Combination of Hand and Gaze Signals During Reaching: Activity in Parietal Area 7m of the Monkey

S. Ferraina, P. B. Johnson, M. R. Garasto, A. Battaglia-Mayer, L. Ercolani, L. Bianchi, F. Lacquaniti, and R. Caminiti. Combination of hand and gaze signals during reaching: activity in parietal area 7m of the monkey. J. Neurophysiol. 77: 1034–1038, 1997. The role of area 7m has been studied by recording the activity of single neurons of monkeys trained to fixate and reach toward peripheral targets. The target was randomly selected from eight possible locations on a virtual circle, of radius 30° visual angle from a central target. Three tasks were employed to dissociate hand- from eye-related contributions. In the first task, animals looked and reached to the peripheral target. In a second task, the animal reached to the peripheral target while maintaining fixation on the central target. In the third task, the monkey maintained fixation on peripheral targets that were spatially coincident with those of the reaching tasks. The results show that cell activity in area 7m relates, for some cells to eye position, for others to hand position and movement, and for the majority of cells to a combination of visuomotor and oculomotor information. This area, therefore, seems to perform an early combination of information in the processing leading from target localization to movement generation.

INTRODUCTION

Reaching for a visual target requires multisensory fusion to generate the appropriate motor commands. Retinal, gaze position, and arm position signals are combined to coordinate eye and hand movements to the target.

We have begun to study the neural bases of this process in the medial parietal area 7m, which receives association inputs from some visual areas of the occipitoparietal cortex (Cavada and Goldman-Rakic 1989; Matelli et al. 1995), and has frontal lobe projections (Cavada and Goldman-Rakic 1989; Matelli et al. 1995), to a reaching-related region of premotor cortex (Caminiti et al. 1996; Johnson et al. 1993, 1996; Tanné et al. 1995). A brief report (Thier and Andersen 1993), based on microstimulation studies, assigned to 7m a role in oculomotor functions. This area may therefore be considered as an early stage where different sources of information are combined in the process leading from target localization to arm movement generation.

The current research was performed to assess whether a relationship exists between neuronal activity and reaching in area 7m and, if so, to elucidate some of the underlying coding mechanisms.

METHODS

Animals and tasks

Two rhesus monkeys (Macaca mulatta; body weights 3.7 and 3.3 kg) were used in this study.

The monkeys sat on a primate chair with head fixed, 17 cm in front of a capacitive touch-sensitive (MicroTouch Systems, Wilmington, MA) computer monitor used to display the tasks and control the animals’ behavior. Monkeys performed three different tasks.

Two arm-reaching tasks were performed with the hand contralateral to the hemisphere where recordings were made. Movements were from a central position to eight peripheral targets (subtending 0.76° visual angle) located on a circle of 13 cm radius (30° visual angle), at 45° angular intervals.

In the reaching task (R), a center light was first presented, and the animals both fixated it (Fig. 1, D and F) and touched it with the hand for a variable center holding time (CHT, 1–1.5 s) after which one of the eight targets was lit, in a randomized block design. Within a reaction and movement time of prespecified ranges (RT, 0.5 s, upper limit; MT, 1 s), the animals moved the eyes (Fig. 1, D and F) and the hand to that target and kept them there for a variable target holding time (TH, 1–1.5 s) before receiving a liquid reward.

In a separate task (Rang), to dissociate the spatial position of the hand from that of the eyes, monkeys were required to maintain fixation on the central target while reaching to peripheral targets. A fixation point (consisting of 2 white bars of 0.4° side, divided by a narrow black gap of similar size) and a center light were presented, with a vertical offset of 3°. The animals fixated the first (Fig. 1, E and G) and touched the second for a variable CHT after which one of the eight targets was lit, while the center light was extinguished. Within prespecified RT and MT, the animals moved the hand, but not the eyes (Fig. 1, E and G), to the target and maintained the hand there for a variable TH, until a 90° rotation of the fixation point occurred. Premature breaking of fixation was detected by the computer, which then aborted the trial. Epochs had the same duration as in the R task.

The eye-position task was used to study the influence of eye-position signals on cell activity. The monkeys maintained fixation (1–1.5 s) on the same eight targets used in the visuomotor tasks.

Eye position signals, derived from implanted search coils, were sampled at 100 Hz, with 1 arc s resolution. Circular windows of 7.5° diam around the targets were used to control fixation accuracy. The position of the hand was measured by the use of the touch screen, with 0.28 × 0.3 mm resolution. Windows for hand accuracy were 3-cm-diam circles centered on the targets.

Neural recording

Neuronal activity was recorded extracellularly by means of glass-coated PT-Ir electrodes “labeled” with the fluorescent carboxyanines DiI or DiI-C5 (Molecular Probes, Eugene, OR), to facilitate reconstruction of the microelectrode tracks. Behavioral control and collection of neural and behavioral data were performed with...
FIG. 1. Insets (A and B) of the brain figure (C) displaying the entry points (dots) of microelectrode penetrations in the left hemispheres of 2 monkeys. IPS, POs, and CGs indicate intraparietal, parietooccipital, and cingulate sulci, respectively. Eye-movement records in the R task (D and F: 4 replications for every movement direction) and in R fix task (E and G: 32 replications) obtained during collection of neural activity of the the cells shown in Figs. 2 and 3, respectively. Crosses indicate target locations (30° visual angle); circles in E and G indicate the size of the fixation window (7.5°).

the use of personal computers. The eye coil, recording chamber, and head holder were implanted aseptically under general anesthesia (pentobarbital sodium, 25 mg/kg iv).

Data analysis

The mean firing rates during the different epochs of the tasks were calculated for each trial. The repeated measures data were analyzed by using the 5V program of the BMDP (Statistical Software, CA) statistical package, to assess 1) significant modulation (Wald $\chi^2$ test) of cell activity during RT, MT, and THT, relative to the control time (CHT); 2) significant variations of cell activity with arm movement direction (during RT and MT) and position (THT) or with eye position during eye-target holding time of the eye-position task; 3) differences in cell activity in R versus R fix tasks. The interaction term (task $\times$ direction) of this last analysis
was used to assess significant difference in the directional properties of cells across task conditions. The significance level for all statistical tests was set to 0.05.

Directional tuning curves (Georgopoulos et al. 1982) and preferred directions (PDs) of cells were determined by fitting, with a two-term harmonic Fourier series, the discrete firing rates measured at the eight target directions during the different epochs (RT, MT, and THT). This was necessary to account for the existence of two peaks of activity (corresponding to 2 different PDs) in many cells.

RESULTS

A total of 234 single cells were studied during 33 successful microelectrode penetrations in area 7m of two hemispheres (Fig. 1, A–C), as determined by the reconstruction of the fluorescent microelectrode penetrations in the histological sections. Sixty-five cells had a complete set of experimental data and were retained for further quantitative analysis. These cells were studied at depths of up to 6,350 μm from the cortical surface.

![Fig. 2](http://jn.physiology.org/content/159/5/1036/F2)

**FIG. 2.** Impulse activity of a neuron in area 7m recorded during the R (A) and Rfix (B) tasks. Rasters of 4 replications for every movement direction (arrows) were aligned to movement onset (M). Longer vertical bars indicate, from left to right, beginning of the trial, target presentation (T), movement onset, beginning (H) and end of target holding time (THT). C: polar plots of mean impulse activity for different epochs of both task conditions (R, continuous line; Rfix, interrupted line). For both task conditions, circles indicate mean frequency of discharge during the control period (CHT), taken as control time. D and E: rasters and polar plots, respectively, of the activity of this same neuron in the eye-position task. Positions of the rasters indicate the different locations in space where the animal was fixating during the eye-target holding time.
Behavioral data collected while recording cell activity in the R task showed that average eye RT was 133.2 ± 12.7 (SD) ms; average eye MT was 87 ± 13.3 ms. Thus the eyes arrived at the target ~220 ms after target presentation. The hand RT was on average 347.2 ± 20.3 ms. Therefore the movement of the hand typically began after the eyes were immobile on the target and ended 262.8 ± 51.1 ms later.

In the reaching tasks, 55 (84.6%) cells were significantly modulated during the RT and/or MT and THT, relative to the CHT. Out of these task-related neurons, 41 cells were directionally modulated during RT and/or MT and were termed directional reaching-related neurons. Forty-one cells displayed static positional effects during THT, because their activity differed while the hand was maintained immobile at the different target locations.

The activity of 27 cells was compared during the R and RT, MT, and THT. Data from an example neuron are shown in Fig. 2. In the R task (Fig. 2, A and C) this cell was significantly modulated during RT, MT, and THT, relative to the control period (CHT). It was directional during both MT and THT.

In the Rfix task (Fig. 2, B and C), cell activity was significantly different from that measured in R task, in all epochs. This neuron was also modulated in the eye-position task (Fig. 2, D and E), while the eyes were maintained immobile at different target locations, which corresponded to those occupied by both eyes and hand during THT of the R task. In the eye-position task the PD of the cell was at 179.7°, very similar to that seen during THT of the R task (175.3°).

These results suggest that eye-position signals play a large role in the modulation of this neuron during reaching. However, the presence of directional tuning during the Rfix task further suggests that the cell processes additional information related to hand motor control. Further, interactions between eye and hand position signals are evident in the different levels of activity when eye and hand together are held motionless at the target, as compared with when eye and hand positions are dissociated.

Another potential type of processing is suggested by the activity of the neuron of Fig. 3. In the R task (Fig. 3A), this cell was significantly modulated and directional during RT, MT, and THT. In the Rfix task, only during MT was cell activity significantly different from that observed in the R task. This neuron was not directionally modulated in the eye-position task (p = 0.128; Fig. 3B). The largest modulation of activity of this cell occurred when the hand approached the visually fixated target (MT R), whereas a significantly smaller modulation was observed when the hand moved to the nonfixated target (MT Rfix).

When considering the different behavioral epochs, in the R versus Rfix tasks, significant differences in cell activity were observed in 11/27 (40.7%) neurons studied during RT, 8/27 (29.6%) during MT, and 11/27 (40.7%) during THT.
During the same epochs, significant changes in directional properties across these task conditions were observed in the activity of 25.9% (RT), 40.7% (MT), and 48.1% (THT) of the neurons studied.

In the eye-position task, 14/27 cells (51.8%) showed significant (Wald test, $P < 0.005$) static eye-position effects.

**Discussion**

In this study of parietal area 7m, we have found diverse types of reaching-related neurons characterized by combinatorial properties.

Many cells exhibited a coherent directional tuning in the oculomotor and in the reaching tasks, indicating a major contribution of eye-position signals. Other cells, however, showed a significant directional tuning only in the visuomotor tasks and not in the oculomotor one. Moreover, most cells in both these groups were directionally tuned when the eyes were held immobile during the reaching movement. Thus one can conclude that eye-position signals may contribute to the modulation of many 7m neurons during reaching, but other signals, relating to hand movement and position, make important additional contributions.

In particular, there exist neurons that are not directionally modulated by the position of eyes in the orbit, but during arm reaching display significant differences in activity levels and directional properties when the eyes are immobile as compared with when they can move freely to the target. Across these two conditions, the retinal positions of both the target and the hand differ. As a working hypothesis, we can speculate that these neurons use retinal error signals, reflecting the difference between target and hand position, to compose motor commands that move the hand to the target. However, they could also be involved in other processes, such as visual monitoring of the hand trajectory. Finally, the influence of selective spatial attention may also play a role in the modulation of cell activity, under the experimental conditions of this study.

The interplay between these different populations of neurons and their relative “weight” in the coding mechanism remains to be determined.

Area 7m’s frontal projections (Cavada and Goldman-Rakic 1989; Matelli et al. 1995) to a reaching-related zone of the frontal lobe, encompassing dorsal premotor cortex and its border with primary motor cortex, have been worked out in detail (Caminiti et al. 1996; Johnson et al. 1993, 1996; Tanne et al. 1995). On the basis of these studies, it has been proposed that this medial parietal area represents an early stage in the processing mechanisms by which the combination of different information leads from target localization to movement composition (Caminiti et al. 1996; Johnson et al. 1993, 1996). The results of the present study illustrate some of the combinatorial features of the cortical network underlying this mechanism.

Reentrant neural signals traveling through the reciprocal association pathways between frontal and parietal cortices are the likely sources of the hand-position and movement-related signals observed in area 7m. The anatomic connections with the parietooccipital cortex and inferior parietal lobe (Cavada and Goldman-Rakic 1989; Matelli et al. 1995) are possible cortical carriers of eye-position signals.

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**References**


