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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 supports the conceptual framework of an anterior-directed gradient of progressively more complex functionality in the SMA.

Keywords

NIRS; SMA; pre-SMA; optical imaging; oxyHb

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1. 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 and colleagues (1986) demonstrated that repetitive bimanual movements, especially finger movements, naturally tend toward 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 Whitall, 2000; Monno et al., 2000; Temprado et al., 1999; Whitall et al., 1999; Zannone 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 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).

Amongst 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 and colleagues (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, which it projects to 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 Whitall, 2000; Whitall 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.

2. Methods and Materials

2.1 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.

2.2 Experimental Paradigm

Participants were seated with their arms in a neutral position, the elbows bent at 90 degrees, 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); 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 Whitall, 2000). Each condition was completed in a single block, which consisted of five alternating trials of self-paced bimanual movements for 15 seconds followed by 25 seconds of no-movement baseline. Thus, each trial lasted 40 total seconds and each block was 200 seconds. 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 was closely monitored by a study staff member.

2.3 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 & Delpy, 1988; Obrig & Villringer, 2003). The overall optical system consisted of eight infrared optode emitters and eight optode detectors, arranged in a square 4 X 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 the International 10/20 system (Jasper, 1958), which is commonly employed in EEG, fNIRS, and TMS studies. First, the distance from the nasion to the inion was measured and a mark was made on the scalp at the 50% point, then the distance between the left and right periauricles was measured and the midpoint was marked. The intersection of the inion/nasion plane and the periaruicle plane is, by definition, Cz. In our experiment, the probe array was positioned so that Cz was midway between the first two rows of optodes in the y-plane (anterior-posterior) and in the exact middle of the array in the x-plane (left/right). Once the array was positioned, the location of each channel could be measured directly in reference to Cz. Importantly, Okamoto and colleagues (Okamoto et al., 2004; Okamoto & Dan, 2005) have developed a method for transforming the scalp-based International 10-20 coordinate system to Montreal Neurological Institute (MNI) based coordinates. Briefly, using a data from a large sample of healthy adults, they developed a probabilistic distribution of the cortical projection points in MNI space that corresponds to input coordinates from the International 10-20 system (Okamoto et al., 2004). Based on their data, coordinates in the International 10-20 system (i.e., scalp-based) can be estimated in MNI space with an average standard deviation of 8 mm (Okamoto et al., 2004), which is equal-to or better than the inherent resolution of fNIRS. Thus, we computed the coordinates of each of our measurement locations (channels) in reference to Cz in the International 10-20 system, and then used the transformation methods provided by Okamoto et al (2004) to obtain the MNI coordinate that corresponded to these scalp based locations. Overall, our optodes were situated with the front part of the array positioned over the posterior aspect of the superior frontal gyrus, and the back part of the array located over the

anterior portion of the superior parietal lobule (Okamoto et al., 2004; Okamoto & Dan, 2005). With this optode positioning, all medial aspects of the anterior and posterior supplementary motor area (SMA), primary motor cortex, and the paracentral lobule were likely sampled based on the transformation methods provided by Okamoto (Okamoto et al., 2004; Okamoto & Dan, 2005). All optodes were connected to lightweight fiber optic cables that allowed for transmission of the infrared light to the Hitachi ETG-4000 workstation.

2.4 fNIRS Data Analyses

The measured oxyHb and deoxyHb concentration waveforms were filtered using a 0.01 Hz high pass filter and a 5.0 s moving average. To increase the signal-to-noise ratio and exclude extraneous biological noise (e.g., respiratory and cardio-artifacts), principal component analyses were conducted on the respective individual-trial waveforms taken from all channels (Boas et al., 2004; Zhang et al., 2005). Components with 0.25 or lower correlation with the reference waveform, which corresponded to the expected hemodynamic response function, were filtered from the data while those with correlations above 0.25 were included in the final reconstruction of the individual channel time series. The reference waveform was a trapezoidal function with an upward slope that started at the onset of finger movements and had a 5 s time-to-peak, a 10 s peak duration, and a 5 s downward slope. We used a trapezoidal function because it closely approximates the actual experimental measurements in fNIRS (Cui et al., 2010, 2011; Leamy et al., 2011; also see Buxton et al. 2004). These reconstructed data were then averaged across trials, per condition and participant, to create average oxyHb and deoxyHb waveforms for each channel while the participant performed either in-phase or anti-phase finger movements. Changes in the oxyHb and deoxyHb concentrations were evaluated relative to their condition-specific baselines, which was defined as the 5.0 s of fNIRS measurements that immediately preceded the onset of movement. Thus, in both conditions the total duration of the analysis epoch was 20 s including the 5.0 s pre-movement baseline.

Relative concentrations of oxyHb and deoxyHb chromophores in the SMA and anterior SMA, between in-phase and anti-phase movement patterns, were assessed by separating the sampled fNIRS channels into two groups that were situated over (a) the most anterior aspects of the supplementary motor area (e.g., pre-SMA), and (b) the SMA proper and potentially very anterior and medial pre-central gyri. The channel composition of these subgroups was based on the automated anatomical labeling template (AAL; Tzourio-Mazoyer et al., 2002) implemented in MRICron, and the probabilistic atlas provided by Okamoto and colleagues who estimated the MNI brain coordinates which correspond to the surface coordinates of the International 10/20 system (see Section 2.3;Okamoto et al., 2004; Okamoto & Dan, 2005). Essentially, AAL was used to determine the precise MNI coordinates of the SMA complex, including the anterior and posterior zones. If the MNI coordinates of a fNIRS measurement location corresponded to an area of the anterior SMA, than the given channel would be grouped with similar channels that were sampling from this brain region, and so on and so forth for the posterior SMA. Channels that were recording from areas outside of the SMA, such as those along the back of the array and the peripheral sides, were not recorded. In sum, the cortical projection in MNI space for each measurement point was computed based on a probabilistic atlas (Okamoto et al., 2004), and the measurement points (i.e., channels) were separated into anterior and posterior groups based on their anatomical sampling location according to the AAL template. For each participant, the concentration values for fNIRS measurement channels in each anterior/posterior group were averaged per condition and chromophore, to yield a mean concentration value per area (anterior SMA, posterior SMA), chromphore (oxyHb, deoxyHb), and condition (in-phase, anti-phase).

Initially, we conducted separate Wilcoxon sign rank tests (two-tailed) to assess whether the baseline and task periods were significantly different for the respective oxyHb and deoxyHb measurements in each channel group per movement pattern (in-phase, anti-phase). For these comparisons, nonparametric tests were used because the concentration values during the baseline period were not normally distributed. In contrast, parametric methods were used to evaluate the task-period data for conditional effects, as these data approximated a normal distribution. Thus, the averaged, task-period concentration values were subjected to repeated-measures ANOVA analyses with movement pattern (in-phase and anti-phase) and neural area (anterior and posterior SMA) as within-subject factors. Significant interaction effects were followed-up using paired t-tests, and all statistical tests were two-tailed and conducted using SPSS for Windows software. Lastly, it should be noted that although we examined deoxyHb responses, our primary focus was on the oxyHb measurements due to their higher signal-to-noise ratios (relative to deoxyHb), reduced inter-subject variability, and their reduced vulnerability to contamination by factors such as cross talk (Leff et al., 2011; Miyai et al., 2001; Strangman et al., 2003).

3. Results

All participants showed robust oxyHb responses and clear deoxyHb responses across both channel groups during each movement pattern. These responses were strong enough to be easily discerned in the channel-level chromophore waveforms, and were in the expected direction during the task period (see Figure 1). Wilcoxon tests indicated that the oxyHb concentrations were significantly greater during the task period compared to the baseline period in both anterior and posterior portions of the fNIRS array for both in-phase and anti-phase movement conditions (all p's < 0.01). Conversely, there were significant decreases in deoxyHb during the task period compared to the baseline period for the anti-phase condition (anterior array: $p < 0.05$, posterior array: $p = 0.06$) and the in-phase condition (anterior array: $p = 0.14$, posterior array: $p < 0.05$).

In regards to the average amplitude of the oxyHb response, a 2 x 2 ANOVA with within-subjects factors indicated a main effect of movement pattern $F(1,11) = 5.77$ ($p < 0.05$), and a movement pattern-by-brain region interaction effect $F(1,11) = 4.69$ ($p < 0.05$; see Figure 2). The brain region main effect was not significant ($p = 0.6$). Follow-up t-tests were conducted to evaluate the interaction effect, and these revealed that the oxyHb responses were stronger in the anterior SMA region during anti-phase $t(11) = 2.88$ ($p = 0.015$) compared with in-phase movements. Finally, the main effect of movement pattern indicated that across both SMA sub-regions, oxyHb concentrations were higher during the anti-phase movements.

In contrast to the oxyHb data, a 2 x 2 ANOVA using the deoxyHb data did not show a main effect of movement pattern or brain region (p's > 0.53), nor an interaction effect ($p = 0.26$). Although summary statistics indicated the same overall pattern as the oxyHb data, with more negative deoxyHb concentrations in the anterior SMA during anti-phase compared to in-phase movements. The opposite pattern was also present in the SMA proper (i.e., lower deoxyHb) during in-phase relative anti-phase movements. Finally, it is worth noting that the lack of significant findings for deoxyHb measurements was likely due to extreme inter-subject variability in these responses, which is consistent with other reports that evaluated both chromophores (Miyai et al., 2001).

4. Discussion

We evaluated activation in the anterior SMA and SMA proper during a bimanual finger flexion-extension task that involved both anti-phase and in-phase movement patterns. Our most important finding was stronger activation in the anterior SMA during anti-phase compared to in-phase movement patterns. The amplitude of oxyHb responses in the SMA

proper did not statistically differ between the respective coordinative patterns. These data suggest that the more anterior aspects of the SMA (e.g., pre-SMA) are critical to programming and maintaining the more unstable anti-phase movement patterns. Moreover, this relationship suggests that the anterior SMA may be relatively more involved in the additional attention demands that are known to be necessary for performing anti-phase coordinative movements (Monno et al., 2000; Temprado et al., 1999; Zanone et al., 2001). Below, we discuss the implications of these findings for understanding the role of SMA subdivisions in bimanual coordination and the putative functional specialization of these subdivisions.

The functional role of the SMA is a complex issue as neurophysiological data from behaving monkeys and functional brain imaging studies in humans have ascribed an exceptionally broad array of behaviors to one or more subdivisions of this neural area(s). For example, there is clear evidence that the SMA complex is involved in internally-generated and externally-triggered movements, planning sequences of movements, learning new movements, inhibiting movements, and cognitive control of complex or extended duration movements (see Nachev et al., 2008 for a review). An early case study of a patient with an infarct affecting the SMA indicated that the integrity of the SMA complex is necessary for producing anti-phase patterned bimanual movements (Chan & Ross, 1988). There is also data from animal models showing that lesions in the SMA produce long lasting deficits in the ability to produce coordinated finger movements (Brinkman, 1981). Together with the results presented in our investigation, it is clear that the SMA complex plays a key role in the planning and production of coordinated bimanual movements. However, several studies in humans have shown that lesions in the SMA complex can produce striking higher-level deficits such as alien-limb syndrome, where the affected limb moves or grasps objects outside the subject's voluntary control, and/or utilization behaviors, where objects appear to drive behavior in a stimulus driven fashion (e.g., just seeing eyeglasses causes the subject to put them on; Boccardi et al., 2002; Feinberg et al., 1992). Given such results, there remains little agreement and no working model or theory of SMA function that explains the full gamut of behaviors linked to the region (Leek & Johnston, 2009; Nachev et al., 2008).

In regards to functional subdivisions or discrete modules with the SMA complex, the only widely agreed upon functional division is the simple rostral-caudal gradient subdivision, which captures the notion of decreasing complexity or abstractness as one moves from rostral (i.e., pre-SMA) to more caudal parts of the SMA; although it should be noted that this gradient is thought to hold within each subdivision as well (Nachev et al., 2007, 2008; Nakamura et al., 1998). An exception to this framework is the well-recognized supplementary eye field, which is a subdivision near the SMA and pre-SMA border that appears to serve complex, especially multi-step or sequential eye movements (Grosbras et al., 1999; Yamamoto et al., 2004). The current findings clearly support the notion that anterior regions of the SMA (e.g., pre-SMA) serve more abstract/complex transformations or movement sequences. Essentially, we observed more robust activation in the anterior SMA when participants were engaged in maintaining the less stable and more cognitively demanding anti-phase movement pattern (Monno et al., 2000; Temprado, et al., 1999; Zanone et al., 2001). In contrast, activation in the SMA proper did not differ between anti-phase and in-phase movements, which may reflect that the two movement patterns involve programming the same actual movements, but with a heightened spatiotemporal awareness in the case of anti-phase movements. Potentially, maintaining an anti-phase movement pattern requires constant monitoring of visual and somatosensory feedback to make online adjustments that would be needed when the stability of the pattern begins to erode, and such attentive monitoring may underlie the increased anterior SMA activation during anti-phase trials. In our task, participants were required to fixate on a distant object throughout the movements, but should have been able to monitor their performance through somatosensory

and proprioceptive feedback to make adjustments as needed. The anterior SMA has strong bidirectional inter-connections with premotor regions and the SMA proper, and receives widespread projections from the prefrontal cortex (Ashe et al., 2006; Nachev et al., 2008). Such connectivity would provide the capacity for the anterior SMA to receive both goal signals and real time sensory signals, which may eventually dictate the adjustments and/or programming needed to maintain movement patterns that are consistent with immediate and near-term motor goals. In our view, the anterior SMA likely performs real time spatiotemporal transformations based on incoming sensory information and goal signals from prefrontal cortices, and implements motor signal perturbations as necessary (e.g., to maintain movements in an anti-phase pattern) through its bidirectional interactions with the SMA proper (Ashe et al., 2006; Hoshi & Tanji, 2004; Kennerley et al., 2004; Makoshi et al., 2011). Understanding the anterior SMA as a center for performing real time spatiotemporal transformations is consistent with the region's involvement in mental rotation and other cognitive tasks, and such functionality has been championed by other investigators (Leek & Johnston, 2009).

In conclusion, we evaluated whether maintaining movements in an anti-phase compared to an in-phase pattern more strongly burdened the anterior SMA (e.g., pre-SMA) cortices using fNIRS. Anti-phase movement patterns are less stable and require greater attentional resources to maintain the coordination dynamics relative to in-phase patterns of bimanual coordination. To our knowledge, this is the first fNIRS investigation of bimanual coordination that has recorded hemodynamic responses in the SMA complex. Our primary results indicated that sustaining anti-phase patterns requires more anterior SMA involvement, and thus supports previous findings of greater anterior SMA activity during anti-phase finger movements in healthy adults (Stephan et al., 1999). This latter study found that the number of significantly activated voxels was greater in the SMA complex during anti-phase compared with in-phase movements, and although no voxels survived the direct comparison of anti-phase and in-phase conditions, at sub-threshold levels greater activity was detected during the anti-phase condition in anterior aspects (Stephan et al., 1999). Our findings are also in agreement with the previous fMRI study of Wu and colleagues (2010) and the conceptual framework of an anterior-directed gradient of progressively more abstract/complex functionality in the primate SMA (Aramaki et al., 2006; Nachev et al., 2008). Beyond enhancing our understanding of the neural bases of bimanual coordination, the current study also supports the notion that fNIRS is a viable technique for probing the SMA cortices in behaving humans (Leff et al., 2011).

The results of this study must be taken in an associative context, as there are a number of limitations. For one, we only investigated self-paced movements that were performed at the participant's preferred rate, and our results cannot be easily generalized to externally cued-movements and/or tasks where participants move at the maximum possible rate. We focused on self-paced coordinative patterns because they reflect the natural and inherent timing tendencies seen in the performance of the neuromuscular system, but other movement patterns would also be of interest. Another limitation is that we did not screen for persons who more often used their fingers for tasks of daily living (e.g., expert model builders, stringed-instrument players). It is possible that activation in the SMA would be different in these participants compared to those without such prior experiences. Finally, we cannot rule out that movement rate differences contributed to some of our neural findings. It is well accepted in the fMRI literature that faster movement rates elicit greater activation. In our study, we closely monitored performance for differences in movement rate between the two conditions, but it is possible that minute differences still existed. However, we would expect any differences in movement rate to favor the in-phase condition as these movements are easier and can be completed more quickly without sacrificing accuracy, and our experimental results did not support this. Thus, while possible, it is not likely that

differences in movement rate significantly affected our results. In spite of these limitations, our results 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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Highlights

- Participants performed in-phase and anti-phase bimanual finger movements.
- fNIRS measurements of oxyHb and deoxyHb were collected from the SMA complex.
- OxyHb concentrations were greater in the anterior SMA during anti-phase movements.
- OxyHb responses in the SMA proper did not distinguish the two movement patterns.
- Anterior SMA may be more critical to maintaining the less stable anti-phase patterns.

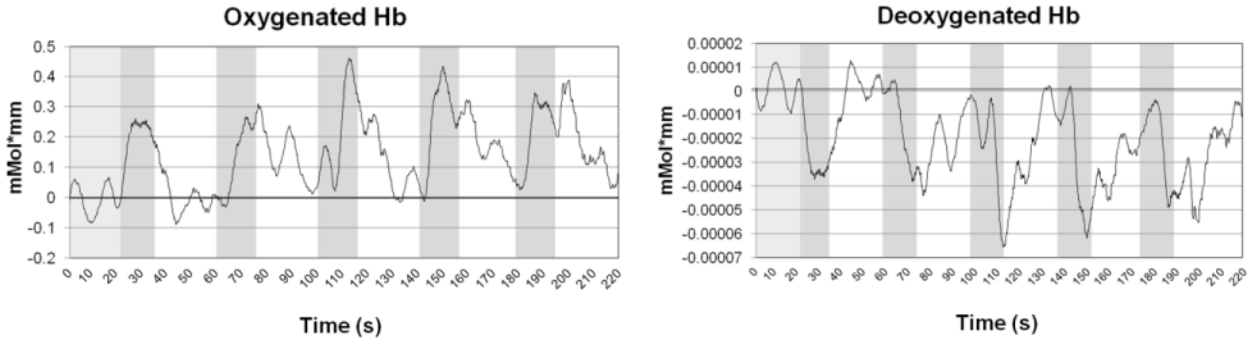

Figure 1.

Representative Un-Averaged Time Series of the OxyHb and DeoxyHb Concentrations. The un-averaged oxyHb (left) and deoxyHb (right) concentration time series for a channel located over the anterior supplementary motor area (SMA) during anti-phase finger movements. Qualitatively similar results were seen in all collected channels. In this figure, time appears on the x-axis in seconds and concentration is on the Y-axis (notice the differences in scale). The white-colored sections indicate the 25 s duration baseline (no movement) periods, the light gray area reflects an initial 20 s pre-scan resting period, and finally the darker gray areas reflect the 15 s duration periods of active movement. As can be discerned, the amount of oxyHb strongly increased during movement periods and decreased during the baseline periods. Finally, as expected, the oxyHb changes were much stronger and in the opposite direction of those for deoxyHb.

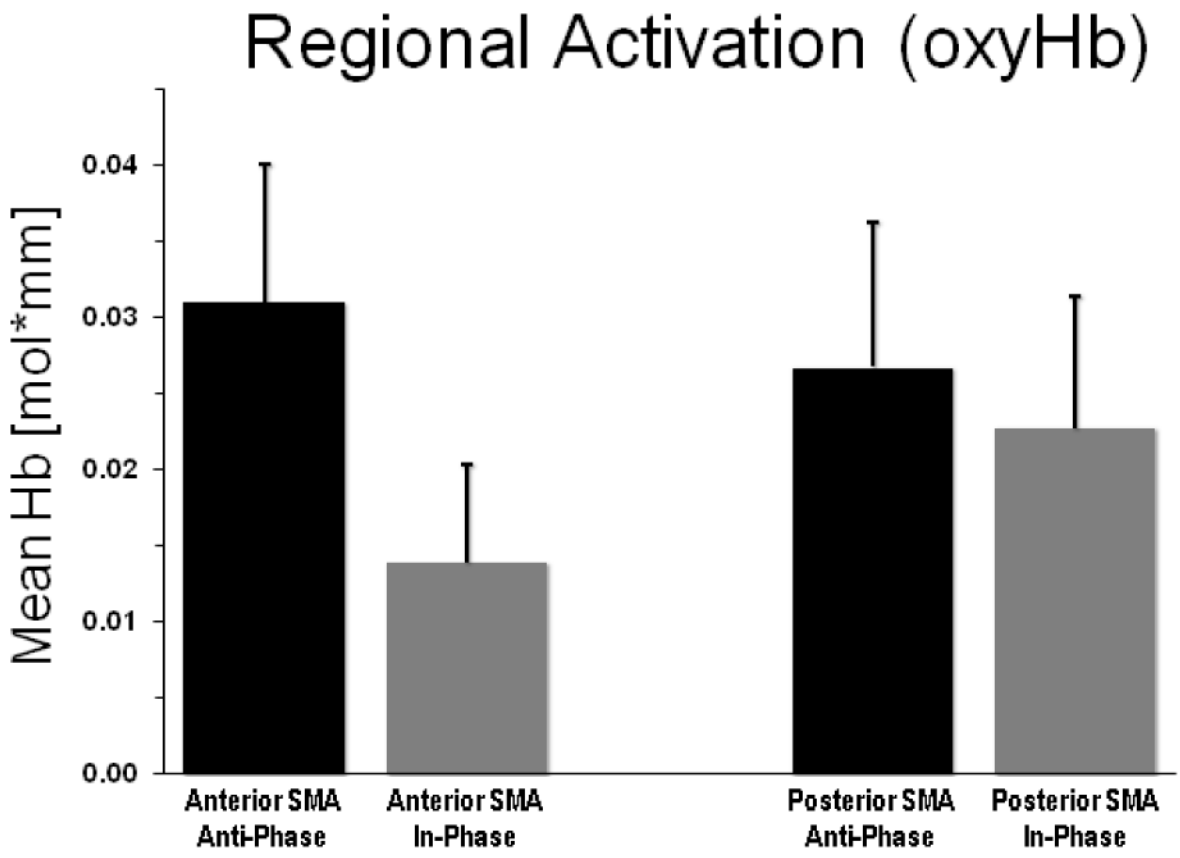

Figure 2.

Regional Activation Indices for OxyHb. The average oxyHb response amplitudes during task performance, per movement pattern and participant, were averaged across subgroups of fNIRS channels to derive regional activation indices for the anterior SMA and SMA proper (see Methods). Group means for these regional activation indices are shown above with activation amplitude on the y-axis. Along the x-axis, data corresponding to the anterior SMA is shown to the left and that for the SMA proper is on the right. Black bars represent the anti-phase data, while grey bars correspond to the in-phase data. Activation was significantly stronger in the anterior SMA during performance of the anti-phase compared to in-phase movement patterns ($p < 0.05$). Error bars indicate one standard error of the mean.