



VENTRAL PREMOTOR CORTEX AND THE LATERALITY OF MOTORIC CHOICES

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1. Abstract

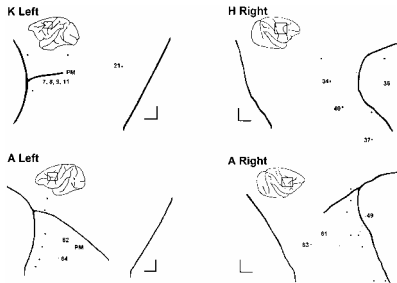
Neurons in the ventral premotor cortex (PMv) have large visual fields in near peripersonal space anchored to specific parts of the face, arms and/or hands, suggesting that the PMv plays an important role in the interaction of these body parts with visually perceived objects (Rizzolatti et al., 1996, Graziano et al., 1997). To elucidate the role of the PMv in visually guided interactions, we studied the reaching behavior of 3 rhesus monkeys while the PMv was reversibly inactivated by intracortical injection of muscimol. Unilateral PMv inactivation produced no overt deficit in a monkey's ability to reach out and grasp a food morsel with the contralateral hand, nor did the monkey have difficulty in extracting a food morsel from a narrow well, or in performing a visually-cued individuated finger movement task. Unilateral PMv inactivation did alter the laterality of the monkey's motoric choices, however. When two food morsels were presented simultaneously to the monkey's right and left, the likelihood that the monkey would make motoric responses contralateral to the inactivated PMv was reduced dramatically. After PMv muscimol injections, a monkey was less likely to initially turn its head contralaterally to inspect food morsels, less likely to reach for the food morsel with its contralateral hand, and less likely to take the morsel on its contralateral side. Catch trials in which a food morsel was present only on one side showed no evidence that the monkey neglected that side. We infer that when equivalent visually perceived objects for behavioral interaction are present bilaterally, the PMv plays a role in choosing the object to which motoric responses will be directed, and the body part that will be used in the response.

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2. Methods

Effects of reversible inactivation of the PMv were studied in three Rhesus monkeys. In each experimental session, BEFORE muscimol injections, the loosely restrained monkey first performed a) a double simultaneous presentation task and b) a food well task. The monkey then was placed in a primate chair, where it performed c) our visually-cued individuated finger movement task. As the monkey performed this task, muscimol was injected intracortically at multiple sites as shown below. Once the monkey was done performing the individuated finger movement task, it again was loosely restrained, and again performed the food well and double simultaneous presentation tasks AFTER muscimol injections, while the PMv was inactivated. After some sessions, the monkey performed the double simultaneous stimulation task again the next day to assess RECOVERY.

Table 1: Summary of muscimol injection sites and parameters for three monkeys (K, H, A). Columns include Monkey, Session, Site, Depth, Volume, and various behavioral metrics.

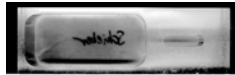


2a. Double Simultaneous Presentation



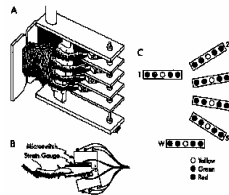
Each double simultaneous presentation trial began as the examiner brought his closed hands together directly in front of the monkey (above left). Once the monkey's gaze was directed at the examiner's closed hands in the midline, the examiner swept one hand to either side and simultaneously opened them, revealing a food morsel (apple piece approximately 0.5 to 1 cc) in one or both hands, at a comfortable reaching distance from the monkey. With no time constraints, the monkey looked at the food morsels (above middle), and then reached with either hand to take the bait from one of the examiner's hands (above right). The examiner then withdrew his other hand without allowing the monkey to take the food morsel that might be there. Though the monkey often looked back and forth at the food morsels on its right and left side, the monkey rarely if ever tried to take both food morsels at once. Instead, the monkey typically glanced back and forth, and then took one food morsel using a precision pinch, all within 1 to 2 sec. The monkey typically performed up to 10 blocks of 6 trials each. Though the examiner's movements were the same on all trials, within each block a food morsel was actually present bilaterally in 4 trials, only on the monkey's right in 1 trial (right catch trial), and only on the left in one trial (left catch trial). The order of these 6 trials was randomized within each block. Each trial was scored for: i) the direction (right or left) in which the monkey first turned its head to look at a food morsel, ii) the hand (right or left) the monkey used to take the food morsel, and iii) the side (right or left) from which the monkey took the food morsel. The side of the initial head turn, the arm used and the side from which the food morsel was taken, each were compared before versus after muscimol injections using Fisher's Exact Test.

2b. Food Well



The monkey also was examined retrieving small food morsels (apple pieces approximately 0.5 to 1 cc) from two wells machined in a block of clear Lucite: one well large enough to permit entry of the entire hand (89 mm high, 38 mm wide, and 45 mm deep), and another well small enough to permit entry of only one finger (29 mm high, 8 mm wide, and 23 mm deep). An investigator presented these food wells to the monkey one at a time, with the monkey minimally restrained as above. The wells were presented at eye level (monkeys K and A) or at floor level (monkey H). To induce the monkey to use the right hand on some trials and the left hand on other trials, the food wells were presented at a comfortable reaching distance to the monkey's right or left, respectively.

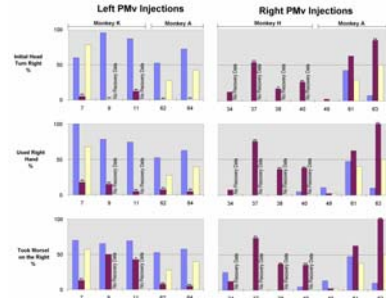
2c. Visually-Cued Individuated Finger Movements



In the individuated finger movement task, the monkey's the right hand was placed in a pistol-grip manipulandum (A) that separated each finger into a different slot. At the end of each slot, each fingertip lay between two microswitches (B). By flexing or extending a digit a few millimeters, the monkey closed the ventral or dorsal switch, respectively. The monkey viewed a display of light-emitting diodes (C) that cued him to flex or extend one finger, closing only one switch at time, for a reward. Each instructed movement is denoted by the number of the instructed digit (1 = thumb to 5 = little finger, w=wrists) and the first letter of the instructed direction (f = flexion, e = extension).

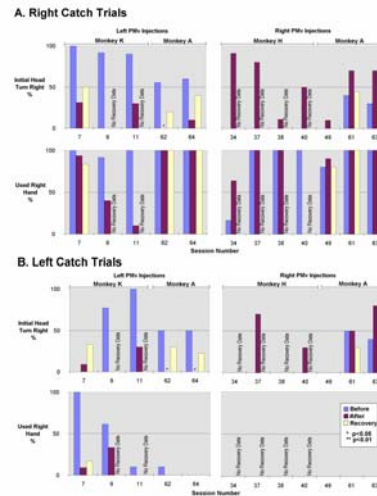
PMv inactivation had no effect on performance of the visually-cued individuated finger movement task, or on the monkeys' dexterity in retrieving food morsels from either the large or small food well.

3. PMv Inactivation Decreased the Likelihood of Contralateral Motoric Choices



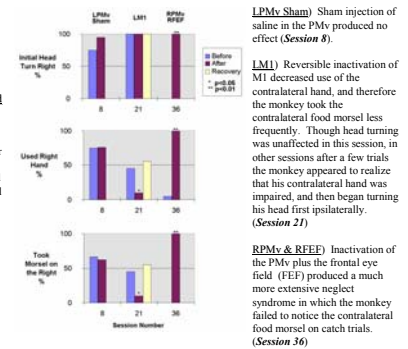
Though the monkeys showed no paresis or inaccuracy in reaching and grasping with either hand after unilateral PMv inactivation, the laterality of their motor behaviors was systematically altered in the double simultaneous presentation task. The figure at left shows the percentage of double simultaneous presentation trials in which the monkey initially turned its head to the right (top), used its right hand to take the food morsel (middle), and took the food morsel on its right (bottom), for each session in which injections were made in the PMv unilaterally. For each session, these percentages are shown for double simultaneous presentation trials performed BEFORE muscimol injection, AFTER muscimol injection, and (where available) after RECOVERY the next day. Only trials in which food morsels actually were present bilaterally are included here. After muscimol injections that inactivated the PMv, the monkey was less likely to turn its head contralaterally, less likely to use its contralateral hand, and less likely to take the food morsel on its contralateral side.

4. Catch Trials Showed No Neglect of the Contralateral Side



Every block of 6 trials included two catch trials: one trial with a food morsel present only on the monkey's right (A), another trial with a food morsel only on the monkey's left (B). In catch trials, none of the three monkeys ever failed to find and take the food morsel promptly. When the monkey initially turned its head toward an empty examiner's hand, the monkey immediately turned toward the opposite examiner's hand and took the food morsel, even when the morsel was contralateral to the inactivated PMv. In catch trials, as in trials with food morsels were present bilaterally, the likelihood that the monkey would turn its head initially to the right tended to be decreased after left PMv inactivation, and increased after right PMv inactivation. The laterality of hand use in catch trials, however, was relatively unaltered by unilateral PMv inactivation. Especially for monkeys A and H, the hand used remained tightly correlated with the side from which the food morsel was taken, here determined by the type of catch trial. Such was the case before muscimol injection, after muscimol injection, and after recovery the next day.

5. Comparison Controls



LPMv Sham Sham injection of saline in the PMv produced no effect (Session 8). LMI Reversible inactivation of M1 decreased use of the contralateral hand, and therefore the monkey took the contralateral food morsel less frequently. Though head turning was unaffected in this session, in other sessions after a few trials the monkey appeared to realize that his contralateral hand was impaired, and then began turning his head first ipsilaterally. (Session 21) RPMv & REEF Inactivation of the PMv plus the frontal eye field (FEF) produced a much more extensive neglect syndrome in which the monkey failed to notice the contralateral food morsel on catch trials. (Session 36)

6. Summary

- 1) Unilateral, reversible inactivation of the PMv decreased the likelihood that a monkey would act contralaterally when presented with a right/left motoric choice. We observed similar effects on: - which way the monkey initially turned his head - which hand the monkey used to take a food morsel - the side from which the monkey took the food morsel
- 2) Catch trials demonstrated that the monkey did not neglect, and was able to attend to, contralateral stimuli.
- 3) Performance of visually-cued individuated finger movements, and dexterity in retrieving morsels from food wells were unaffected by PMv inactivation.
- 4) Alterations in the laterality of motoric choices thus occurred - without alteration in the monkeys' ability to attend to contralateral stimuli - without motoric impairment of the contralateral arm and hand

7. Conclusions

- 5) When multiple objects are present the PMv may play a role in choosing which object to target for motoric interactions, as well as choosing which body part to deploy for the interaction. While the present study deals only with right/left choices, we speculate that the PMv may be involved in choices among other features as well.

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