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**Prediction of sensorimotor feedback from efference copy of motor
commands: A review of behavioral and functional neuroimaging studies**

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Hirorshi IMAMIZU

*National Institute of Information and Communications Technology (NICT) and
Advanced Telecommunications Research (ATR) Institute International*

15

Address for correspondence:

20

Hiroshi Imamizu

Biological ICT Group

National Institute of Information and Communications Technology

2-2-2 Hikaridai, Seika-cyo, Soraku-gun, Kyoto 619-0288

Tel: +81 774 95 1220

25

Fax: +81 774 95 1236

e-mail: imamizu@gmail.com

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Abstract

5 Humans can rapidly and smoothly control their own bodies and external objects such as tools. Because sensorimotor feedback of movements is inevitably delayed by many factors, including delay for transmission of motor commands from the brain to muscles and time for processing of sensory information, many studies have suggested the existence of mechanisms in the brain that can predict the precise motor commands
10 necessary for realizing intended motions and sensorimotor feedback from the motor commands before movement. This article focuses on mechanisms for prediction of feedback and summarizes how the predicted feedback can contribute to rapid, efficient and flexible control of movements and processing of sensory information. Possible neural correlates for the prediction mechanisms and their contribution to higher-order
15 cognitive functions are discussed.

Key words: movement control, sensorimotor feedback, forward model, functional neuroimaging

20 **Running head:** Prediction of sensorimotor feedback

Introduction

Skilled manipulation of objects, including our own bodies, relies on the brain learning to control the object and predict the consequences of this control. The ability to learn the relationships between actions and the resultant changes in states of external objects is particularly important for rapid and smooth control of movements. It has been suggested that such abilities are largely dependent on neural mechanisms that can model or simulate the relationships between an action and its consequences before the action's execution. Neural mechanisms that can mimic the input-output properties of controlled objects are called internal models (Kawato, 1999; Kawato, Furukawa, & Suzuki, 1987; Wolpert, Ghahramani, & Jordan, 1995).

The central nervous system (CNS) is thought to use two forms of internal models: an inverse internal model and a forward internal model. In the context of arm reaching movements (Fig. 1a), forward models transform efference copies of motor commands into the resultant trajectory or sensorimotor feedback (Kawato, et al., 1987; Miall, Weir, Wolpert, & Stein, 1993; Wolpert, et al., 1995). Here, an efference copy is an internal copy created with a motor command and sent to other brain regions. Inverse models transform an intended motion of the arm into the motor commands used to realize the motion (Kawato, et al., 1987). Inverse and forward models can also contribute to predictive control of external objects such as tools. **For example, skilled manipulation of a computer mouse requires the ability to predict how the cursor will move on the screen if the mouse is moved in a particular direction (forward model: Fig. 1b) and how the**

mouse should be moved in order to move the cursor to a particular position on the screen (inverse model).

In this article, I will focus on forward models for prediction of feedback and review behavioral and functional imaging studies that clarify the contribution of forward models to human behaviors. These studies demonstrate how predicted sensorimotor feedback helps flexible, rapid and precise control of movements as well as processing of sensory information.

Grip force - load force coupling using forward models

When an object is held with the tips of the thumb and index finger at the sides, grip force allows the development of frictional force to counteract the load force (Fig. 2a). In a series of studies, Johansson and colleagues (Johansson & Cole, 1992; Johansson & Westling, 1984) have shown that when lifting objects or pulling on fixed loads grip force is adjusted in parallel with changes in load force, in such a way that it is always slightly greater than the minimum required to prevent slip. If grip force is measured during rapid arm movements with hand-held objects, it is modulated in parallel with, or even prior to, fluctuations in the acceleration-dependent inertial load (grip force - load force coupling: Fig. 2b). This finding indicates that the CNS is able to precisely predict the movement-induced load, and it has been suggested that this prediction is based on an internal model of the motor apparatus and external load (Flanagan & Wing, 1997).

This grip force - load force coupling is explained by a framework that contains a forward model of the arm (Kawato, 1999) (Fig. 2c). Take, for example, a point-to-point arm-reaching movement that takes place while the hand is grasping an object. A controller for the arm calculates the motor commands needed to realize the desired motion of the arm. These commands are sent to the arm muscles as well as to the forward dynamics model as the efference copy. Then, the forward model can predict an arm trajectory that is slightly in the future. Given the predicted arm trajectory, the load force is calculated; then, by multiplying a friction coefficient and a safety factor, the necessary minimum level of grip force can be calculated in a grip force controller. To realize this grip force modulation, motor commands are sent to hand muscles.

This framework has already been supported by theoretical and empirical studies as follows. Many studies have indicated that forward models can be acquired more quickly than the appropriate controllers (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008; Flanagan & Wing, 1997). Because grip force modulation utilizes output signals from the forward model, this framework predicts that the learning rate of the grip force - load force coupling is quicker than that of arm control. This prediction has been supported by behavioral studies (Flanagan & Wing, 1997; Ugata, Kuroda, Imamizu, Yoshioka, Wada, & Kawato, 2003), indicating quicker learning of grip force - load force coupling than that of the appropriate control of arm movement in a novel environment. These studies suggest that forward models are used in grip force - load force coupling.

Based on the above framework, we have explored the possible sites of forward models through an experiment using a functional magnetic resonance imaging (fMRI) (Kawato, Kuroda, Imamizu, Nakano, Miyauchi, & Yoshioka, 2003). In this experiment, subjects held an object in a precision grip and made cyclic up-and-down movements of their right arm according to sounds generated by a computer (Fig. 3a; test condition).

Brain activity during the test condition is expected to include not only activity related to grip force - load force coupling but also activity related to arm movement and activity related to modulation of grip force. Theoretically, if we remove the last two types of activity from activity in the test condition, we can extract the brain activity exclusively related to grip force - load force coupling or to the coordination of arm movement and grip force modulation. Therefore, we added two baseline conditions to the experiment.

One was an "arm-movement" condition (Fig. 3c) where subjects moved their arms in the same fashion as the test periods but the object was attached at the tips of the fingers by tape. In this condition, the arm movement was the same as that in the test condition but the grip force - load force coupling was not needed because the object would never slip from the subjects' hands. **By measuring the grip force during the experiment, we**

confirmed that a change in the grip force in the arm-movement condition (thick curve in Fig. 3d) was very small compared to that in the test condition (Fig. 3b). The other was a

"grip-force-modulation" condition (Fig. 3e) where subjects held the object in the same grip as in the other conditions and periodically changed the grip force without arm movements. Corresponding to the above framework, the test condition activates all components, **the arm-movement condition mainly activates the arm controller**, and the

grip-force-modulation condition activates the grip force controller. Therefore, subtraction of activity in the latter two conditions from activity in the test condition would extract activity related to the forward model from the other activity.

Brain activity related to the arm-movement condition was mainly found in the large portion of the sensorimotor region (Fig. 4a), while activity related to the grip-force-modulation condition was found in a smaller portion in nearly the same region (Fig. 4b). These results are consistent with the notion that the sensorimotor region contributes to control of arms and fingers. Importantly, when activities in the two baseline conditions were subtracted from the activity in the test condition, we could find the residual activity only in the cerebellum (Fig. 4c). This means that parts of the cerebellum acquire forward internal models and contribute to the grip force - load force coupling. This activity was found in the contra-lateral (left) part to the moving hand and arm (right), although it is known that the hand and arm movements on one side activate the ipsi-lateral parts of the cerebellum (e.g., Grodd, Hulsmann, Lotze, Wildgruber, & Erb, 2001). However, activity in the left or bi-lateral cerebellum is often reported when subjects manipulate an external object using the right hand (e.g., Imamizu, Miyauchi, Tamada, Sasaki, Takino, Putz, Yoshioka, & Kawato, 2000; Schmitz, Jenmalm, Ehrsson, & Forssberg, 2005; Tamada, Miyauchi, Imamizu, Yoshioka, & Kawato, 1999). This suggests that the activity found in the above experiment reflects forward models for not only arm movement but also object manipulation.

Coordination between effectors based on prediction of forward models

The above studies show that a forward model contributes to coordination between movements of different effectors, i.e., the arm and fingers, to accomplish grip force - load force coupling. There are several studies indicating that forward models play
5 important roles in coordination between effectors in the other context.

Miall and colleagues investigated brain activity related to eye-hand coordination using a tracking task (Miall, Reckess, & Imamizu, 2001). In their experiment, subjects followed a moving target with their eyes while simultaneously moving a joystick to control the cursor. The temporal offset between targets for eye and hand motions caused
10 parametric variation in the degree of eye-hand coordination (Δt in Fig. 5). The behavioral data indicated that manual tracking performance was optimal when the target for eye motion was anticipated before the target for hand motion by 38 ms.

Synchronous movements of two effectors with such a small offset cannot be achieved simply by reaction to proprioceptive or visual feedbacks. This suggests that a forward
15 model predicts the movement outcome based on motor commands for the eye muscles and that the predicted outcome is sent to the hand-control system for programming or modifying the manual movement. They conducted fMRI experiments and found that activity in the lateral cerebellum and the oculomotor vermis (medial part of the cerebellum) parametrically increased as performance of the eye-hand coordination
20 improved. This result suggests a contribution of the cerebellum to eye - hand coordination by predicting the movement outcome.

Another fMRI study investigated mechanisms for coordination between a finger (thumb) and arm movements (Diedrichsen, Criscimagna-Hemminger, & Shadmehr, 2007) in a different context from grip force - load force coupling. Using thumbs, subjects pressed a button attached to the handle of a device that they grasped during arm reaching movements. Subjects were trained to press the button depending on the state of the arm movements without relying on sensorimotor feedback. Theoretically, it was necessary for the CNS to predict the future state of the arm from motor commands to accomplish this task. Brain activity during the state-dependent motor control was compared to activity in a baseline condition where the subject pressed the button at a particular timing independent of the arm state (timing control). Activity related to the state-dependent control was found in the arm regions of the anterior cerebellum, suggesting that a forward model of the arm is acquired in the CNS and predicts the future state of the arm.

Cancellation of sensory inputs using prediction of sensory feedback

It has been suggested that another important function of a forward model is to predict sensory inputs caused by our own movements to cancel the inputs. A behavioral study was conducted to investigate why we cannot tickle ourselves (Blakemore, Wolpert, & Frith, 2000). They examined two hypotheses on the reasons for this. One is that there is a general gating of all incoming sensory stimulation when we tickle ourselves. The other is that the CNS precisely predicts, probably using forward models, the sensory

consequences of motor commands for tickling behavior and then cancels these sensory inputs using the predicted sensory consequences.

In their experiments, they asked subjects to rate the sensation of a tactile stimulus on the palm of the hand and then examined the perceptual effects of altering the correspondence between self-generated movement and its sensory (tactile) consequences. The alteration was achieved by a mechanical device, which was designed to introduce parametrically varied degrees of delay or angular discrepancy between the subject's movement and the resultant tactile stimulation. If the CNS simply shuts down sensory input, then the tickled sensation would remain at the same level under all delays and angular discrepancies, since movement occurs regardless of delays and discrepancies. By contrast, if the CNS utilizes an accurate prediction of the sensation to cancel sensory inputs, the tickled sensation increases as the delay or angular discrepancy increases because the difference between the predicted and actual sensory inputs would increase. Results of their experiments showed that subjects rated the sensation increasingly tickly as the delay or discrepancy increased, thus supporting the hypothesis that the CNS precisely predicts the sensory consequences of motor commands for tickling behavior.

Furthermore, these researchers conducted functional neuroimaging studies using positron emission tomography and fMRI to investigate corresponding neural mechanisms (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 1998). They subtracted brain activity in a condition where subjects tickled themselves from

activity in the other condition, where subjects were tickled by another person. They found residual activity mainly in the secondary somatosensory cortex (SII) and the cerebellum. Because the SII receives sensory inputs, activity in the SII probably reflects tickled sensation itself. Furthermore, they also found a negative correlation between activity in the SII and activity in the cerebellum, suggesting that the more the cerebellum was activated the less the SII was activated. This can be interpreted as the output signals from the cerebellum being used to cancel input signals to the SII.

Switching of internal models based on prediction of sensorimotor feedback

Humans interact with myriad objects and environments that often change in a discrete manner. If the CNS maintains only a small number of global internal models, relearning is needed whenever objects and environments change. However, if the CNS maintains a large number of internal models or modules for different objects and environments, less relearning is needed, and thus learning interference is avoided. Moreover, initial learning of objects and environments may be facilitated by a combination of stored modules. Many lines of behavioral studies have shown the multiplicity and modularity of internal models: dual adaptation to prismatic displacements of visual feedback in opposite directions (Welch, Bridgeman, Anand, & Browman, 1993), independent learning of internal models for kinematic and dynamic control of reaching (Krakauer, Ghilardi, & Ghez, 1999), and composition of output signals from stored modules (Flanagan, Nakano, Imamizu, Osu, Yoshioka, & Kawato, 1999; Ghahramani & Wolpert,

1997). Our previous imaging studies first found cerebellar activity related to an internal model of a novel tool (Imamizu, et al., 2000) and, second, indicated the modularity of internal models by showing activation in different sets of cerebellar regions, reflecting different input-output properties of tools (Imamizu, Kuroda, Miyauchi, Yoshioka, & Kawato, 2003).

If multiple internal models exist in the CNS, a question arises about how models are selected or switched appropriately from the current context, i.e., how the CNS solves the problem of modular selection. Behavioral studies have reported that humans can flexibly switch internal models based on contextual information. For example, an auditory-tone cue can induce context-dependent adaptation to prismatic displacement (Kravitz & Yaffe, 1972). Cognitive contextual cues can help simultaneous learning and switching of internal models for different dynamic environments (Osu, Hirai, Yoshioka, & Kawato, 2004; Wada, Kawabata, Kotosaka, Yamamoto, Kitazawa, & Kawato, 2003; Yamamoto, Kawato, Kotosaka, & Kitazawa, 2007). However, little is known about neural mechanisms for internal-model switching.

Empirically, two types of information are crucial for the switching of internal models: contextual information, such as color or shape of the objects that can be perceived before movement execution, and information on the difference between actual and predicted sensorimotor feedbacks calculated during or after execution. For example, when we lift a transparent bottle, the CNS can switch between internal models for light and heavy objects in a predictive fashion, since we know whether the bottle is

empty or full beforehand (upper panel of Fig. 6a). However, when lifting up a paper milk carton (upper panel of Fig. 6b), we cannot estimate the weight, and the CNS relies on the error between actual and predicted sensorimotor feedbacks (prediction error) as shown in the diagram in Fig. 6c. In the latter case, switching during or after the

5 movement is needed. We call this a "postdictive" switch in contrast to the predictive switch. The above example illustrates switching during control of forces (dynamics), but we often encounter similar situations during kinematic control in which forces do not play an important role. That is, for example, when you want to reduce or increase the brightness of a room light by adjusting a slide volume control (lower panel of Fig.

10 6a), you can decide the direction and amount of movement of the controller in a predictive fashion if you often use the same controller (e.g., if the room is yours) or if a label illustrating the relationship between brightness and lever position is attached to the controller. However, we generally have to rely on the difference (error) between predicted sensory feedback (expected brightness of the light) and actual feedback, i.e.,

15 we typically use a controller for the first time without the benefit of such a label (lower panel of Fig. 6b). As we have already mentioned, forward models play crucial roles in prediction of sensorimotor feedback and thus contribute to the postdictive switch of internal models based on prediction error.

We conducted a behavioral experiment to investigate whether the predictive

20 mechanism is functionally independent from the postdictive mechanism (Imamizu, Sugimoto, Osu, Tsutsui, Sugiyama, Wada, & Kawato, 2007). Subjects learned to move

their index fingers to targets while visual feedback of the finger movements was rotated clockwise (CW) or counterclockwise (CCW) by 40° around the initial position (i.e., kinematic alteration of the relationship between the finger movement and the cursor movements). When subjects adapted to alternating blocks of opposing rotations, we investigated the effects on the subjects' performances due to contextual information (a verbal instruction) on the forthcoming direction of rotation. We measured the effect of such contextual information on the predictive mechanism by measuring the performance error at the beginning of each block and that on the postdictive mechanism by measuring the speed of gradual decrease of the error within blocks. Consequently, the contextual information selectively improved predictive switching performance but did not affect postdictive switching performance based on prediction errors, suggesting the existence of functionally independent mechanisms.

Based on the results of our behavioral study, we planned an fMRI experiment to examine whether these two mechanisms are based on separate neural substrates. In the fMRI experiment, discrete pointing movements and event-related fMRI were used to separate activity related to the presentation of the cognitive cue from that related to sensorimotor feedback (Imamizu & Kawato, 2008). The task for subjects followed that in our behavioral study, and subjects sufficiently learned the 40° CW and 40° CCW visuomotor rotations before scanning of brain activity. During the fMRI experiment, the direction of rotation changed in a block-random fashion. A cue was presented at the beginning of each trial and before movement initiation. The color of the cue

corresponded to the direction of rotation of the feedback in an instructed condition, and thus predictive switching was possible. However, the color did not correspond to the direction in the non-instructed condition, and thus subjects relied on prediction errors calculated from sensorimotor feedback for switching in a non-instructed condition.

5 Switching-related activity was identified as activity that transiently increased after the direction of rotation was changed. The switching-related activity in cue periods in the instructed condition, when a predictive switch is possible, was observed in the superior parietal lobule (SPL) (Fig. 6d). However, the switching-related activity in feedback periods in the non-instructed condition, when prediction error is crucial for the
10 postdictive switch, was observed in the inferior parietal lobule (IPL) and prefrontal cortex (PFC) (Fig. 6e). These results clearly demonstrate regional differences in neural substrates between the predictive and postdictive mechanisms.

Our results are consistent with previous studies indicating that the SPL is involved in modulation of behaviors based on visual information as follows. For example, fMRI
15 studies of the SPL identified activity related to discrimination of visual surface orientation (Shikata, Hamzei, Glauche, Knab, Dettmers, Weiller, & Buchel, 2001) and control of steering according to visual future path information (Field, Wilkie, & Wann, 2007). Many studies indicated a contribution of the SPL to planning of action based on visual information (Culham, Cavina-Pratesi, & Singhal, 2006; Medendorp, Goltz,
20 Crawford, & Vilis, 2005). Kimberg et al. (Kimberg, Aguirre, & D'Esposito, 2000) investigated activity when subjects switched between different stimulus-response

mappings during a task in which subjects pressed a key according to a letter presented on a screen, and they reported that the SPL is related to switching based on contextual information. Our study suggests that the SPL associates contextual information with the degree of contribution of each individual internal model.

5 In contrast to the SPL, our study suggested that the IPL contributes to the postdictive switch by integrating sensorimotor feedbacks obtained by vision and proprioception and then comparing this with predictions by forward models to calculate prediction error. Many studies have suggested the IPL contributes to integration of multisensory information. It is known that the lateral bank of the intraparietal sulcus in
10 the IPL is related to control of grasping movements guided by vision (Castiello, 2005). Grefkes et al. (Grefkes, Weiss, Zilles, & Fink, 2002) reported the contribution of the IPL to cross-modal integration between visual and somatosensory information. Furthermore, a study on anatomical pathways in the monkey brain indicated that a region in the IPL (area 7b in monkeys) is the target of output from the cerebellum
15 (Clower, West, Lynch, & Strick, 2001). This suggests that prediction of sensorimotor feedback made by cerebellar forward models is sent to the IPL and compared with the actual sensory feedback and that the results of the comparison (prediction error) contribute to switching of internal models.

20 Discussion

In this article, I reviewed behavioral and imaging studies related to neural mechanisms

for prediction of sensorimotor feedback from the efference copy of motor commands.

These mechanisms are called (internal) forward models. Actual sensorimotor feedbacks

that can be obtained during or after movement **are** inevitably delayed by many factors:

transmission of motor commands from the brain to muscles, mechanical delay of

5 muscles and external objects, and processing of visual and proprioceptive feedback

information. Therefore, internal prediction of sensorimotor feedback without relying on

an external feedback loop is useful for rapid, efficient, flexible, and precise control of

our own bodies and objects. Studies reviewed in this article have shown examples of

such control: a grip force - load force coupling, coordination of effectors, cancelation of

10 sensory inputs caused by one's own movement, and switching of sensorimotor tasks.

So far, I have mainly reviewed functional neuroimaging studies indicating that

forward models are acquired in the cerebellum. In the following, I refer to studies that

directly measured electrophysiological activity of neurons. These studies found neural

activity reflecting forward models not only in the cerebellum but also in the other

15 cortical regions. Miall and colleagues proposed that simple spike activity of Purkinje

cells (neurons in the cerebellar cortex) represent prediction of sensory feedback and is

corrected by complex spike activity representing a discrepancy between the prediction

and actual feedback (Miall, et al., 1993). They found, as supporting evidence, that the

interval between an increase in simple spike activity and the resulting complex spike

20 activity is about 150 ms, which is equivalent to visuomotor feedback delay and

necessary for synchronizing the prediction and feedback (Miall, Keating, Malkmus, &

Thach, 1998). Recently, it has been suggested that simple spike discharge of Purkinje cells has several characteristics of a forward internal model of the arm (Ebner & Pasalar, 2008).

Another stream of studies has suggested that neural activity in parietal or frontal regions reflects forward-model computation or signals related to forward models. A study recorded activity in the posterior parietal cortex when monkeys moved a cursor toward a target by controlling a joystick, and it found neurons encoding a forward estimate of the state of the cursor, that is, the direction of cursor movements caused by joystick movement (Mulliken, Musallam, & Andersen, 2008). Their encoding properties were available from neither sensory feedback nor outgoing motor commands but from sensory signals predicted by a forward model. Studies on neuronal activity during eye-movement tasks have also found data related to forward models. For example, eye movement causes a shift in the visual image on the retina, but a study has shown that the location of receptive fields of neurons in the lateral intra-parietal area shifts before the initiation of the eye-movement based on prediction of a shift of a target on the retinal image (Duhamel, Colby, & Goldberg, 1992). This suggests that parietal neurons use information about intended eye movements and update the representation of visual space. Such update cannot be done without prediction of the movement outcome from an efference copy of motor commands sent to the eye muscles. Another study investigated a pathway that conveys an efference copy of motor commands for saccadic eye movements, and it identified an ascending pathway from the superior

colliculus to the frontal eye field via the mediodorsal thalamus (Sommer & Wurtz, 2002). According to this result, the frontal eye field is a target location of the efference copy and a possible neural correlate of a forward model.

Many studies have indicated that the cerebellum is an important locus of forward-model computation, but parietal and frontal regions have also been suggested as contributing to the computation or having relationships with the input signals to and output signals from forward models. Probably, the locus of forward models is not unique, and several regions contribute to the computation according to different contexts and requirements of tasks. Future studies that can extract neural information simultaneously from multiple regions in the brain will enable us to elucidate the outlines of the brain network used for the forward-model computation as well as the functional differences among the regions.

Although I mainly focused on the contribution of forward models to control of movements, many researchers are now interested in the contribution of forward models to higher-order cognitive functions. By using forward models, the CNS can construct internal simulation loops without relying on external feedback. Hurley proposed a "Shared Circuit Model" in which cognitive functions such as mirror systems, imitation, mental simulation of social interactions, and mind reading (theory of minds) use such internal simulation loops for sensorimotor control and additional systems that inhibit motor outputs and generate virtual sensory inputs during the simulation (Hurley, 2008). More specifically, Oztop and colleagues conducted computer simulations of tasks that

are closely related to mirror systems (Oztop, Kawato, & Arbib, 2006; Oztop, Wolpert, & Kawato, 2005). In their simulations, an observer estimated the goal of reaching movements or the intention of an agent performing grasping movements. The results indicated that, in theory, forward models for sensorimotor control contribute to effective
5 inferring the goals or mental states of others, suggesting that the models contribute to mirror systems and theory of minds. These internal circuits support "mental simulations" of interactions between one's own actions and the resultant changes in the environment, and they can increase accuracy based on recursive computation in sophisticated planning and selection of behaviors necessary for social interactions and
10 achievement of long-term goals. **It is well known that immediate feedback of error is important for motor learning that depends on the cerebellum (Ito, 1984; Kitazawa, Kohno, & Uka, 1995). However, feedback in social interaction is often delayed, and this delay can be on the order of hours or days. Therefore, the internal circuits include not only the cerebellum but also other brain regions, such as prefrontal regions that can**
15 **compensate for these variable and unpredictable delays.**

Because neural mechanisms for such cognitive functions are more complex than those for simple reaching and grasping movements, future theoretical and empirical studies are needed to fully understand how internal simulation loops support higher-order functions. However, the current studies will give us important clues to
20 understanding how human intelligence has emerged from fundamental brain functions, such as control of movements, which are common with other species including

non-human primates.

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Figure Legends

Figure 1

Examples of internal forward models and inverse models. **(a)** Internal models for arm
 5 reaching movement. **(b)** Internal models for an external object and a tool (e.g., a
 computer mouse).

Figure 2

Illustrations of grip force - load force coupling. **(a)** An object held with the tips of the
 10 index finger and thumb. When lifting the object, the normal grip force on the contact
 surface allows for the development of a frictional force, which prevents the object from
 slipping. **The figure illustrates the load force in the deceleration phase of the upward
 movement.** **(b)** Examples of time courses of grip force (solid curve) and load force
 (broken line) when lifting up and down an object. A dash-dotted line indicates a peak
 15 latency of the grip force. **(c)** A framework explaining mechanisms for grip force - load
 force coupling based on inverse and forward models of the arm. Reproduced with
 permission from reference (Kawato, 1999) © Elsevier.

Figure 3

20 **Three conditions in an fMRI experiment investigating brain activity related to grip force
 - load force coupling (a, c and e) and typical change in grip force and load force
 measured during each condition (b, d and f).**

Figure 4

Brain activity related to arm movements **(a)**, grip force modulation **(b)** and coordination between arm movement and grip force modulation **(c)**. White regions enclosed by thick curves indicate activated regions. In panels **a** and **b**, activated regions are indicated on the brain surface. In the top image of panel **c**, activity is rendered on the coronal slice as indicated by the bottom panel.

Figure 5

Examples of target trajectories used in an experiment investigating eye - hand coordination (Miall, et al., 2001). Solid curves indicate target trajectory for hand (joystick) tracking as time courses of the horizontal (x) position **(a)** and the vertical (y) position **(b)**. Dashed curves indicate target trajectory for eye tracking, which is advanced or delayed from the target for the hand tracking by a parameter Δt . **(c)** A target trajectory for the hand tracking is represented in $x - y$ coordinates. Each position is represented in pixel coordinates of a computer screen.

Figure 6

Illustrations of two types **(a)**, **(b)** of switching in sensorimotor tasks. **(a)** Examples of predictive switch. When we lift a transparent bottle, the CNS can switch between internal models for light and heavy objects in a predictive fashion, since we know whether the bottle is empty or full beforehand (an example for control of dynamics:

upper panel). When we control the brightness of a room light, we can decide the direction and amount of movement of the control lever before moving the controller if a label is attached to the controller indicating the relationship between the brightness and position of the lever or, otherwise, if we are familiar with the controller (an example for

5 control of kinematic control: lower panel). **(b)** Examples of postdictive switch. When lifting up a milk carton, we cannot estimate the weight, and the CNS relies on the error between actual and predicted sensorimotor feedbacks. In such a case, switching during or after the movement is needed (upper panel). In the case of light control, we have to

rely on sensory feedback (brightness of the light) if no label is attached to the controller

10 (lower panel). **(c)** A schema for calculation of prediction error of sensorimotor feedback.

Brain activity related to predictive switch **(d)** or postdictive switch **(e)** as found by an fMRI study (Imamizu & Kawato, 2008). Activated regions (white regions enclosed by thick curves) are indicated on the brain surface viewed from the top. SPL: Superior parietal lobe, IPL: Inferior parietal lobe, PFC: prefrontal cortex.

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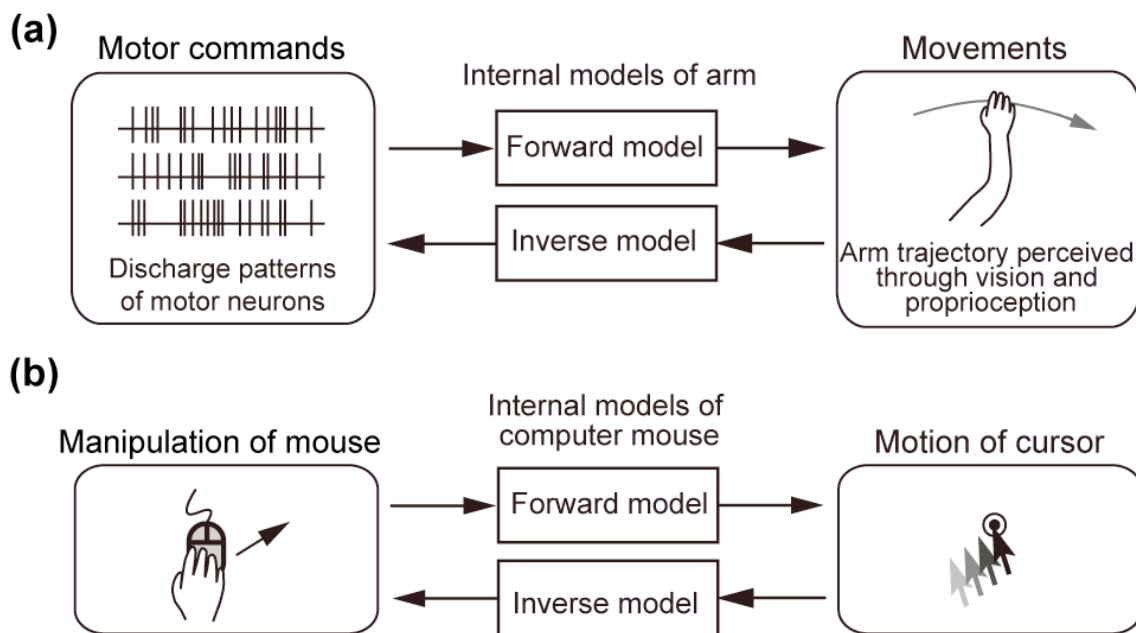


Figure 1

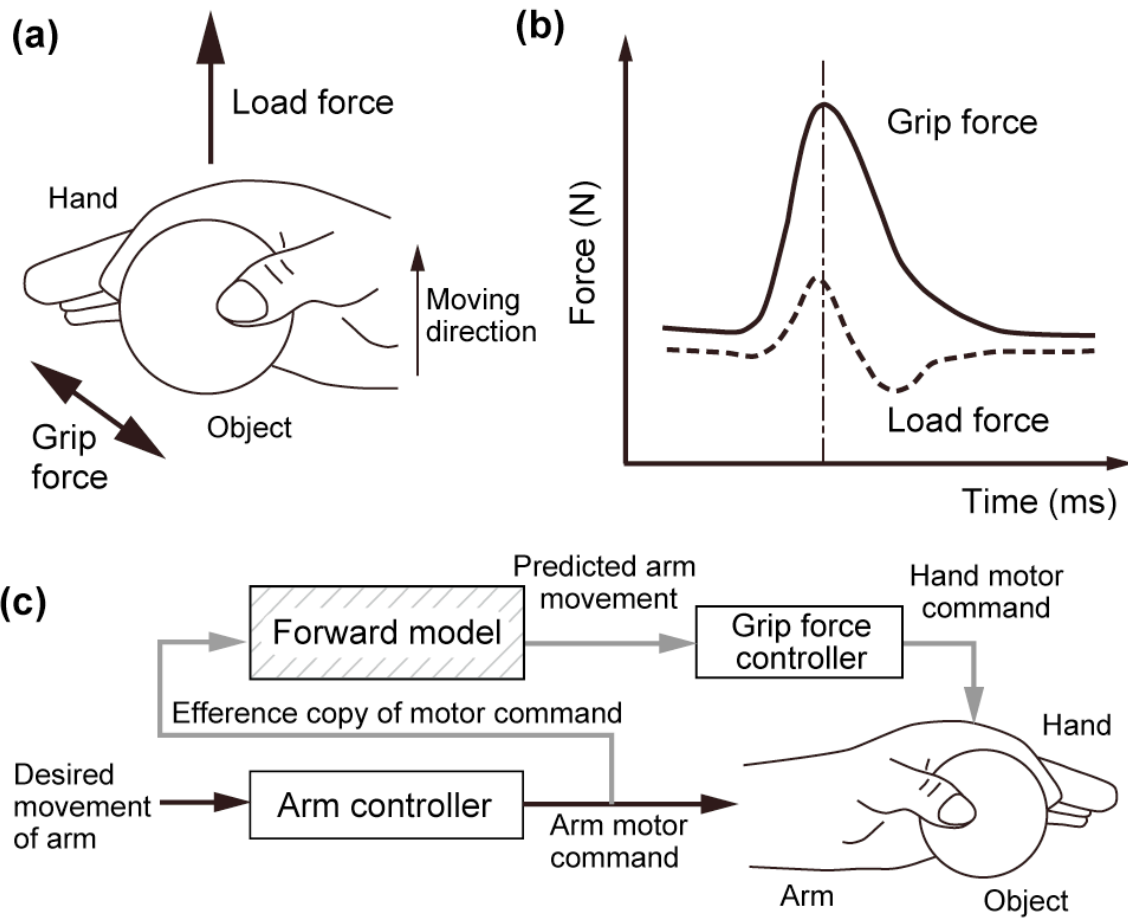


Figure 2

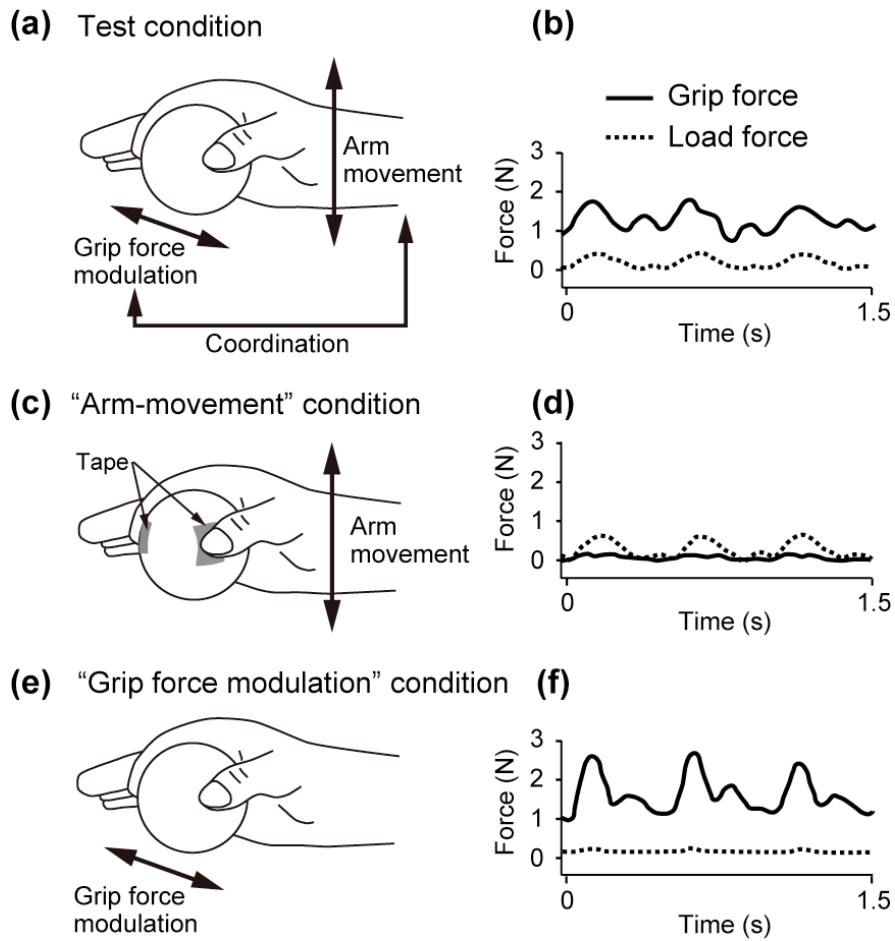
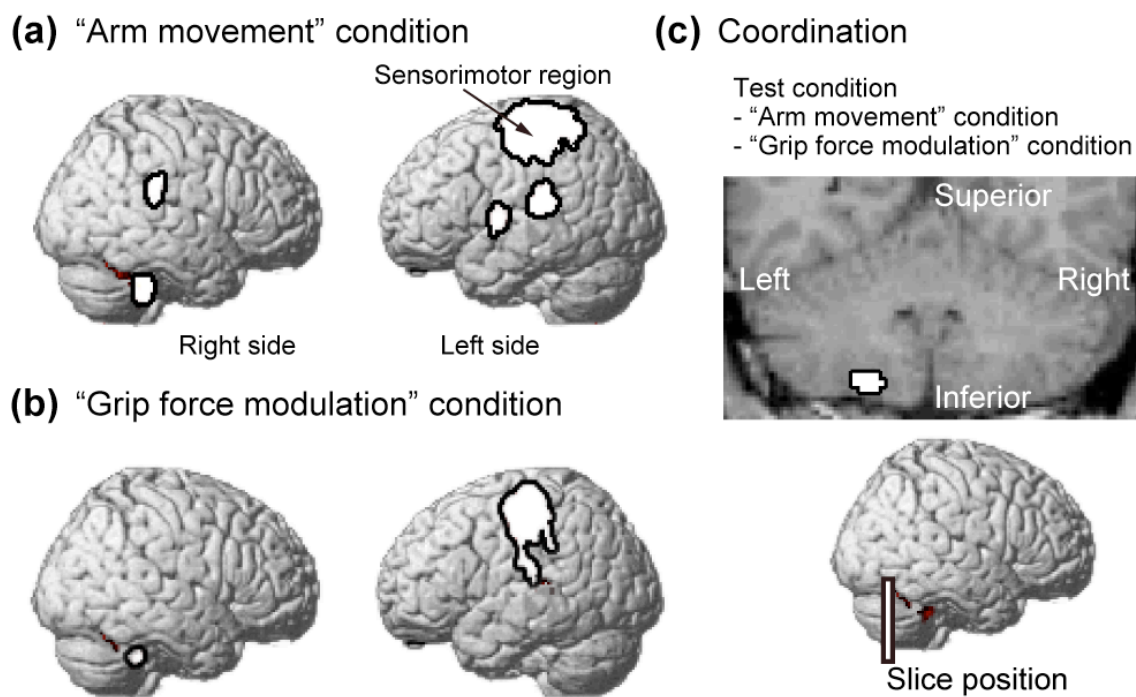
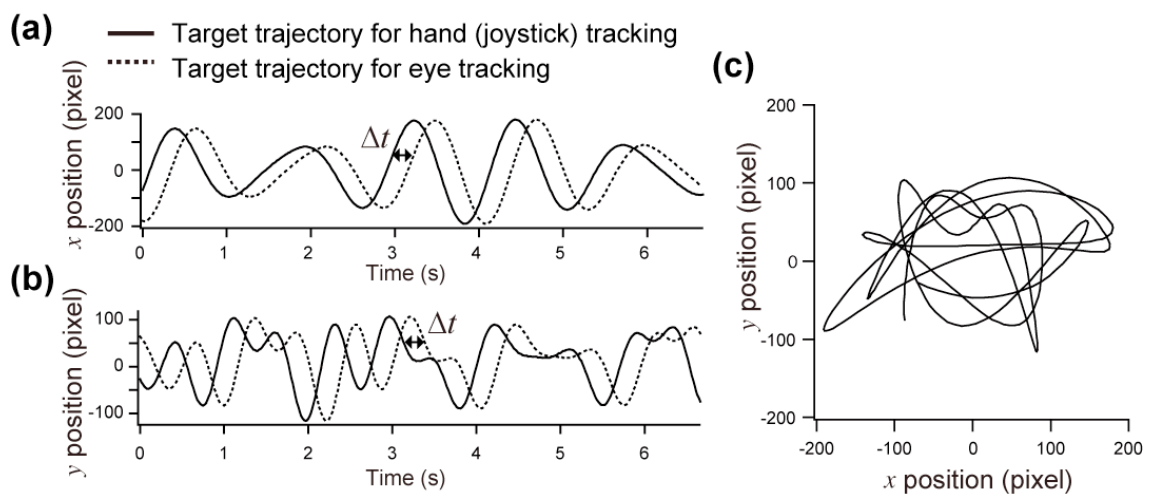


Figure 3



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Figure 4



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Figure 5

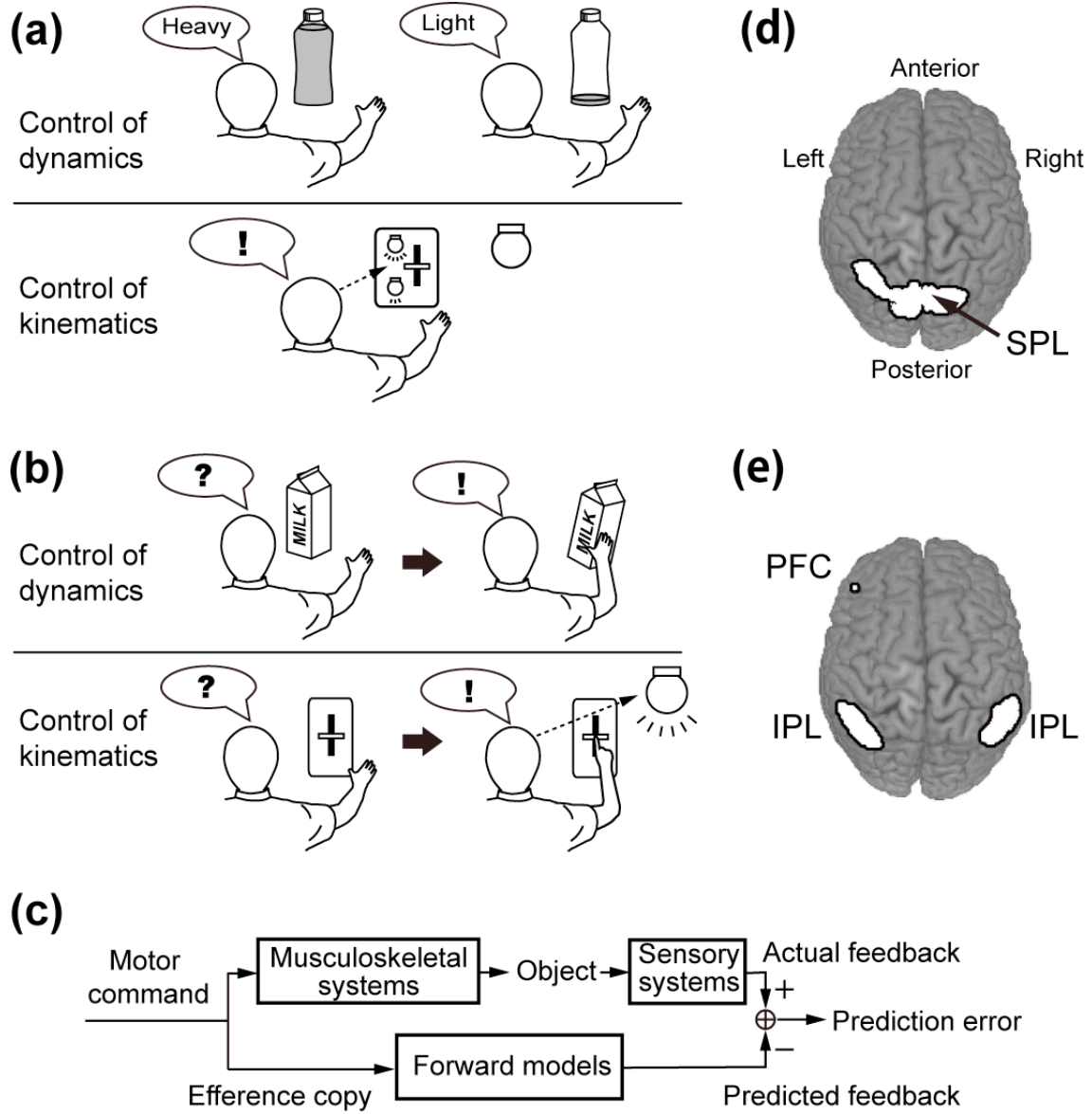


Figure 6