Effects of Image Motion in the Dorsal Premotor Cortex During Planning of an Arm Movement

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Ochiai, Tetsuji, Hajime Mushiake, and Jun Tanji. Effects of image motion in the dorsal premotor cortex during planning of an arm movement. J Neurophysiol 88: 2167–2171, 2002; 10.1152/jn.00102.2002. This study examined whether neuronal activity in the dorsal premotor cortex (PMd) covaries with image motion or actual movement of the arm while planning a target-capturing task when the motor task is guided by an image of the moving arm. For this purpose, we trained a monkey to capture a target on a video screen with the part of the arm displayed on the screen. The target-capturing body part was either the right or left side of the hand image. Because the actual arm movement was invisible, the motor task was guided by the arm image, which was at times right-left inverted on the screen. We found that neuronal activity in the PMd predominantly reflected arm-image movement rather than the actual arm movement, and for half of PMd neurons, the activity differed depending on the target-capturing body-part defined in the right or left side of the arm image.

METHODS

We trained a monkey (Macaca fuscata) to move the image of its right arm captured with a video camera and projected on a screen using a video system. The animal was cared for in accordance with the Guiding Principles in the Care and Use of Laboratory Animals of the National Institutes of Health. The motor task was to capture a target spot displayed on the screen with the specific part of the arm image specified by an instruction spot-signal. The target spot and the instruction were overlaid with the arm image, using an image-superimposing system (Fig. 1D). The task began when the animal placed its hand within a hold position displayed on the screen for 1.0 s (Fig. 1A), and a red spot illuminated either the right or left side of the hand for a duration of 1.0 s, indicating the body part with which the spatial target was to be captured. Subsequently, after a delay period of 1.0 s, a green spot appeared at one of four target positions. For 1.5 s after the appearance of the target spot, the animal had to wait until the initial hold position disappeared from the screen, serving as a go signal to start the target-capturing movement within 500 ms. Actual arm movement was either straight ahead or 30° to the right or left in the horizontal plane. Under the visual image, the arm movement appeared upward or to the right or left on the screen. We used conventional electrophysiological techniques for single-cell recording in the monkey (Mushiake et al. 1991). We applied intracortical microstimulation (ICMS) with 10–20 pulses of 0.2-ms duration at 333 Hz.

The monkey was also trained to perform the motor task when the video image was inverted horizontally, in which case, the image motion was dissociated from the true motion of the arm. Under the image inversion, when the monkey moved its actual arm forward and to the right, the mirror-image arm moved upward and to the left on the screen. After extensive training, the animal was able to adapt to the dissociation and captured the spatial target without much difficulty. After a transition period of 10 trials in the inverted-view condition, the actual movement trajectories and muscle activities were indistinguishable from those observed under the normal-view condition (Fig. 1B). Therefore we analyzed the neuronal data after the initial 10 trials in the inverted-view condition. Hand position was monitored by infrared position detector system (CS949-01, Hamamatsu Photonics) at 250-Hz sampling rate. Eye position was monitored by infrared eye-camera system (R-21C-AS, RMS) at 250-Hz sampling rate. We used magnetic resonance imaging of the brain to identify recording sites with reference to three-dimensional images of cortical sulci. In this study, we focused on preparatory activity and did not deal with the arm image. A preliminary account of this study appeared in abstract form (Ochiai et al. 2001).

INTRODUCTION

The dorsal premotor cortex (PMd) of primates has been implicated in the sensorial guidance of arm movements (Kurata 1994; Rizzolatti et al. 1998; Wise 1985). Recent studies have stressed the importance of visual as well as somatosensory information (Fogassi et al. 1999; Johnson et al. 1996; Wise et al. 1997) sent to the PMd by anatomical connections (Caminiti et al. 1996; Matelli et al. 1998). To guide arm movements, visual inputs are necessary to provide information about the target and also about the configuration of the moving arm (Hoshi and Tanji 2000; Rossetti et al. 1994; Wise et al. 1997). It is not known, however, to what extent neuronal activity in the PMd reflects visual information about the moving arm under behavioral conditions where the image of the moving arm is crucial for guiding the reach movement. Here, we examined whether neuronal activity in the PMd reflects image motion or actual movement of the arm while planning a target-capturing task. For this purpose, we trained a monkey to capture a target on a video screen with an image of the animal’s arm. In addition to movement direction, two other experimental conditions were varied: the right or left side of the hand (hand-side) was used to capture the target. The animal’s hand was shown either as a normal view or inverted image. We found that the majority of neuronal activity in the PMd reflects image motion rather than the actual motion of the arm and the activity also reflects the target-capturing hand-side defined in the right or left side of the arm image.
activity differed from the control-period activity (Mann-Whitney test, $P < 0.05$). Furthermore, we did not detect changes in activity during the preparatory period before the go signal. We also analyzed eye position and movement and did not detect any influence of image-inversion or right-left location of the body part that captured the target.

We then analyzed 138 PMd neurons that were judged as preparatory related. The recording sites of these neurons were concentrated close to the precentral dimple (Fig. 1C), and all were located at least 3 mm rostral to the border between the premotor and the precentral motor cortices as tentatively determined with cortical ICMS (Kurata and Tanji 1986). Of these, 72 neurons were found to be selective for the direction of the target-capturing movement ($P < 0.001$ by ANOVA).

Did this selectivity reflect the direction of image motion or the direction of the actual motion of the arm? To answer this question, we inverted the motion image on the screen horizontally so that rightward motion of the arm would appear leftward and vice versa. Remarkably, in the majority of cases, the PMd neuronal activity reflected the image motion as exemplified in Fig. 2A. For this neuron, the activity was greatest when the image (and actual) motion was directed to the right, regardless of whether the right or left side of the hand captured the spatial target (bottom left). Activity was not seen when the image motion was directed leftward (top left). When the image was inverted horizontally, the same neuron was also active when the image motion was directed rightward (top right), despite the fact that the monkey was actually moving its arm in the leftward direction. Obviously, this neuron did not reflect the actual motion because, with the inverted view, the rightward arm motion was not preceded by detectable activity. A similar trend reflecting image motion was found in 44 PMd neurons tested with image inversion, while in 12 neurons the activity was selective for the actual motion.

We subsequently investigated whether the neuronal activity reflected which side of the hand image captured the target. We found that the activity of 67 neurons of 138 preparatory-related PMd neurons (49%) differed depending on the hand-side that captured the target. Figure 2B shows a typical example in which a PMd neuron is selectively active when the animal used the right side of its hand to capture targets (right) but not when capturing them with the left side of the hand (left).

Did this selectivity reflect the anatomical body part (radial or ulnar) in the image or the relative position (right or left side) of the image? To answer this question, we analyzed neuronal activity with the inverted view. Figure 3 shows a typical result of such an analysis. With the normal view, the neuronal activity was greater when the right side of the hand image (the ulnar side in this case) captured the target (right in A). With the inverted view, the neuronal activity was also greater when the right side of the image was used to capture the target (right in B), although the part capturing the target was the radial side. Thus the selectivity was for the relative position in the image.
that captured the target and not for the anatomical body part. We further found that among the 67 hand-side selective PMd neurons, a majority (n = 36) of the PMd neurons also exhibited image-direction selectivity, while in the remaining 31 neurons the direction selectivity was not significant. We, then, tested the effect of image inversion for 34 of the 67 hand-side selective PMd neurons. It turned out that the hand-side selectivity remained unaffected in 30 neurons (88%), similarly as shown in Fig. 3, while in the remaining 4 neurons, the selectivity was lost when the image was inverted.

**DISCUSSION**

In this study, we found that neuronal activity in the PMd predominantly reflected image motion rather than the real motion of the arm while planning an arm movement guided by an image of the arm. We also found that in half of the PMd neurons the activity depended on which part of the arm was to capture the spatial target. These findings point to a role for PMd neurons in planning arm movements under visual guidance.

The influence of visual signals on neuronal activity in the PMd has been reported extensively (Godschalk et al. 1985; Weinrich et al. 1984; Wise et al. 1997). Reports describing the activity during a preparatory or motor planning period are of particular relevance to our study (Kurata and Wise 1988). It is generally agreed that the motor significance, rather than the attentional or visuospatial significance, of the sensory signals given as instructions affects a large part of the preparatory activity in the PMd (Boussaoud and Wise 1993; Crammond and Kalaska 1994; di Pellegrino and Wise 1993; Hocherman and Wise 1991; Riehle and Requin 1989). Subsequently, Shen and Alexander (1997) found that PMd neurons have directional responses that reflect the spatial target of an intended movement rather than the physical properties of the movement itself when they used a two-dimensional delayed reaching task that dissociated target location from the trajectory of limb movement. Our present findings are in accord with this report in that a majority of PMd neurons did not reflect the direction of actual movement performed. On the other hand, it can be argued that the direction of the image motion may be interpreted as the position of the spatial target, just as Shen and Alexander concluded in their study. Concerning this possible
interpretation, we will perform further analysis in a future study. It should also be mentioned that the image motion-related activity may, at least in part, be related to spatial attention to the target.

Our study also demonstrated that neuronal activity in the PMd reflected the hand side that was instructed to capture the spatial target. This finding may be taken to indicate that some PMd activity is moving-object centered. This property is reminiscent of object-centered activity reported in the supplementary eye field (SEF) (Olson and Gettner 1999), although the reported activity reflected the relative position of target within visual object to which saccades were oriented. We tested whether the 67 neurons exhibiting this selectivity were also selective for the location of the spatial target. ANOVA analysis indicated that 38 neurons did not exhibit selectivity for the location of the spatial target ($P > 0.05$). For these 38 neurons, selectivity reflected the point of interest in the arm image without being sensitive to the spatial target. For the remaining 29, the target selectivity was significant ($P < 0.05$), indicating that the neurons were selective to both the target-capturing part in the image and the location of the spatial target. It is interesting, however, that the image-location selectivity was not anchored to the anatomical body part but reflected relative position in the image (cf. Graziano 2001; Kakei et al. 2001). Taken together, PMd activity during preparation for an upcoming reach movement seems to be closely involved with processing visual information for the spatial guidance of the movement trajectory.

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REFERENCES


