

Mechanisms of Human Sensorimotor-Learning and Their Implications for Brain Communication

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SUMMARY Humans have a remarkable ability to flexibly control various objects such as tools. Much evidence suggests that the internal models acquired in the central nervous system (CNS) support flexible control. Internal models are neural mechanisms that mimic the input-output properties of controlled objects. In a series of functional magnetic resonance imaging (fMRI) studies, we demonstrate how the CNS acquires and switches internal models for dexterous use of many tools. In the first study, we investigated human cerebellar activity when human subjects learned how to use a novel tool (a rotated computer mouse, where the cursor appears in a rotated position) and found that activity reflecting an internal model of the novel tool increases in the lateral cerebellum after learning how to use the tool. In the second study, we investigated the internal-model activity after sufficient training in the use of two types of novel tools (the rotated mouse and a velocity mouse, where the cursor's velocity is proportional to mouse's position) and found that the cerebellar activities for the two tools were spatially segregated. In the third study, we investigated brain activity associated with the flexible switching of tools. We found that the activity related to switching internal models was in the prefrontal lobe (area 46 and the insula), the parietal lobe, and the cerebellum. These results suggest that internal models in the cerebellum represent input-output properties of the tools as modulators of continuous signals. The cerebellar abilities in adaptive modulation of signals can be used to enhance the control signals in communications between the brain and computers.

key words: *internal models, sensorimotor learning, tool use, task switching brain-machine communication*

1. Introduction

An ideal brain-machine interface should utilize as control signals the natural brain activities that arise in performing everyday tasks. However, due to technical limitations, many interfaces, especially non-invasive ones, require humans to acquire skills to generate specific brain activities that can be easily read-out by the interfaces. Using fMRI, we have been investigating how skills for controlling a computer mouse, a representative man-machine interface, are acquired and adaptively switched in the human brain. In a series of our experiment, we investigated brain activity during learning how to use novel computer mice: a rotated mouse, where the cursor appears in a rotated position, and a velocity mouse, where the cursor's velocity is proportional to mouse's position. We studied activity related to each-type of the mouse and activity related to switching of the mouse-type. In this review article, we summarize the results of our studies and discuss their implications for brain-machine interfaces, i.e.

communications between the brain and a machine. Our results illustrate how humans acquire skills for controlling the interfaces and suggest effective designs of non-invasive brain-machine interfaces that require the users to modulate their brain activities as control signals for a computer cursor or a robot arm.

2. Neural Correlates of Internal Models

Knowing the input-output properties of tools is important for rapid and smooth use of tools. For example, when we manipulate a computer mouse that we have used for a long time, we can predict how its cursor will move on a screen if we move the mouse in a particular direction, and how we should move the mouse if we want to move the cursor to a particular position on the screen. Many studies have suggested that internal models in the CNS represent input-output properties of control objects such as human bodies and tools [1]–[6]. It has been proposed that Purkinje cells in the cerebellum play an important role in representing the input-output properties (Fig. 1, for example [7]). Purkinje cells receive major inputs from parallel fibers and climbing fibers and send the sole output signals from the cortex. Climbing fiber inputs carry performance errors between the desired and actual movements and guide the learning acquisition of internal models by changing synaptic efficacy. In the case of motor learning, after repetitive training, a Purkinje cell becomes capable of transforming planned movements carried by parallel fibers to the appropriate motor commands that realize the desired movements. This learning mechanism was computationally modeled by a feedback-error-learning schema [1], [8], and its biological plausibility has been investigated by neurophysiological studies in monkeys [9]–[12].

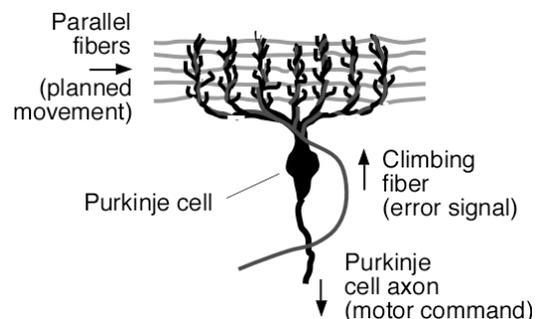


Fig. 1 Information flow around Purkinje cell in the cerebellar cortex.

Manuscript received November 14, 2007.

Manuscript revised March 5, 2008.

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DOI: 10.1093/ietcom/e91-b.7.2102

3. An fMRI Study Investigating an Internal Model for a New Tool

We examined whether activities reflecting an internal model and its acquisition process could be visualized in the human cerebellum using fMRI [13]. Subjects manipulated a computer mouse in an MR scanner so that the corresponding cursor followed a randomly moving target on a screen (tracking task). In test periods, the cursor appeared in a position rotated 120° around the center of the screen to necessitate subject learning (novel mouse; Fig. 2), while during baseline periods it was not rotated (normal mouse). The subjects' performance was measured by tracking errors, i.e., the distance between the cursor and the target. The errors in the test periods significantly decreased as the number of sessions increased, while the errors in the baseline periods were constant (Fig. 3A, bottom), suggesting that learning progressed in the test periods. Activation maps obtained by subtraction of brain activity in the baseline periods from that in the test periods (Fig. 3A, top) indicated that the activity in the lateral cerebellum became smaller as learning progressed.

The decreasing activity in the lateral cerebellum may reflect performance error that also decreased as learning proceeded. To evaluate this possibility, the subjects underwent

an 'error-equalized' experiment: the target velocity in the baseline periods was increased so that the baseline error was equal to the test error (Fig. 3B, bottom). There was no significant difference between the test and the baseline errors, but we could find similar cerebellar activity to that observed in the last stage of learning (Fig. 3B, top). This activity cannot be related to the tracking error. The most plausible explanation is that the remaining activity reflects the acquired internal models, whereas the decrease in activity as learning progresses may largely reflect the error signals.

We examined the time courses of signal intensity during the training sessions averaged over two regions of interest. First, the error-related region was defined as voxels whose signal intensity in the training sessions was significantly and positively correlated with the tracking error (white regions enclosed by solid lines in Fig. 4A). Second, the internal-model-related region was defined as voxels whose signal intensity was significantly higher in the tests periods than the baseline periods in the error-equalized experiments (hatched regions in Fig. 4A). The activity in the error-related region markedly decreased as the number of training sessions increased (Fig. 4B, middle). In contrast, the activity in the internal-model-related regions did not markedly decrease (Fig. 4B, left), and its correlation with the error was low ($r^2 = 0.25$) in comparison to the activity

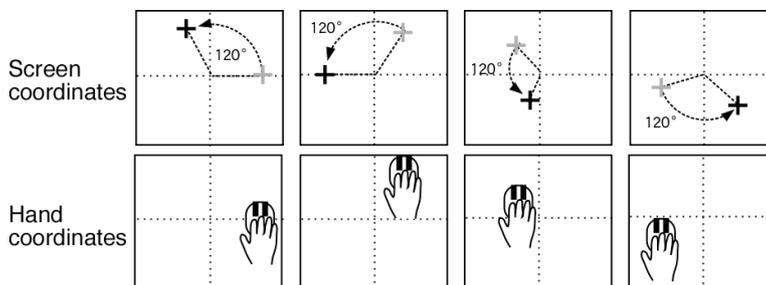


Fig. 2 Relationship between a cursor and a rotated mouse at various positions. The cursor (black cross) on a computer screen appears in a position rotated 120° around the screen's center. Gray cross indicates the cursor of a normal mouse.

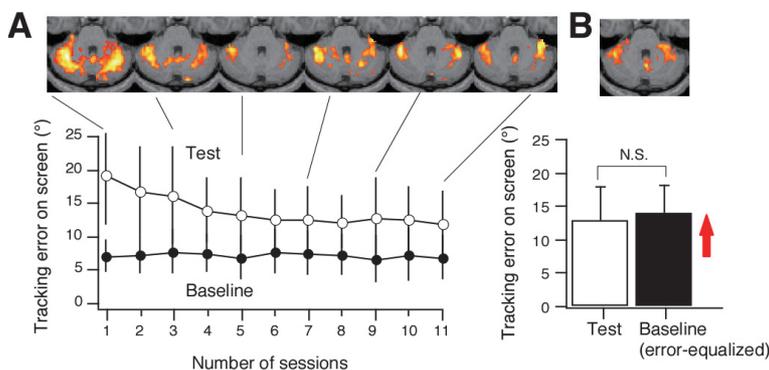


Fig. 3 Cerebellar activity that decreased with learning progress (A), and the activity that remained when the tracking error was equalized (B). A: The upper panels show the activation maps of the regions significantly activated in the test periods in comparison to those in the baseline periods. The lower panel shows tracking error (mean ± SD) in the training sessions. B: The upper panel shows the activation map in the error-equalized session (see main text). The lower panel indicates tracking error (mean + SD) in the same session.

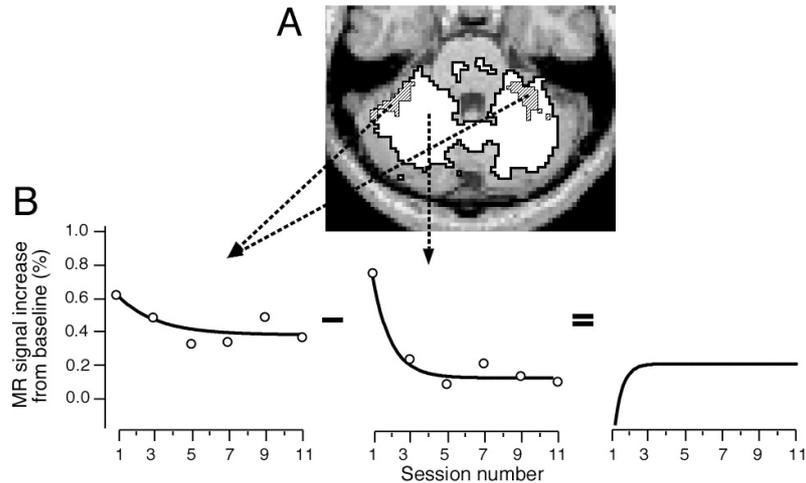


Fig. 4 A: Cerebellar activity related to error signals (white regions enclosed by solid line) and activity related to the acquired internal model (hatched regions). B: Left panel shows activity change in the hatched regions in Fig. 4A. Middle panel shows activity change in the white regions in Fig. 4A. Right panel shows the subtraction of the activity change in the middle panel from that in the left panel. Each curve indicates the exponential function fitted to the circles.

in the error-related regions ($r^2 = 0.82$). This result indicates that the activity in the internal-model-related regions may include components that cannot be explained solely by the error. By subtracting activity in the error-related regions (middle panel) from that in the internal-model-related regions (left panel), we could confirm that activity reflecting the acquired internal model increased as learning progressed (Fig. 4B, right). The acquired internal model in this experiment is expected to represent the relationship between the cursor movement and the mouse movement, i.e., the input-output property of the novel mouse.

4. Multiple Internal Models Corresponding to Different Input-Output Properties

To confirm that the above internal-model-related activity reflects input-output properties of the novel mouse, we examined cerebellar activity after sufficient learning of the other type of mouse that has different input-output properties [14]. The activity pattern in the lateral cerebellum is expected to change according to the different properties. In this experiment, subjects intensively learned to manipulate two novel mice. One is the rotated mouse, which was used in the previous experiment, and the other was a velocity mouse whose cursor velocity was proportional to the mouse position (Fig. 5). The velocity mouse has remarkably different input-output properties from the rotated mouse, but the difficulty in manipulation is almost the same as that of the rotated mouse. Thus, we can compare brain activity related to the rotated mouse to that related to the velocity mouse under relatively equivalent conditions. There were two types of sessions when brain activity was scanned. In a rotated session, the subjects manipulated the rotated mouse during the test periods and the normal mouse during the baseline periods. In a velocity session, the subjects manipulated the

velocity mouse during the test periods and the normal mouse during the baseline periods. By increasing the target velocity during the baseline periods, the errors during the baseline periods were matched to those during the test periods according to the methods explained in the previous section (error-equalized experiment).

We subtracted activity during the baseline period from that during test periods for each session and obtained two activation maps, each of which is related to manipulation of the rotated mouse or the velocity mouse. Figure 6 shows three-dimensional displays of the maps. The yellow and blue regions indicate activity for the rotated mouse and the velocity mouse, respectively. Similar regions in the lateral cerebellum were activated, but the rotated mouse activations tend to be located more anteriorly and laterally than the velocity mouse activations. To investigate overlap between the two types of activity, the activated volume was measured in each subject's activity map and then averaged. The overlapping region is only 2.1% of the total activated volume by using a moderate threshold ($P < 0.05$ corrected for multiple comparisons; $t > 4.1$) and 6.3% even at a considerably lower threshold ($P < 0.001$ uncorrected; $t > 3.1$). The sizes of the yellow (57.5%) and blue (40.4%) regions are comparable at the moderate threshold. The different tools evoked activities in distinct locations with small overlap, demonstrating the modularity and multiplicity of internal models for tools. In our recent study [15], we confirmed the modularity in the cerebellum for more common tools than a computer mouse (e.g., a hammer, scissors, chopsticks, a knife, and so on). In another study [16], we found brain activity in prefrontal regions, suggesting that the CNS attempts to cope with a new tool by blending outputs from internal models previously acquired.

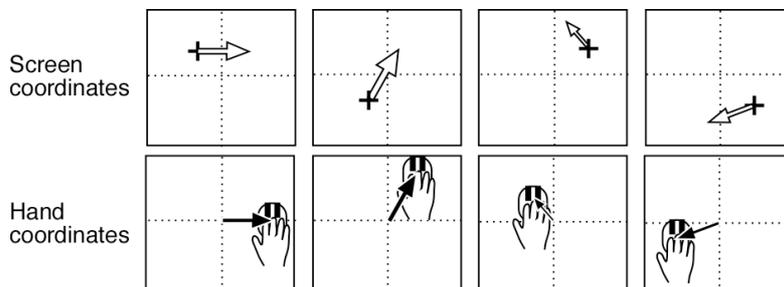


Fig. 5 Relationship between a cursor and a velocity mouse. The cursor's (black cross) velocity (white arrow) was proportional to the mouse displacement from the center position (black arrow).

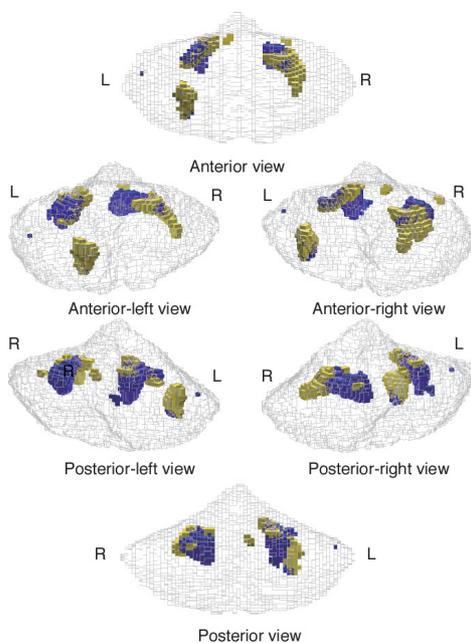


Fig. 6 Cerebellar regions related to manipulation of the novel mice shown in various views. Yellow and blue colors indicate regions where activation was more highly and positively correlated with manipulation of a rotated or velocity mouse, respectively, than manipulation of a normal mouse. L: left, R: right.

5. Switching of Multiple Internal Models

The above study suggests that there exist multiple internal models in the cerebellum. Because we use many tools in daily life, there must exist a switching mechanism that can select and activate the internal model, depending on the tool being used and the situation. In the following experiment, we investigated the switching mechanism [17]. Subjects sufficiently learned to use the three types of mice (normal, rotation and velocity mice), and the brain activity was scanned during a tracking task using a mouse. The mouse type was changed at random timing during the task, and we found brain regions whose activity transiently increased immediately after switching the mouse type (Fig. 7A).

Our close examination of activation time courses revealed that there exist two types of temporal profiles in ac-

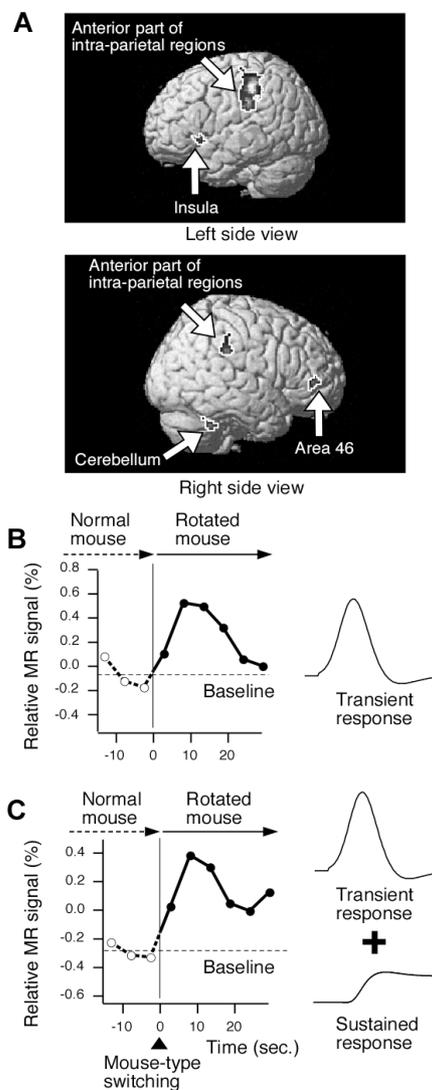


Fig. 7 A: Brain regions whose activity increased immediately after switching mouse-type. B: Activation time course in area 46. C: Activation time course in the cerebellum.

tivity change depending on the brain region. One type of profile transiently increased immediately after the switch, but the levels of sustained background activity 20 sec after switching were almost the same as those before switching, suggesting that the dominant component of this profile is

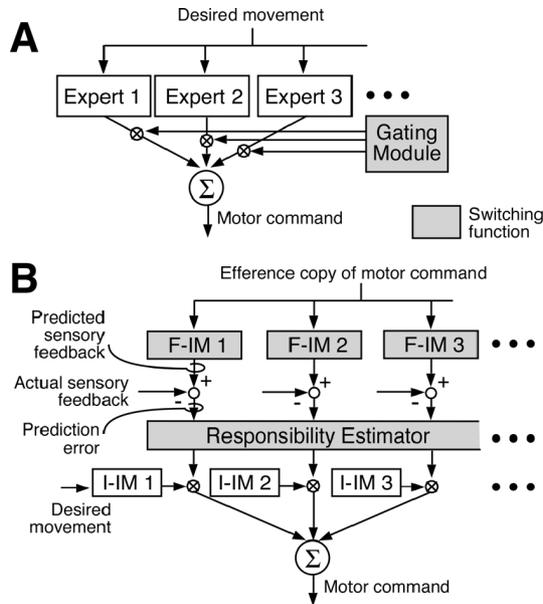


Fig. 8 Two representative computational models for switching internal models. A: mixture-of-experts model in which a gating module estimates the current context and decides the contribution of each expert (internal model) independently of the activity of the experts. Switching functions (hatched parts) are concentrated in the gating module. B: MOSAIC model in which a forward internal model (F-IM) and an inverse internal model (I-IM) are tightly coupled. The responsibility estimator decides the contribution of inverse internal models according to the goodness of prediction made by the forward internal model. Thus, internal models (forward internal models) contribute to switching functions.

transient response (Fig. 7B). This transient response is related to the switching of internal models corresponding to the change of mouse type. This type of profile was found in Brodmann area 46 and the insula. In the other profile, we could observe not only a transient increase of activity but also a change in the sustained activity level. In Fig. 7C, the level of activation was low before the switch when the subjects used the normal mouse (open circles). It transiently increased immediately after switching and then remained high as long as the subjects used the rotated mouse (filled circles). Thus, this type of profile consisted of both transient activity and sustained activity. The sustained activity can be considered activity related to internal models. This type of profile was mainly observed in the cerebellum and the anterior part of the intra-parietal regions. In the following, we discuss the computational meaning of the two types of profiles.

Two representative computational models have been proposed for task switching. One is a mixture-of-experts model for centralized switching [18], [19] (Fig. 8A). The other is the MOSAIC model for parallel-distributed switching [20], [21] (Fig. 8B). In the mixture-of-experts architecture, expert modules are specialized in the subparts of input data. Furthermore, switching is commanded by a single executive architecture called a gating module. In the case of tool use, each expert module is specialized in the use of each tool, and the gating module decides which module is appropriate for the current situation. Thus, the switching

function is centralized in the gating module. In the MOSAIC model, internal models themselves largely contribute to selection and switching. Multiple pairs of an inverse internal model and a forward internal model are tightly coupled as functional units. The forward internal model predicts the sensory feedback from an efference copy of motor commands. The prediction of each forward model is then compared with actual sensory feedback. The inverse model is paired with the forward model, with a small prediction of error, that is considered an appropriate model for the current context. Furthermore, the degree of the inverse internal model's output to the total output is increased. Therefore, the mixture-of-experts model predicts that an activity related to switching is segregated from an activity related to internal models. In contrast, the MOSAIC model predicts that the switching activity spatially and temporally overlaps with the internal-model activity. This is because a prediction by forward internal models is essential for selecting appropriate models.

The temporal profile of activity in area 46 and the insula mainly consists of the transient response related to switching (Fig. 7B), whereas the profile in the intra-parietal regions and the cerebellum consists of both transient activity (switching) and sustained activity (internal models). Therefore, switching mechanisms modeled by the mixture-of-experts model are implemented in area 46 and the insula, whereas mechanisms modeled by the MOSAIC model are implemented in the parietal regions and the cerebellum. Our recent behavioral study [22] suggested that there exist two separate switching mechanisms: a predictive switching mechanism based on prior contextual information and a postdictive switching mechanism based on the difference between actual and predicted sensorimotor feedbacks. We suppose that the predictive switching mechanism is located in prefrontal regions (area 46 and insula) while the postdictive mechanism is located in a network between the parietal regions and the cerebellum.

6. Implications for Communication between Brain and Machines

The above studies demonstrate that the human cerebellum acquires internal models reflecting input-output properties of controlled objects such as tools. Functions of the cerebellar internal models can be considered effective translators or modulators of continuous signals. We speculate that the following changes of information flow occurred in the brain during learning of the rotated mouse. At the early stage of the learning, various regions in the cerebral cortex were involved in the generation of motor commands for control of the mouse (dashed arrows in Fig. 9A). Information processing in these regions is thought to be inefficient and inaccurate because the subjects could not manipulate the mouse appropriately at the early stage. However, after intensive learning, particular regions in the cerebellum learn input-output properties of the mouse, and these come to be substituted for significant parts of the processing in the cerebral

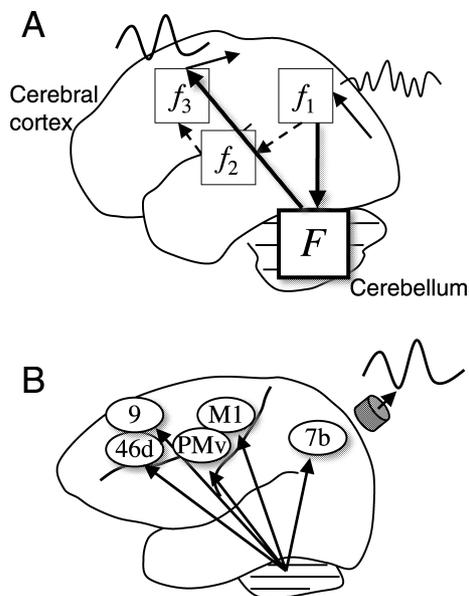


Fig. 9 A: Information flow in the human brain assumed at early stage (broken arrows) and late stage (thick arrow) of learning how to use the rotated mouse. F or f indicates information processing in each brain region. B: Projections from the cerebellum to cerebral cortex in monkey brain. 9: Brodmann area 9, 46d: dorsal part of area 46, M1: primary motor cortex, PMv: ventral part of premotor cortex, 7b: a part of posterior parietal regions.

regions as learning progresses (thick arrows). The processing in the cerebellum is thought to be efficient and automatic [23].

Due to technical limitations, many brain-machine interfaces, especially non-invasive ones, require humans to acquire skills to generate specific brain activity that can be easily read-out by the interfaces. Furthermore, most of these interfaces are designed to extract signals from the brain and to utilize them to control a computer cursor or a robot arm. As our series of studies suggested, the cerebellum is one of the most suitable neural mechanisms to acquire information processing necessary for the control of objects, including a cursor and tools in various environments. Therefore, signals extracted from the cerebellum are expected to be the most suitable control signals in comparison to those from the other brain regions. However, it is difficult to measure activity in the cerebellum using portable and handy non-invasive methods such as near infrared spectroscopy (NIRS) or electroencephalography (EEG) because the cerebellum exists behind the neck muscles.

An effective method for measuring control signals from the cerebellum using NIRS or EEG may be to record activity in cerebral regions that receive projections from the cerebellum. It is known that the cerebellum has strong projections to the primary motor cortex (for example [24] and [25]). In recent studies, transneuronal virus tracing techniques demonstrated that the output of the cerebellum of primates projects not only to the primary motor cortex but also to “non-motor” cerebral regions in the prefrontal (e.g., area 46, [26]) and posterior parietal cortex (e.g., area 7b, [27])

(Fig. 9B).

It is important from where control signals for brain-machine interfaces are extracted in the brain when users have no experience in manipulation of an interface. If the signals are extracted from brain regions where activity can be modulated after training, users can adapt to a new interface even if they have no experience in manipulation. However, if the signals are extracted regions where users cannot modulate activity, it is difficult to adapt to a new interface. Activity in cerebral regions that receive output signals from the cerebellum can be modulated based on intensive training. Therefore, by extracting control signals from the above cerebral regions, we can expect to utilize the learning abilities of cerebellar internal models and to help users adapt to an interface.

7. Conclusion

A series of our studies indicate that 1) internal models in the cerebellum represent input-output properties of the tools as modulators of continuous signals, 2) multiple internal models each of which represent different input-output property are acquired in the cerebellum and 3) cerebro-cerebellar communication loops contribute to selection and switching of internal models. These results suggest that the cerebellum has abilities in adaptive modulation of control signals for manipulation of objects including our own body. These abilities can be used to enhance the control signals for brain-machine interfaces.

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