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Parietal cortex neurons of the monkey related to the visual guidance of hand movement

M. Taira, S. Mine*, A.P. Georgopoulos, A. Murata, and H. Sakata**

1st Department of Physiology, Nihon University School of Medicine, 30-1 Ohyaguchi-kamimachi, Itabasiku, Tokyo 173, Japan

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Summary. A class of neurons specifically related to hand movements was studied in the posterior parietal cortex while the monkeys manipulated different types of objects. We examined the neuronal activity during manipulation of objects by the hand in the light and in the dark. Fifty-five neurons were active during manipulation in the dark and were classified as "hand-movement-related" neurons. Of these, 38/55 (69%) cells were also influenced by the visual stimulus. Most of the hand-movement-related neurons were selective in the type of objects manipulated. Moreover, some of these cells were selective in the axis of orientation of the object. These results suggest that the hand-movement-related neurons of the parietal cortex are concerned with the visual guidance of the hand movement, especially in matching the pattern of movement with the spatial characteristics of the object to be manipulated.

Key words: Hand movement – Parietal cortex – Visual guidance – Monkey

Introduction

The hand of the primates is specialized for prehensile movements to grasp a variety of objects in the environment (Napier 1962). These movements are usually performed under visual guidance to ensure high precision and skillful manipulation of the object of interest. Visual information is particularly important in order to adapt the posture of the hand and fingers to the shape, size and orientation of the object to be manipulated (Jeannerod 1988). Yet visually guided movements of the hand and fingers have received relatively little attention, partly because of the large number of degrees of freedom of these movements which makes them difficult to analyze experimentally (Jeannerod 1988).

The posterior parietal cortex is concerned with the control of visual reaching as suggested by clinical observations in human subjects (Balint 1909; Hecaen and de Ajuriaguerra 1954; Rondot et al. 1977) and lesion experiments in monkeys (Bates and Ettlinger 1960; La Motte and Acuna 1978). Moreover, parietal lesions result in disturbances in the formation of grip and the adjustment in orientation of the hand both in monkeys and human subjects (Haaxma and Kuypers 1975; Faugier-Grimaud et al. 1978; Jeannerod and Biguer 1982; Jeannerod 1986; Perenin and Vighetto 1983). In previous studies of single cell activity in the parietal association cortex in behaving monkeys, many neurons were found to be related to the visual reaching and hand manipulation (Mountcastle et al. 1975; Hyvärinen and Poranen 1974). However only the neurons related to reaching were studied quantitatively using specific motor tasks (Mountcastle et al. 1975; Kalaska et al. 1983). No such studies have been performed for neurons related to hand manipulation. The present experiments were designed to study the activity of hand manipulation neurons of area 7 with appropriate tasks of hand movements. For that purpose, monkeys were trained to manipulate objects of various configurations that required different types of movement. The results obtained suggest that there is a population of hand-movement-related neurons in the posterior bank of the intraparietal sulcus, which may play an important role in matching the motor commands to the spatial characteristics of the object to be manipulated.

Methods

Behavioral procedure

Experiments were carried out on three awake Japanese monkeys (Macaca fuscata). The monkeys were seated in a primate chair with

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Present addresses: * Department of Neurosurgery, Chiba University School of Medicine, Chiba 280, Japan

** The Philip Bard Laboratories of Neurophysiology, Department of Neuroscience, Johns Hopkins University, School of Medicine, Baltimore, MD 21205, USA

Offprint requests to: H. Sakata (address see above)

the head fixed. They were trained to manipulate various types of objects connected with microswitches that required different patterns of hand movement (object-manipulation task). They were also trained to fixate their gaze on the object without manipulating it, in order to assess visual responses of cells to the sight of the object (object-fixation task).

In both tasks, a small red/green light emitting diode (LED) was placed at 57 cm in front of the monkey at eye level as an initial fixation spot (L1). A second LED spot (L2) was attached to the top of the object to indicate the time to release. The object was mounted on a versatile stand, which allowed changes in its location and orientation, and was generally placed within arm's reach about 15 cm below the eye level.

Fig. 1 shows the paradigm of the object-manipulation task. First, when L1 was turned on, the monkey fixated it and pressed a key at the lap level for 1.0–1.5 s. Next, when L1 changed its color from red to green, the animal released the key, while shifting its gaze to L2, reached to the object, and pulled or pushed, as needed, for 1.0–1.5 s until the L2 changed its color. Then the monkey turned the switch off quickly to get a drop of juice. Thus the task was divided into two periods, 1) the "set" period when the monkey was prepared to move its hand, and 2) the "manipulation" period when it reached and manipulated the object. The latter was further subdivided into, a) the "initial" period when the animal reached and grasped the object to turn the switch on, and b) the "hold" period when it maintained the same posture to keep the switch on.

In the object-fixation task, the light shifted from L1 to L2 immediately when the monkey pressed the key, and the animal was required to fixate it without reaching to the object until L2 changed its color. The immediate shift of light spot served as a cue to restrain the animal from making hand manipulation movements.

We used four types of objects for manipulation and fixation: a pull knob in a groove (Fig. 3A), a pull lever (Fig. 3B), an open pull knob (Fig. 3C) and a push button (Fig. 3D). The same object was presented in a series of 10–20 trials and was changed manually after the series was over. The task was performed in the dark as well as in the light in order to determine the contribution of visual components. Great care was taken to keep the luminance of LED spot so low that the monkey could not see the object nor his own hand even in the dark adapted condition.

Data recording and analysis

After the behavioral training, surgery was performed under general anesthesia (pentobarbital sodium) and a stainless steel cylinder was implanted over a trephine hole in the skull overlying the parietal cortex. Extracellular recordings of single unit activity were made with glass insulated platinum iridium microelctrodes according to the standard electrophysiological techniques (Sakata et al. 1980). Microelectrode penetrations were made mainly in the posterior bank of the intraparietal sulcus.

Eye movements were recorded using the magnetic search coil technique (Robinson 1963; Judge et al. 1980), monitored with an oscilloscope and sampled by the A/D converter every 10 ms (Fig. 1 EM). We used video tape to analyze the shape of the hand during the task. In some sessions, a position sensing system using an infrared LED fixed on the wrist (HAMAMATSU PHOTO Ltd.) was used for monitoring the hand movement (Fig. 1 HM). In one monkey, the EMG's were recorded with a set of Teflon coated stainless steel wire electrodes implanted in eleven muscles of upper arm, forearm and shoulder during the task for analysis.

During recording sessions, we first examined the activity of the parietal neurons in natural behavior by letting the monkey grasp a piece of food or other objects in the laboratory, and selected those cells for study which showed a clear increase of activity during active hand movement. We excluded the somatosensory neurons which were activated by passive movement of joints or cutaneous stimulation. We also excluded purely visual neurons and eye-movement-related cells (visual fixation neurons, visual tracking neurons. etc.).

Statistical analysis (Student t-test) of neuronal discharge was made to determine the increase of activity and the difference in activity change among different tasks and conditions. The onset of neuronal activity was determined on the histograms with a bin width of 20 ms as three consecutive bins exceeding the mean control level by 50% or more (Georgopoulos et al. 1982).

Histological studies

After finishing the recordings in both hemispheres, a series of electrolytic lesions (40 μA cathodal current for 10 s) were made in several guide penetrations. The monkey was deeply anesthetized with an overdose of pentobarbital (50 mg/kg) and was perfused with saline followed by 10% formalin. The brain was sectioned frontally at 50 μm and was stained by Klüver-Barrera method. The location of the penetrations and the sites of unit recording were determined indirectly from their relative positions to the guide penetrations.

Results

The data base for this study consists of 124 cells with task-related activity recorded in 51 penetrations made in the inferior parietal lobules of five hemispheres. Eighty-five of these cells were examined with the task both in the lighted room and in the dark. Fifty-five cells were activated during performance of the hand manipulation task in the dark, and were classified as "hand-movement-related" neurons, although many of them were less active in the dark than in the light. Twenty-three cells were not activated at all in the dark room during hand movement and were classified as "visual dominant" neurons. The remaining 7 cells were not classified as hand-movement-related neurons because a clear-cut increase of discharge during manipulation period in the light disappeared in the dark, although a moderate increase of discharge throughout the task appeared instead.

Figure 2 illustrates the site of recording of hand-movement-related neurons, as determined from the histological sections, on three representations of the frontal sections of the parietal lobe. The great majority of neurons were localized in the posterior bank of intraparietal sulcus (area P0a of Seltzer and Pandya, 1980) adjacent to the hand and arm areas of SI. This area is more medial and dorsal than area 7b, and we stopped going further anterolateral when we recorded a group of cutaneous neurons that characterized area 7b.

Figure 3 shows an example of activity of a hand-movement-related neuron during the object-manipulation task in the lighted room. The cell showed differential changes in activity with different objects. Its activity increased markedly with the pull knob in a groove (A), slightly increased at the beginning of reaching to the lever (B), but did not change with open pull knob (C), and decreased with the push button (D). There was an abrupt increase of discharge immediately after the release of the key, forming a transient peak of activity during the initial period, followed by a maintained discharge during the hold period. Most of the neurons studied showed an initial transient increase and maintained their level of discharge during manipulation of the preferred object as illustrated

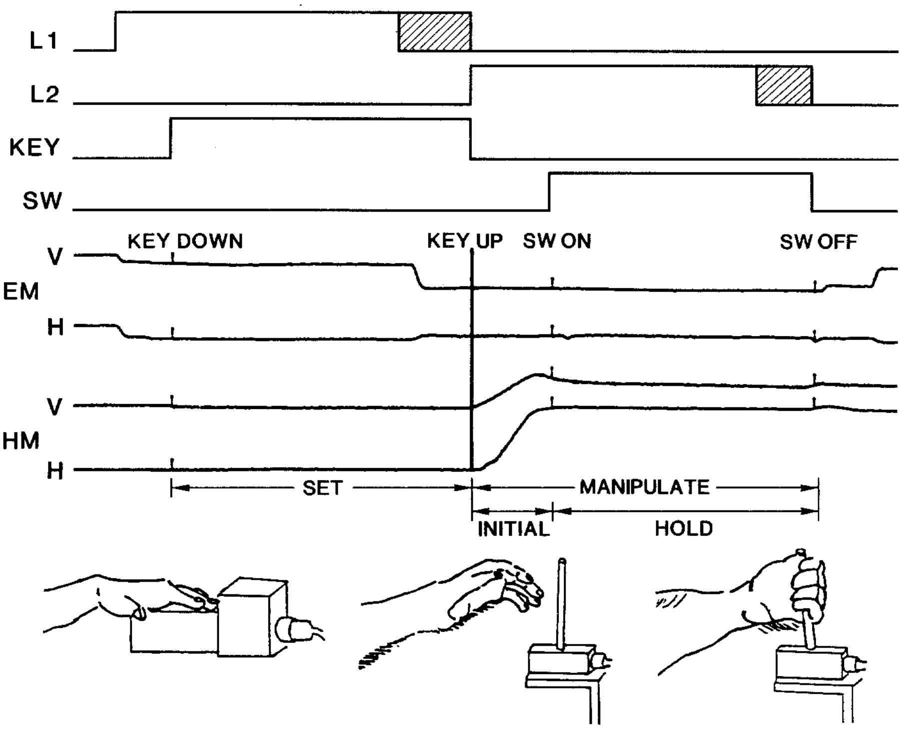

Fig. 1. Schematic representation of the object-manipulation task. L1: fixation spot, a small red/green LED at monkey's eye level. L2: instruction spot attached at the top of each object. In both traces an upward deflection indicate that the LEDs turned red and during the hatched area, the LEDS turned into green. KEY: a key at lap level. SW: a microswitch which was connected to the object. Upward deflection in each trace denotes time during which the key was pressed and the switch was held on respectively. EM: eye movement (V: vertical. H: horizontal). HM: hand movement. The whole sequence was divided into two periods: 'set' and 'manipulate' period. The latter was subdivided again into two periods: 'initial' and 'hold' period. The shape of monkey's hand during each period is shown below

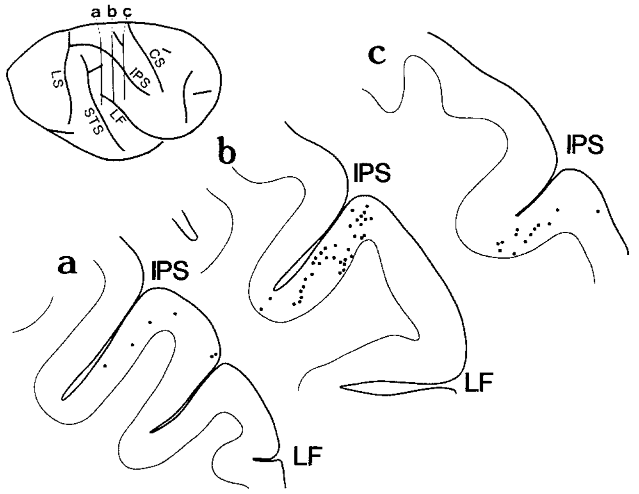

Fig. 2a–c. Location of 'hand-movement-related' neurons in 5 hemispheres. Each diagram (a, b, c) is the trace of frontal sections at the levels indicated in the small diagram of the brain surface. Recording sites of the neurons in the thickness of 4 mm was plotted in each diagram. Note that most of the neurons were localized in the posterior bank of the intraparietal sulcus. STS: superior temporal sulcus. LF: lateral fissure

in Fig. 3A. Several neurons showed only a transient increase of activity during the initial period, and four neurons showed a partial increase of discharge rate during the set period before reaching, just like the "set + movement" cells of premotor cortex (Weinrich and Wise 1982). The time of onset of the hand-movement-related discharge was usually very close to the time of the release of the key (mean ± SD = 9 ± 105 ms N = 51).

Figure 4 illustrates examples of three type of cells studied in the light and the dark. Cell A is an example of a neuron which showed no significant difference in activity during hand manipulation between the two conditions and gave no response when the monkey fixated its eyes on the spot attached to the object in the light. Eleven cells were similar to cell A and six other cells showed larger response during hand manipulation in the dark than in the light with no response during fixation on the object. We called both of these cells "motor dominant" neurons. In contrast, the response of cell B during manipulation of the push button was much smaller in the dark than in the light, and a marked response was elicited when the animal fixated on the push button in the light. The majority of hand-movement-related neurons (38/55) were less active in the dark than in the light. Since there was no essential difference in the pattern of movement between the task in the light and in the dark as far as we examined by EMG recordings, we assumed that the difference in cell activity between the two conditions was likely to be due to some visual input received by these cells. Therefore, we called this type of cells "visual and motor" neurons. More than half of this group of cells tested (18/34) was activated by the fixation on the object of manipulation in the light, as illustrated in Fig. 4B. Whereas the rest of them (16/34) were not activated by object fixation, and we could not find any effective visual stimulus for them.

Cell C (Fig. 4) is an example of a "visual dominant" neuron. The cell was activated when the monkey pulled the knob in the groove in the lighted room, but it was not activated during the same manipulation in the dark. Moreover, the increase of activity during object fixation task was comparable to that observed during manipulation. The majority of the "visual dominant" neurons tested

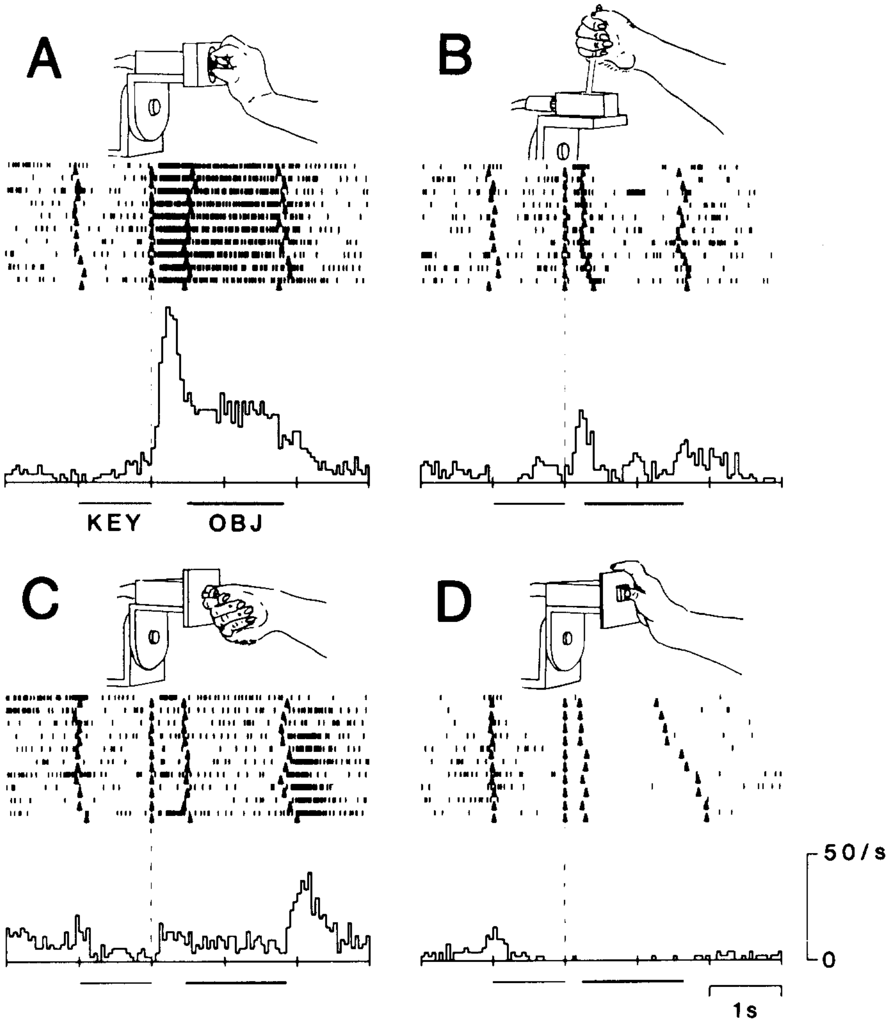

Fig. 3A–D. A typical example of the hand-movement-related neuron in area 7a. **A** Neuronal activity during manipulation of a pull knob in a groove, **B** a pull lever, **C** an open pull knob, **D** a push button, in the lighted room. The shape of the monkey's hand during manipulation of each object is shown above. The rasters and histograms are aligned with the moment when the monkey released the key. The histogram were constructed from 10 trials which are shown in a raster display above the histograms. Bin width is 50 ms. The four arrow heads beneath each raster row indicate the onset of key down, key up, switch on and switch off respectively. The thin line below the histogram shows the mean duration of pressing the key down calculated from the 10 trials (KEY). The thick line shows the mean duration of holding the switch on (OBJ)

(11/19) were activated during fixation of the object to be manipulated. Therefore, the "visual dominant" neurons activated during the manipulation task are likely to receive visual signals relevant to the hand manipulation. However, for the remaining eight cells (8/19) we could not find any effective visual stimulus for their activation.

There was usually a strong preference, among different cells, for specific objects, as illustrated in Fig. 3. Twenty-eight (51%) of the hand-movement-related neurons were highly selective, since their discharge in association with a particular object was significantly greater than that for other objects ($p < 0.01$, t-test). Seventeen cells (31%) were moderately selective, in the sense that two or three objects were equally effective, but ten cells (18%) were non-selective. In contrast, selectivity in position was rarely observed in the hand-movement-related neurons we examined (2/10).

Cell activity was often influenced by the orientation of the object in space. In particular, an effect of the orientation of the lever was most commonly observed. An example is shown in Fig. 5 which illustrates the activity of a cell that was maximally activated with the lever pointing upward and to the right. An orientation selectivity was present in eleven cells for which lever manipulation was effective. Nine of them preferred one particular direction toward which the lever was pointing, and two of them were "bidirectional". In a few other cases, cell activity varied with the orientation of the groove housing the pull knob, or with surface orientation of the push button.

Discussion

The results of the present study are in agreement with those of previous investigations which demonstrated the existence of a group of area 7 neurons related to the active movement of the hand (Hyvärinen and Poranen 1974; Mountcastle et al. 1975). However, more strict criteria were used in the present experiments to classify hand-movement-related neurons than previously. We included in this class only those neurons which were activated during the hand manipulation both in the light and in the dark, and excluded "visual dominant" neurons which were not activated in the dark. We also excluded those neurons which responded to passive movement of joints or cutaneous stimulation. Only a small number of such somatosensory neurons (N = 16) were encountered in the region of

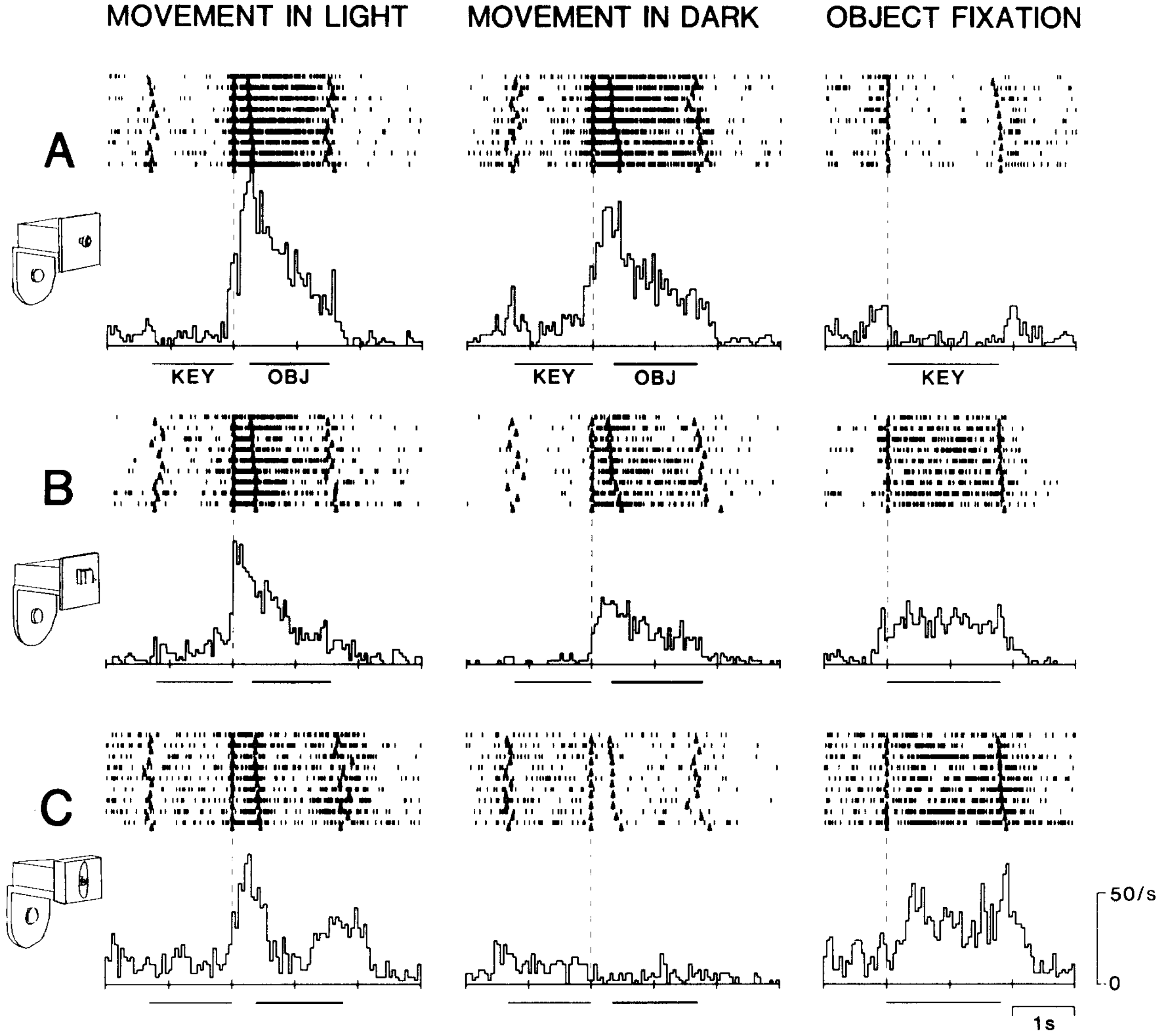

Fig. 4A–C. Comparison of the activity of three types of neurons among three task conditions (hand movment in light, hand movement in dark, object fixation). **A** An example of "motor-dominant" type neuron. **B** "Visual and motor" type neuron. **C** "Visual dominant" type neuron. The objects used in three tasks for each cell are shown with inserts on the left side: from above, open pull knob (**A**), push button (**B**), pull knob in groove (**C**). The histograms were constructed from 9 trials. Other conventions in the left and the middle column are the same as in Fig. 1. In the right column, the histograms are aligned with the onset of key press, and the two arrow heads beneath each raster indicate the onset of the key press and the onset of the key release, respectivley. The thin line below the histogram shows the mean duration of object fixation (KEY)

area 7 where we recorded hand-movement-related neurons. This is in sharp contrast to the neurons of area 5 (Sakata et al. 1973) and area 7b (Leinonen et al. 1979) which responded frequently to somatosensory stimulation. Therefore, the changes in cell activity during object manipulation in the dark could be attributed to the active movement of the hand, but not to concomitant sensory stimulation as suggested previously (Robinson et al. 1978). However, the activity of these neurons were not likely to be directly related to the initiation of movement, since the onset time of the increase of discharge of them was very close to the onset of movement. Thus it is more likely that their activity was due to a corollary discharge of motor command signals as suggested previously for area 5 neurons related to reaching (Kalaska et al. 1983).

It is noteworthy that the majority of hand-movement-related neurons in area 7 showed greater changes in activity when the task was performed in the light than in the dark. This suggests that these cells might have received visual input related to the object to be manipulated and/or the moving hand. Therefore, we classified such neurons as "visual and motor" type, in distinction from the "motor dominant" type which showed no significant difference between the two conditions or enhancement of activity in the dark. Indeed, more than half of "visual and motor" type of hand-movement-related neurons responded to the sight of the object when the animal fixated on it without

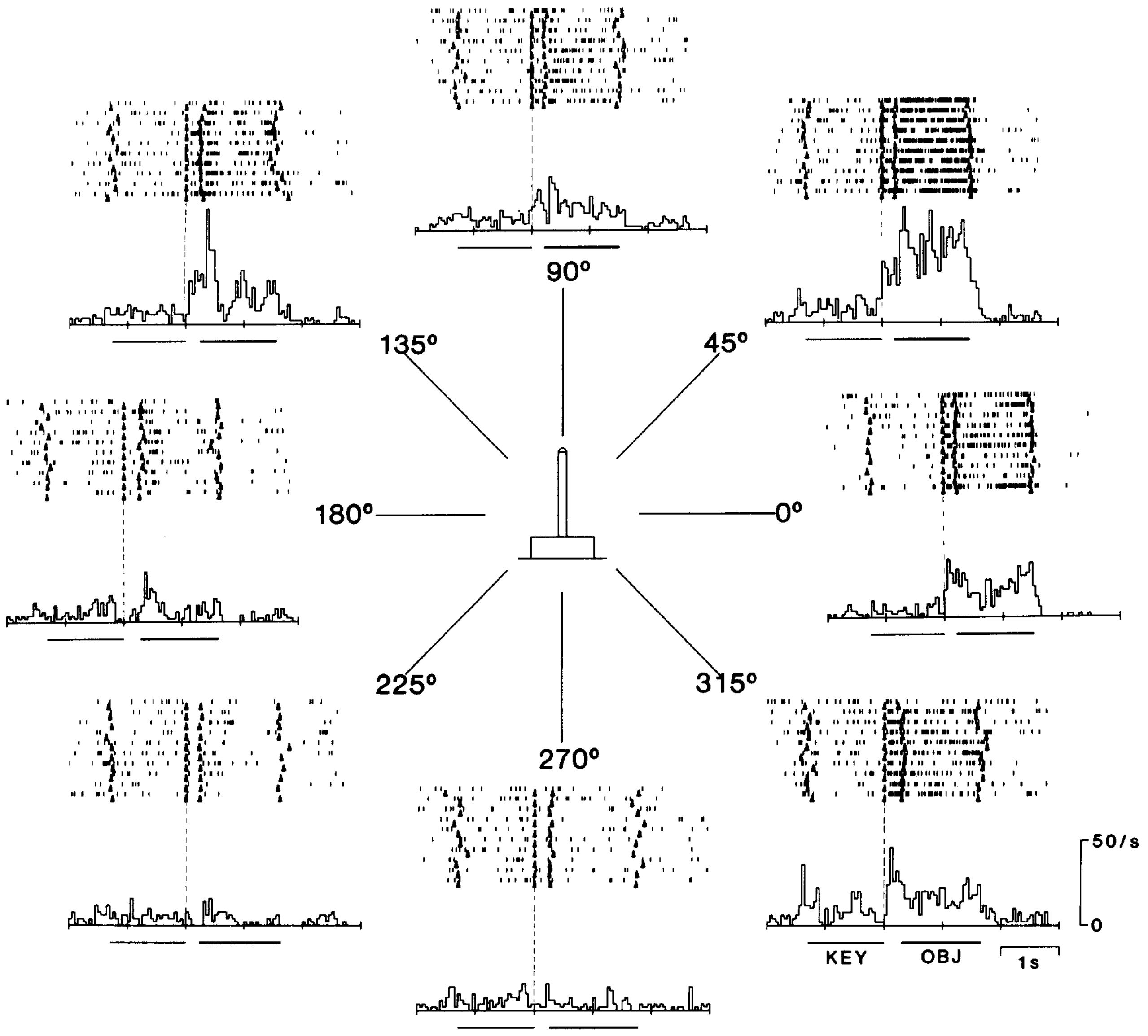

Fig. 5. An example of a hand-movement-related neuron which showed selectivity for the orientation in the space of the lever switch. The rasters and histograms correspond to the angle of orientation of the lever measured from the horizontal axis pointing to the right. Maximum response was obtained when the lever was tilted 45 degrees to the right

moving its hand, although the effect of the view of the moving hand remains to be examined.

The most important finding of the present study was that many hand-movement-related neurons in area 7 were selective for their activation, depending on the configuration and orientation of the object to be manipulated. The use of different objects was associated with different motor pattern of hand and fingers, whereas the proximal movement of reaching was common to all objects. Therefore, the difference in cell activity observed among different objects during hand manipulation in the dark could be attributed to the different pattern of hand movement. It may also be noted that the position selectivity, which is specific to reaching was relatively rare among the hand-movement-related neurons. The activity of the hand-movement-related neurons is likely to represent a particular pattern of hand movement as a whole, since most of them showed a maintained increase of activity throughout the period of object manipulation as well as the transient peak of activity at the beginning.

The selectivity of "visual and motor" cells depended also on the visual signals. The view of the object appeared to accentuate the selectivity in motor pattern, since our preliminary investigation (Sakata et al. 1989) showed that the preferred object in the fixation task was the same as the preferred object for manipulation, in most of the cells examined (12/16). The visual input to these neurons is probably processed within area 7, because various visual neurons related to the space perception have been recorded in this area (Motter and Mountcastle 1981; Andersen and Mountcastle 1983; Sakata et al. 1985; Steinmentz et al. 1987). Moreover, the "visual dominant" neurons in the present study were recorded in the same region as the hand-movement-related neurons, and the majority of them responded to the sight of the object for manipulation. It is likely that the "visual dominant" cells provided visual input to the "visual and motor" cells within the same region in the posterior bank of the intraparietal sulcus.

The most likely source of motor signal is the input from premotor cortex (area 6) by way of corticocortical connections, since a reciprocal connection was demonstrated between the postarcuate cortex and the posterior bank of the intraparietal sulcus (Godschalk et al. 1984; Matelli et al. 1986). Recently Rizzolatti et al. (1987, 1988) recorded in the rostral part of inferior area 6, on the posterior bank of arcuate sulcus, a group of neurons that were related to movements of hand and fingers. The premotor neurons which they designated as "grasping-with-the-hand neurons" were selective for a particular type of grasping, just like the hand-movement-related neurons of area 7. This suggest that there may be an intimate functional relationship between these two groups of neurons. The premotor neurons are likely to generate motor command signals, since they project directly to the motor cortex (Muakkassa and Strick 1979; Godschalk et al. 1984), whereas the parietal neurons are more likely to monitor the ongoing motor activity, and mediate the matching of the movement pattern to the spatial characteristics of the target object by integrating the motor and visual signals.

The clinical symptom of the deficit in shaping of the hand before grasping (Jeannerod and Biguer 1982; Jeannerod 1986) and the error in hand orientation test (Perenin and Vighetto, 1983) observed in patients with parietal lesion, may be explained by the lack of this visuomotor integration in the posterior parietal cortex. The present results are in accordance with the matching of perceptual schemes of different aspects of the object to different motor schemes in the theory of coordinated control programs for hand movement (Arbib et al. 1985). Indeed, if an element is added to integrate perceptual and motor signals to that system, as suggested by the "visual and motor" type of hand-movement-related neurons found in the present study, it should make the system more stable and more precise in performance.

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