Bilateral Motor Control during Motor Tasks Involving the Nondominant Hand

Kenichi Shibuya1,2) and Naomi Kuboyama3)

1) Center for General Education, Nagasaki Institute of Applied Science
2) Research Institute of Physical Fitness, Japan Women’s College of Physical Education
3) The Faculty of Human Science, Hiroshima Bunkyo Women’s University

Abstract It is generally thought that fatigue is modulated during prolonged exhaustive motor tasks by the bilateral motor cortex. It remains unclear, however, how fatigue is modulated during motor tasks and how information about fatigue affects motor cortex activities in healthy humans. These results may help explain why fatigue is so prevalent in patients with neurological disorders. The purpose of the present study was to investigate the time course of oxygenation of the ipsilateral motor cortex during an exhaustive pinching task. Seven healthy right-handed subjects participated in the study. Near-infrared spectroscopy over the bilateral motor cortices was used to measure activity throughout the pinching task. Subjects performed a sustained maximal voluntary contraction of 50–60% with their left hands until voluntary exhaustion was reached. After the start of the motor task, oxygenation to the contralateral motor cortex increased significantly compared with the resting value (p<0.05). However, with the passage of time, it decreased significantly compared with the resting value (p<0.05). In addition, oxygenation of the ipsilateral motor cortex significantly increased after the start of the motor task, and then decreased significantly at voluntary exhaustion compared with the resting value (p<0.05). These results suggest an interaction between the bilateral motor cortices during motor tasks. J Physiol Anthropol 28(4): 165–171, 2009 http://www.jstage.jst.go.jp/browse/jpa2 [DOI: 10.2114/jpa2.28.165]

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Introduction

A fundamental organizational principle of the human motor system is the contralateral control of distal movements. Reflected in part by the nearly complete crossing of corticospinal fibers innervating the distal musculature (Brinkman and Kuypers, 1973), right-hand movements are associated with neural activity in the left motor cortex and left-hand movements with neural activity in the right motor cortex. The two hemispheres may not contribute in a symmetric manner to motor control as in the case of other brain functions. The role of ipsilateral cortical activity in the control of hand and finger movements remains controversial.

Muscle fatigue is reflected by a reduction in force-generating capacity of the muscle. Muscle fatigue can be categorized as being of central and peripheral origin. There have been a number of studies of central changes during fatiguing exercise. Transcranial magnetic stimulation (TMS) measurements have shown increased excitation and inhibition in primary motor cortex during fatiguing exercise (Taylor et al., 1996; Sacco et al., 1997, 2000; Chen et al., 2003). Recent functional magnetic resonance imaging (fMRI) studies have shown that bilateral of right-handed subjects in the primary motor cortex well as secondary and association cortices during dominant hand unimanual fatiguing exercise, suggesting the presence of a more widespread central response to a fatiguing exercise (Liu et al., 2002; Liu et al., 2003).

Handedness refers to the well-defined preference whereby one hand is used in favor of the other in a consistent manner. It is a fundamental behavioral characteristic that becomes stabilized during development (Miller, 1982) and can be evaluated in terms of preference or performance, although both expressions are closely related. About 90% of humans are more skilled with the right than the left hand, although the degree of manual asymmetry varies as a function of age and task complexity (Bryden et al., 2000; Roy et al., 2003).

Knowing the effect of motor tasks involving the dominant and nondominant hand on the bilateral motor cortices may reveal the delicacy inherent in motor control. This delicacy may explain the ambidexterity of dominant hand movements. Interaction between the bilateral hemispheres may play an important role in accurate motor control.

Several experiments have demonstrated increased activation of the ipsilateral motor cortex in association with unimanual motor task (Hess et al., 1986; Rossini et al., 1987; Tinazzi and Zanette, 1988; Zwarts, 1992; Stedman et al., 1998; Muellbäcker et al., 2000). The left hemisphere may play a greater role in ipsilateral motor control than the right
hemisphere (Ziemann and Hallet, 2001).

Near-infrared spectroscopy (NIRS) allow for noninvasive monitoring of regional changes in cortical tissue oxygenation in response to various stimuli with a high temporal resolution (Kleinschmidt et al., 1996; Obrig et al., 1996, 2000; Colier et al., 1999; Mehnagol-Schipper et al., 2000), even during exercise (Kuboyama et al., 2004, 2005; Shibuya et al., 2004a, 2004b, 2008, 2009; Shibuya and Tachi, 2006; Shibuya and Kuboyama, 2007). In addition, compared with other techniques, NIRS can monitor changes in cerebral oxygenation during dynamic motor tasks by low restriction (e.g., fMRI, positron emission tomography (PET), and TMS). With the NIRS techniques, it is possible to examine oxygenation of the bilateral motor cortices during the course of sustained motor tasks reaching voluntary exhaustion and at the exact moment of voluntary exhaustion (Shibuya and Kuboyama, 2007).

Kim et al. (1993) reported the difference in activation pattern in bilateral motor cortex between dominant and nondominant hand motor tasks in right-handed subjects. A recent study revealed the significant increase of oxygenation in the contralateral motor cortex in the early phase of a motor task with the dominant hand. In that study, oxygenation of the contralateral motor cortex significantly decreased at exhaustion in all subjects (Shibuya and Kuboyama, 2007). At the same time, oxygenation of the ipsilateral motor cortex did not increase in the early phase of the motor task and significantly decreased at exhaustion in all subjects. However, the activity and haemodynamics of the bilateral motor cortices during exhaustive motor tasks remain unclear.

In right-handed subjects, there is evidence that the role of the right hemisphere in motor organisation would be under the rule of the left hemisphere (Haaland et al., 2004; Serrien et al., 2006). However, it is not clearly defined whether oxygenation of the bilateral motor cortices decreases in a similar manner during the motor task until voluntary exhaustion is reached. Therefore, there would be differences in the activation pattern of the bilateral motor cortex during nondominant hand exhaustive motor task from that during a dominant hand exhaustive motor task. The purpose of the present study was to examine oxygenation changes at voluntary exhaustion during a motor task involving the nondominant hand using high temporal resolution NIRS.

**Materials and Methods**

**Subjects**

Seven normal, right-handed, healthy volunteers (21.7±8.4 yr, 169.3±8.3 cm, 61.6±8.4 kg) participated in the present study. Handedness of subjects was confirmed by the side of use for all movements in daily life. Informed consent was obtained from each subject after detailed explanation of the procedure and noninvasiveness of the study. Throughout the study, subjects were lying on a comfortable bed in a quiet room. The criteria for participation were a medical history free of cardiovascular, pulmonary, renal, endocrinological, and neurological disorders. The subjects were told not to train hard on the day prior to testing and not to exercise on the day of testing. They were also asked to refrain from consuming food or beverages containing caffeine before the test.

**Near-infrared spectroscopy**

NIRS techniques have been described elsewhere (Elwell et al., 1994). We used four wavelengths (775, 810, 850, and 905 nm) of NIRS (NIRO-300L, Hamamatsu Photonics, Japan) to analyze motor cortex oxygenation. The optical probe consisted of two emitters and two detectors (comprising three separate sensors). The NIRS probes were guided on the subjects' heads through glass fiber bundles. The probes were positioned over the bilateral motor cortex areas enclosing C3 and C4, according to the modified international EEG 10-20 system (American Electroencephalographic Society, 1994). The distance between the transmitting and receiving probes was 3.5 cm. The positioning of probes around the motor area for the hand was checked during a pinching task of the right hand to induce functional oxygenation. If no oxygenation changes were detected in response to the pinching task, the probes were moved several millimetres until, by trial and error, a consistent oxygenation response was obtained.

The probes were fixed to the bilateral motor cortex areas with a light sealed tape and a strap. A description of room luminance and any procedures implemented to reduce light interference with measurements. For quantification of changes in [HbO2], [Hb] (Delpy et al., 1988), a modified Lambert–Beer law was used, which describes optical attenuation in a highly scattering medium:

$$\text{Attenuation (OD)} = \log \frac{I_\text{in}}{I_\text{det}} = A\text{cLB} + G$$

In this equation, OD is the optical density, $I_\text{in}$ is the incident light intensity, $I_\text{det}$ is the detected light intensity, A is the absorption coefficient of chromophores in mmol/L, L is the interprobe distance in centimetres, and B is the differential optical path-length factor that takes into account the scattering of light in tissue. G is a factor related to the tissue geometry. The NIRS data were collected with a sample frequency of 2 Hz. The baseline values of [HbO2] and [Hb] were calculated from the average of 120 data (60 sec) during 3 min before the start of the exercise. The values of [HbO2] and [Hb] during exercise were calculated using an average of 5 sec before and after each section. NIRS data could not compare between another data set, i.e., contralateral vs. ipsilateral, because the data from NIRS are not numerical values. Therefore, in the present study, the pattern of changes in values in the contralateral and ipsilateral motor cortex was not compared. The value in each side motor cortex compared only with each baseline value.

The oxygenation signals in the bilateral motor cortex were measured simultaneously. The data block was delimited every 10 sec for data stability (baseline, 10 sec, 20 sec, 30 sec, after the start of exercise, and at exhaustion), because the minimum value of the duration of exercise was 37.5 sec, as mentioned in
the Results section.

Protocol
Before the start of study, the subjects were familiarized with the protocol. Subjects performed a static left-hand pinching task at 50–60% of maximal voluntary contraction (MVC) until they were no longer able to sustain 50%MVC. Subjects were on an inclined surface and pinched the hydraulic pinch meter, which was held at the heart level. A nylon tube connected the pinching device and the transducer. During the NIRS experiment, subjects pinched the device to match a target force provided by a visual feedback system. The force applied by pinching was sensed and converted to a voltage signal by the pressure transducer in the hydraulic system. The laboratory was air-conditioned and the temperature was kept constant at 19–22°C.

Electrophysiological (Siemionow et al., 2000) and neuroimaging (Dai et al., 2001; Detmers et al., 1995) studies have reported a proportional relationship between cortical signals and exerted joint force in human subjects, indicating that brain signals are positively correlated to voluntary effort, as a higher level of effort is required for exerting greater muscle force.

Statistical analysis
Each change in oxygenation in the contralateral and ipsilateral motor cortex with the passage of time was assessed using repeated ANOVA. Post-hoc analysis using paired T-test was performed on the time-series oxygenation changes in [HbO₂] and [Hb] compared with the baseline value. A p value <0.05 was considered statistically significant.

Results
The mean value of MVC was 7.5±0.9 kg. The value of 50%MVC was 3.8±0.5 kg. The duration time to voluntary exhaustion from the start of the motor task was 66.3±20.4 sec (37.5–99.6 sec) in the left hand.

Contralateral (left-side) motor cortex oxygenation
The oxygenation kinetics of the contralateral motor cortex during the course of the motor task is described in Fig. 1 and Table 1. The contralateral [HbO₂] significantly changed during the motor task ($F=9.302$, $p<0.0001$). [HbO₂] was significantly increased at 10 sec ($T=−11.510$, $p=0.0001$) after the start of the motor task compared with the resting value. In seven subjects, the contralateral [HbO₂] was increased at 10 sec after the start of the motor task, and the contralateral [HbO₂] was increased at 20 sec after the start of the motor task in six of seven subjects compared with the resting value. [HbO₂] significantly decreased, however, at voluntary exhaustion ($T=2.903$, $p=0.0337$) compared with the resting value. In four of seven subjects, contralateral [HbO₂] decreased at 30 sec after the start of the motor task, and decreased at exhaustion in all subjects compared with the resting value.

The contralateral [Hb] did not change significantly

![Fig. 1 Changes in the contralateral motor cortex from resting values in (a) oxyhaemoglobin concentration ([HbO₂]) and (b) deoxyhaemoglobin concentration ([Hb]) during a pinching motor task. Values are expressed as mean±SE. Asterisks show significant differences, $p<0.05$.](image)

<table>
<thead>
<tr>
<th>Table 1</th>
<th>The changes of [HbO₂] and [Hb] from resting value after the start of motor task. Results are mean number±SD. Asterisks show significant differences compared with the resting value, $p&lt;0.05$</th>
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<td>Ipsilateral Motor Cortex</td>
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<td>$\Delta$ [HbO₂]</td>
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<tr>
<td>0 sec</td>
<td>$−0.004±0.006$</td>
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<tr>
<td>10 sec</td>
<td>$0.728±0.630^*$</td>
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<tr>
<td>20 sec</td>
<td>$−0.078±0.674$</td>
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<tr>
<td>30 sec</td>
<td>$−0.130±1.200$</td>
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<tr>
<td>Exhaustion</td>
<td>$−1.006±0.829^*$</td>
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Fig. 2 Changes in the ipsilateral motor cortex from resting values in (a) oxyhaemoglobin concentration [HbO₂] during a pinching motor task and (b) deoxyhaemoglobin concentration [Hb]. Values are expressed as mean±SE. Asterisks show significant differences, p<0.05.

throughout the motor task (F=2.623, p=0.0544). In four of seven subjects, the contralateral [Hb] was decreased at exhaustion compared with the resting value.

Ipsilateral (right-side) motor cortex oxygenation

The oxygenation kinetics of the ipsilateral motor cortex during the motor task is described in Fig. 2 and Table 1. Ipsilateral [HbO₂] changed significantly during the motor task (F=4.462, p=0.006). The ipsilateral [HbO₂] significantly decreased at exhaustion (T=3.201, p=0.0186) compared with the resting value. In five of seven subjects, [HbO₂] was increased at 10 sec after the start of the motor task, and it decreased in all subjects at exhaustion compared with the resting value. Ipsilateral [Hb] did not change significantly during exercise (F=1.207, p=0.3284). In four of seven subjects, the ipsilateral [Hb] was decreased at exhaustion compared with the resting value.

Discussion

Changes in cerebral oxygenation reflect cerebral functional activation (Kleinschmidt et al., 1996; Obrig et al., 1996; Colier et al., 1997, 1999). In the present study, a bilateral reduction in motor cortex oxygenation was observed during a sustained motor task with the nondominant hand until voluntary exhaustion was reached. The important findings in the present study were the decline in oxygenation in the bilateral motor cortex and the synchronized decline in oxygenation between contralateral and ipsilateral motor cortices during the unimanual motor task until exhaustion was reached. In the present study, the exhaustion point at which a subject could no longer sustain the pinching force over 50%MVC was determined. The declining oxygenation of the contralateral motor cortex was observed not only at exhaustion but also at 10 sec before exhaustion. Simultaneously, a change in oxygenation of the ipsilateral motor cortex occurred that was similar to the change in the contralateral motor cortex.

Little is known of central changes that occur during the course of a motor task until voluntary exhaustion is reached, although previous studies using fMRI and TMS have demonstrated a decrease in activity during the intervals between and after a fatiguing motor task, not only on the contralateral but also on the ipsilateral motor cortex (Ferbert et al., 1992; Netz et al., 1995; Benwell et al., 2005). In our previous and present studies, we explored motor cortex oxygenation changes during an exhaustive motor task using NIRS, which is a high temporal resolution technique (Shibuya and Kuboyama, 2007). In the previous study, it was proposed that a decline occurred in the oxygenation of bilateral motor cortices with the passage of time and that in all subjects, bilateral oxygenation decreased at voluntary exhaustion in a dominant-hand exhaustive motor task (Shibuya and Kuboyama, 2007). The present results are similar to those in our previous study. These results were also consistent with other investigations, which showed fatiguing accompanied by changes in the level of activation in the primary motor cortex (Liu et al., 2002, 2003).

In our previous study using a dominant exhaustive motor task, the [HbO₂] of the ipsilateral motor cortex did not increase in three of eight subjects at 10 sec after the start of the motor task, and it decreased in five of eight subjects at 20 sec after the start of the motor task, but these changes were not statistically significant (Shibuya and Kuboyama, 2007). In the present result, however, the [HbO₂] of the ipsilateral motor cortex increased significantly. [HbO₂] of the ipsilateral motor cortex increased in five of seven subjects at 10 sec after the motor task, and it increased in five of seven subjects at 20 sec after the motor task. In six of seven subjects, [HbO₂] increased at either 10 sec or 20 sec after the start of the motor task.

Two models have been proposed to explain the presence of cortical activation in the motor cortex ipsilateral to an active hand as well as hemispheric asymmetries in the control of motor activity. One model assumes that most movements of the distal extremities are first generated bilaterally (Rossini et al., 1987; Britton et al., 1991). In this model, the dominant hemisphere exerts a more potent action on the nondominant hemisphere via asymmetric interhemispheric inhibition and activation (Ziemann and Hallett, 2001). The second model assumes that activation starts in the hemisphere that is contralateral to the active hand and spreads into the ipsilateral hemisphere, with more influence of the left hemisphere over
the right hemisphere than vice versa. Furthermore, one correlate of this model suggests that motor programs are stored in the left hemisphere and are transferred via callosal projections to the right hemisphere to command skilled movements with the left hand. Both models assume that the left hemisphere possesses better developed motor programs and the presumed interhemispheric interactions rely on transcallosal fiber systems. Our finding that both hemispheres were activated in the early phase of a motor task using the nondominant hand suggests that the motor cortex of the left hemisphere is activated, and that this activation in the left hemisphere allows it to influence the right hemisphere’s motor systems when subjects are using their left hand to perform a skilled task. Further, this influence adds to the ability of the right hemisphere to perform agile and dexterous movements with the left hand. Alternatively, interhemispheric activation might reduce the left hemisphere’s inhibition of the right hemisphere. Furthermore, in the present study, the reductions in oxygenation in the bilateral motor cortices were observed at exhaustion. According to the previously mentioned models, the reduction of oxygenation in the motor cortex of the left hemisphere might influence the motor cortex of the right hemisphere, although the mechanisms for this phenomenon remain unclear. The pathways mediating bilateral responses and their relationship to contralateral corticospinal projection have not been fully defined (Chen et al., 2003). Further research is needed to clarify the interaction between the bilateral hemispheres.

The meaning of the data obtained from NIRS is still under discussion, in particular, whether the NIRS signals reflect intracerebral blood volume of pial and, probably, also the blood volume of more superficial circulation. For example, hyperventilation at rest induces a reduction of [HbO2] but not less cerebral oxygenation because the blood volume was reduced due to peripheral vasocostriction (Rostrup et al., 2002). In addition, the spatial resolution and cerebral penetration depth are limited in NIRS measurements. Therefore, further studies are needed to confirm the validity of the present results.

In conclusion, the present study provides important evidence that a decline in oxygenation occurred in bilateral motor cortices and that a synchronized decline in oxygenation occurred between contralateral and ipsilateral motor cortices during the course of a unimanual motor task performed to exhaustion. We determined the exhaustion point at which a subject could no longer sustain the pinching force at more than 50% MVC. The decline in oxygenation of the contralateral motor cortex was observed not only at exhaustion but also 10 sec before exhaustion. Simultaneously, the change in oxygenation of the ipsilateral motor cortex was similar to that of the contralateral motor cortex. These results suggest that the ipsilateral motor cortex as well as the contralateral motor cortex activates during a motor task until exhaustion is reached.

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Correspondence to: Kenichi Shibuya, Ph.D., Center for General Education, Nagasaki Institute of Applied Science, 536 Aba-machi, Nagasaki 851–0123, Japan
Phone: +81–95–838–4489
e-mail: shibuya_kenichi@nias.ac.jp