



Review article

The body and objects represented in the ventral stream of the parieto-premotor network

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ABSTRACT

The network between the parietal cortex and premotor cortex has a pivotal role in sensory-motor control. Grasping-related neurons in the anterior intraparietal area (AIP) and the ventral premotor cortex (F5) showed complementary properties each other. The object information for grasping is sent from the parietal cortex to the premotor cortex for sensory-motor transformation, and the backward signal from the premotor cortex to parietal cortex can be considered an efference copy/corollary discharge that is used to predict sensory outcome during motor behavior. Mirror neurons that represent both own action and other's action are involved in this system. This system also very well fits with body schema that reflects online state of the body during motor execution. We speculate that the parieto-premotor network, which includes the mirror neuron system, is key for mapping one's own body and the bodies of others. This means that the neuronal substrates that control one's own action and the mirror neuron system are shared with the "who" system, which is related to the recognition of action contribution, i.e., sense of agency. Representation of own and other's body in the parieto-premotor network is key to link between sensory-motor control and higher-order cognitive functions.

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1. Introduction

The hands have many functional roles during daily activities. Kamakura (1989) categorized eight functional roles of the hands: (1) exploring (i.e., sensing or exploring the environment), (2) contacts (i.e., holding an object or ones own body), (3) acting as a

joint (i.e., working like a joint between the body and an object), (4) tools (i.e., being used as a tools), (5) grasping, (6) manipulating objects or tools, (7) responding (i.e., as an object of action by another hand), and (8) symbolizing (i.e., making a sign). Recently, it has been revealed that the motor control system in the brain not only controls these complex hand actions, but also concerns body representation. The motor control system contributes to perception of the hands as part of the own body. Since the perception of one's own body is the fundamental process of self-recognition (Gallagher, 2005), the hands are not only effectors in movement, but are a link between the mind and motor control.

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As discussed in the next section, connections between the parietal cortex and premotor cortex play a pivotal role in sensory-motor control. The network between the inferior parietal cortex and the ventral premotor cortex (F5), namely the ventro-dorsal stream, plays a role in visually-guided hand actions. The body is represented in the brain according to spatiotemporal dynamic manner (Berlucchi and Aglioti, 1997). The system for body representation is based on visual, somatosensory, and intrinsic motor signals that update the internal representation of one's own body state, and therefore is key for sensory motor control. This is the "who" system described by Jeannerod (2003), which is involved in recognition of action contribution to whether own self or other. In this line of thinking, it is suspected that the ventro-dorsal stream is shared with common neural substrates with the "who" system. Furthermore, in this stream, neurophysiological studies have found mirror neurons that are active during execution of a goal-directed hand action and during observation of the same action performed by another individual (Rizzolatti and Craighero, 2004). Mirror neurons are usually discussed in the principle of shared representation of other's hand action with the own action. We postulate that the mirror neurons contribute to not only shared representation of self and other, but also to the distinction between self and other. As described afterwards, our most recent study supports this hypothesis (Maeda et al., 2015). In this review, we discuss the functional role of the ventro-dorsal stream to the internal representation of the object and the body, and the importance of this link between motor control and cognitive function.

2. Anatomy of the parieto-premotor network

In this section, we would mention about anatomical configuration of parietal-premotor network that is connected with dorsal visual stream. Classically, the parietal association cortex has been thought to be involved in the dorsal visual stream, which contributes to the space perception. However, the parietal cortex is not a terminal station of this stream, and has very strong reciprocal connections with the premotor cortices. This network is key for sensory-motor control. As shown in Fig. 1, there are several parallel pathways between the parietal and premotor cortices that have been revealed in the monkey (Rizzolatti et al., 1998; Galletti et al., 2003), and recent physiological studies have revealed that these parallel pathways have different roles, such as arm reaching and/or hand grasping, along with body mapping (Murata and Ishida, 2007; Rizzolatti et al., 2014).

The dorsal visual pathway is separated into two channels: the dorso-dorsal pathway and the ventro-dorsal pathway (Tanne-Gariepy et al., 2002; Galletti et al., 2003; Rizzolatti and Matelli, 2003). The input to the dorso-dorsal pathway is from area V3/V3A and passes through V6, which is the most caudal dorsal part of the parietal cortex (Galletti et al., 2003). V6 has connections with V6A and the middle intraparietal area (MIP) in the superior parietal lobule. These two areas have strong connections with the dorsal premotor cortex (F2). Neurons in V6A, MIP, and F2 are related to reaching (Battaglia-Mayer et al., 2003) or grasping (Fattori et al., 2004) movements (Fig. 1).

The ventro-dorsal pathway passes through the anterior intraparietal area (AIP), which is located in the anterior part of the lateral bank of the intraparietal sulcus, or the PFG/PF on the lateral convexity of the posterior parietal cortex (Fig. 1). The convexity of the posterior parietal cortex is separated into PF, PFG, and PG (Rizzolatti and Matelli, 2003). According to cytoarchitecture and connections with other areas, classical area 7b involves PF and part of PFG (Pandya and Seltzer, 1982; Gregoriou et al., 2006; Rozzi et al., 2006). AIP and PFG/PF have connections with F5 (Luppino et al., 1999; Lewis and Van Essen, 2000; Rizzolatti and Luppino, 2001;

Tanne-Gariepy et al., 2002; Rizzolatti and Matelli, 2003). Many of the neurons in AIP and PFG are related to distal hand movements (Sakata and Taira, 1994; Sakata et al., 1997; Rozzi et al., 2008).

In between these two streams (Rizzolatti and Matelli, 2003), in the fundus of the intraparietal sulcus, lies the ventral intraparietal area (VIP). VIP is on the border of the superior parietal lobule and the inferior parietal lobule (Fig. 1). According to the definition by Rizzolatti's group (Rizzolatti and Matelli, 2003), VIP is involved in the ventro-dorsal stream. The visual afferent input to this area originates from middle temporal area (MT)/medial superior temporal area (MST), and somatosensory afferent input originates from primary somatosensory cortex (SI) and secondary somatosensory cortex (SII) (Lewis and Van Essen, 2000). The VIP has a connection with the caudal part of the ventral premotor cortex (F4), either directly or via PEa (Rozzi et al., 2006) that is in medial bank of intraparietal sulcus and part of area 5 (Luppino et al., 1999; Lewis and Van Essen, 2000; Rizzolatti and Luppino, 2001). Because neurons in V6A, MIP, PEa, PF/PFG, and VIP (shaded area in Fig. 1B) show bimodal sensory properties (i.e., visual and somatosensory properties) (Colby et al., 1993; Iriki et al., 1996; Colby, 1998; Breveglieri et al., 2002), these areas are thought to be involved in the integration of somatosensory and visual information. As described later, the pathway from the VIP to F4, which includes PEa and PF/PFG, is involved in the representation of peripersonal space and body parts (Rizzolatti et al., 1997; di Pellegrino and Ladavas, 2015), and also in hand/arm movement control (Graziano and Cooke, 2006; Rozzi et al., 2008; Rizzolatti et al., 2014).

3. Object affords hand action in the AIP-F5 network

Now, we would like to concentrate on functional properties ventro-dorsal pathway that is related to control object manipulation with the distal hand. Since the end of the last century, several studies have revealed neural mechanisms for distal hand movement control in the monkey parieto-premotor network (Rizzolatti et al., 1988; Sakata et al., 1995; Fogassi et al., 1999; Fattori et al., 2004). Activity of neurons in AIP and ventral premotor area F5 changed when the monkey was manipulating different objects (Rizzolatti et al., 1988; Taira et al., 1990). We will discuss the properties of neurons in the monkey parietal cortex and premotor cortex to reveal functional difference between the two regions.

Sakata's group compared neural activity in AIP during hand manipulation tasks in which a monkey was required to manipulate objects with one hand using full vision and in the dark, and to just fixate on the object for manipulation without grasping it (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000) (Fig. 2). When a red spotlight was presented, the monkey fixated on it, and then press a home key switch. At the same time, the object was illuminated and the monkey could see the object. The monkey fixated on the object until the green light turned on (go signal), then the monkey was required to reach and grasp the object, and hold onto it for a while (movement in the light). The task was the same in the full vision and the dark conditions (movement in the dark), except that in the dark condition the monkey did not have any vision apart from that provided by the spotlight. Sakata and colleagues identified three different types of AIP neurons activated during the task: motor-dominant neurons, visual-dominant neurons, and visual-motor neurons (Fig. 2) (Taira et al., 1990; Sakata et al., 1995; Murata et al., 2000). Motor-dominant neurons fired during movement in the light and in the dark condition, but did not show any significant difference in the level of activity between the two conditions. These neurons did not respond to the presentation of objects, nor to any somatosensory stimuli, and were thus considered as being related to the motor component of the task. Visual-dominant neurons fired during movement in the light but not during

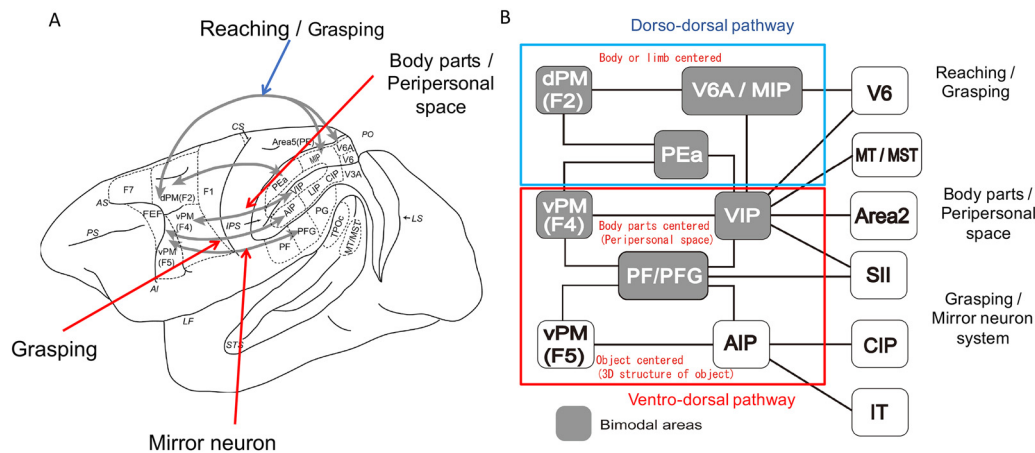


Fig. 1. (A) Parieto-premotor connections in the monkey cerebral cortex. Lateral view of the monkey brain. AIP, anterior intraparietal area; VIP, ventral intraparietal area; LIP, lateral intraparietal area; CIP, caudal intraparietal area; MIP, middle intraparietal area; dPM, dorsal premotor cortex; vPM, ventral premotor cortex; MT, middle temporal area; MST, medial superior temporal area; PS, principal sulcus; AS, superior arcuate sulcus; AI, inferior arcuate sulcus; CS, central sulcus; IPS, inferior parietal sulcus; PO, parieto-occipital sulcus; LF, lateral fissure; LS, lunare sulcus; STS, superior temporal sulcus. IPS, STS, and LS are opened, showing the inside of the sulci. (B) Parieto-premotor connections for reaching, grasping, and mapping of the body parts/peripersonal space. Shaded areas indicate visual-tactile bimodal area. IT, inferior temporal cortex; SII, secondary somatosensory cortex.

Modified from Murata and Ishida (2007).

manipulation in the dark condition. Visual-motor neurons were less active during movement in the dark condition than in the light. Some of these visually responsive neurons (i.e., visual-motor neurons and visual dominant neurons) fired during fixation on the object, being involved in coding the three-dimensional properties of the object, namely object type. That is, each of these neurons was selective to a particular shape, orientation, or size of object (Murata et al., 2000). Importantly, in visual-motor object type neurons, the selectivity for shape, orientation, or size of the object was consistent across manipulation and fixation. The remaining visually responsive neurons (visual-motor neurons and visual dominant neurons) did not show any activity related to the sight of the object, designated as non-object type. This type of neuron showed selectivity for the type of grasping; therefore, it was suspected that the activity reflected the view of the moving hand configuration.

AIP receives visual information about three-dimensional objects, such as shape, orientation, and size. This means that the three-dimensional identity of an object that affords a particular action is represented in the parietal cortex of the dorsal visual pathway. Supporting this idea, visual neurons in AIP are sensitive to binocular disparity (Durand et al., 2007; Srivastava et al., 2009; Janssen and Scherberger, 2015). The source of the efferent visual information is thought to be the caudal intraparietal area (CIP) (Taira et al., 2000; Tsutsui et al., 2001) or the inferior temporal cortex (IT) (Uka et al., 2000), where three-dimensional visual cues activate neurons. AIP has an anatomical connection with CIP and IT (Borra et al., 2008).

In daily life, there can be several affordances of the object to be manipulated. Arbib and Mundhenk (2005) proposed that perceptual affordance to achieve the goal of action is selected in AIP, according to a signal from the prefrontal cortex. A recent study showed that hand-manipulation-related neurons in AIP were differentially activated dependent on the context (Baumann et al., 2009). In this experiment, a contextual cue and an object were presented, and then after some delay period in the dark, the monkey was required to grasp the object in one of two different ways (precision or power grip) according to the contextual cue. AIP neurons showed differential activity immediately after the visual stimulus according to the contextual cue. Furthermore, if only the contextual cue (i.e., grip information) was presented without an object, these neurons did not represent the grip information informed by

the contextual cue. According to Sakata's definition (Sakata et al., 1995), these neurons would be classified as visual-motor neurons, object type. This means that activity during object presentation and the delay period before context-dependent activity is not related to the motor term (i.e., how to grasp the object), but rather to part of the object identity that is useful to afford a particular motor behavior, likely perceptual affordance. Some hand-manipulation-related neurons in AIP show relative position selectivity (WinNyiShein et al., 1999). In this study, the monkey was trained to push a button mounted on the surface of a box. The position of the button was constant in the body-centered frame, but differed relative to the box (i.e., front, back, right, left, top, or bottom of the box). The neurons responded selectively to the position of the button relative to the box (Fig. 3A). Activity was independent of position of the object in the body-centered frame of reference and the retinotopic coordinate system (Fig. 3B and C). This may be related to the position of affordance relative to the object. Probably, this relative position coding was correlated with view point of the subject rather than world-centered position.

Neurons in F5 showed selectivity to the type of hand grip required, i.e., precision grip, finger prehension, or whole-hand grasping (Rizzolatti et al., 1988). Rizzolatti's group coined the term "motor vocabulary" for these different types of movement representation (Jeannerod et al., 1995). The functional properties of neurons in F5 were similar to those in AIP, and a number of neurons in F5 were activated when the monkey fixated on the object to be grasped, designated as canonical neurons (Murata et al., 1997; Raos et al., 2006), showing disparity sensitivity (Theys et al., 2013). These canonical neurons were active during grasping in the dark, like visual-motor object-type neurons in AIP. Furthermore, remaining grasping neurons in F5 did not show any visual properties, and were similar to motor-dominant neurons in AIP. The context dependent modulation of grasping related activity was also found in F5 neurons (Fluet et al., 2010; Vargas-Irwin et al., 2015). However, there were some differences in the functional properties of neurons between F5 and AIP (Raos et al., 2006; Murata and Ishida, 2007; Janssen and Scherberger, 2015). No purely visual neurons, such as the visual-dominant neurons in AIP, were found in F5; all neurons showed motor-related activity during grasping in the dark (as seen in visual-motor neurons and motor-dominant neurons in AIP) (Raos et al., 2006). Furthermore, neurons in F5 showed sustained activity

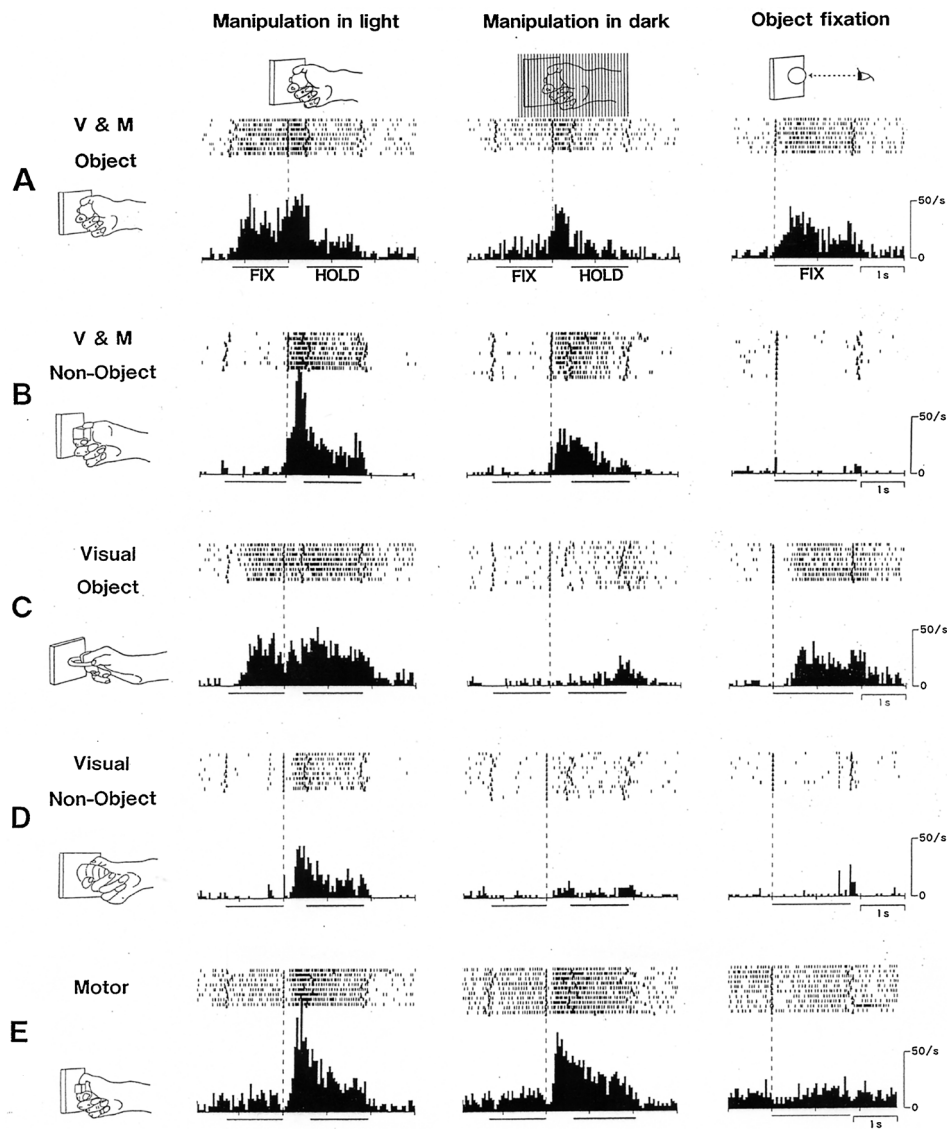


Fig. 2. Five types of hand-manipulation-related neurons in AIP in each of three task conditions. (A) Visual-motor neurons (V&M), object type. (B) Visual-motor neurons, non-object type. (C) Visual-dominant neurons, object type. (D) Visual-dominant neurons, non-object type. (E) Motor-dominant neurons. Manipulation in the light: hand manipulation task performed in the light. Manipulation in the dark: hand manipulation task performed in the dark. Object fixation: object-fixation task performed in the light. Raster plots and histograms represent moment of recorded spike and spike rate (/s) in each 50 ms/bin respectively, and are aligned with the moment at which movement onset in the manipulation task and object presentation in the object-fixation task. FIX, fixation of LED spot; HOLD, holding object.

From Murata et al. (2000).

after object presentation and prior to the onset of hand movement (called set-related activity) (Raos et al., 2006) (Fig. 4). This may reflect the process of visuo-motor transformation, which involves selection of a proper motor plan according to the visual identity of the object. Actually it was revealed that this set-related activity was less common in AIP than in F5 (Murata et al., 1996).

F5 grasping neurons encode goal of action rather than movement per se (Umiltà et al., 2008). In their experiment, the monkey was trained to grasp food with two types of pliers. Normal pliers required the monkey to open the hand to open the pliers and then close the hand to grasp the food, and “reverse pliers” required the opposite sequence, that is, the monkey had to close the hand to open the pliers and then open the hand to grasp the food. Even though the movements during the use of these two types of pliers were different, the goal remained the same and the neurons remained active.

In total, these results suggest that AIP and F5 work together in transforming visual object representations into motor signals

(Rizzolatti et al., 2014). Sakaguchi et al. (2010) calculated the time course of mutual information using a single-unit recording from AIP, and revealed that the temporal pattern of mutual information differed across types of neurons (i.e., visual dominant, visual-motor and motor dominant neuron). They proposed a Gantt chart that represented the temporal/causal relation between AIP and F5 (Fig. 5). Perceptual affordance is probably selected by object-type visual-motor neurons in AIP. This information is sent to F5, where the object information is transformed to motor planning, action selection, and command or goal by canonical neurons (Oztop et al., 2006). This motor information is then sent to the primary motor area. At the same time, a copy of the motor representation, that is, the efference copy, is returned to AIP. This efference copy predicts sensory feedback (corollary discharge). This efference copy/corollary discharge in AIP is reflected by activity of motor-dominant neurons. This is matched with the visual object representation (coded by the activity of visual-motor neurons in AIP) (Sakata et al., 1995). Finally, some non-object type

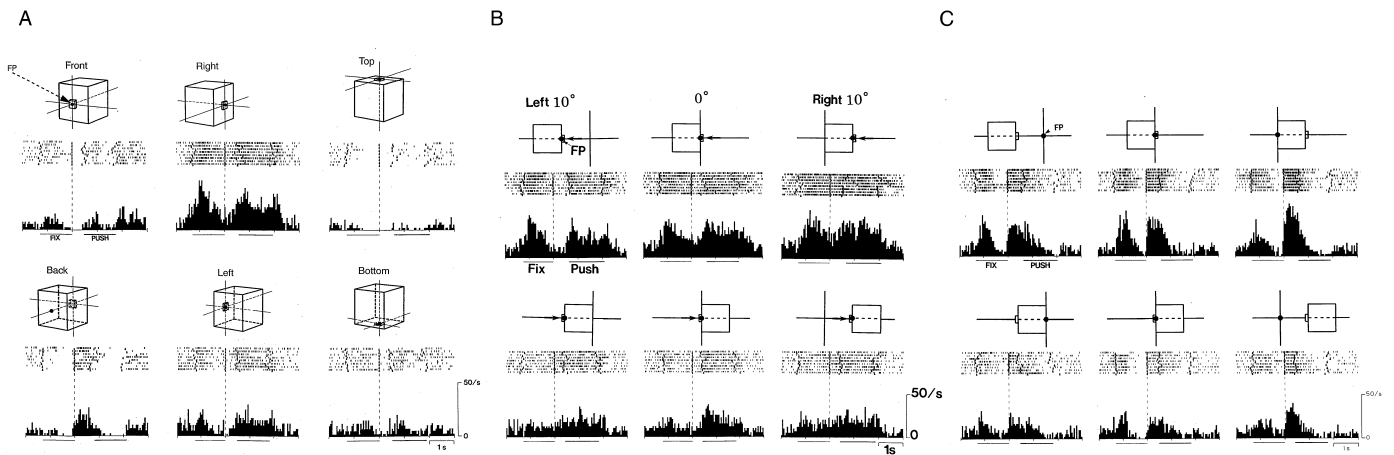


Fig. 3. An example of neuron encoding relative-position in AIP. (A) The monkey was required to fixate on the fixation point (FP) on the push button (PUSH) mounted on the BOX. FIX; the period of fixation on FP, PUSH; the period of pushing button. The FP was always at the same position in the body-centered coordinate system. (B) Position invariance in the body-centered coordinate. The body centered position of the BOX was shifted with FP. (C) Position invariance in the retinotopic coordinate. Position of FP was fixed in the center position. The neuron had a high level of activity when the relative position of the target was on the right of the box. The neuron is a visual-dominant neuron.

From WinNyiShein et al. (1999).

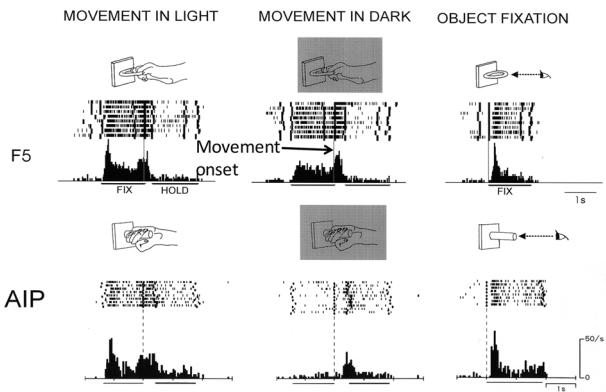


Fig. 4. Examples of canonical neuron in F5 and visual-motor object type neuron in AIP. Both types of neurons were active during the object fixation task, in which the monkey was not required grasping movement. A difference in neuronal behavior between the two brain regions was found before movement onset. Raster plots and histograms are the same as for the manipulation task shown in Fig. 2.

Modified from Murata et al. (1997).

visual-motor and/or visual dominant neurons in AIP are supposed to be the visual feedback signals that monitor ongoing hand movement. In the next section, we discuss the functional properties of non-object type neurons that contribute to monitoring body state.

4. Parietal mirror neurons driven by visual feedback

The ventro-dorsal pathway does not only represent object for manipulation, but also encode visual configuration of the hands during execution of action. AIP and PFG neurons have strong visual properties and grasping related activity. As mentioned above, non-object type visual-dominant neurons and visual-motor neuron in AIP do not respond to visualization of the object, and instead are selective for the shape of the handgrip (Murata et al., 2000). Mirror neurons in PFG and F5 are active during execution of goal-directed actions and during observation of the same action performed by another individual (di Pellegrino et al., 1992; Fogassi et al., 1998). It is hypothesized that mirror neurons activate the intrinsic motor vocabulary during action observation, and that this allows understanding of the observed action, similar as motor theory in recognition of spoken language (Rizzolatti et al., 2014). This is a

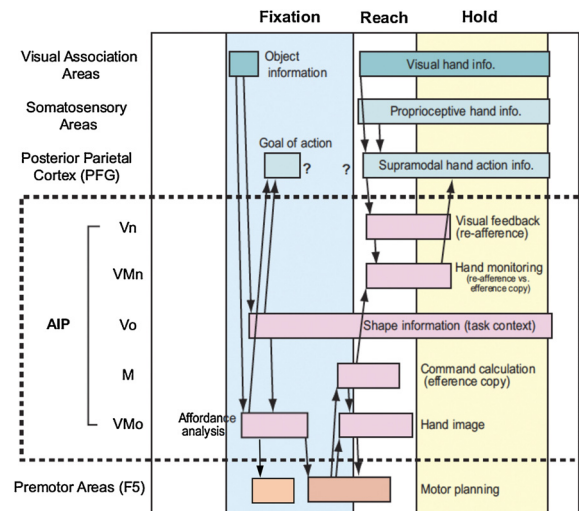


Fig. 5. A Gantt chart for the grasping AIP-F5 network. This chart shows the temporal relations among different types of neurons in AIP, and the proposed relation between neurons in AIP and other related areas. Information flow is speculation, based on mutual information analysis using single-unit data from AIP. Vn; visual-dominant neuron, non-object type. VMn; visual-motor neuron, non-object type. Vo; visual-dominant neuron, object type. M; motor-dominant neuron. VMo; visual-motor neuron, object type.

Modified from Sakaguchi et al. (2010).

reason why mirror neurons discussed in the context of social recognition (Rizzolatti and Sinigaglia, 2010; Rizzolatti et al., 2014).

Our hypothesis is that non-object type neurons and mirror neurons may both be involved in the monitoring of ongoing hand movements (Murata and Ishida, 2007). The most recent our findings proved this hypothesis. Maeda et al. (2015) recorded the activity of single neurons in PFG and AIP of the monkey while the monkey performed the hand manipulation and fixation task as described above. However, in this study, the monkey was required to reach and grasp the object while watching a video monitor on which the image of the monkey's own hand and the object was presented in real time. The monkey could not directly see its own hand or the object (Fig. 6A). In the fixation task, the monkey was required to fixate on the screen, and a movie of the monkey's own hand movement was presented from the first-person perspective. Some AIP and PFG

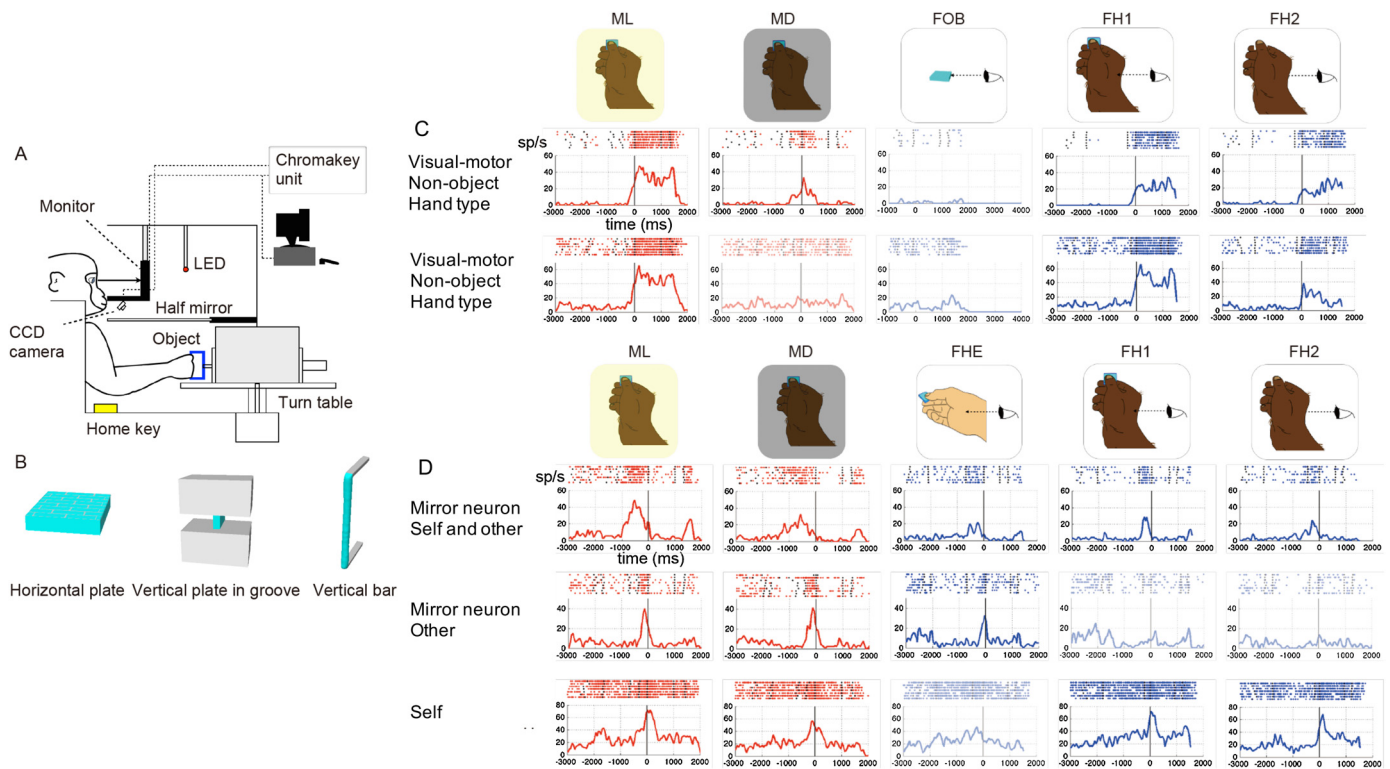


Fig. 6. (A) Experimental setup. (B) Objects used in the experiment. (C and D) Five neurons that responded to the movie of hand action. The image of the hand movement and object was taken by a video camera, and was presented in the first-person perspective on a monitor. In the hand manipulation task in the light (ML), the monkey fixated on the object and pressed a key, then reached for and grasped the object. In the hand manipulation in the dark (MD), the monkey performed the same task in the dark. In the fixation task (FOB, FH1, FH2, and FHE), the monkey fixated on a green spotlight until a red light came on. FOB; just static image of the object was presented on the monitor. FH1; a movie was shown of the hand movements of the monkey recorded in the ML condition. FH2; the same movie was shown but without the object. FHE; a movie of the experimenter's hand performing the task was shown in the third-person perspective. The two neurons shown in (C) were active in FH1 and FH2, but not in FOB, suggesting that they encoded the hand image (non-object hand type neurons). The neuron shown in the upper trace of (D) is a mirror neuron that responded to the image of both the monkey's own action and the movie of the experimenter's action. The neuron shown in the middle trace of (D) is a mirror neuron that responded only to the video of the experimenter's hand action. The neuron shown in the bottom trace of (D) responded only to the movie of the monkey's own action.

Modified from Maeda et al. (2015).

neurons related to the hand manipulation task responded to the movie of the monkey's own hand movement (Murata and Ishida, 2007; Maeda et al., 2015). This is also supported by the results of Pani et al. (2014). The neurons remained active even after the image of the object was erased from the movie (Fig. 6C), and thus the response could be considered a response to the configuration of the hand, and the neuron was designated as a hand-type neuron. Many hand-type neurons were previously called non-object type neurons, as they did not show much activity during fixation on the object (Fig. 6C). Furthermore, some of object-type neurons (i.e., neurons that were active during the object fixation task) and motor-dominant neurons (i.e., neurons that showed the same magnitude of activity with movement in the light and the dark conditions) also responded to the movie of the monkey's own hand.

In this same study (Maeda et al., 2015), we also checked the mirror properties of hand-manipulation-related neurons in AIP and PFG by presenting a movie of the experimenter's hand performing a grasping action shot from a lateral view. As shown in Fig. 6D, a hand-type neuron was active when the monkey observed a movie of his own hand action and when the monkey observed a movie of the experimenter's hand action. This neuron was also active during movement in the dark, and was classified as mirror neuron. It is noteworthy we also found mirror neurons in AIP, as in a preliminary study (Rizzolatti et al., 2014). The majority of hand-type neurons responded to the movie of the experimenter's hand action (Fig. 6D). As discussed in the previous section, the motor-related activity might reflect an efference copy/corollary discharge that originated in F5. We consider that hand-manipulation-related

neurons, including mirror neurons in AIP and PFG, compare corollary discharge (predicted feedback) and actual visual feedback, thus monitoring one's own action (Fig. 7).

Transcranial magnetic stimulation (TMS) of the human homologue of AIP disrupted online adjustments of grasping (Tunik et al., 2005). Some grasping-related neurons and mirror neurons in F5 (Fadiga et al., 2013; Maranesi et al., 2015), and the primary motor cortex also were modulated by visual feedback (Fadiga et al., 2013). Fadiga et al. suggested that this modulation of activity in F5 was due to direct input from AIP. As presented in Fig. 7, feedback control has been established in the AIP-F5 network. This framework also suggests an ontogenetic origin of mirror neurons, as in Heyes' associative sequence learning theory (Heyes, 2010). This theory describes how, during development, a baby will commonly have a visual image of his or her own hand as visual feedback contingent to an action. Hence, it may be easy for the visual image of the hand to become associated with the motor signal. This process of association between vision and action also could lead to matching between one's own motor representation and observed action performed by another individual (Fadiga et al., 2013). In support of this, some mirror neurons in F5 were modulated by the view point of the observer, but others were not, suggesting the occurrence of this matching process in mirror neuron system (Caggiano et al., 2011).

It is noteworthy that mirror neurons recorded in Maeda et al.'s study (Maeda et al., 2015) were associated with the kinematics of the movement, because hand-type neurons were active even if only the movie of the hand was presented. This property of the mirror neurons is different to those previously reported.

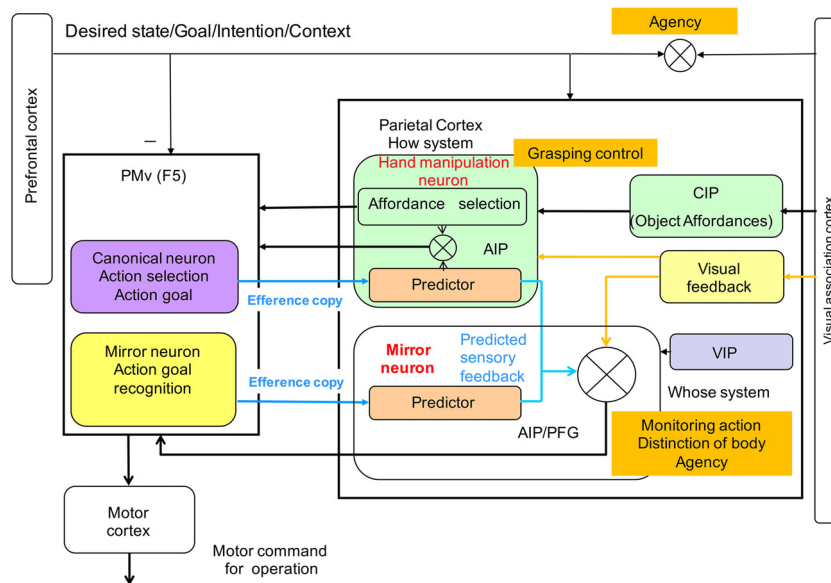


Fig. 7. Conceptual framework for body representation and sensory motor control in the parieto-premotor network. See text for details.

Mirror neurons in F5 were active according to the goal of the action rather than detailed kinematics of the action (Umiltà et al., 2001). Future experiments are required to reveal whether mirror neurons in the parietal cortex represent kinematics or whether we recorded another category of mirror neurons in parietal cortex.

5. Distinction between actions performed by oneself and others in the mirror neuron system

In this section, we would introduce distinctive representation of one's own and other's action in mirror neuron system. Usually, mirror neurons are discussed in the context of the shared representation of self and other. The results by Maeda et al. (2015) are likely consistent with this concept. However, is one's own action distinguishable from other's action in the mirror neuron system? We postulated that there are some distinct representations of self and other in the mirror neuron system. Maeda's study also revealed that some neurons were active only during observation of one's own hand, or only during observation of the action performed by another (Fig. 6D) (Maeda et al., 2015). In the AIP and PFG neurons that responded to observed action, almost 33% of them were active during observation of action performed by only another individual, and 28% were active only for one's own action, although 39% were active for both one's own and another's actions.

As discussed, many mirror neurons in F5 are modulated by the visual perspective of the observed action (Caggiano et al., 2011). This may also reflect a distinct representation of self and other. Bonini et al. (2014b) reported that a subset of neurons in F5 discharged not only when the monkey executed a grasping action, but also when the monkey itself refrained from performing the action. Another subset of neurons was active during the execution of grasping but not when the monkey refrained from performing the action. These neurons were active during action observation (i.e., were mirror neurons) and also discharged when the observed agent did not act grasping. This inaction-related activity was associated with either one's own inaction or other's inaction, but not both. The activity of these neurons was likely related to mental rehearsal of action, which is attributed only to one's self or to another.

In humans, the motor-evoked potential (MEP) by TMS on the motor cortex was enhanced by action observation (Fadiga et al., 1995). This phenomenon is evidence that motor system is

facilitated by mirror neurons during action observation. It was reported that the change in MEP during observation of action was modulated by self-attribution of observed action; that is to say, if the observer felt sense of ownership to that observed hand, the MEP was not much enhanced (Schutz-Bosbach et al., 2006). We believe that, in the mirror neuron system, there are some classes of neurons that encode either one's own action or another's action, and other classes of neurons that encode both.

6. Sense of agency and the parieto-premotor network

As described previous section, one's own and other's action can be distinguishable in the mirror neuron system. Now, we will discuss mechanisms how the parieto-premotor network distinguish own and the other's action. A sense of agency is a subjective awareness that one's generated action attributes to one's self. A sense of agency occurs when an executed action is recognized as being generated by one's own body parts. This occurs only during voluntary movement, which implies that internal motor signals (i.e., motor commands) have a crucial role in generating sense of agency. The comparator model has been proposed to explain sense of agency (Blakemore et al., 1999). In this model, a copy of the motor command, that is, the efference copy, can pass into the forward model to predict feedback (i.e., corollary discharge reflect predicted feedback) in response to a given motor command. Ongoing movement is monitored by the comparison of sensory feedback and the corollary discharge, and this enables more precise movement. This comparator also contributes to recognition of who generated the observed action. If the efference copy matches with sensory feedback, the action is detected as self-generated (Blakemore et al., 2001, 2002; Jeannerod, 2003). This is consistent with the properties of neurons in the AIP-F5 network and the mirror neuron system.

Fig. 7 shows a conceptual framework of the parieto-premotor cortical network for bodily self-recognition. In some parietal neurons, observation of self-action cannot be distinguished from observation of the action of others. The origin of the visual feedback signal may be the superior temporal sulcus, which is involved in the visualization of body action or the extrastriate body area; this is not yet clear in the monkey brain (Astafiev et al., 2004; Keysers and Perrett, 2004). Mirror neurons in the PFG and AIP show a motor component, possibly reflecting the efference copy/corollary

discharge (Murata and Ishida, 2007; Maeda et al., 2015). Comparison of the motor representation of action and the sensory representation of action occurs in the PFG/AIP, and this works for feedback control of movement. Moreover, if the motor representation of action matches the sensory representation of action in the PFG/AIP, it is possible to distinguish the agency of action.

Neuropsychological and imaging experiments in humans have revealed that the inferior parietal cortex is involved in the sense of agency. Patients with damage to the inferior parietal cortex have difficulty with agency recognition (Sirigu et al., 1999). In addition, a number of human brain imaging studies have reported that the inferior parietal cortex is involved in the detection of agency of action (Farrer et al., 2003, 2008; Decety and Grezes, 2006; Chambon et al., 2013). A decreased sense of controlling one's own action (generated by increased spatial distortion of the visual feedback) was associated with increased activation of the right inferior parietal cortex angular gyrus and decreased activation of the insula (Farrer et al., 2003). This supports the hypothesis that the inferior parietal cortex detects any discrepancy between the intrinsic motor component of self-generated action and sensory feedback.

Of course, the sensory-motor control system consists of more than only the parieto-premotor network. The sensory-motor system is controlled by higher order areas that process action goals, desired state of behavior, working memory and task constraints, as suggested by Blakemore et al. (2002). Neurophysiological studies have revealed that AIP-F5 network are influenced by intention of behavior. For example, grasp-related neurons in PFG and F5 responded differentially depending on whether the monkey grasped food to eat or grasped food to place on a tray, even though the same movement was performed in the two condition (Fogassi et al., 2005; Bonini et al., 2010). As described above, AIP neurons are modulated by contextual cue (Baumann et al., 2009). Since the ventrolateral prefrontal cortex has a very strong connection with AIP, PFG, and F5 (Rozzi et al., 2006; Borra et al., 2008, 2011), these higher-order control signals may originate from the prefrontal cortex.

Top-down signals, that is intentional goal or desired state, are crucial for sense of agency (Chambon et al., 2014). For example, task performance modulates sense of agency (Metcalf and Greene, 2007; Wen et al., 2015). Wen et al. (2015) proposed that both action-feedback association and task performance influenced the judgment of agency. In their experiment, human subjects were required to control an object on the computer screen by pressing keys to move the object left or right, with the goal of reaching a particular location as quickly as possible (Fig. 8). The interval between the key press and response of the object was manipulated to change the difficulty of the task. In an assisted condition, the computer ignored erroneous key presses, thus improving task performance and weakening the association between the participant's commands and the movement of the object. In the self-control condition the computer responded to all key presses. Even though the participant's command was not always executed in the assisted condition, the improved task performance influenced the participant's judgment of sense of agency, that is to say that sense of agency was greater in the assisted condition than in the self-control condition when the delay in feedback was 400-ms delay or more (Fig. 8). This suggests that sensory-motor comparator is influenced by a top-down signal, or there is another module to compare intentional goal and results of behavior.

Recently, subliminal priming was shown to influence fluency of action selection process, and this modulated subjective sense of agency (Chambon et al., 2013). This change in sense of agency is related to monitoring the action selection process prospectively rather than retrospective comparison between predicted feedback and actual results of behavior (Chambon et al., 2014). Neuroimaging

data revealed that the angular gyrus was involved in this process (Chambon et al., 2013).

7. Visuo-tactile integration for body perception

From now on, we also mention about own body perception by multimodal sensory integration, especially vision and somatosensory. When the visual event around or related to the body or to specific body parts is correlated with tactile stimulation on the body, that visual event is attributed to one's own body. The sense of ownership, that is, the feeling that the body is owned by one's self, is based on multimodal sensory integration (Tsakiris, 2010; Blanke, 2012). Multimodal sensory integration is used to monitor the position of the body during action. Neurons in PEa, in the medial bank of the intraparietal sulcus, show a visuo-tactile bimodal property. They exhibited a dynamic response to passive wrist movement and moving visual stimuli (Tanaka et al., 2004), whereby responses to both proprioceptive and visual stimuli were directionally tuned and the preferred directions were spatially correspondent. In this experiment, Tanaka et al. (2004) inverted wrist orientation posture by changing arm posture, and found that the preferred direction of passive joint movement was inverted in relation to the hand so as to match the preferred visual direction movement in extrinsic space. They concluded that the neurons were related to re-calibration of the intrinsic image of arm movement relative to the extrinsic coordinates. This re-calibration also occurred when the visual image of the hand was occluded (Obayashi et al., 2000). Obayashi et al. (2000) studied visuo-tactile bimodal neurons in the PEa and found that visual receptive fields were anchored to the hands, i.e., followed movement of the hand, even when the subject could not see. They covered the hand with an opaque plate and found that the visual receptive fields remained above the invisible hand and moved with displacement of the invisible hand. They concluded that the subjective image of the one's own body could be updated by bimodal neurons in the PEa. In the same way, when we use a stick to explore a ball in a narrow space, the stick becomes a part of our arm (Maravita et al., 2003; Maravita and Iriki, 2004), and plastic modification of neuronal activity during tool use has been reported in the PEa (Iriki et al., 1996).

The neurons respond to vision not only of the body itself, but also to visual stimuli presented in the space surrounding the body. This space is called peripersonal space (Rizzolatti et al., 1997; di Pellegrino and Ladavas, 2015). This way of space coding represents a correlation between the environment and the body, and is also contribute action, that is reaching, avoidance object, and so on. The neurophysiological correlates of peripersonal space are somatosensory and visual bimodal areas in VIP, PFG, ventral premotor F4, and putamen (Hyvarinen and Poranen, 1974; Gentilucci et al., 1988; Colby et al., 1993; Graziano and Gross, 1993; Iriki et al., 1996).

The properties of bimodal neurons in the VIP are well studied (Colby et al., 1993; Bremmer et al., 2001; Avillac et al., 2005). In many cases, the visual receptive fields of these neurons are located very close to the body. The neurons respond to moving stimuli within the visual receptive fields. The tactile receptive fields of the neurons are usually anchored to the face, head or hands, and the visual receptive field is in a location congruent with that of the tactile receptive field. Because the location of the visual receptive fields is often independent of eye position and moved with that body parts, the neurons are considered to encode body-part-centered coordinates. Neural activity in this area seems to encode the location of an object in the peripersonal space in a supramodal way (Bremmer et al., 2001; Holmes and Spence, 2004), also responding to auditory stimuli. Supporting this idea, electrical microstimulation of the VIP induced eye blinking and face, ear, and limb movement (Cooke et al., 2003). The VIP is thought to be related to defensive-like movements designed to protect the body from attack

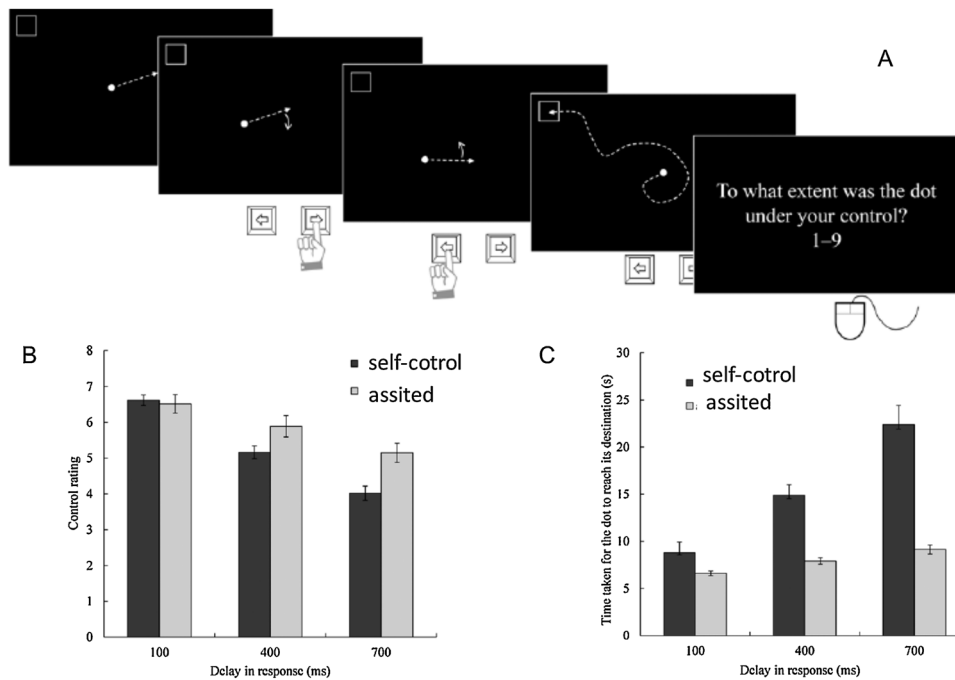


Fig. 8. Sense of agency was influenced by performance. (A) Experimental setup. The subject was required to move the dot into the target area on the monitor screen by pressing two keys. A delay between the key press and the response of the dot was introduced. In some trials, the computer ignored the key press and helped to get the goal if it was incorrect, and thus assisted the performance of the subject (assisted condition). After each trial, the subjects were asked to what extent they felt the dot had been under their control (control rating). (B) Control rating. When the delay was more than 400 ms, the control rating was higher in the assisted condition than in the self-control condition. (C) Mean duration of the trial. Task performance was worse with longer delay between the key press and the response of the dot, but was better in the assisted condition than in the self-control condition for all delays.

Modified from [Wen et al. \(2015\)](#).

or collision by external objects ([Graziano and Cooke, 2006](#)). Evidence suggests that the VIP contributes to the encoding of multiple body-part-centered frames of reference.

Neurons in the ventral premotor area (F4) showed very similar activity to those in VIP, and had visual and somatosensory bimodal properties. VIP has a strong anatomical connection with F4 ([Gentilucci et al., 1983](#); [Fogassi et al., 1996](#)). The visual receptive fields of many F4 neurons are anchored on the tactile receptive fields, and are independent of eye position ([Fogassi et al., 1996](#)), although for some F4 neurons the visual receptive field is in retinotopic coordinates ([Mushiake et al., 1997](#)). Visual and somatosensory receptive fields of F4 neurons moved together with limb movements ([Graziano et al., 1994](#); [Graziano and Cooke, 2006](#)). This means that the receptive fields of neurons in F4 have multiple frames of reference ([Gentilucci et al., 1988](#); [Fadiga et al., 2000](#)), coding body-part-centered coordinates. Like PEa neurons, F4 neurons invert their preferred direction of active wrist joint movement to match to the preferred direction of movement in space ([Kakei et al., 2001](#)). In total, evidence suggests that the VIP/PEa-F4 network has pivotal role in mapping body and peripersonal space, and in updating the intrinsic representation of the body.

8. Other's bodies mapped on one's own body

The brain perceives not only one's own body, but also another's body. Now, we proposed that the map of own body parts is a reference for perception of body parts of another individual. Actually considering properties of mirror neurons, it is suspected that the brain may represent the body parts of other individuals to percept other's action. [Blakemore et al. \(2005\)](#) reported a subject with vision-touch synesthesia, who experienced touched feeling on her body when she observed another person being touched equivalent body part in way of mirror image. Using functional magnetic resonance imaging, [Blakemore et al. \(2005\)](#) found

activation of the mirror neuron system when normal subjects observed another human being touched. Furthermore, the synesthetic subject was much higher activation in bilateral SI, SII and anterior insula and premotor cortex than normal subjects. This suggests that the representation of another individual's body shares some of the representation of one's own body.

As mentioned above, neurons in the VIP that represent one's own body exhibit bimodal visual-tactile properties. We suspected that these bimodal neurons also represented other's body. [Ishida et al. \(2010\)](#) investigated neuronal response in the VIP and PFG when a monkey observed the experimenter's body. Visual receptive fields typically existed <30 cm from the monkey's face or limb, and no activation was found with stimuli >120 cm from the monkey's face or limb. The experimenter faced the monkey at a distance of 120 cm, and the monkey observed visual stimuli presented close to the experimenter's body parts. Some of the bimodal neurons had visual receptive fields <30 cm from the experimenter's body that were congruent with the bimodal receptive fields on the monkey's body ([Fig. 9](#)). Almost half of these visual receptive fields lateralized in the manner of a mirror image of visuo-tactile receptive fields on the monkey, and the remaining half had receptive fields located bilaterally or on the center of the body. For the very small number of neurons receptive fields on the experimenter's body anatomically corresponded with those on the monkey's body. [Ishida et al. \(2010\)](#) designated these neurons as "body-matching neurons". The robustness of body-matching neurons was tested by changing the position of the experimenter. Even if the experimenter shifted position to the left or the right, the location of the receptive field on the experimenter's body did not change. This suggests that the body parts of other were encoded in the same neuron that represents one's own body parts, and that the map of own body parts was referred to for recognition of the other's body. As described before, tactile and visual integration is crucial factor to represent one's own body, however there are also other's representation sharing with one's

Mirror image

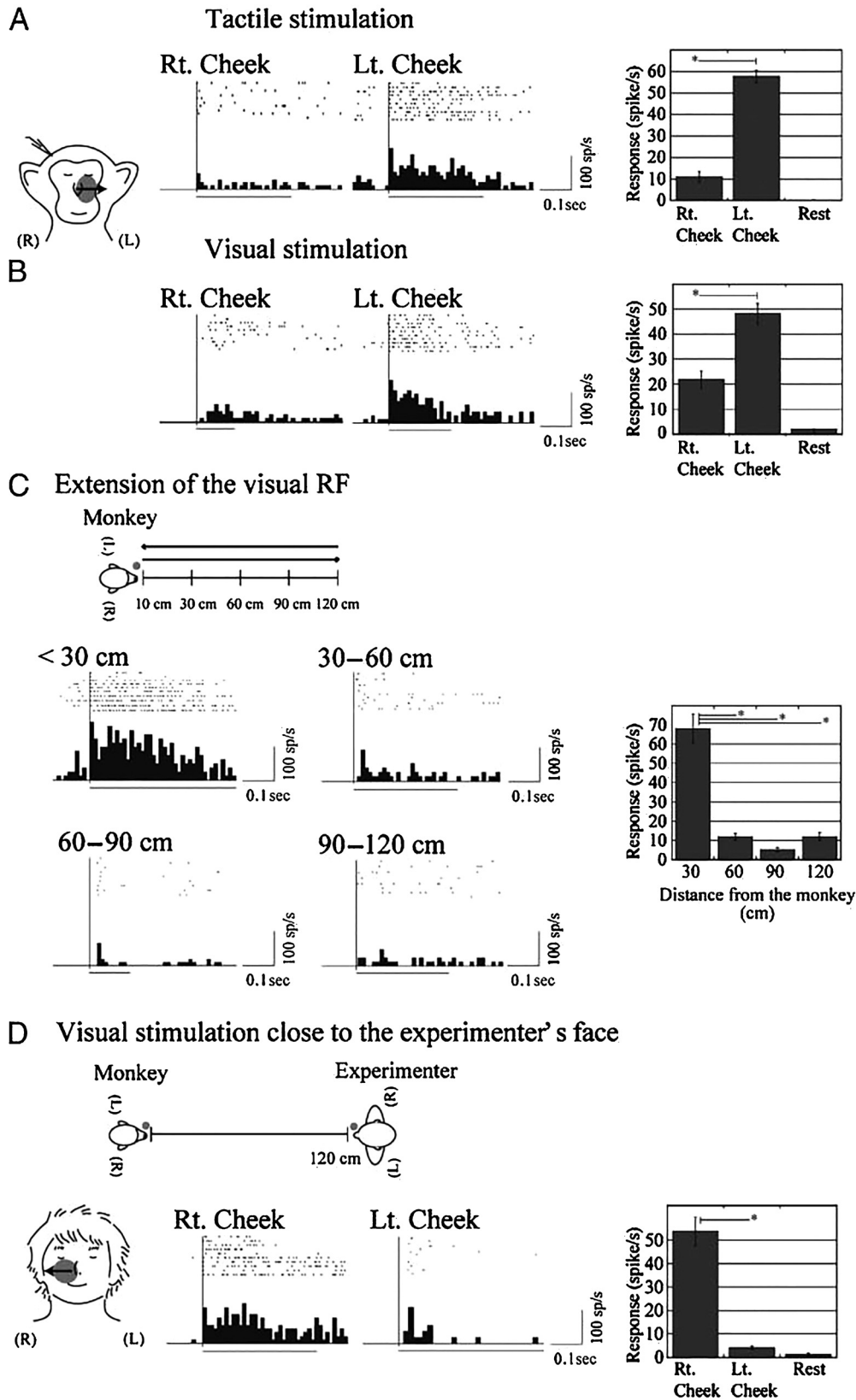


Fig. 9. An example of a body-matching neuron. (A and B) The neuron responded to stimuli presented in visual and tactile receptive fields on the monkey's left cheek. (C) The visual receptive field was in just the peripersonal space around the face less than 30 cm from the monkey. (D) When the monkey observed an experimenter situated 120 cm from the monkey, the neuron was activated by visual stimuli presented close to the experimenter's right cheek. Rasters and histograms of single-unit activity (10 trials and bin width, 10 ms) are aligned on stimulus movement onset (long vertical line); the horizontal bar below the histogram indicates mean duration of stimulation. Bar graphs (right) show mean discharge frequencies of the histogram during tactile stimulation of the right or left cheek, along with visual stimulation close to each body part. From Ishida et al. (2010).

own body, like a mirror neuron system. With this system, even if spatial configuration of the body parts has a different perspective, the brain can easily match one's own body parts to another's body parts.

The VIP has a strong anatomical connection with PFG (Rozzi et al., 2006). Mirror neurons in F5 showed differential activity according to whether an action was observed in peripersonal space or extrapersonal space (Bonini et al., 2014a). In some cases, neurons were activated by actions observed in both peripersonal and extrapersonal space. The body-matching neurons may supply information about other's body to mirror neuron system.

9. Summary and conclusions

In this paper, we have discussed multimodal representation of the body in the brain. The body interacts with the environment. If the environment affords action, then the action changes the extrinsic information and also the intrinsic state of the body. The production of action is a fundamental process of body representation in the brain. Hence, the physical body is not only the end-effector, but also affects the brain. The representation of objects in the parieto-premotor network is in relation to the body. Affordances in the external world are also affected by the body.

Typically, mirror neurons are discussed in the context of shared representation of self and other. However, even in the mirror neuron system, action is attributed to either one's self or another. We believe that the mirror neuron system is also shared by the "who" system. In this review, we discussed the contribution of the mirror neuron system to representation of the body and consciousness of the body, and we proposed multiple comparators in the parieto-premotor network (Fig. 7). The comparison of corollary discharge and actual sensory feedback is a fundamental process in sensory-motor control and sense of agency. The mirror neuron system also has a comparator that matches one's own body parts with the body parts of another. The representation of one's own body is a reference for perception of the bodies of others. Furthermore, top-down signals, intention, decision, or context cues are also compared with sensory feedback or results of behavior (i.e., performance). The mirror neuron system probably works with other systems that have executive function, i.e., the prefrontal cortex. More experimental evidence is needed to support discussion of the relation between the parieto-premotor network and other brain regions for body representation.

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