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	キーワード (Ja):
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	作成者: 久保山, 直己, KUBOYAMA, Naomi
	メールアドレス:
	所属:
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Functions of the Ipsilateral Prefrontal Cortex during a Unimanual Timing Task

Naomi Kuboyama

Introduction

Right hand movements are associated with neural activity in the left motor cortex, and left hand movements are associated with neural activity in the right motor cortex (Brinkman and Kuypers 1973).

However, several experiments have demonstrated increased activation of the ipsilateral motor cortex in association with a unimanual motor task (Hess et al. 1986, Muellbacher et al. 2000, Zwarts 1992). Thus, numerous reports have addressed the activation of the contralateral and ipsilateral cortices during motor tasks. However, the hemodynamics in the ipsilateral cortex and contralateral cortex during motor tasks had not been made clear.

The prefrontal cortex (PFC) plays an important role in motor control (Ullsperger and von Cramon 2006, Jueptner et al. 1997, Durstewitz et al. 2000). In a previous experiment, Jueptner et al. (1997) showed that the PFC was sequence-learning activated during new learning but not during automatic performance. A number of neurobiological models of PFC function and connectivity are consistent with the general organizational framework of top-down control in mental timekeeping and highlight the role of the PFC as the apex of this hierarchy (Miller and Cohen 2001). Lesions in the PFC have been shown to cause general deficits in executive abilities, such as working memory, with few if any discernable deficits in more basic sensory discrimination and motor performance (Diamond and Goldman-Rakic 1989, Duncan et al. 1996, Vendrell et al. 1995). The right PFC was involved in sustained attention and errors, finding that conflicts with the conception of the left PFC as having a role in the inhibition of automatic responses (Vendrell et al. 1995). However, the relationship between the contralateral-PFC and the ipsilateral-PFC and the hemodynamics of both PFCs during motor tasks remains controversial. Studying the effect of motor tasks involvement of the bilateral PFCs may reveal the delicacy inherent in motor control, and may clarify whether the interaction between the bilateral PFCs plays an important role in accurate motor control.

Studies in humans through the use of positron emission tomography (PET) and regional cerebral blood flow (rCBF) signal changes as an indirect index of brain activity have explored the effect of stimulus rate on the central nervous system, particularly in the primary visual cortex (Fox and Raichle, 1984). The rCBF change in the striate cortex is proportional to the repetition rate of photic stimulation between 0 and 7.8Hz (Fox and Raichle 1984). In other studies, a linear relationship was also observed in the primary auditory cortex (Price et al. 1992). These studies underscore the signi?cance of the stimulus rate as a determinant of rCBF response. Moreover, research has also been conducted on the relationship between frequency and rCBF using a movement stimulus (Jenkins et al., 1997). Jenkins et al. (1997) examined the effect of joystick movement, in frequencies that ranged from 1/sec to 1 every 5.5sec in 0.5s steps, on cerebral activation. They observed no signi?cant relationship between movement frequency and cerebral activation. Furthermore, Sadato et al. (1997) measured rCBF by PET and reported that the relationship between motor cortex activation and movement frequency was not signi?cant, and tended to plateau as the frequency reached 4Hz. In these studies, cerebral activation showed a nonlinear increase, indicating an exponential rise. Thus, the relationship between stimulus frequency and brain activity differs in terms of the region of the brain and the type of stimulation. In brain activity studies using movement stimulus, movement was restricted by the limitations of the test equipment and was not performed with high frequency stimuli of over 4.0Hz. Due to noise interference while the body is being measured, measurement of movements of high frequency is impossible. For this reason, the relationship between a movement stimulus and brain activity has not been examined at high frequencies (over 4.0Hz). Therefore, brain activity at high frequencies is still unknown. The prefrontal cortex (PFC) plays an important role in motor control in humans. However, function of the ipsilateral-PFC during motor tasks remains unclear. It is possible to examine the ipsilateral-PFC during a simple motor task, such as unimanual finger tapping, using near-infrared spectroscopy (NIRS), in which it is assumed that increased oxygenation reflects cortical activation.

Near-infrared spectroscopy (NIRS) is a non-invasive method used to measure the oxygenation and de-oxygenation of tissues within the human body, and its use as a measure of brain activity has been proposed. Brain activation is thought to be accompanied by increases in the regional cerebral blood flow (CBF) and oxygen metabolic rate, with neuronal activation accompanied by an increase in oxyhemoglobin (HbO2) and a decrease in deoxyhemoglobin (HHb) (Boushel et al. 2001, Madsen and Secher 1999, Obrig and Villringer 2003).

The purpose of this study was to examine the contralateral-PFC and ipsilateral-PFC activation in response to frequency during a unilateral finger task using high-temporal-resolution NIRS.

Methods

Subjects

Eleven right-handed females participated in the study. Their mean (± SD) age, height, and weight were 20.3 (± 1.4) yrs, 159.6 cm (± 5.4) and 54.0 kg (± 10.4), respectively. The subjects were asked to lie in a supine position on a bed and perform a finger-tapping exercise. Each subjects tapped the index finger of her right hand. Each subject stretched out one's arm along her body and tapped her finger on the bed. The frequencies of the finger-tapping were 2, 3, 4, 5 and 6Hz. Each finger-tapping exercise continued for 20 seconds. The subjects then rested for 40 seconds, and then performed the tapping exercise at next frequency. The subjects were shown the next frequency during the rest. The order of the frequencies differed with every subjects. The subjects matched their finger-tapping with the rhythm of a digital metronome sound. During the rest, the subjects were asked to relax and not move any of their fingers.

NIRS

Blood-oxygenation-level-dependent evaluations of CBF are important in imaging studies of brain function (Silva et al. 1999), whereas the capillary-oxygen-level-dependent (COLD) control of brain oxygen diffusion is the basis for an emerging understanding of the neuroenergetics of brain function (Gjedde et al. 2005). Capillary oxygenation can be monitored noninvasively by NIRS in real time during situations ranging from surgery (Skak et al. 1997) to strenuous whole-body exercise (Nielsen et al. 2001). We used a three-wavelength (775, 810 and 850 nm) NIRS (NIRO-200; Hamamatsu Photonics, Japan) to measure the ipsilateral-PFC and the contralateral-PFC oxygenation. The NIRO-200 makes it possible to quantify tissue oxygenation. However, this measurement requires optically homogenous tissue so that the signal-to-noise ratio can be reduced, and this requirement is unlikely to be by cerebral tissue (Greisen 2006). As the accuracy of this parameter is under discussion, at least concerning cerebral tissue, we here report results based on changes in oxy-Hb concentration [HbO2], the most sensitive parameter of hemodynamic responses (Strangman et al. 2002, Hoshi et al. 2001). The optical probe comprised one emitter and one detector (with a total of three separate sensors), guided on the subjects' heads through glass fiber bundles. The probes were positioned over the bilateral frontal cortex areas (AF3 and AF4) according to the modified international EEG 10-20 system (American Electroencephalographic Society Guidelines, 1994). The distance between the transmitting and receiving probes was 4.0 cm. The probes positioned around the ipsilateral-PFC and contralateral-PFC areas were checked by inducing functional oxygenation with a right-index-finger-tapping task. If no oxygenation changes were detected in response to the handgrip task, the probes were moved by several mm until a consistent oxygenation response was achieved by trial and error.

The probes were fixed to the ipsilateral-PFC and contralateral-PFC areas with light sealing tape and a strap. The NIRS data were collected with a sample frequency of 2Hz. Relative concentration changes were measured from the resting baseline of [HbO2].

Statistical analyses

The average values were expressed as means ± S.D. The criterion for significance was $P < 0.05$. In order to determine the significance of [HbO2], one-way repeated measures analysis of variance (ANOVA) and a post-hoc Tukey-HSD test were performed.

Results

Contralateral PFC oxygenation changes during the finger task

This study reported results here based on changes in oxy-Hb concentration, the most sensitive parameter of hemodynamic responses.

All subjects completed the designated finger-tapping tasks. The changes in [HbO2] in the contralateral-PFC during the finger-tapping task are shown in Fig. 1. The contralateral PFC [HbO2] levels changed significantly during the finger-tapping task ($F = 4.221$, $p < 0.01$) (Fig. 1). Compared with the 2Hz value, the contralateral frontal [HbO2] levels were in a steady state from 3Hz to 5Hz. However the 6Hz value increased markedly ($p < 0.01$).

Ipsilateral frontal cortex oxygenation changes during finger task

The changes in [HbO2] in the contralateral frontal cortex during the finger-tapping task are also shown in Fig. 1. The contralateral frontal [HbO2] levels changed significantly during the finger-tapping task ($F = 4.799$, $p < 0.01$) (Fig. 1). Compared with the 2Hz value, the contralateral frontal [HbO2] levels were in a steady state from 3Hz to 5Hz. However the 6Hz value increased markedly ($p < 0.01$).

Discussion

Eleven right-handed females participated in this study. The subjects performed a tapping task with the index finger of the right hand. This study showed that the oxygenation of the contralateral-PFC and that of the ipsilateral-PFC were synchronized during finger-tapping at all frequencies.

A NIRS study found different kinetics in the contralateral and ipsilateral frontal cortices during the maximal handgrip task (Kuboyama and Shibuya 2015). In that study, the activity of the contralateral frontal cortex increased and then decreased during the motor task, while that of the ipsilateral frontal cortex increased throughout the task. That study suggested a connection between the ipsilateral and contralateral frontal cortices and that the ipsilateral cerebral cortex provided complementary activity to the insufficient activity of the contralateral cerebral cortex. However, the results of that previous study differed from the results of this study. In this study, the oxygenation of the contralateral-PFC did not decrease in all tasks. Thus, it was difficult to provide complementary activity to the insufficient activity of the contralateral cerebral cortex. During the finger-tapping task, the oxygenation of the ipsilateral-PFC and that of the contralateral-PFC were synchronized. The oxygenations of the contralateral-PFC is explained by the right-hand movements are associated with neural activity in the left hemisphere and the left hand movements are associated with neural activity in the right hemisphere (Brinkman et al. 1970). In this study, all subjects performed the finger-tapping with the right index finger. Therefore the oxygenations in the ipsilateral-PFC during finger-tapping cannot be explained in this way. However, it is possible that the ipsilateral-PFC is related to the precise coordinate motor control during the timing task. The ability to precisely coordinate

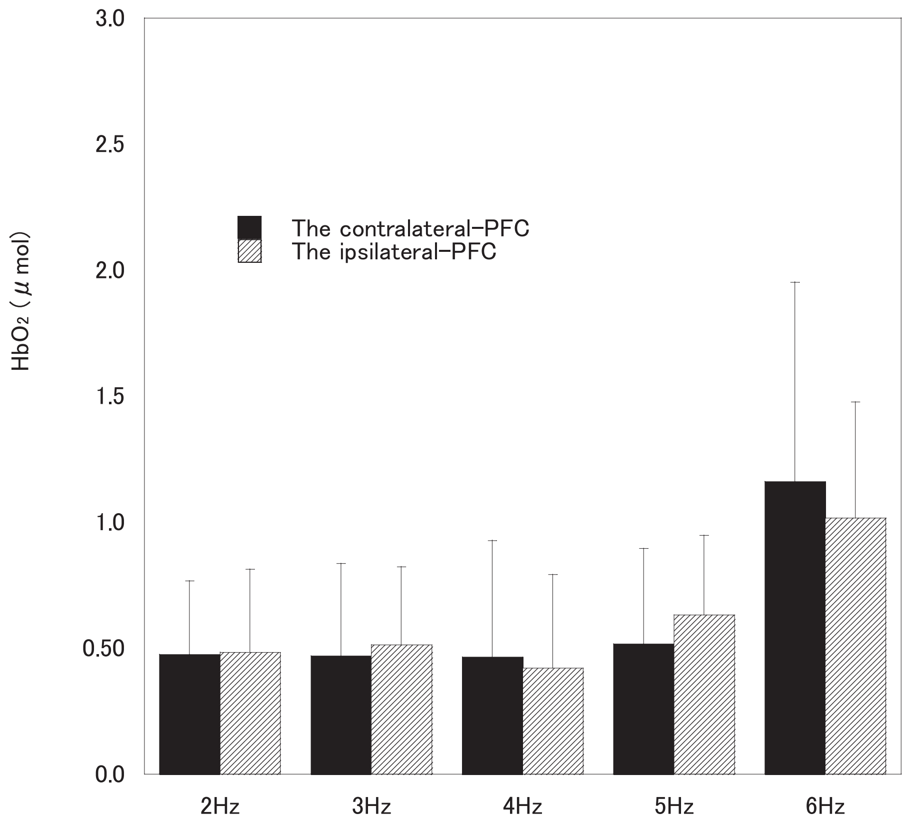

Figure1. Oxygenation in the contralateral prefrontal cortex and the ipsilateral prefrontal cortex. Changes from the baseline values in oxyhemoglobin concentration (HbO2) in the prefrontal cortex during tapping task. Values are mean ± SD. ** indicated $p < 0.01$.

motor control with regularly-paced sensory stimuli requires an ability often called 'mental timekeeping', thought to be a distinct form of cognitive function (Wiener et al. 2010). Wiener et al. (2010) suggested that the processing of temporal information is mediated by a distributed network that can be differentially engaged depending on the task requirements. A consistent feature among numerous conceptual models of the internal clock mechanism (Matell and Meck 2004, Meck and Benson 2002), such as pacemaker-accumulator models, is an element of 'top-down' cognitive control. A NIRS study proposed that variations in the hemodynamics response of the PFC may represent individualized neuronal activity (Ekkekakis 2009). Therefore measures of the hemodynamics response from multiple areas of the PFC could potentially indicate functional activation (i.e. top-down regulatory [cognitive control] processes) due to affective processing (Tempest et al. 2014). A number of neurobiological models of PFC function and connectivity are consistent with the general organizational framework of top-down control in mental timekeeping and highlight the role of the PFC as the apex of this hierarchy (Miller and Cohen 2001).

A sensorimotor timing study suggested that both the right and left PFCs were found to exert control over timing-behavioral accuracy, but there were distinctly lateralized roles with respect to optimal performance (Witt and Stevens 2013). That study reported that the right PFC and the left PFC were connected with the left motor cortex. Therefore, in this study, it was possible that the oxygenation of the ipsilateral-PFC exerted control over the timing-behavioral accuracy. On the other hand, this study cannot fully rule out the possibility that the contralateral-PFC participates in exercise control. However, the contralateral-PFC is considered to have little influence on timing control there will be little influence of the contralateral-PFC in timing control because right-hand movements are associated with neural activity in the left hemisphere (Brinkman et al. 1970). That is to say, it is possible that the ipsilateral-PFC is more likely to control timing than the contralateral-PFC. In conclusion, the present study provides important evidence that a synchronized activation was found over the contralateral-PFC and ipsilateral-PFC areas at all frequencies investigated during a unimanual finger-tapping task. This study determined the oxygenation of the contralateral-PFC and the ipsilateral-PFC at task frequencies ranging from 2Hz to 6Hz. The synchronized activation was found over both PFC areas at all frequencies investigated. In the ipsilateral-PFC, the oxygenation levels at 6Hz were significantly higher than at other frequencies ($p < 0.01$). In the contralateral-PFC, the oxygenation levels at 6Hz were also significantly higher than at other frequencies ($p < 0.01$). There were no significant differences between the contralateral-PFC and the ipsilateral-PFC at any of the frequencies. It was possible that the ipsilateral-PFC was more strongly related with precisely coordinate motor control than was the contralateral-PFC during the timing task.

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