparietal areas (Lloyd et al. 2003). This hypothesis and variations of it are supported by evidence from TOJ tasks (Heed and Azañón, 2014) as well as a variety of other tasks (for review, see Badde and Heed, 2016). In contrast, the motion-projection hypothesis, proposed by Kitazawa et al. (2007), states that the reversed TOJ occurs as touches are perceived to arise from a single object in continuous motion. There is some support for this hypothesis; for example, when local motion consistent with the global motion is contained within each stimulus, TOJ accuracy improves (Craig, 2003). Furthermore, if visual stimuli that are congruent with the global motion are added, the TOJ is biased in this direction (Kitazawa et al. 2007; Takahashi et al. 2013). This transformation could be performed in the human MST as tactile information from the hand projects to it and it responds moving stimuli (Beauchamp et al. 2007). The current study did not differentiate between these two accounts of tactile remapping but did confirm that they are both anatomically plausible.

Having found that posterior alpha rhythms influence tactile TOJ in "top-reversers," the authors tested "bottom-reversers" to determine whether the effect generalized to those with a smaller crossed-hands deficit. Although these bottom-reversers did show the same posterior alpha-rhythm-dependent effect, it was reduced and delayed an additional 60 ms. Takahashi and Kitazawa (2017) offer this difference as an explanation for the commonly observed between-subject variability of the crossed-hands deficit. They suggest that bottom-reversers depend less on pathways that signal skin-based information. There is also some evidence that these reference frames are subject to different weighting depending on the task. For instance, localizing the finger and the hand relies on skin-based and external representations to different degrees (Heed and Azañón, 2014). Thus, it is also conceivable that reference frame weighting differs by individual.

When Yamamoto and Kitazawa (2001) first described the N-shaped curve in the crossed-hands deficit, they proposed that it might arise from individual differences in the prestimulus period. This new study provides good evidence for this hypothesis. How could future studies determine what differs and why in the prestimulus period? Differences in attention, elicited using a tactile cue, have robust effects on localization of a tactile motion stimulus (Kilgard and Merzenich, 1995). One possibility is that the preceding trial could cue attention on the next trial in tactile TOJ tasks. A study using one paradigm showed that exogenous cueing with a tactile stimulus has robust inhibitory effects (∼20–40 ms) on reaction time to a tactile target presented at up to 6 s after the cue (Cohen et al. 2005). This time period is not dissimilar to that used in many previous crossed-hands deficit studies, and the inhibition is proposed to take place in the superior colliculus (Tassinari and Campara, 1996), which projects to the precuneus and to human MST. Tactile cueing effects act in skin-based space only (Röder et al. 2002). Therefore, inadvertent cueing from the previous trial could influence tactile TOJ. Future tactile spatiotemporal processing studies could explore whether attention is naturally cued at a location and whether it interacts with the alpha rhythm. Given that it was recently shown that the size of alpha-rhythm-dependent effects on simultaneity judgments in vision are modulated by attention (Milton et al. 2016), one might expect a similar effect in touch.

Importantly, the new results of Takahashi and Kitazawa (2017) account for a substantial amount of both the intraindividual and interindividual variation of tactile temporal order judgments. They demonstrate that a large part of the trial-to-trial variation is dependent on the posterior alpha rhythm. These findings provide exciting new avenues to determine the mechanisms by which tactile events are represented in space and how they are modulated by attention. But whether the crossed-hands deficit occurs from reference frame conflict or inverted apparent motion signals remains an open question.

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