



Functional specialization within the supplementary motor area: A fNIRS study of bimanual coordination

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ABSTRACT

Bimanual movements can be performed by flexing and extending the target effectors (e.g., hand muscles) in unison, or by flexing units on one side in unison with extension of the same units on the opposite side. The former movement patterns are generally referred to as in-phase or parallel, whereas the latter patterns are often termed anti-phase movements. It is well known that anti-phase patterns are unstable and tend to spontaneously transition to in-phase movements at higher repetition rates, but the mechanisms and brain regions involved are not fully understood. In the current study, we utilized functional near-infrared spectroscopy (fNIRS) to evaluate whether anterior/posterior subdivisions of the supplementary motor complex (SMA) have distinct functional roles in maintaining in-phase and anti-phase movement patterns. Twelve healthy adult participants completed a bimanual coordination task comprised of anti-phase and in-phase trials as 24-channel fNIRS data was recorded from dorsal-medial motor areas. We examined the relative concentrations of oxygenated and deoxygenated hemoglobin in the channels that were located over the anterior SMA (e.g., pre-SMA) and the SMA proper. Our most interesting results indicated that oxygenated hemoglobin responses were greater in the anterior SMA during performance of anti-phase compared to in-phase movements. In the SMA proper, oxygenated hemoglobin responses did not differ between the two movement patterns. These data suggest that the anterior SMA is critical to programming and maintaining the less stable anti-phase movement patterns, and support the conceptual framework of an anterior-directed gradient of progressively more complex functionality in the SMA.

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Introduction

The human neuromuscular system can produce an extensive variety of bimanually-coordinated movement patterns, and each of these patterns can vary in their spatiotemporal organization based on the constraints of the given task dynamics. Although these coordinated movements appear relatively effortless, further inspection reveals that the resulting motor commands are likely quite complex and probably require additional attention and programming if the homologue muscles in the contralateral limb are not performing the same movement (Monno et al., 2000; Swinnen, 2002; Temprado et al., 1999; Zanone et al., 2001). For example, drawing a circle with one hand and a figure eight with the other hand (in unison) requires substantial attentional resources to maintain a smooth and coordinated movement pattern. A considerable amount of effort has been directed towards identifying and characterizing the behavioral changes that

occur when one attempts to perform distinct coordinative patterns with the respective limbs (Kelso, 1995; Kelso et al., 1986; Monno et al., 2000; Semjen et al., 1995; Swinnen, 2002; Temprado et al., 1999; Zanone et al., 2001), although we presently have little understanding of the key neural areas that are involved in the production of these movement patterns.

The seminal work of Kelso et al. (1986) demonstrated that repetitive bimanual movements, especially finger movements, naturally tend towards mirror symmetry as the movement frequency increases. That is, there is a spontaneous transition from less stable asymmetrical (anti-phase) movement patterns to the more stable symmetrical (in-phase) patterns as the repetition rate of the movement reaches some sort of critical threshold. More recent investigations of bimanual coordination have also demonstrated that anti-phase patterns are less stable, and that they require a greater amount of attention to maintain the coordination dynamics (Forrester and Whittall, 2000; Monno et al., 2000; Temprado et al., 1999; Whittall et al., 1999; Zanone et al., 2001). This notion of greater cognitive demand is further substantiated by studies showing that the inadvertent switching from an anti-phase to an in-phase movement pattern occurs at a lower movement rate in elderly participants (Bangert et al., 2010; Fling et al., 2011; Goble

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et al., 2010; Lee et al., 2002; Wishart et al., 2000), which has been tentatively linked to smaller corpus callosum volumes and less integrity of callosal microstructure within regions connecting sensorimotor cortices (Fling et al., 2011). Moreover, there is extensive evidence that anti-phase movements are more difficult to perform and error prone in patients with movement disorders like Parkinson's disease (Almeida et al., 2002; Geuze, 2001; Ponsen et al., 2006; Wu et al., 2010). These results may be traceable to a network-level abnormality involving dysfunction within the supplementary motor area (SMA) and basal ganglia, along with compensatory over-connectivity of these brain regions with other cortical motor areas (Wu et al., 2010).

Among all of the brain regions involved in hand movements, the SMA complex has garnered special interest as activity in this region appears to be closely linked to performance in anti-phase movement tasks. Several studies have shown that activation magnitude in the SMA complex is positively correlated with performance during anti-phase trials in healthy participants and those with age-related motor declines, and negatively correlated with the severity of motor symptoms in patients with Parkinson's disease (Goble et al., 2010; Wu et al., 2010). Moreover, in their event-related fMRI study, Aramaki et al. (2006) demonstrated that the SMA complex was not only activated during anti-phase and in-phase movements, but was also crucial to the involuntary phase transition (from anti-phase to in-phase) that occurs when participants reach their particular rate limit (Aramaki et al., 2006). The traditionally defined SMA is now generally understood as including at least two separate areas. The SMA proper occupies an expanse of medial frontal agranular cortex that is anterior to the primary motor cortex, to which it projects directly along with direct projections to the spinal cord. The most anterior aspect of the SMA, or pre-SMA, is more distant from the primary motor cortex and receives projections from the prefrontal cortices and cingulate motor regions (Hoshi and Tanji, 2004; Nachev et al., 2008; Tanji, 1994; see also Kim et al., 2010). Beyond structural characteristics, both areas are involved in bimanual coordination and appear to have some functional specializations with respect to receiving and processing associative movement cues, planning of motor behavior, and movement execution (Ashe et al., 2006; Hanakawa et al., 2008; Hoshi and Tanji, 2004; Nachev et al., 2008). There is clear evidence that the pre-SMA preferentially receives complex sensory input (somatosensory, proprioceptive, and visual), and that it may perform multifaceted transformations which potentially serve future movement planning and guidance of ongoing movements through interaction with the SMA proper (Ashe et al., 2006; Hoshi and Tanji, 2004; Nachev et al., 2008). Performing these real time spatiotemporal transformations, based on incoming sensory information and goal signals from prefrontal regions, would position the anterior SMA as a crucial brain center for maintaining anti-phase pattern movements, and there is at least strong circumstantial evidence supporting such functionality (Aramaki et al., 2006; Hoshi and Tanji, 2004; Kennerley et al., 2004; Leek and Johnston, 2009; Makoshi et al., 2011).

In this investigation, we examined specialization along the anterior-to-posterior plane of the SMA complex using functional near-infrared spectroscopy (fNIRS). Healthy participants performed a self-paced finger flexion–extension task with anti-phase and in-phase conditions as fNIRS data were acquired from regions of the SMA. Self-paced coordinative patterns were evaluated in this investigation because they reflect the natural and inherent timing tendencies seen in the performance of the neuromuscular system (Forrester and Whittall, 2000; Whittall et al., 1999). Our primary goal was to illuminate how neural activity in the anterior SMA and SMA proper varies as movement programming becomes more complex due to increasingly sophisticated bimanual coordination patterns. Only one previous fNIRS study has examined finger flexion movements (Strangman et al., 2002) and this was a unimanual study that did not involve a coordinative pattern. Several other fNIRS studies have utilized bimanual tasks, but these studies focused on prefrontal or primary motor cortices and did not sample fNIRS data from the SMA complex (Holper et al., 2009; Leff et al., 2008). Nonetheless, a

recent review did highlight the sensitivity of fNIRS to activation in the SMA and pre-SMA (Leff et al., 2011). Our primary hypothesis was that anti-phase movements would more strongly burden the anterior region of the SMA (i.e., the pre-SMA) compared to in-phase movements.

Methods and materials

Subject selection

We studied 12 healthy adults (mean age: 23.5 years-old; 5 males), all of whom were recruited from the local community. Exclusionary criteria included any medical illness affecting CNS function, psychiatric or neurological disorder, history of head trauma, and current substance abuse. Written informed consent was obtained in accord with the guidelines of the University of Nebraska Medical Center's Institutional Review Board, who also approved all study procedures.

Experimental paradigm

Participants were seated with their arms in a neutral position, the elbows bent at 90°, and the forearm supinated such that the thumbs pointed upward. Prior to the beginning of each movement condition/block, participants were asked to keep the index finger extended and the remaining fingers flexed into a fist position. Once positioned, participants were told to remain still and listen for an auditory tone, which cued them to start flexing and extending their respective index fingers at the first metatarsal phalangeal joint. The overall experiment consisted of two conditions per participant, which were performed in a pseudo-randomized order: a) flexion of one index finger in unison with extension of the opposite index finger (i.e., “anti-phase” relative to midline); and b) mirror symmetric, flexing and extending both index fingers in unison (i.e., parallel, or “in-phase” relative to midline). In either case, the frequencies of the respective coordinated finger movements were performed at a self-prescribed pace that was to be held constant across the two conditions. We evaluated a self-paced movement because it has been previously shown that the use of an external cue (e.g., a metronome) introduces extrinsic information, which can confound the natural self-organized coordinative behavior between the fingers (Forrester and Whittall, 2000). Each condition was completed in a single block, which consisted of five alternating trials of self-paced bimanual movements for 15 s followed by 25 s of no-movement baseline. Thus, each trial lasted 40 total seconds and each block was 200 s. Note that participant's maintained a constant arm and hand position throughout the 25-second baseline period. Participants were required to maintain a stable head position and to fixate on a visual target that was positioned in front of the person above eye-level. Throughout the recording, the movement rate and gaze position of each participant were closely monitored by a study staff member.

Data acquisition

A continuous-wave fNIRS system (ETG-4000 Optical System; Hitachi Medical Corporation, Tokyo, Japan) utilizing two different wavelengths (~695 and ~830 nm) was used for this study. Relative changes in the absorption of near-infrared light were sampled at 10 Hz, and these measures were converted into relative concentration changes of oxygenated hemoglobin (oxyHb) and deoxygenated hemoglobin (deoxyHb) based on the modified Beer–Lambert approach (Cope and Delpy, 1988; Obrig and Villringer, 2003). The overall optical system consisted of eight infrared optode emitters and eight optode detectors, arranged in a square 4 × 4 array, with 3 centimeter inter-optode spacing. All optodes were affixed to a custom-made Lycra hat that was worn on the head. This configuration provided 24-channels of hemodynamic response measurements of the underlying neural tissues. The optodes were positioned on each participant's head using

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