Processing of Visual Signals for Direct Specification of Motor Targets and for Conceptual Representation of Action Targets in the Dorsal and Ventral Premotor Cortex

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Yamagata T, Nakayama Y, Tanji J, Hoshi E. Processing of visual signals for direct specification of motor targets and for conceptual representation of action targets in the dorsal and ventral premotor cortex. J Neurophysiol 102: 3280–3294, 2009. First published September 30, 2009; doi:10.1152/jn.00452.2009. Previous reports have indicated that the premotor cortex (PM) uses visual information for either direct guidance of limb movements or indirect specification of action targets at a conceptual level. We explored how visual inputs signaling these two different categories of information are processed by PM neurons. Monkeys performed a delayed reaching task after receiving two different sets of visual instructions, one directly specifying the spatial location of a motor target (a direct spatial-target cue) and the other providing abstract information about the spatial location of a motor target by indicating whether to select the right or left target at a conceptual level (a symbolic action-selection cue). By comparing visual responses of PM neurons to the two sets of visual cues, we found that the conceptual action plan indicated by the symbolic action-selection cue was represented predominantly in dorsal PM (PMd) neurons with a longer latency (150 ms), whereas both PMd and ventral PM (PMv) neurons responded with a shorter latency (90 ms) when the motor target was directly specified with the direct spatial-target cue. We also found that excited, but not inhibited, responses of PM neurons to the direct spatial-target cue were biased toward contralateral preference. In contrast, responses to the symbolic action-selection cue were either excited or inhibited without laterality preference. Taken together, these results suggest that the PM constitutes a pair of distinct circuits for visually guided motor act; one circuit, linked more strongly with PMd, carries information for retrieving action instruction associated with a symbolic cue, and the other circuit, linked with PMd and PMv, carries information for directly specifying a visuospatial position of a reach target.

INTRODUCTION

The premotor cortex (PM) is essential for the visual guidance of motor behavior (Passingham 1993; Wise 1985). Three major factors have been proposed as relevant in this regard. The first involves using visual information to directly guide the movements of proximal or distal limbs. PM’s role in specifying the spatial location of the targets of reaching movements (Caminiti et al. 1991; Cisek and Kalaska 2005; Godschalk et al. 1981; Kurata and Hoshi 2002; Mushiake et al. 1991; Pesaran et al. 2008; Weinrich and Wise 1982) and in shaping the hand to grasp an observed object (Murata et al. 1997; Rizzolatti and Luppino 2001; Rizzolotti et al. 1988) is well established. The second factor concerns the arbitrary manner in which visual signals are associated with specific movements. The involvement of PM in establishing a conditional association between visual signals and movements (or visuomotor mapping) has been demonstrated among primates (Chen and Wise 1995; Mitz et al. 1991; Murray et al. 2000; Wise and Murray 2000) including humans (Grafton et al. 1998; Picard and Strick 2001). The third factor emerged in a recent study demonstrating the crucial role played by PM in representing forthcoming actions at a conceptual level before information is transformed into a motor plan (Nakayama et al. 2008). That study found that PM neurons retrieve motor instructions at an abstract level even when the location of actual motor targets was not available.

Thus it will be of great interest to examine how visual signals with different behavioral meanings are processed in this area. The aim of this study was to examine whether visuospatial information about motor targets and action-selection information at a conceptual level are transmitted to the same cells or if such information is channeled into separate groups of cells. This issue is important for clarifying the brain circuits involved in the two aspects of behavioral guidance based on visual information. However, it is not easy to detect the input stage of a series of information processing in the frontal association cortex because sustained neuronal activity reflecting a forthcoming motor act is also initiated once a movement is determined regardless of the mode of cue presentation (Ferrera et al. 1999; Kurata and Wise 1988; Weinrich and Wise 1982). Thus it is necessary to dissociate activity reflecting the input stage from the output stage reflecting the forthcoming movement.

We consider that four major solutions are available. The first one is to use a task that asks animals to make a response as fast as possible after a cue appears; this strategy has made substantial success in dissociating sensory input stage from motor output stage (Sato and Schall 2003; Tanji and Kurata 1982; Thompson et al. 1997). The second one is to ask animals to make a movement away from a visuospatial cue (Crammond and Kalaska 1994; Funahashi et al. 1993; Gail and Andersen 2006; Johnston et al. 2009; Schlag-Rey et al. 1997; Yoshida and Tanaka 2009). The third one is to present a sensory cue while animals engage in a fixation task. This strategy is widely used in examining response properties of neurons in visual association areas. In the current study, we adopted this strategy in examining neuronal activity reflecting visuospatial information of motor targets. Finally, the fourth one is to present a motor instruction while the forthcoming movement itself is kept undetermined (Bastian et al. 2003; Nakayama et al. 2008); this strategy was adopted in investigating neuronal activity reflecting action-selection information at a conceptual level.
PM is thought to be subdivided into at least two regions on the basis of anatomy and physiology: the ventral and the dorsal PM (PMv and PMd) (Barbas and Pandya 1987; Dum and Strick 2005; Hoshi and Tanji 2007; Passingham 1993; Rizzolatti and Luppino 2001). A recent report compared the neuronal activity in the two regions. PMv neuronal activity was typically characterized as reflecting the spatial position of a visual cue, whereas PMd neuronal activity was characterized as reflecting a motor plan that signaled where to reach with which arm (Hoshi and Tanji 2000, 2006). This finding prompted us to compare PMd and PMv neurons in terms of the role of visual responses in directly signaling motor targets or in representing action selection at a conceptual level. In this study, we further examined neuronal activity from a perspective of the laterality preference. This was because prior studies have shown that visuospatial responses, especially in the parietal cortex, are biased toward the contralateral space from the recorded hemisphere (Barash et al. 1991; Battaglia-Mayer et al. 2005; Blatt et al. 1990; Colby and Duhamel 1991; Duhamel et al. 1998; Mountcastle et al. 1975; Rozzi et al. 2008), whereas our prior study has revealed that PM retrieves a motor instruction concerning ipsilateral, as well as as contralateral, aspect of arm use and target location (Hoshi and Tanji 2006). The contrast of laterality representation raised an intriguing possibility that direct specification of motor targets and retrieval of action selection at a conceptual level are achieved in an essentially distinct manner.

We show here that conceptual action plans associated with symbolic cues are represented predominantly by PMd neurons, whereas PMv and PMd neurons are similarly involved in specifying motor targets indicated directly by visuospatial cues. We show further that representations of the two classes of information are different in terms of the laterality preference, the time course of the selectivity development, and the selectivity coding by activity increase or decrease. These results provide evidence that the premotor cortex receives signals generated in a pair of distinct circuits for visually guided motor act; one circuit, linked more strongly with PMd, carries information for retrieving action instruction associated with a symbolic cue, and the other circuit, linked with PMd and PMv, carries information for specifying a visuospatial position of a reach target.

METHODS

Subjects and experimental conditions

We used two monkeys (Macaca fuscata; 1 male weighing 6.0 kg and 1 female weighing 5.0 kg) that were cared for in accordance with the National Institutes of Health guidelines and the guidelines of our institute. During the experimental sessions, the monkeys sat in chairs with their heads and left arms restrained. We installed a button in front of their chair at waist level. A 19-in video monitor equipped with a touch-sensitive screen was placed in front of the monkeys (22 cm away from the eye). Eye positions were monitored at 240 Hz with an infrared eye-tracking system (resolution, 0.25° in visual angle; RHS-M; Applied Science Laboratories). Neuronal activity was recorded with glass-insulated Elgiloy-alloy microelectrodes (0.5–2 MΩ at 1 kHz), which were inserted through the dura mater using a hydraulic microdrive (MO- 81-S; Narishige). Single-unit potentials were amplified with a multichannel processor and sorted using a multispike detector (MCP Plus 8 and MSD; Alpha Omega Engineering). Muscle activity was recorded with stainless-steel wire electrodes. The electromyographic activity was amplified, A-D converted, and stored. We monitored activity in the following muscles during task performance: the biceps and triceps brachii, deltoid (anterior, lateral, and posterior heads), trapezius, supraspinatus, infraspinatus, pectoralis major, rhomboid major, and neck and paravertebral muscles. We did not find any systematic changes in the muscle activity before the appearance of the go signal. We used the TEMPONET system (Reflective Computing) to control the behavioral task and to collect data at 1,000 Hz for off-line analyses.

Behavioral task

The monkeys were trained to perform two behavioral tasks. Each trial of both tasks commenced when the monkey pushed the button with the right hand and gazed at a fixation point (white circle, 1.4° in visual angle) that appeared at the center of the touch-sensitive screen after an inter-trial interval of >3 s. In the first task (symbolic cue task, Fig. 1A), after the gaze was maintained on the fixation point for 1200 ms, an instruction cue (size, 11 × 11°) was presented on the fixation point for 800 ms to tell the animals to select either the right or left target. At this stage, no information about future targets was given. The monkeys were required to select right or left based on the color and shape of the instruction cue. For monkey 1, a green circle or yellow square indicated that the target on the right should be selected, whereas a red diamond or blue cross indicated that the left target should be selected (Fig. 1B). For monkey 2, a green circle and a red diamond specified the selection of the right and left targets, respectively. These cues were presented randomly. If the monkey fixated on the fixation point for 1,200 ms during the subsequent delay period, a choice cue consisting of two gray squares (size of each box, 7 × 7°; 11° separation between the centers of adjacent two gray squares) appeared at one of six different locations on the screen (Fig. 1C). After a delay period of 1.500–2.500 ms, the color changed from gray to white, which served as the go signal. If the monkey reached for the target with the right arm within the next 1.5 s, s/he received a fruit juice reward 500 ms after touching the correct square.

In the second task (direct cue task, Fig. 1D), after the gaze was maintained on the fixation point for 1,200 ms, a gray square (size of box, 7°) was randomly presented for 800 ms at one of five different locations on the screen (Fig. 1E) as an instruction cue. If the monkey fixated on the fixation point for 1,200 ms during the subsequent delay period, the same gray square was presented as a set cue at the same location as the instruction cue. After a delay of 1,500–2,500 ms, the color changed from gray to white if the monkey gazed at the set cue for 300–600 ms; the color change served as the go signal. If the monkey reached for the target with the right arm within the next 1.5 s, s/he received a fruit juice reward 500 ms after touching the target. The animal’s oculomotor behavior was controlled at three periods of the behavioral tasks; the animal was required to gaze at the fixation point 1) for 1,200 ms before the instruction cue onset, and 2) for 1,200 ms before the choice-cue or set-cue onset, and the animal was required to gaze at the choice cue or set cue 3) for 300–600 ms before the go signal onset. After the go signal onset, the monkey was free to move the eyes. Because the monkey’s gaze was maintained at the fixation point for 1,200 ms before each visual cue’s onset, it was secured that the visual cues (the instruction cue, the choice cue, and the set cue) appeared at a constant location in retino- and craniocentric coordinates.

The progress of the task, the requirement of gazing at the fixation point, and the location of reach targets (T1–T3, Fig. 1, C and E) were the same in the two tasks. However, in the symbolic cue task, the right or left reach was cued indirectly according to the learned association with each visually observable object. By contrast, in the direct cue task, the spatial location of the instruction cue directly indicated the direction of the future movement. Thus after the appearance of the instruction cue, information processing was essentially different in the two tasks. The two tasks were alternated in blocks of 30–60 trials.
Data analysis and definition of task-related activity

To detect the task-related activity, we first counted the number of spikes from each neuron in successive 200-ms bins focused on four task events: the onset of the instruction cue (10 bins; 4 before, 1 around, and 5 after the onset), the onset of the choice cue (10 bins; 4 before, 1 around, and 5 after the onset), the onset of the GO signal onset (5 bins; 4 before, and 1 around the onset), and the onset of the movement (5 bins; 2 before, 1 around, and 2 after the onset). We classified a neuron as “task-related” if the distribution of the discharge rate (in spike/s) was significantly different in H11 of the 10 trial types in the symbolic cue task (5 positions of the target on the screen, T1–T5 in Fig. 1C, each of which could be associated with a left or right target; ANOVA, P < 0.001, not corrected). Because we applied the ANOVA repeatedly for 10 times, we set the of each analysis to 0.001. All of the neurons in the database were confirmed to be task-related. The task-related activity was observed in H11 of the neurons that we encountered during the physiological recording. Details of other statistical analyses are described in RESULTS.

RESULTS

Database of neuronal activity recorded from PMd and PMv

While two monkeys were performing the tasks, extracellular neuronal activity was recorded from the postarcuate premotor cortex in the left hemisphere (Fig. 1F, see also Fig. 8). At the end of each experimental session, we checked the neuronal responses to somatosensory and visual stimuli and applied intracortical microstimulation (ICMS) through the tip of an inserted electrode (11–44 pulses of 200-μs width at 333 Hz; current, <50 μA). At the most caudal part of the frontal cortex and rostral to the central sulcus, forelimb movements or muscle twitches were evoked (with >50% probability) by shorter trains (11 pulses) of ICMS with currents of <40 μA. We also found that some neurons responded to somatosensory stimuli but not to visual stimuli. We operationally defined this area as the primary motor cortex. In the region that was located rostral to the primary motor cortex and medial to the spur of the arcuate sulcus, we observed that only longer trains (i.e., 44 pulses) of ICMS evoked forelimb movements. However, we did not elicit saccadic eye movements at any sites where we collected neuronal activity for this report, suggesting that the recording sites were outside the rostral part of PMd or the frontal eye field where saccadic eye movements can be evoked with ICMS (Bruce et al. 1985; Fujii et al. 2000). Thus this dorsal area corresponds to the caudal division, or area F2, of the dorsal premotor cortex (PMd) (Matelli et al. 1985; Picard and Strick 2001). In the region that was located ventral to the spur of the arcuate sulcus and rostral to the primary motor cortex, we observed that some neurons showed bimodal response properties, responding to both the tactile and visual stimuli (Fogassi et al. 1996; Graziano et al. 1997). We also

FIG. 1. Behavioral tasks, instructions, and cue signals, and the recording site. A: temporal sequence of behavioral events in the symbolic cue task. B: visual signals used to designate the selection of the left or right forthcoming choice cue in the symbolic cue task. C: locations of the choice cue and target on the screen in the symbolic cue task. For the choice cue, 2 gray squares appeared at neighboring positions (locations 0–6 depicted with dotted squares). The target position was selected from 5 potential targets (T1–T5), which were either to the left or to the right of the choice cue. T3 was located at the center of the screen, aligned with the center of the monkey’s body. D: temporal sequence of behavioral events in the direct cue task. The time structure was the same as in the symbolic cue task. E: locations of the instructions, set cues, and targets on the screen in the direct cue task. The position was selected from five potential targets (T1–T5) as in the symbolic cue task (shown in C). F: cortical map of recording sites. Neuronal activity was recorded from ventral premotor cortex (PMv) and caudal dorsal PM (PMd; colored in blue and pink, respectively). PS, principal sulcus; AS, arcuate sulcus; CeS, central sulcus. Scale bar, 10 mm.
found that the longer trains of ICMS evoked forelimb movements. This region was judged to correspond to the caudal sector, or area F4, of PMv (Matelli et al. 1985). Rostrally, we collected neuronal activity up to the posterior bank of the inferior limb of the arcuate sulcus. In the anterior bank, we could evoke saccadic eye movements with 11 pulses of ICMS with currents of $<$40 $\mu$A (Bruce et al. 1985); this area was judged as the frontal eye field, and data recorded from this area were excluded. Taken together, the ventral area corresponds to the forelimb area of the ventral premotor cortex (PMv), including areas F4 and F5 (Matelli et al. 1985). The recording sites were verified by observing the central and arcuate sulci, the arcuate spur, and the superior precentral dimple during craniotomy, by examining magnetic resonance images (Siemens, Sonata 1.5 T) taken after a recording chamber was implanted and by checking the depth at which we observed neuronal activity for the first time after penetrating the dura mater (we encountered the 1st neuronal spikes at a deeper point in and around the sulcus).

We recorded the activity of only one (74%) or two (26%) neurons in isolation with each electrode. Special care was taken to avoid contamination by other neurons by rigorously inspecting the waveform of monitored single-neuron spikes. In 593 PMd neurons (254 in monkey 1 and 339 in monkey 2) and 498 PMv neurons (316 in monkey 1 and 182 in monkey 2), we sampled activity in $\geq$50 successful trials for the symbolic cue task and in $\geq$30 successful trials for the direct cue task. The data for PMd were a subset of those reported in our prior report (Nakayama et al. 2008). All of the neurons in the database were confirmed as task-related in the symbolic cue task (see METHODS). Data collection was initiated by recording neuronal activity in $\geq$50 trials in the symbolic cue task. If the condition of cell isolation was judged to be stable, we switched the task to the direct cue task and collected data in $\geq$30 trials. Then we again switched the task to the symbolic cue task to confirm that we collected activity from an identical cell in the two tasks. Recording sites were frequently switched among PMd, PMv, and the primary motor cortex to reduce the effect of sampling bias to a minimum. We advanced the electrode to find task-related neuronal activity while the monkey was performing the symbolic cue task. After encountering a new spike waveform, we monitored the activity in raster plots sorted according to the trial types and behavioral events. If the activity was judged as task-related by visual inspection after collecting data $>20$ trials, we continued recording. If not, we advanced the electrode slowly looking for new cellular spikes. It was unlikely that we missed the activity specific to the direct cue task because the visuospatial processing was also required after the choice cue onset in the symbolic cue task.

In this study, we focused on these neurons’ activity that occurred in response to the instruction cue in the two tasks. The reaction time (time interval between the go signal onset and the button release) and the movement time (time interval between the button release and the target touch) for each animal were short and indistinguishable in the two tasks (Table 1), suggesting that they performed the two tasks with comparable attentiveness. Because the success rate exceeded 95% under each behavioral condition for both animals, we addressed responses for successful trials only.

### Reaction time and movement time

<table>
<thead>
<tr>
<th>Subject</th>
<th>Task</th>
<th>Reaction Time, ms</th>
<th>Movement Time, ms</th>
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<tbody>
<tr>
<td>Monkey 1</td>
<td>Symbolic cue task</td>
<td>451 ± 59</td>
<td>212 ± 38</td>
</tr>
<tr>
<td></td>
<td>Direct cue task</td>
<td>469 ± 71</td>
<td>219 ± 37</td>
</tr>
<tr>
<td>Monkey 2</td>
<td>Symbolic cue task</td>
<td>314 ± 17</td>
<td>311 ± 35</td>
</tr>
<tr>
<td></td>
<td>Direct cue task</td>
<td>322 ± 22</td>
<td>305 ± 41</td>
</tr>
</tbody>
</table>

Times are expressed as means ± SD.

**Neuronal activity in response to symbolic action-selection cue or direct spatial-target cue**

We found that a subset of PM neurons responded selectively to either the symbolic action-selection cue or the direct spatial-target cue but not to both. Figure 2 presents an example of the subset of premotor neurons responding to the action-selection cue. The PMd neuron illustrated in Fig. 2 responded to the appearance of the red diamond or blue cross in the symbolic cue task (Fig. 2, left). In other words, the visual responses were observed if the cue called for the selection of the left target. The same neuron, however, did not respond at all to the appearance of the direct spatial-target cue (Fig. 2, right) even if it appeared at the center of the screen (i.e., the same place as the action-selection cue at T3) or at the left side of the screen (T1 and T2). In contrast, a subset of premotor neurons reflected the visuospatial location of the cue on the screen in the direct cue task (Fig. 1E). The PMv neuron illustrated in Fig. 3 showed transient visual responses when a spatial cue appeared on the right side (T4 and T5) of the screen (Fig. 3, right). This neuron, however, showed negligible responses to the action-selection cue (Fig. 3, left) appearing at the center of the screen. The same neuron responded to the appearance of the spatial cue at the same location (T3, right), although to a rather modest extent. The discovery of these selective responses to the symbolic action-selection cue and direct spatial-target cue led us to compare the visual response properties of the whole population of PMd and PMv neurons.

**Latency of neuronal activity exhibiting laterality difference**

We examined when the direction selectivity appeared in response to the symbolic action-selection and direct spatial-target cues by analyzing the time at which selectivity for the laterality of neuronal activity first appeared after the onset of the instruction cue. We defined the latency as the first of two consecutive 20-ms bins with significant activity differences depending on the left or right location of the cued information (Mann–Whitney U test, $P < 0.05$, for each bin); we here used the nonparametric test because the normal distribution could not be assumed because of the small bin size (20 ms). The latency was calculated for each neuron separately during the two behavioral tasks.

The distribution of the latency in response to the symbolic action-selection cue is shown in Fig. 4A for PMd neurons ($n = 593$) and in B for PMv neurons ($n = 498$). The distribution of the latency among PMd neurons was concentrated immediately after the cue onset, during 400 ms after cue onset (33.7%, colored in red in the histogram in Fig. 4A). By contrast, among PMv neurons, the concentration of the distribution was less obvious; only 11.6% of latencies for PMv neurons fell within this period (red-colored in Fig. 4B). The first bin in which the number of neurons exceeded baseline level (at least mean +5 SD of the number during the baseline period, 500-ms period...
preceding the cue onset) was that centered at 150 ms for PMd neurons and at 190 ms for PMv neurons (dotted lines).

The distribution of the latency calculated for the spatial-target cue responses is presented in Fig. 4C for PMd neurons (n = 593) and in D for PMv neurons (n = 498). The distribution of PMd and PMv latencies was similar during the 400 ms after the onset of the cue (20.4% in PMd and 19.7% in PMv, colored in blue in Fig. 4, C and D). The first bin in which the number of neurons exceeded the control value during the baseline period (at least mean ± 5 SD) was centered at 90 ms for both PMd and PMv neurons (dotted lines). The distributions of PMd and PMv neurons did not differ significantly (P = 0.6310, Kolmogorov–Smirnov test).

The preceding analyses suggested that the latency was shorter after the direct spatial-target cue than the symbolic action-selection cue. However, the spatial positions of the cue used for the analysis in the two tasks were different; the visual cue in the symbolic cue task was presented at the center of the screen (T3, Fig. 1E), whereas the analysis for the direct cue task was conducted using trials in which the cue was presented at the left or right side of the screen (i.e., T1-2 or T4-5; Fig. 1E). Thus the latency difference could be affected by the spatial position effect. To examine this possibility, we examined the response latency to the appearance of the visuospatial cue. We calculated it separately for neurons with highest discharge rates at the center (T3) or at the periphery (T1, 2, 4, and 5). The analysis showed that the latency of the former group was 125 ± 97.6 (mean ± SD), whereas that of the latter group was 129 ± 87.0 ms; the latency did not differ significantly between the two groups (P = 0.4957, Kolmogorov–Smirnov test). Thus the result revealed that the latency for the spatial cue was not much influenced by the spatial position.

Proportion of PMd and PMv neurons exhibiting right/left selective responses to symbolic action-selection and direct spatial-target cues

To examine the proportion of neurons that showed significant right/left selectivity in response to the symbolic action-
selection cue, we conducted ANOVAs for the activity during the 400-ms period after the cue onset. For the data of monkey 1, to which four visual objects were presented, we applied a two-way ANOVA; two independent variables were the right/left instruction (red diamond/blue cross vs. green circle/yellow square) and the object (red diamond/green circle vs. blue cross/yellow square). For the data of monkey 2, to which only a pair of objects were presented, we applied one-way ANOVA with the right/left instruction an independent variable. These analyses revealed that 29% of PMd neurons (172 of 593) and 11% of PMv neurons (54 of 498) exhibited significant instruction selectivity ($P < 0.01$; Tables 2 and 3, sum of “the symbolic cue” and “both”). Object selectivity was detected as significant interaction between the instruction and the object ($P < 0.01$). Because the four objects were used in monkey 1, we obtained information about the object selectivity from this animal. We found that only eight neurons (1.4% of PM neurons in monkey 1, $n = 570$) exhibited significant relationship with the identity of the cue.

We then assessed the proportion of neurons showing significant selectivity for the direct spatial-target cue in two ways. First, we conducted ANOVA ($P < 0.01$) on the neuronal activity during 400 ms after the onset with the five spatial targets (T1–T5) an independent variable. The result revealed that 24% of PMd neurons (143 of 593) and 15% of PMv neurons (74 of 498) showed significant selectivity (Table 2, sum of both and direct cue only). Second, we conducted ANOVA ($P < 0.01$) on the neuronal activity during 400 ms after the onset with the left location (T1–T2) and the right location (T4–T5) an independent variable. The result revealed that 24% of PMd neurons (141 of 593) and 17% of PMv neurons (83 of 498) showed significant selectivity (Table 3, sum of both and direct cue only). Because the two sets of analyses did not reveal any differences, we describe the results of the latter analysis.

Based on the preceding analyses, we classified PM neurons with significant selectivity into three groups (Table 3); neurons selective only for the instruction in the symbolic cue task, neurons selective only for the direct spatial-target cue, and neurons selective for both.

### Table 2. The number of neurons with significant right/left selectivity in symbolic cue task and with cue location selectivity in direct cue task in PMd ($n = 593$) and PMv ($n = 498$)

<table>
<thead>
<tr>
<th>Task</th>
<th>PMd</th>
<th>PMv</th>
<th>$\chi^2$ Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbolic cue only</td>
<td>109 (18.4)</td>
<td>36 (7.2)</td>
<td>*$P &lt; 0.0001$</td>
</tr>
<tr>
<td>Both</td>
<td>63 (10.6)</td>
<td>18 (3.6)</td>
<td>*$P &lt; 0.0001$</td>
</tr>
<tr>
<td>Direct cue only</td>
<td>80 (13.5)</td>
<td>56 (11.2)</td>
<td>$P = 0.3046$</td>
</tr>
<tr>
<td>Subtotal</td>
<td>252 (42.5)</td>
<td>110 (22.1)</td>
<td></td>
</tr>
</tbody>
</table>

In both tasks, the period of analysis covered 400 ms after cue onset. Numbers in parentheses indicate the percentage of neurons out of the total. *: a statistical significance ($P < 0.01$). PMd and PMv, dorsal and ventral premotor cortex, respectively.

### Table 3. The number of neurons with significant right/left selectivity in symbolic cue task and direct cue tasks in PMd ($n = 593$) and PMv ($n = 498$)

<table>
<thead>
<tr>
<th>Task</th>
<th>PMd</th>
<th>PMv</th>
<th>$\chi^2$ Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbolic cue only</td>
<td>106 (17.9)</td>
<td>33 (6.6)</td>
<td>*$P &lt; 0.0001$</td>
</tr>
<tr>
<td>Both</td>
<td>66 (11.1)</td>
<td>21 (4.2)</td>
<td>*$P &lt; 0.0001$</td>
</tr>
<tr>
<td>Direct cue only</td>
<td>75 (12.6)</td>
<td>62 (12.4)</td>
<td>$P = 0.9948$</td>
</tr>
<tr>
<td>Subtotal</td>
<td>247 (41.7)</td>
<td>116 (23.3)</td>
<td></td>
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</table>

In both tasks, the period of analysis covered 400 ms after cue onset. Numbers in parentheses indicate the percentage of neurons out of the total. *: a statistical significance ($P < 0.01$).
neurons selective both for the instruction and for the spatial target location in the direct cue task, and neurons selective only for the spatial target location. The distribution of the three groups of neurons was different between PMd and PMv ($\chi^2$ test, $P = 0.0023$). Further examination revealed that the first and second groups of neurons were found more often in PMd ($P < 0.0001$, $\chi^2$ test), whereas the proportion of neurons selective only for the visuospatial cue location was not different between PMd and PMv ($P = 0.3046$, $\chi^2$ test). These results revealed that PMd neurons were more selective during the symbolic cue task than were PMv neurons, whereas neurons in both PMd and PMv were selective during the direct cue task.

Laterality preference and excitatory/inhibitory responses

We first examined whether the right or left instruction cue led to greater changes in the instruction period activity (activity during 400 ms after the cue onset) compared with the baseline period activity (activity during 500-ms period preceding the cue onset), irrespective of increase or decrease of activity; we defined the cued side that led to greater changes in activity as the preferred side and the opposite side as the nonpreferred side. The laterality preference for action-selection responses in the symbolic cue task was defined as ipsilateral or contralateral, depending on whether the preferred side of neuronal responses (i.e., left or right instruction) coincided with or was opposed to the left hemisphere, from which we recorded neuronal activity. For the direct spatial-target cue responses, the preference was defined as ipsi- or contralateral depending on whether the preferred side of the target-cue position [i.e., leftward (T1–T2) or rightward (T4–T5) direction] coincided with the left hemisphere. Subsequently, instruction responses were classified from the perspective of excitation and inhibition of neuronal activity by separating the population of neurons into two groups: neurons the activity of which for the preferred side increased during the instruction period compared with the baseline period (excited response) and neurons the activity of which decreased for the preferred side during the instruction period compared with the baseline period (inhibited response).

Based on the preceding classifications, we calculated population activity separately for excited and inhibited groups. To detect overall activity profiles in each area, we included all neurons in the database, irrespective of significance in the laterality selectivity ($n = 593$ in PMd and $n = 498$ in PMv). Results of the analyses applied to the activity during the symbolic cue task are shown in Fig. 5. The population activity of PMd neurons is shown in Fig. 5A for the excited response ($n = 346$) and in B for the inhibited response ($n = 247$). Figure 5C shows the difference in activity between the preferred and nonpreferred sides for the excited (red line) and inhibited (magenta line) response groups. The results of the same analyses for PMv neurons are shown in Fig. 5D for the excited response group ($n = 315$), in E for the inhibited response group ($n = 183$), and in F for the activity differences. By comparing the laterality differences between PMd and PMv for the excited and inhibited groups separately, we found that the selectivity was greater for PMd than for PMv in both groups (during the period of 400 ms, Kolmogorov–Smirnov test; $P < 0.0001$ for the excited group, $P = 0.0014$ for the inhibited group).

Results of the analyses applied to the activity during the direct cue task are shown in Fig. 6. To detect overall activity profiles in each area, we included all neurons in the database, irrespective of significance in the laterality selectivity ($n = 593$ in PMd and $n = 498$ in PMv). The population activity of PMd neurons is shown in Fig. 6A for excited responses ($n = 346$) and in B for inhibited responses ($n = 247$). Figure 6C shows the difference in activity between the preferred and nonpreferred sides for the excited (purple line) and inhibited (blue line) response groups. Figure 6D shows results of the analyses for PMv neurons with regard to excited responses ($n = 310$), E shows results of the analyses for inhibited responses ($n = 188$), and F shows results of the analyses for laterality selectivity. We then compared laterality selectivity between PMd and PMv neurons separately for the excited and inhibited groups. We found that selectivity of PMd and PMv neurons were not distinguishable for excited responses, and the selectivity was greater for PMd than PMv neurons in inhibited responses (during 400 ms; Kolmogorov–Smirnov test, $P = 0.0062$ for the excited responses, $KS = 0.0438$; $P = 0.0120$ for the inhibited responses, $KS = 0.1529$).

Time course and magnitude of right/left selectivity for symbolic cue and direct cue task

To examine the time course and magnitude of activity of neurons with significant right/left selectivity in symbolic cue task or direct cue task (Table 3), we calculated population activity of these selective neurons (Fig. 7). We pooled the data from PMd and PMv because the selective neurons themselves showed similar responses. In the symbolic cue task, the right/left selectivity reached to 10 and 9 spike/s for excited response and inhibited response, respectively (Fig. 7A). In the direct cue task, the selectivity reached to 17 and 15 spike/s for excited and inhibited activity (Fig. 7B). The extent of selectivity was comparable to that for the motor plan during the motor preparation period preceding the motor execution (Fig. 8 in Nakayama et al. 2008).

We calculated the latency of the selectivity defined as the time when the selectivity exceeds the mean $\pm 5$ SD of the baseline period (500-ms period preceding the cue onset). We found that the latency of excited response was slightly shorter than inhibited response both in the symbolic cue task (150 ms for excited, 170 ms for inhibited response) and in the direct cue task (90 ms for excited, 110 ms for inhibited response). The data also revealed that the latency was generally longer in the symbolic cue task than the direct cue task, which is consistent with the result obtained by analyzing the activity of each neuron (Fig. 4).

Relationship between laterality preference and excited/inhibited responses

In Table 4, we summarized the relationship between the laterality preference and the excited/inhibited responses of PM neurons that showed significant right/left selectivity in either of the two tasks. The following findings emerged from this analysis. 1) In the symbolic cue task, a substantial proportion of PMd neurons encoded the right/left selectivity information by decreasing activity (33%, 57 of 172 PMd neurons). 2) In the symbolic cue task, the number of neurons encoding contralateral or ipsilateral side was not different in both the excited and inhibited response groups. 3) In the direct cue task, inhibited responses were found more often in PMd than PMv (chi-square test,
In the direct cue task, excited response group showed contralateral preference (binominal test, \( P = 0.0001 \) in PMd, \( P = 0.0080 \) in PMv), whereas inhibited group did not (binominal test, \( P = 1 \)).

**Distribution of selective activity**

Figure 8 shows the spatial distribution of neurons exhibiting right/left selectivity in response to the symbolic action-selection cue (A) and the direct spatial-target cue (B). The proportion of right/left selective neurons is presented as a fraction of the total number of task-related neurons, projected onto a 1 × 1-mm pixel of the cortical surface. Neurons selective for the symbolic action-selection cue were found throughout the surveyed area of the caudal PMd with a tendency toward higher concentration caudodorsal to the genu of the arcuate sulcus, corresponding to the ventral part of F2 (Matelli et al. 1985). We counted the number of selective neurons separately in a rostral sector (posterior bank and convexity region of the arcuate sulcus) and a caudal sector (closer to the border with the primary motor cortex) to examine the relationship between rostrocaudal localization and neuronal selectivity. The arbitrary rostrocaudal boundary is indicated with a green dotted line in Fig. 8A. The number of selective neurons in the rostral sector of PMd was significantly greater (37 vs. 22%, \( P = 0.0001 \); \( \chi^2 \) test). By contrast, the density of selective PMv neurons was greatly reduced, and the number of right/left selective neurons was not different between rostral and caudal sectors of PMv (11 vs. 10%, \( P = 0.8869 \); \( \chi^2 \) test). We then analyzed the number of right/left selective neurons in the direct cue task separately for rostral and caudal sectors (the boundary is indicated with a green dotted line in Fig. 8B). The analysis revealed that the selective neurons were found more frequently in rostral than caudal sector in both PMd (29 vs. 19%, \( P = 0.0032 \); \( \chi^2 \) test) and PMv (22 vs. 10%, \( P = 0.0008 \); \( \chi^2 \) test). By contrast, we did not find any differences dorsoventrally. We did not find any regional differences in the latency of the selective activity.

**DISCUSSION**

This study examined the properties of PM neurons responding to two different visual instructions: the symbolic action-
selection cue indicating whether to select the right or left target at a conceptual level and the direct spatial-target cue directly indicating the location of the forthcoming target. The comparison of neuronal responses to the two sets of instructions revealed that the conceptual action plan associated with the symbolic cue is represented predominantly in PMd neurons with a longer latency (150 ms), whereas both PMd and PMv neurons are involved with a short latency (90 ms) when the motor target is directly specified. We confirmed that the latency difference could not be explained by the fact that the symbolic cue was presented at the center of the screen (on the fixation point) because the response latency to the appearance of the visuospatial cue was not different depending on whether the cue appeared at the center or at the periphery of the screen. The second major finding was that PM neurons receive information from symbolic visual cues for ipsilateral as well as contralateral action selection, whereas excited responses of PM neurons to the direct spatial-target cue are biased toward the visual cues presented contralaterally. These findings suggest a pair of distinct brain circuits feeding into the PM.

**Exploring input stages of information processing in the premotor cortex**

This study examined response properties of PM neurons to the appearance of visual signals in two different conditions. In the direct cue task, we expected that by asking the monkey to gaze at a fixation point before the appearance of the first cue, we would be able to observe activity mostly reflecting a visuospatial input rather than the motor preparation. We observed that neuronal activity exhibited a transient spatial selectivity, which dropped shortly after the cue onset (Fig. 7B). Obtaining this type of activity suggests that the animal hardly initiated motor preparation toward the target at this stage although it detected its appearance. Based on this observation, we wish to propose that the two-step presentation of cues is useful for detecting the activity reflecting input signals. In the symbolic cue task, we presented a motor instruction while the forthcoming movement itself was kept undetermined. Thus in this study, we used the two strategies to examine the input stage of information processing in the PM. In either case, we found right/left selective neuronal responses with magnitudes

**FIG. 6.** Time courses of the excited and inhibited responses to the direct spatial-target cue. A and D show excited responses, whereas B and E show inhibited responses. Purple and blue lines represent the time course of activity in response to the cue that appeared at a preferred side, and the gray lines represents the nonpreferred side. C and F: bin-by-bin plots of differences in activity calculated as the difference between the data for the preferred and nonpreferred sides; purple line represents excited responses (A and D), and blue line represents inhibited responses (B and E). A–F: the translucent ribbons around the solid line indicate SE.
of >8 spike/s on average. Because the magnitude of selective activity was comparable to that of the movement selective activity during the motor preparation period (10 spike/s, see Fig. 8D in Nakayama et al. 2008), the visual responses in the two tasks were deemed to be substantial.

It is of note that PM neurons responding to visual cues may often exhibit modulations of activity characterizing a diverse aspect of visuomotor behavior at later stages of behavioral tasks. For example, the neuron illustrated in Fig. 3 showed short-latency visual responses when the cue appeared on the right side of the screen in the direct cue task. On the other hand, the same neuron showed delay-period activity when the right-side target reach was instructed in the symbolic cue task. This observation suggests that a single PM neuron plays multiple roles depending on a task demand or a behavioral context. In the future, it is of interest to examine multi-functionality of neurons possessing sensory responses; dynamic task-phase-dependent changes in the representation of multiple sets of information might play an important role in sensorimotor integration.

### TABLE 4. Relationship between the laterality preference and the excited/inhibited responses

<table>
<thead>
<tr>
<th>Task</th>
<th>Response Type</th>
<th>PMd (Ipsilateral/Contralateral)</th>
<th>PMv (Ipsilateral/Contralateral)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbolic cue</td>
<td>Excited</td>
<td>60/55 $P = 0.7093$</td>
<td>18/25 $P = 0.3604$</td>
</tr>
<tr>
<td></td>
<td>Inhibited</td>
<td>27/30 $P = 0.7914$</td>
<td>7/4 $P = 0.5488$</td>
</tr>
<tr>
<td>Direct cue</td>
<td>Excited</td>
<td>32/58 *$P = 0.0080$</td>
<td>17/55 *$P &lt; 0.0001$</td>
</tr>
<tr>
<td></td>
<td>Inhibited</td>
<td>25/26 $P = 1.0000$</td>
<td>6/5 $P = 1.0000$</td>
</tr>
</tbody>
</table>

The $P$ values indicate the result of binomial test. *, a statistical significance ($P < 0.01$).
Involvement of PMd and PMv in direct specification of target

Many lines of evidence have shown that neurons in PMd and PMv reflect the visuospatial information specifying a target (Boussaoud et al. 1993; di Pellegrino and Wise 1993; Godschalk et al. 1985; Lebedev and Wise 2001; Rizzolatti et al. 1981; Shimodzono et al. 1997; Weinrich et al. 1984). The present study directly compared the visuospatial response properties of neurons in PMd and PMv of the same animals. We found no differences with respect to response latency (90 ms for both PMd and PMv), frequency of appearance of neurons selective only for the visuospatial position (13% in PMd, 12% in PMv), and contralateral dominance of excited response (64% in PMd, 76% in PMv). Furthermore, the extent of selectivity of excited responses was comparable in the two areas, although inhibited responses were found more often in PMd than PMv (χ² test, Ρ = 0.0004; Table 4) and the extent of selectivity of inhibited responses was greater in PMd (Fig. 6, C and F). The similarity in these diverse aspects of visual responses was unexpected because PMd and PMv are interconnected with different portions of the parietal cortex. The spatial information of PMd (F2 and the ventrorostral part F2) is thought to derive from PEC, V6A, and the medial intraparietal area (MIP), whereas that of PMv is viewed as originating from the ventral intraparietal area (VIP) and area 7b (Caminiti et al. 1996; Colby and Duhamel 1991; Galletti et al. 2003; Luppino et al. 1999; Matelli et al. 1998; Pesaran et al. 2008; Shipp et al. 1998; Snyder et al. 1997; Tanne-Gariepy et al. 2002; Tomassini et al. 2007; Wise et al. 1997). Further studies are needed to compare the nature of the spatial representation in the two areas, with respect to, e.g., the frame of reference.

By separately examining the laterality selectivity for the excited and inhibited responses (Table 4), we found that contralateral preference is evident only for the excited responses, suggesting that they are driven by the excitatory inputs originating from other structures, such as the parietal cortex. By contrast, we did not find the laterality bias in the inhibited responses (Table 4). The 20-ms delay in the development of the selectivity (Fig. 7B) might suggest that local circuits make the inhibited response within PM. However, it is possible that the inhibited response is provided by the interaction with other structures, such as the indirect pathway of the basal ganglia.

Involvement of PMd and PMv in selecting action cues based on visual instruction cues

The crucial involvement of PMd in retrieving motor instructions from visual-object cues (i.e., conditional visuomotor mapping) has been suggested by lesion or interference studies (Halsband and Passingham 1985; Kurata and Hoffman 1994; Petrides 1986; Schluter et al. 1998) and by studies examining neuronal activity in task-performing monkeys (Boussaoud and Wise 1993; Kurata and Wise 1988; Mitl et al. 1991). In our current behavioral task, the visual object indicated the motor instruction only at an abstract level (i.e., the virtual action plan) because the actual motor target remained undetermined until the choice cue was presented later. We found that the conceptual action-selection information retrieved from the symbolic cue was represented predominantly in PMd and minimally in PMv. We also found that both the excited and inhibited responses possessed bilateral preference. This is in sharp contrast to the responses to the direct spatial-target cue; the excited responses were biased to the space contralateral to the hemisphere from which the neuronal activity was recorded. The functional significance of the bilateral representation of the motor instruction is unclear. However, the bilateral representation might be advantageous for the process of motor planning because local circuits in a single hemisphere could collect and integrate all necessary information.

It is noteworthy that the selectivity for the conceptual action-selection appeared in PMd as early as 150 ms after the onset of the cue. A comparable response latency of 110 ms was reported for the specification of a motor target based on a color cue (Cisek and Kalaska 2005). Another study reported selectivity for the Go/No-Go instruction starting earlier than 200 ms after a visual cue (Wallis and Miller 2003). These early responses are remarkable, because PMd is not directly connected with the areas in the ventral stream (Ungerleider and Mishkin 1982), such as the area V4 or the inferior temporal cortex (IT) where neuronal activity reflects the identity of visual objects (Desimone et al. 1984; Miyashita and Chang 1988; Tanaka 1996).

Three major candidates have been proposed as pathways linking the IT to PMd to provide visually cued information: the prefrontal cortex, the posterior parietal cortex, and the basal ganglia (Murray et al. 2000; Wise and Murray 2000) but not the cerebellum (Glickstein et al. 1985; Nixon and Passingham 2000). With respect to the first possibility, two studies have shown that the start of instruction selectivity, or Go/No-Go selectivity, occurred later in the prefrontal cortex than in PMd (Hoshi and Tanji 2004, 2006; Wallis and Miller 2003). Furthermore, the direction selectivity for the conditionally instructed motor response started at 250 ms in the prefrontal cortex (Asaad et al. 1998), as much as 100 ms later than in PMd. Thus in learned and familiar contexts, motor information appears earlier in PMd than in the prefrontal cortex, rendering the first possibility unlikely. As for the second pathway, the IT is connected with the anterior part of the inferior parietal cortex (AIP), which in turn is connected preferentially with PMv (Rozzi et al. 2006). Our findings indicating minor roles for PMv neurons in cueing actions provide evidence against the second possibility. It is more likely that the IT-AIP connection serves other purposes, such as guiding hand actions (Sakata et al. 1995) and/or perceptual processing of visual objects (Durand et al. 2007). Another route via the parietal cortex is through areas centered at the lateral intraparietal area (area LIP); LIP is interconnected with the area V4 and IT (Blatt et al. 1990). LIP neurons have been shown to be sensitive to the color or shape of visual object (Sereno and Maunsell 1998; Toth and Assad 2002). Although LIP is not directly connected with PM, its widespread connection with other parietal areas, including area 7a, area 7b, and the ventral intraparietal area might serve as a substrate for a visuomotor transformation (Blatt et al. 1990). Because PMd is under the strong influence of the superior parietal lobule (Caminiti et al. 1996; Galletti et al. 2003; Matelli et al. 1998; Wise et al. 1997), it would be of interest to examine systematically the object selectivity in this parietal region although a study negated a possibility of object representation (Calton et al. 2002). The remaining candidate is the third one, namely the basal ganglia. The crucial involve-
ment of the basal ganglia in conditional motor behavior has been revealed in single-cell studies (Brasted and Wise 2004; Buch et al. 2006; Hadj-Bouziane and Boussaoud 2003; Inase et al. 2001; Tremblay et al. 1998) and lesion studies (Canavan et al. 1989; Nixon et al. 2004) of monkeys and by activation studies in humans ( Toni and Passingham 1999; Toni et al. 2001); to prove the crucial involvement of the basal ganglia in the abstract stimulus-response mapping, it remains to be proved that human patients with the lesion cannot perform the task. The basal ganglia have been reported to bias the direction of a forthcoming action (Lauwereyns et al. 2002). Direct comparisons of the onset of direction selectivity in the prefrontal cortex and striatum found that directional information appeared earlier in the striatum (Pasapathy and Miller 2005). The striatum receives afferent connections from the IT (Saint-Cyr et al. 1990; Van Hoesen et al. 1981). On the other hand, the output of the basal ganglia can affect the cerebral cortex through direct and indirect pathways (Alexander and Crutcher 1990). A prevailing view holds that these pathways allow focused selection of a relevant motor program by inhibiting competing opponents (Mink 1996). Our results raise a possibility that excited and inhibited responses might be provided by direct and indirect pathways, respectively (Houk and Wise 1995). Another possibility is that the inhibited response is formed by inhibitory neurons in the cerebral cortex ( Kawaguchi and Kubota 1997). The current study revealed that the latency of inhibited response was 20 ms longer than the excited response (Fig. 7) in both the symbolic cue task and the direct cue tasks. It would be of interest to examine whether the delay of the signal arrival to PM or extra processing within PM caused the delay for the inhibited responses. In relation to the inhibited response, the anticipatory activity before the cue onset, which develops as learning progresses (Buch et al. 2006), can be viewed as a preparatory elevation of activity occurring before the representation of motor information by subsequent decreases in activity. Finally, although we here focused on the three major candidates, the action plan representation is reminiscent of the activity reported in the supplementary eye field ( Olson and Gettner 1995, 1999) and the superior colliculus (Horwitz et al. 2004). In the future, it would be of interest to compare the onset latency of the action plan in these structures. Further, relationship between the hippocampus and PMd should be examined because neuronal activity in the hippocampus has been shown to reflect visuomotor mapping ( Miyashita et al. 1989; Xiang and Brown 1999; Yanike et al. 2004).

**Rostrocaudal functional specification in PMd and PMv**

Our previous report showed that the PMd area dorsal to the genu and the spur of the arcuate sulcus was involved in retrieving a motor instruction from a visual signal (Hoshi and Tanji 2006). In the current study, we again found that neurons in this region responded more frequently to both the symbolic action selection cue and the direct spatial-target cue. Raos et al. (2004) found neurons in this region reflecting a three-dimensional visual feature of targets for grasping. It has been shown that activity of PMd neurons in this region reflect spatial attention to a cue ( Boussaoud 2001; Lebedev and Wise 2001). Wallis and Miller (2003) found that many PMd neurons with rule-selective activity were located dorsal to the spur. Two studies showed that neurons in this region reflected target location regardless of the arm use ( Cisek et al. 2003; Hoshi and Tanji 2006). Cisek and Kalaska further revealed that neurons in this region reflected a potential reach direction ( Cisek and Kalaska 2005) and a process of mental rehearsal ( Cisek and Kalaska 2004). Taken together, these results suggest that the subregion of PMd located dorsal to the genu and spur of the arcuate sulcus plays a central role in the attentional and cognitive control of motor behavior. In the future, it would be of interest to examine the relationship between this area defined functionally and the areas (F7, F2d, and F2vr) classified by anatomical methods ( Luppino et al. 2003; Matelli et al. 1985).

We found that PMv neurons responding to the spatial-target cue were mainly concentrated in the rostral part of PMv: in the caudal bank of the arcuate sulcus and its convexity region. In our previous study, we found that visuospatial feature of the cue was reflected in the same rostral region (Hoshi and Tanji 2006). By touching the skin or moving a small piece of object around the face, we confirmed that neurons in the caudal PMv showed bimodal response properties, responding to tactile stimuli and to an object presented in the peripersonal space ( Fogassi et al. 1996; Graziano et al. 1997). However, neurons...
in this region were less responsive to the visual stimulus presented on the monitor. The existence of two separate groups of PMv neurons either responding to a visual stimulus presented in the peripersonal space or at the reaching distance is consistent with a previous report (Rizzolatti et al. 1981).

Processing of visual signals for direct specification of motor targets and for conceptual representation of action targets

Figure 9 presents a schematic drawing of neural circuits involving PMd and PMv to represent our hypothesis regarding the processing of two sets of information originated from other brain structures. Inputs from the posterior parietal cortex seem to be important for specifying the spatial characteristics involved in reaching for targets: from V6a/MIP/Pe to the PMd and from VIP/PF/PFG to the PMv. These pathways probably contribute to the primate frontal lobe: a novel role for the superior parietal lobule. Cereb Cortex 6: 319–328, 1996.

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