

# Posterior Parietal Association Cortex of the Monkey: Command Functions for Operations Within Extrapersonal Space

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THE LARGE EXPANSE of the cerebral cortex of primates traditionally termed the association areas was differentiated early in experimental neurology from the primary motor and sensory areas. Association cortex is characterized by a eulaminate or heterotypical cytoarchitecture, thought by some to contain many structurally differentiated areas, by others to be virtually uniform from one region to another, but by all to differ markedly from the agranular motor cortex and the koniocortex of the sensory areas. The notion evolved among experimental neurologists that it is within these regions that afferent input from two or more sensory channels is brought into conjunction with a hypothetical neural concomitant of "ideas" or concepts with the resulting perception of an object in the external world, as distinct from but additive to the simpler sensing of that object. The defects in the more complex aspects of sensation which occur in humans with lesions, for example, of the posterior parietal association cortex, lend some credence to this concept. The general idea has lost favor in recent decades, however, for it does not explain the panorama of abnormal function in humans with lesions of the association areas. Moreover, it is unlikely that cerebral operations fit hierarchical series like those the association model presupposes. Undoubtedly, parallel processing mechanisms are superimposed within the brain on a basic hierarchical design. Sensory input is processed through different levels leading to neural and behavioral events of quite different natures,

from direct reflex reactions to storage in memory.

The development of new methods (28) for the simultaneous observation of behavioral acts and the neural events thought relevant to them has allowed direct study of the association cortex of the frontal (31, 52, 53), temporal (34), and parietal lobes (10, 21, 23, 46, 47, 73). We present here the results of a survey of the functional organization of the posterior parietal areas of the monkey cerebral cortex, made in waking monkeys trained to respond with simple behavioral acts on detection of certain sequences of sensory stimuli. Our results lead to a hypothesis of the function of the posterior parietal cortex: these regions receive afferent signals descriptive of the position and movement of the body in space, and contain a command apparatus for operation of the limbs, hands, and eyes within immediate extrapersonal space. This general command function is exercised in a holistic fashion. It relates to acts aimed at certain behavioral goals and not to the details of muscular contraction during execution. These details are, on this hypothesis, made precise by the motor system, for which it is well suited by virtue of its powerful mechanisms for specifying movement exactly.

We believe that our findings provide a positive image of some of the behavioral defects that appear in humans and monkeys after lesions of the posterior parietal areas.

*Parietal lobe syndrome in humans and other primates*

Lesions in the parietal association cortex of humans produce profound disturbances

of behavior. These syndromes have in common alterations in the perception of the body form and its relation to surrounding space, and in stereotactic exploration of that space. The syndrome differs with the hemisphere affected, the site and extent of the lesion, and the time since its onset (17).

A major difficulty for systematization has to do with what is to be regarded as the parietal lobe. In humans the term commonly includes the postcentral somatosensory cortex, the superior parietal lobule, and the inferior parietal lobule with its expansions into the angular and supramarginal gyri. The transitional zones between the parietal, temporal and the occipital lobes are vaguely defined. Naturally occurring injuries and disease processes of course disregard any cartography, and there is only one series of patients in whom lesions of known size and location were placed, under neurosurgical control, in the nondominant hemispheres of 17 patients, as a therapeutic measure for parietal lobe epilepsy. The careful study of these cases is particularly valuable for this reason (37).

The varieties of parietal lobe syndrome can be divided into *a*) those in which a unilateral lesion produces changes in function that are strictly contralateral, a syndrome Denny-Brown termed amorphosynthesis (19), and *b*) those in which even unilateral lesions produce bilateral disturbances of behavior. Of these latter, those caused by lesions of the major and minor hemispheres differ substantially.

The purely contralateral syndrome is more common with right than with left hemispheric lesions, in right-handed individuals, presumably because enlarging lesions on the left rapidly compromise the neural mechanisms for language. There is neglect and/or denial of the existence of the left side of the body and of the left half-field of extracorporeal space, and a failure to represent the left side of objects in drawings. There may be a neglect of the toilet and dressing of the contralateral side, the so-called apraxia for dressing. There is perceptual rivalry between stimuli applied to the two sides, with extinction, usually for both somesthetic and visual stimuli, in the absence of primary sensory defects (20). Commonly there occurs some loss of the capacity to recognize the size and form of an object by manual examination in the

dark; whether such an astereognosis ever occurs without defect in primary mechanoreceptive sensibility is uncertain (15). A poverty of spontaneous contralateral movements supervenes, and errors are made in reaching into the contralateral half-field of space. In general, these patients avoid and turn away from all stimuli that approach from the contralateral side, and exhibit a release of the tactile avoiding reactions. The contralateral limbs may be held persistently in unusual postures. Extension of the lesion to produce a left-sided hemiplegia reveals one of the remarkable aspects of the syndrome: the insistent denial that paralysis exists.

In other cases, supposedly when the lesions in the right hemisphere of dextrals are larger, the syndrome takes on more global dimensions, inducing changes in behavior that affect both sides of the body and the patient's capacity to orient himself in and to operate within the immediate space that surrounds him (3). The additional signs are the appearance of constructional apraxia (57, 58), which is more common with right but does appear with left hemispheric lesions (4, 6, 59, 60, 70), and difficulty in map reading and route finding. The latter disorder of the topographical sense occurs using either tactile or visual cues; it appears more often after right- than after left-sided lesions, in right-handed individuals (11, 17, 74).

How and in what way the syndrome produced by lesions of the left parietal lobe in dextrals differs from that just described is the source of some disagreement. Denny-Brown (18) describes the occasional appearance of the purely contralateral syndrome (of amorphosynthesis). This must occur rarely, for in the majority of patients this simpler syndrome is overlaid with disorders of behavior that affect both sides. Constructional apraxia occurs less commonly with lesions of the left side, but the ideomotor and ideational forms of apraxia appear only after lesions on the left (38). This is true also for the agnosias and the disorders of language: finger agnosia, right/left disorientations, dysphasia, alexia, agraphia, acalculia—these and similar disorders appear in conjunction with the contralateral syndrome described above, with destructive lesions in

the left parietal lobes of right-handed individuals (5, 16, 32).

**EFFECTS OF REMOVAL OF POSTERIOR PARIETAL ASSOCIATION AREAS IN MONKEY.** The parietal association areas of the monkey occupy the superior and inferior parietal lobules. The former is largely area 5 of Brodmann (8, 9), and more or less equivalent to the area designated PE by von Bonin and Bailey (7), who used the nomenclature of von Economo; the latter is more or less equivalent to area 7 of Brodmann, and areas PF and PG of von Bonin and Bailey. There is no evidence that the monkey brain contains homologies of the angular and supramarginal gyri of the human brain, areas 39 and 40 of Brodmann. The syndrome which follows removal of the parietal lobules in the monkey is contralateral and symmetrically equivalent on the two sides. We have found no description of a case in which a global disorder of behavior was produced in a monkey by a unilateral parietal lesion. The changes in behavior which do result resemble the contralateral syndrome of amorpho-synthesis of Denny-Brown (19). Such animals show a neglect of the contralateral limbs, a paucity of spontaneous movements, and errors in reaching with the contralateral arm into either half of extrapersonal space (22, 25). In this latter, they differ from humans with parietal lesions; for humans the error in reaching is related to the contralateral half of space and holds for either arm with unilateral lesions (35). After parietal lesions monkeys display a catatonic persistence of unusual limb postures, and with bilateral lesions there is a marked reduction in all exploratory behavior. Perceptual rivalry with extinction occurs for somatic sensory, auditory, and visual stimuli (24, 39), and animals with such lesions are impaired on tests of tactile form discrimination in the contralateral hand (26, 62, 63). There is a remarkable release of the tactile avoiding reaction, indeed of all avoiding reactions, so that such animals show excessive responses to even mildly noxious stimuli delivered anywhere on the contralateral side. In sum, the parietal lobes appear to contain an essential neural mechanism for stereotactile exploration of and orientation within the immediately surrounding extrapersonal space.

## METHODS

Laboratory digital computers were used in all experiments to control stimuli, monitor behavior, and collect relevant data. In our early experiments we used the original LINC in the manner described by Talbot (76); for later experiments, including those in which moving targets were used, the computer was a PDP 11/20 suitably interfaced to the laboratory. Each experimental paradigm was implemented by a program written expressly for the purpose. Programs were controlled by sets of behavior and stimulus parameters entered at the computer's keyboard or retrieved from a data file. These parameters, and remarks typed by the user, were stored with collected data as a permanent label. Most collected data were in the form of interevent time intervals, one table for each relevant trial. Each interval was labeled, implicitly or explicitly, with the name of the event or events that terminated the interval. These stored data provide a nearly complete record of the course of each experiment and are the basis for all graphic and numerical analyses of experimental results. Detailed protocols were dictated, as well.

### *Behavioral tasks*

Two general behavioral paradigms were used, a detection and a detection-reach task. In early experiments, the stimulus used in the detection task was a mechanical sinusoid delivered to the glabrous skin of the monkey's hand (77). The monkey manipulated the telegraph key and press panels or levers with his contralateral hand. In later experiments a visual stimulus was used as the signal. This was commonly a light-emitting diode, 6.5 mm in diameter, placed 34 cm from the monkey's eyes. Each correct response was followed by a liquid reward.

The detection paradigm is outlined by the upper diagram of Fig. 1. When the target light was turned on, under computer control, the monkey depressed a telegraph key and waited for the duration of the foreperiod delay. At the end of this delay the light dimmed slightly (or in some experiments began to flicker), and the monkey was required then to release the key within a specified time. In experiments in which the somesthetic stimulus was used the paradigm was similar, except that a 550- $\mu$ m step indentation of the skin by the probe tip corresponded to light onset, and a superimposed 30-Hz vibration to light dimming. Correct key release caused the light to go out (or the probe tip to be withdrawn from the skin); a 0.2-ml reward of liquid was delivered and

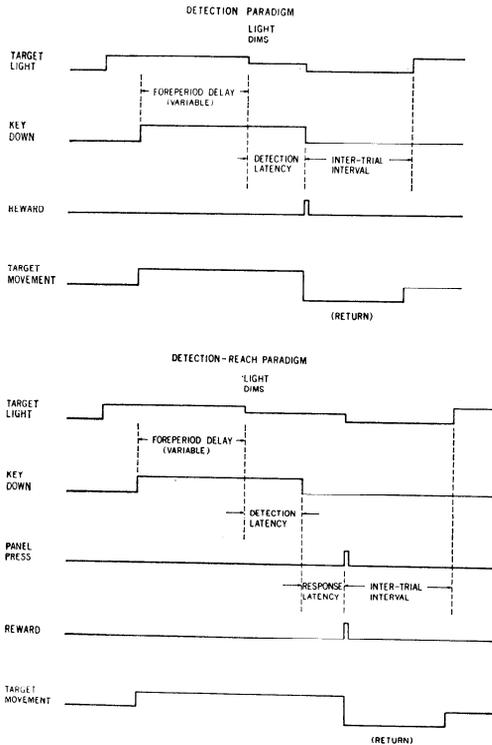


FIG. 1. Schematic representation of two tasks used in studies of the posterior parietal cortex of the monkey. The target light and signal key are those shown in Fig. 2. Tasks are described in detail in the text.

initiated the intertrial interval. At the end of that interval, the beginning of the next trial was signaled by the onset of the target light or of the mechanical indentation of the skin. If the monkey made an error in the course of a trial (if he released the key too soon or held it down too long), the program went directly to the intertrial interval. Stimulus magnitudes were well above detection thresholds, although for visual tracking the diameter of the moving spot and the degree of dimming were small enough to require foveation for successful detection of the change in light. Two or three foreperiods were commonly used in a run, sequenced randomly, so that the monkey could not develop timing or position habits. When a moving target was used (Fig. 1) the trial began with the target stationary at  $37^\circ$  to one side of the midline; the target began to move when the monkey depressed the key. Successful completion of a trial, or an error in the course of a trial, caused the target light to go out and the target carriage to return immediately to the start position.

In the detection-reach paradigm, after a properly timed key release, the monkey was

required to reach out and press a panel or pull a lever within a specified time. In an early version of this test, two horizontal 1-cm diameter bars were mounted in 5-cm<sup>2</sup> recesses 18 cm apart, in a 30-cm<sup>2</sup> panel. The panel was placed at arm's length in front of the monkey (usually about 30 cm), with the levers 5 cm below his eye level. In order to make a correct response, the monkey grasped the lever and pulled it 2 cm toward himself. The stimulus light was mounted between the two levers, at eye level. When the monkey correctly detected a stimulus change, the stimulus light went out and another light turned on in one of the two lever recesses, to indicate which lever the monkey should pull on that trial. The monkey was thus required to project his arm through one of two spatial trajectories to targets about  $32^\circ$  apart, as specified by the computer program.

A later version of our apparatus is shown in Fig. 2. In this case the monkey manipulated the key and the press panel mounted on the carriage with his left hand; his right arm was loosely restrained by a padded metal holder. The target is mounted in the center of a 28-mm-diameter press panel, and the carriage can be moved around the circumference of the 69-cm-diameter brass channel, under computer control. Thus the target can be held stationary at any point in the monkey's field of vision throughout a training or collection run, or moved at either  $12^\circ$  or  $21^\circ/s$  for eye-tracking experiments. Figure 2 also illustrates the head-holding technique, the stepping microdrive (see Fig. 4) mounted over the right parietal region, the field-effect input stage preamplifier, and the reward tube.

### Training procedure

Monkeys were deprived of fluid during periods of training and recording. If any day's performance left an animal short of a day's fluid requirement, he was given sufficient fluid to make it up after the working session. No fluid was given elsewhere. Each animal was transferred from his living cage to a primate chair for each training session, and returned to the cage immediately afterward.

Animals were trained using standard operant conditioning techniques until they performed at 80+% correct, at delays up to 2.5–3.0 s. Typically, three to six training runs of 200 trials each were given each day. The lengthening of the prestimulus delay required from 26 to 43 days. In contrast, when a monkey had learned the detection task well, addition of the lever pull or panel press to the task required only one training session; interhemispheric transfer to the opposite side required

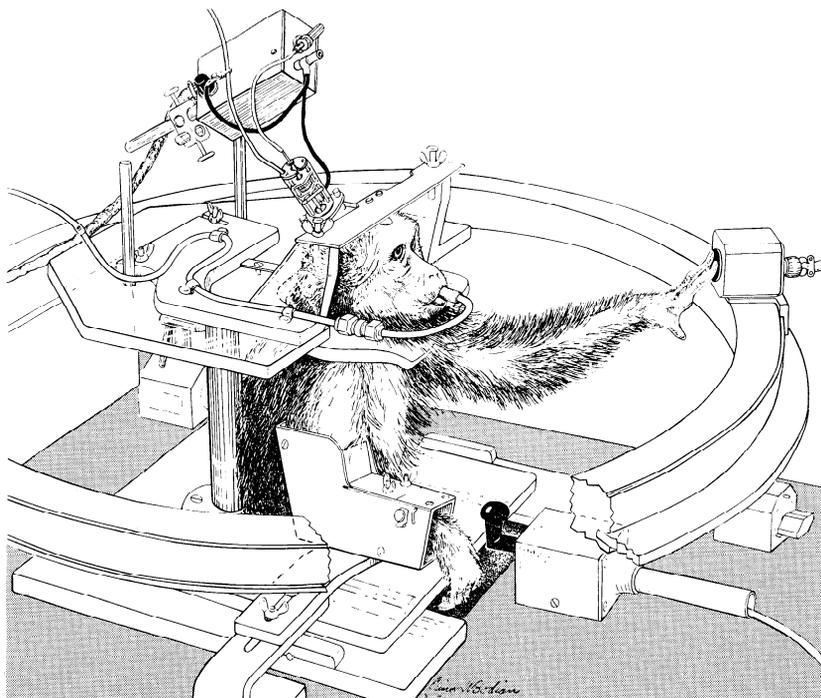


FIG. 2. Drawing of a *M. arctoides* working in the test apparatus used for studies of the posterior parietal cortex of the monkey. The head-fixation apparatus, implanted microdrive, cathode follower, and reward tube are shown upper left. The signal key is shown through the cutaway of the circular race. The animal has just released the key with his left hand and projected that arm and hand forward to contact the lighted switch mounted on the moving carriage, shown upper right. The carriage can be moved from any preset position in either direction at speeds of 12 or 21°/s for preset distances. All parameters under PDP-11 program control. (Drawing courtesy Mrs. E. Bodian.)

no more than two training sessions. Finally, four animals learned within one to three additional training sessions to track the stimulus light as it moved around the circumference of the apparatus shown in Fig. 2, and to project accurately to contact it.

*Animal preparation and method of recording*

The monkey's head was held in a normal upright position by a stainless steel positioner fixed to the skull with anchoring screws and dental acrylic (Fig. 2). A 2-cm trephine opening was made, centered a bit posterior to the intraparietal fissure, directly behind the hand and arm area of the postcentral gyrus. The opening was closed with a thin, fitted Lucite plug, cemented in place with dental impression compound. The recording chamber was oriented over the closed opening, its axis normal to the surface, and fixed in place with an external seal of impression compound and several layers of dental acrylic. The chamber position was varied from one experiment to another to

allow access to different zones of parietal cortex. The wound was cleaned daily, and an antibiotic was given. In two animals the horizontal electrooculogram was recorded via Ag-AgCl cup electrodes implanted in the bone of the lateral orbital rims; the leads were brought subcutaneously to a small pedestal plug fixed in the acrylic implant.

On each recording day the head was fixed, the chamber opened, the dental impression compound seal between its inner wall and the skull repaired if necessary, and the Lucite plug removed. The baseplate of the microdrive was fixed to the chamber top (see Fig. 3), the microdrive with electrode in place mounted on the lock-down device, the air within the chamber displaced with mineral oil, and the electrode moved to the locus selected for penetration. At the end of each day's recording the microdrive was removed, the chamber emptied of oil, and the Lucite plug refixed in the cranial opening, thus closing the head. A cap was placed on the chamber, the head released, and the animal transferred to a living cage in which

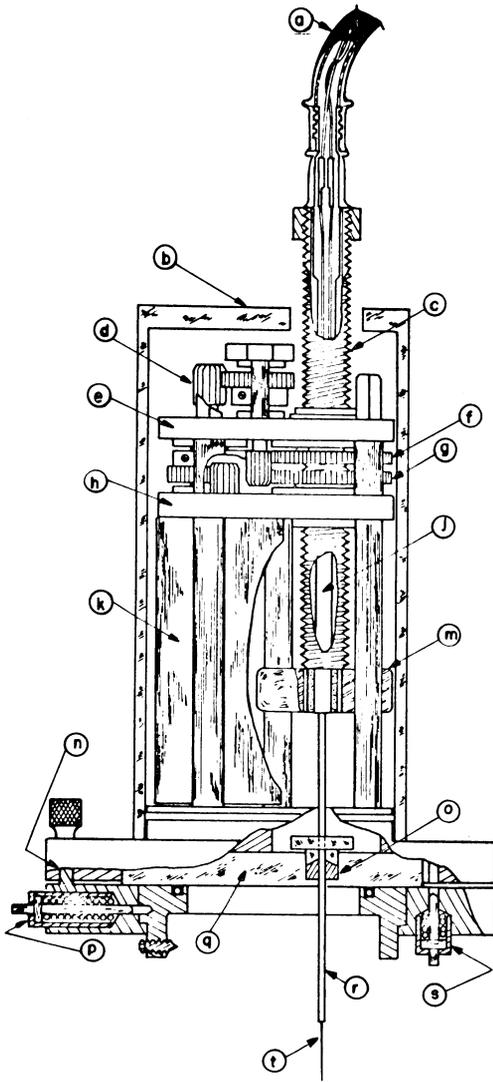


FIG. 3. Cutaway drawing of stepping, electromagnetically driven microdrive designed by Chubbuck (13). The structures labeled include: a, coaxial cable; b, Plexiglas enclosure; c, lead screw; d, 53.7 to 1 gear reduction; e, middle bearing hanger; f, pre-load follower gear; g, lead screw drive gear; h, lower bearing hanger; j, guard tube; k, three-phase synchronous motor; m, slide-way follower; n, base pivot; o, silicone rubber seal; p, rotational detent; q, Plexiglas closure plate; r, carrier tube; s, radial detent; t, electrode. For recording, the base of the microdrive is attached to a Plexiglas chamber permanently fixed to the monkey's skull. Neoprene O rings provide hermetic seal to the chamber.

he was free until the next day's session. In six of our animals (see Table 1), after recording in one hemisphere was completed, a second opening was made on the contralateral side, a

chamber implanted, and the recording procedure repeated.

#### *Microdrive and microelectrodes*

The microdrive used is an electromechanical device weighing 80 g that allows precise, reproducible, 1  $\mu\text{m}$  axial movements of the microelectrode (13) (see Fig. 3). The drive is mounted on a circular baseplate which, for use, is placed eccentrically on and is supported by the circular, detented, lock-down device. The latter is attached to the implanted cortical-recording chamber. The polar coordinate system allows insertion of the microelectrode at any of more than 700 positions within the central 18-mm-diameter circle of the hydraulically closed recording chamber. A control box placed at a distance provides angular displacement commands to the miniature, custom-wound motor which, via a 54-1 reduction-gear train, drives the lead screw and the microelectrode; the net movement is displayed digitally. Motor artifacts are reduced below the noise level of the input amplifiers by Monel metal shielding of the motor and by the guard tube that surrounds the microelectrode and is driven by the amplified electrode signal. Capacitance losses to surrounding metal are reduced by spacing and, when necessary, by negative capacitance feedback.

We used etched, platinum-iridium alloy microelectrodes coated with glass (80), and chose for use those of 2.0- to 2.5-M $\Omega$  impedance, measured at 1,000 Hz, with maximal axial linearity.

#### *Amplification and display of electrophysiological events*

Potential changes occurring at the microelectrode tip were fed to an adjacent, 10 $\times$ , field-effect transistor amplifier with variable capacitance feedback. The amplified signals were then inserted in parallel to a number of recording and display devices. Signals of behavioral and electrophysiological events were collected in computer memory, as described above, and later transferred to digital tapes for storage (76). Electrophysiological data were displayed in the form of impulse replicas and simple histograms shown in several figures.

#### *Search for and classification of neurons*

Action potentials were identified by criteria described in an earlier paper (66). As the electrode was moved down in small steps, we attempted to establish the relation of peripheral events to multiunit activity as well as to each single neuron studied. In either case, tests for

passive driving by sensory stimuli included the gentle rotation of joints, mechanical stimulation of the skin, pressure on muscle bellies, auditory stimuli, by presentation of objects in the visual field and, in some experiments, by the projection of images on a tangent screen confronting the animal at about 1 m distance. We then tested for a correlation of neural activity with behavioral events by presenting objects of interest, usually food, within arm's reach, with and without the freedom to reach for the object. On the basis of these observations we made a tentative assignment of the neuron to one or another of the classes of neurons in Tables 2 and 6, chose a behavioral task appropriate to the neuron type, and proceeded with combined behavioral-electrophysiological data collection. Auditory masking was used when appropriate.

*Anatomical considerations*

The experiments we designed required careful and often prolonged examination of our

monkey subjects—the passive rotation of their limbs at their joints and deep palpation of muscles, as well as tests for arm projection. We found the placid, friendly, and easily trainable *M. speciosa* (*M. arctoides* (30)) to be especially well suited to our needs, and 8 of our 17 experiments (hemispheres) were made in monkeys of this species, the remainder in *M. mulatta*. Consequently, we have studied the cytoarchitecture of the parietal lobes and the thalamic projections to areas 5 and 7 in the two monkeys, for comparison. We found these areas to be indistinguishable in the two species, and the physiological observations made in the two have been treated as one population in the description of our results. A summary diagram of the parietal cortical areas in *M. arctoides* is given in Fig. 4. The eulaminate cortex of areas 5 and 7 is readily distinguished from most of the areas which surround them, and the two differ clearly but to a lesser extent from each other. Along most of its extent the depth of the intraparietal sulcus marks the re-

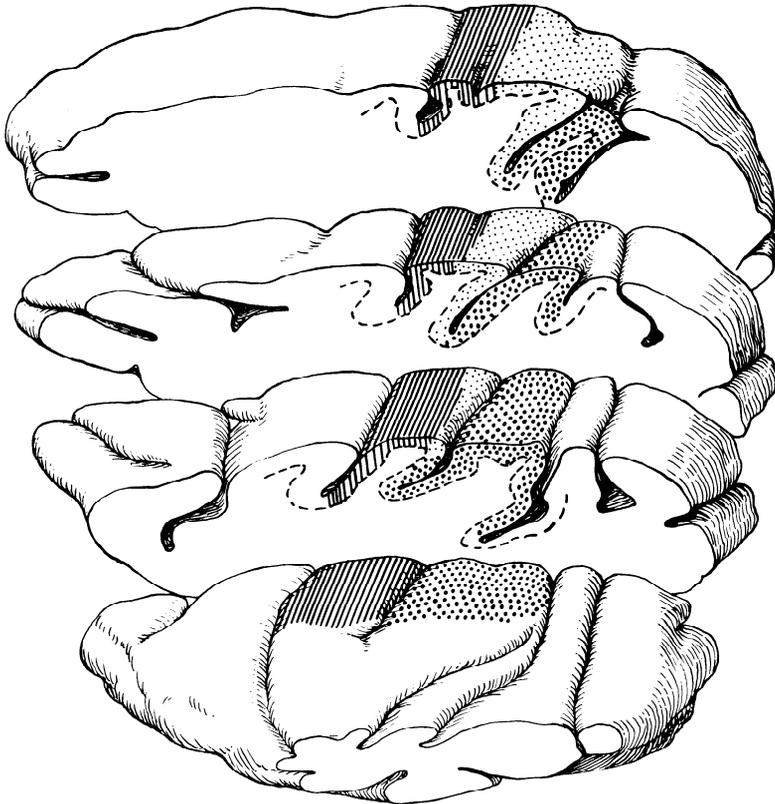


FIG. 4. Drawing prepared from results of cytoarchitectural study of the parietal lobe of the left hemisphere of a *speciosa* monkey (*M. arctoides*). Areas 3, 1, and 2, the postcentral somatosensory cortex, are shown by vertical striping; area 5 of the superior parietal lobule, by light dots; and area 7 of the inferior parietal lobule, by heavy dots. The analysis was not carried laterally beyond the lateral end of the intraparietal fissure. (Drawing courtesy of Mrs. E. Bodian.)

gion of transition between areas 5 and 7, and it is in this mediolateral region that our microelectrode penetrations were made. Toward the lateral end of the fissure, area 5 disappears and area 7 extends onto its anterior wall to meet area 2. Anteriorly, it is obvious that area 5 differs from the koniocortex of area 3, and that the two are separated by a broad band of transitional cortex with identifying features of its own. Whether this consists of areas 1 and 2 in anteroposterior order or of an anteriorly placed area 1 and a transitional region between 1 and 5 seems to us a semantic distinction. The precise location of the transition from area 2 to area 5 differs in different mediolateral planes, and is in all places difficult to mark exactly; it is possible that the population of cells we have defined as area 5 cells is contaminated with some that other viewers would place in area 2. What is certain is that the structure of the cortex and the functional properties of its neurons differs sharply from that just in front to that just behind the transition. Posteriorly, the transition from area 7 to area 19 is reasonably clear, and the extent of areas 5 and 7 onto the medial wall equally so, but the transition from area 7 to the temporal fields laterally is, at least for us, difficult to define. For this reason the analysis shown in Fig. 4 stops at the lateral end of the intraparietal fissure.

At the conclusion of each experiment animals were deeply anesthetized with sodium pentobarbital and perfused through the left heart with 0.9% NaCl solution, followed by 10% formalin. Two small guide wires were inserted into each hemisphere, marking a line for blocking perpendicular to the intraparietal fissure and normal to the cortical surface. Brains were embedded in celloidin and serial sections made at 20  $\mu\text{m}$ ; every section was mounted and stained with Thionine. Several brains were cut entirely for cytoarchitectural study. Penetrations were located by identification of small lesions placed electrolytically during microelectrode penetrations. Each identified penetration was reconstructed on a projected drawing of its section and the cytoarchitectural zones marked on the drawing. We then identified each neuron and each 500- $\mu\text{m}$  segment of a penetration in terms of *a*) the cytoarchitectural area in which it lay, and *b*) the cortical layer(s) containing it. The midpoint of each segment was projected along the cortical radiations to the pial surface and the distance of that intercept to the depth of the intraparietal fissure measured along the pial surface. These measurements provide the abscissas for the histograms of Fig. 13.

## RESULTS

### *General description of electrophysiological results: data base*

Our data base is given in Tables 1, 2, and 6. Successful experiments were made in 17 hemispheres in 11 monkeys. Recording sessions were made on an average of 6 days in each hemisphere; each lasted about 6 h, during which one successful microelectrode penetration was made. In 125 successful penetrations, 1,451 neurons were identified. A neuron entered this population if *a*) its action potential could be identified and remained stable for 10 min or more, and *b*) if the behavioral state found to correlate with, or the sensory stimulus found to drive, the activity of the cell could be identified by at least two observers; 180 (12.4%) neurons were studied in a quantitative way during runs in which behavioral and neural events were identified, timed, and the resulting data stored in computer memory.

Table 1 shows that about 75% of all the penetrations made were later identified in serial sections of the brains and the cytoarchitectural location of each determined. Of the remainder, the large majority were located with reasonable accuracy within one or another area by identification of adjacent penetrations. Tables 2 and 6 show that there is no difference in the distribution of neuron types in either areas 5 or 7 between those observed in identified penetrations and the total population. This suggests that our inferred identifications of the remaining 25% were, for the most part, correct.

### *Properties of neurons of area 5*

**GENERAL CHARACTERISTICS.** Neurons of area 5 differ consistently in their functional properties, so they can be classified into the groups shown in Table 2. We wish to describe the general characteristics of these types; contrast them with the properties of cells of the postcentral somatosensory area, SI; and specify each in some detail.

Area 5 neurons differ from those of SI in several ways. Firstly, they are less active in the absence of an appropriate peripheral sensory or motor event than are those of SI; many of them may otherwise be virtually inactive, and their presence near the tip of the recording microelectrode discovered

TABLE 1. Summary of data base

Expt No.	Species	No. of		Hist Ident		Quant Studies
		Pen	Neurons	Pen	Neurons	
25-L	M. mul.	2	19	2	19	0
32-L	M. mul.	2	13	2	13	0
34-L	M. mul.	3	16	3	16	0
34-R	M. mul.	2	15	2	15	0
36-L	M. mul.	8	150	8	150	8
36-R	M. mul.	5	36	5	36	0
37-R	M. mul.	10	73	9	70	4
37-L	M. mul.	3	41	0	0	0
39-R	M. spec.	7	132	7	132	6
42-L	M. spec.	13	237	0	0	24
42-R	M. spec.	5	111	5	111	5
45-R	M. mul.	9	127	7	110	1
61-L	M. spec.	7	43	7	43	17
61-R	M. spec.	10	68	8	54	18
62-R	M. spec.	16	141	16	141	51
62-L	M. spec.	5	48	5	48	21
63-R	M. spec.	18	181	8	100	25
Totals		125	1,451	94	1,058	180

Summary of all the observations made in the present experiments. Separate totals are given for each of 17 experiments (9 *M. mulatta* and 8 *M. speciosa*): the number of penetrations made and neurons isolated; the number of penetrations identified histologically, and the number of neurons isolated in them; and the number of neurons studied quantitatively in computer-controlled runs. M. mul. = *Macaca mulatta*; M, spec. = *Macaca speciosa* or *Macaca arctoides*. Hist Ident = histologically identified penetrations and neurons.

only on sensory testing or when the waking and behaving animal initiates movements of a certain type, described below. Secondly, those area 5 cells that are driven by peripheral sensory stimuli are less closely linked to that input than are neurons of the somatosensory cortex; this relation never changes in quality, but may vary greatly in security with changes in the state of alertness of the animal. For example, sensory

neurons of area 5 become undrivable during periods of drowsiness or sleep, only to become drivable once again with returning alertness. Thirdly, a proportion of the sensory neurons of area 5 differ from those of SI in the complexity of their relation to the periphery; for a small fraction that relation suggests a higher order of neuronal processing than is common in SI. Lastly, there is within area 5 a class of neurons never ob-

TABLE 2. Classification of neurons of cortical area 5

	Histologically Identified		Total	
	No.	%	No.	%
Projection and hand manipulation	74	10.9	90	9.2
Joint rotation, passive	440	64.4	628	64.3
Other deep tissues, passive	72	10.6	91	9.3
Muscle, passive	21	3.1	29	3.0
Cutaneous, passive	60	8.9	119	12.2
Special	8	1.2	14	1.4
Visual	6	0.9	6	0.6
Totals	681	100.0	977	100.0

Classification of neurons studied in area 5, given as totals and percents, and the numbers and percents in histologically identified penetrations. There were 45 identified and 19 unidentified penetrations into area 5; of the latter, 11 were made in one animal, *BM 42*, who survived so long that the lesions made in the first hemisphere had regressed to invisibility. 80 neurons studied quantitatively in computer-controlled runs.

served in SI, for they are not sensory in nature. We classify these as projection and hand-manipulation neurons because of their functional properties, which we describe in a later section. Cells of this type occur also in the anterior part of area 7 (see Fig. 13).

**JOINT NEURONS OF AREA 5.** Table 2 reveals that two-thirds of the cells identified in area 5 responded to passive rotation of the limbs at their joints. Many of these resemble the joint neurons of area 2 of SI in that *a*) about 82% of them are related to single joints on the contralateral side of the body, and *b*) many of them are sensitive indicators of the steady joint position, at least over the time scale of a few seconds. A smaller number differ from the joint neurons of area 2 in that *a*) about 10% of the total is related to two or more joints on the contralateral side, and *b*) about 7.5% can be activated by rotation of joints on the ipsilateral side of the body, a relation never observed by us for joint neurons in area 2 (see Table 3). Moreover, many area 5 joint neurons are much more active during active movements of the limbs than when the latter are passively displaced. It was a common observation that while passive rotation of the appropriate joint might evoke only a few impulses, the same neuron was driven to high rates of discharge during an active movement which involved rotation of the same joint. The results of study of one such neuron are shown in Fig. 5. This cell discharged at a very slow rate when the shoulder was passively protracted and abducted. The histograms and impulse discharge records of Fig. 5 indicate the high-frequency discharge which occurred during active shoulder protraction and movement of the arm toward

the target, as the animal worked in the task outlined in Fig. 1. The explanation of this difference is not obvious; it will be the subject of a later discussion. What is certain from our study of this group of cells is that each active movement of the limbs is signaled accurately by the patterns of activity in these neurons of area 5.

**CUTANEOUS NEURONS OF AREA 5.** Neurons activated by light mechanical stimulation of the skin are relatively uncommon in area 5 (see Table 2), and the properties of many of them differ from those of cutaneous neurons of the postcentral somatic central cortex. Firstly, their receptive fields are much larger; many located on the contralateral arm, for example, cover the entire palm and volar surface of both the fore- and upper arm. Secondly, these fields may contain both glabrous and hairy skin, a static property which is rare for cutaneous neurons of as well as the ventrobasal complex or of SI, for the mechanoreceptive afferent fibers of beta size which innervate the skin of the arm and hand. Thirdly, large numbers of cells of this class are especially sensitive to moving as opposed to stationary stimuli, and of these many display directional sensitivity (see Table 4). Our criterion for the latter was that a cell be differentially sensitive to the movement of a mechanical probe no matter where in the receptive field the movement began. For many of these cells this differential sensitivity is almost absolute; i.e., a high-frequency discharge is evoked by movement in one direction, none in the other. This property was observed for a small number of cells in an earlier study of the postcentral gyrus (66). Whitsel et al. (79) studied them quantitatively and found that this small proportion is located almost exclusively in layers III and V of SI.

These properties support the idea that the cutaneous neurons of area 5 receive an intramodal convergence that sets them at a higher level in the chain of neural processing than that occupied by cells of the postcentral gyrus.

**PROJECTION AND HAND-MANIPULATED NEURONS OF AREAS 5 AND 7.** The most novel neurons encountered in the posterior parietal areas are not activated by any form of passively

TABLE 3. *Laterality of receptive fields for joint neurons*

	No.	%
Contralateral, single joint	513	82.2
Contralateral, two or more joints	64	10.3
Contralateral and ipsilateral joints	12	1.9
Ipsilateral joints only	35	5.6
Totals	624	100.0

Properties of joint neurons of area 5, as regards laterality and number of joints to which each neuron was related. 43 of the 64 multijoint neurons were related to two or more interphalangeal joints.

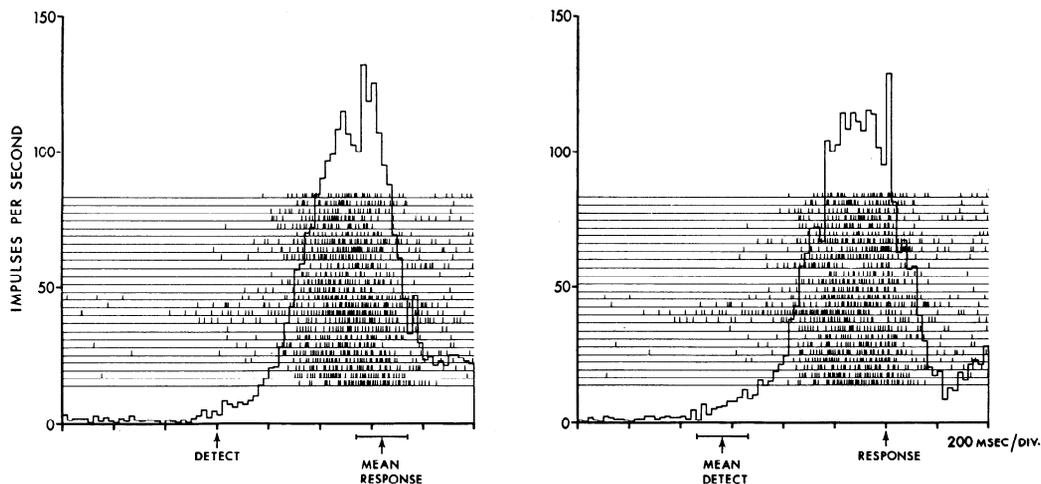


FIG. 5. Replicas of original records, and pre-, intra-, and postresponse histograms of a joint neuron of area 5 of a waking, behaving monkey, working in the detect-projection task schematized in the lower half of Fig. 1. Each horizontal line is the time course of a single trial; each upstroke, the instant in time at which a nerve impulse occurred; only a portion of trials averaged in the histogram are shown. Bin size for histograms = 20 ms. *Left*: records and histograms are oriented by aligning trials at the instant of detection; the bar indicates the mean response (i.e., projection) time  $\pm 1$  SD. *Right*: the same records and the histogram are oriented by aligning trials at the instant of closure of the target switch by the projected hand. The bar shows at its midpoint the mean instant of detection, by its length  $\pm 1$  SD. This neuron responded to passive protraction of the contralateral shoulder with only a few impulses, in contrast to the high-frequency discharge that occurred during active projection of the arm toward the target, in which movement the animal actively protracted the shoulder. Neuron 42-23, located in area 5, left hemisphere.

delivered mechanical stimulation of the peripheral tissues which our monkeys would tolerate; they are equally insensitive to vi-

TABLE 4. *Properties of cutaneous neurons of area 5*

	No.	%
Distribution by laterality of receptive fields		
Contralateral only	108	90.7
Ipsilateral only	3	2.6
Contra- and ipsilateral	8	6.7
Totals	119	100.0
Distribution by skin type		
Glabrous skin	38	32.0
Hairy skin	60	50.4
Glabrous and hairy skin	21	17.6
Totals	119	100.0
Directionally Sensitive Neurons		
Distal to proximal	14	
Proximal to distal	5	
Totals	19	

Properties of cutaneous neurons of area 5, as regards laterality, skin type, and directional sensitivity. The 19 directionally sensitive neurons are 16% of the population, and 14 had fields which included both glabrous and hairy skin, 4 hairy alone, and 1 glabrous alone.

sual or auditory stimuli. Cells of the first set discharge at high rates when the waking animal projects his arm into the immediate extrapersonal space that surrounds him; those of the second when he manipulates within it. However, this activity occurs only if the projected movement or the manipulation is aimed at securing for the animal an object he desires, such as food when he is hungry; or, as in our experimental paradigm, contacting a switch or pulling a lever that provides fluid when he is thirsty. The large majority of these cells (199/218 = 92%) is silent during other active movements, such as those of an aggressive or aversive nature in which the arm and hand may be manipulated in the same zones and with the same muscles as those used during movements aimed at satisfying an appetitive drive. The properties of these cells were first observed in naive animals, untrained in the projection task of Fig. 1. This population of cells is divided in Table 5 as regards cortical area and laterality. It can be seen there that the large majority was active only during actions of the contralateral limbs, that 16% discharged during actions of

either arm, and that 4% were active during ipsilateral projections or manipulations. Bior ipsilaterality is more than 4 times as common for the projection and hand-manipulation neurons of area 7 as for those of area 5.

We show in a later section (see Fig. 13) that neurons of this class are found in both the anterior (area 5) and the posterior (area 7) banks of the intraparietal fissure, in a continuous anteroposterior distribution.

Replicas of the impulse discharges of such a neuron are shown in Fig. 6. The recordings were made as the animal worked in the experimental paradigm of Fig. 1, in which he was required to detect the modulation of a lighted switch placed at arm's length in front of him, and to reach forward to touch the switch to earn a liquid reward. Records such as those shown can be oriented at any one of a number of the accompanying behavioral events; the averages that result will differ slightly because the detection-response times will vary from trial to trial. The records to the left of Fig. 6 are oriented at the instant of key release (signal detection), those to the right at the instant of target switch closure (response). The histograms show that neuronal activity, on the average, began to accelerate before the release of the detect key, reached a peak as the arm moved

through the air toward the target, and declined virtually to zero before the hand contacted the switch.

Figure 6 illustrates the results obtained in a run with a single foreperiod. More commonly, in any given run, trials with different foreperiods followed each other in a random sequence. The histograms for three other projection neurons studied in this way are shown in Fig. 7. The tasks were similar to that outlined in Fig. 1; in each case the target was stationary and placed directly ahead of the animal, at arm's length. For each neuron, the histograms of the neuronal activity during responses made in each of the foreperiod classes of trials are superimposed, in Fig. 7. The results illustrated show that the pattern of neuronal activity during such a motivated projection of the arm is not influenced by the duration of the foreperiod. This general statement is true for all the neurons of this class we have studied.

The histograms shown at the top of Fig. 7 illustrate that the frequency of discharge of a projection neuron may begin to increase before release of the detection key and before any movement of the arm is visible. The histograms of the lower panel of Fig. 7 illustrate another common feature of projection neurons. That is, they may be

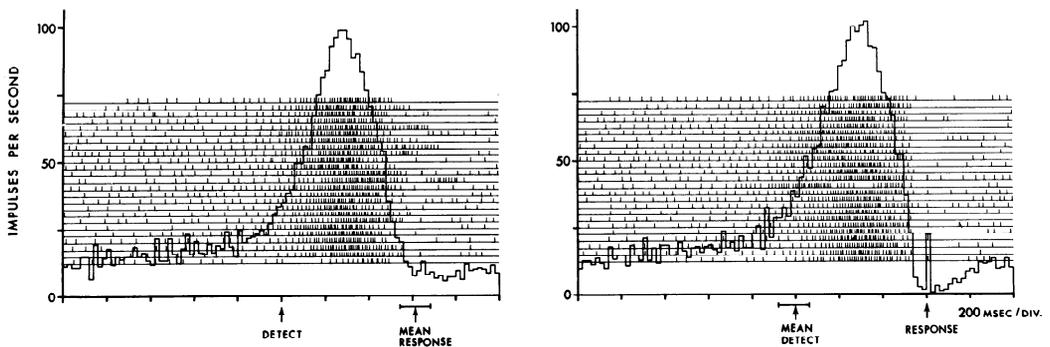


FIG. 6. Replicas of original records, and pre-, intra-, and postresponse histograms, made during study of an active projection neuron. The cell never responded to any passively delivered mechanical stimulus to the arm, to visual or auditory stimuli, or during aversive-aggressive movements of the contralateral arm. Results illustrated were obtained as the animal worked in the task outlined in the lower half of Fig. 1. Each horizontal line is the time course of a single trial, each upstroke the instant at which a nerve impulse occurred; only a portion of trials averaged in the histogram is reproduced. Bin size for histogram = 20 ms. *Left:* records and histograms are oriented by aligning trials at the instant of detection; the bar indicates the mean response time  $\pm 1$  SD. *Right:* the same records and a histogram, now oriented by aligning trials at the instant of closure of the target switch by the projected contralateral hand. The bar shows the mean instant of detection  $\pm 1$  SD. Neuronal activity began to accelerate before release of the detect key, reached its peak as the arm moved through the air toward the target switch, and declined virtually to zero before the hand contacted the switch. Neuron 42-21, area 5, left hemisphere.

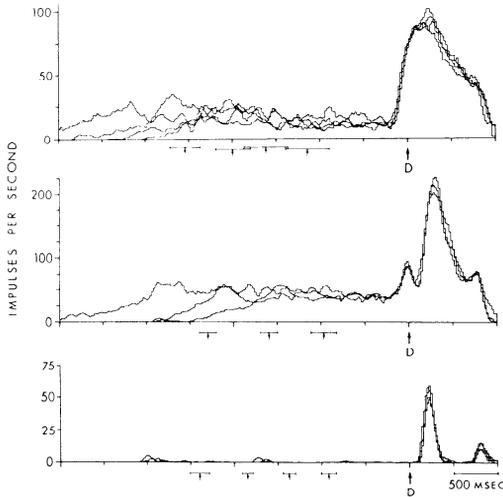


FIG. 7. Suprimposed histograms of responses of three projection neurons in area 5 of the left hemisphere of a *M. arctoides* as he worked in the task schematized in the lower part of Fig. 1 and in the apparatus shown in Fig. 2. For the run on each cell, trials are all oriented at the moment of release of the detect key, but are separated into classes by the duration of the foreperiod, the period of time the monkey must wait before he may correctly detect and project. The near identity of histograms for each class, for each of the three neurons, suggests the time course and frequency of the neuronal activity of projection neurons during arm projection is not a function of the duration of the waiting time. The result above illustrates a case in which neuronal activity began before release of the detect key; that below, a case in which the cell was almost inactive except during the actual projection of the arm. No one of the neurons was activated by any form of stimulus delivered passively. Each was isolated and studied in a separate microelectrode penetration into the left hemisphere of monkey 62, on different recording days. *Upper*: neuron 62-4, layer VI, area 5. Bin size, 20 ms; parabolic smoothing, 8 bins. Foreperiods: 500, 1,000, 1500, and 2,000 ms. For each of these classes the mean time of depression of the key is indicated by the small arrow; the bar is 2 SD of the key down-detect time. *Middle*: neuron 62-5, layer IV, area 5. Bin size, 20 ms; parabolic smoothing, 8 bins. Foreperiods: 500, 1,200, and 1,900 ms. Classes indicated as above. *Lower*: neuron 62-6, layer VI, area 5. Bin size, 20 ms; parabolic smoothing, 8 bins. Foreperiods: 500, 1,000, 1,500, and 2,000 ms. Classes indicated as above.

completely inactive unless such a motivated projection of the arm into extrapersonal space occurs.

*Relation of pattern of activity of projection neurons to spatial trajectory of movement of arm.* An important question for concepts of the function of the posterior

parietal cortex is how closely the activity of projection and hand-manipulation neurons is linked to the associated movements; i.e., are the details of movement specified by them? The parietal cells differ from neurons of the precentral motor cortex, for the relation of their activity to movement is not obligatory; it occurs only during that class of movements aimed at a particular end. Moreover, we found that the pattern of projection neurons is independent of the particular spatial trajectory of the arm toward the target. An example is given in Fig. 8. In this case the monkey worked in the paradigm of Fig. 1, with the lighted switch carried on a target moving at  $21^\circ/\text{s}$ . The inset drawing indicates the average point in space, for each of the foreperiod delays, at which the projected hand reached the target. The superimposition of the histograms for the neuronal responses in each of the three classes indicates that, on the average, there was no difference in the pattern of neuronal activity which correlated with the different spatial trajectories of the arm.

This question was tested again in a task in which the animal was required, on detection of a somatosensory stimulus, to reach forward to pull a lever on one of two panels placed at arm's length before him,  $32^\circ$  apart. The lever indicated as correct by a small light was randomly paired, on any given trial, with one of two foreperiods; there resulted four classes of responses. The impulse replicas and the histogram for one of these are shown to the left of Fig. 9, oriented at the instant of release of the detect key. They show that the activity of this neuron began just before the key release, and reached its peak and declined as the arm moved forward and upward toward the lever. The histograms for the four classes of responses are superimposed to the right in Fig. 9. They indicate that neither the trajectory of the arm nor the critical period of waiting prior to the movement is correlated with any significant difference in the patterns of neuronal discharge of this cell.

We conclude that the activity of this class of parietal cells is not related to the details of movements, but to the act of arm projection or of hand manipulation, considered as a whole.

*Relation of pattern of activity of projec-*

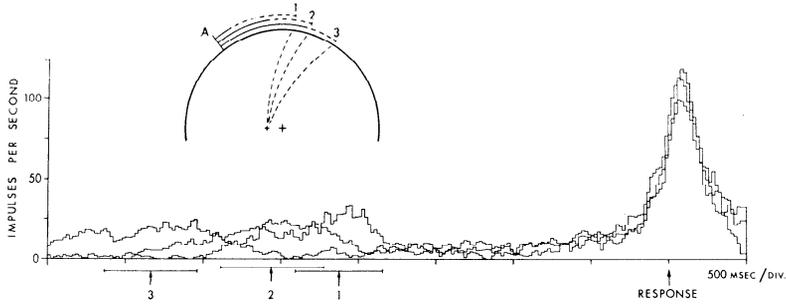


FIG. 8. Superimposed histograms of the activity of an arm-projection neuron during the task outlined in lower Fig. 1, executed in the apparatus of Fig. 2. The identity of the amplitude and time course of the neuronal discharge during arm movements through different trajectories suggests that these command signals do not contain detailed instructions for muscle contractions. Histograms are oriented on the instant at which the moving target was closed by the monkey's extended hand. The three horizontal bars to the left on the abscissa show the mean detection time  $\pm 1$  SD for each of the three foreperiod classes. The inset is a diagram of target movement around the circular track, showing the start position, A, and schematics of the hand trajectories to the mean target positions for each of the three foreperiod delays, 1, 2, 3. The final target position in each case is the sum of the movement during the foreperiod delay of 500, 1,500, or 2,500 ms (solid lines), and movement during the mean detection times plus that during the mean response times (dashed lines). Histogram bins, 20 ms. Neuron 62-43, area 7, right hemisphere. Left arm projecting.

*tion neurons to channel used for sensory signals.* The possibility exists that the pattern of activity of neurons of this class is related to the unique combination of arm

projection and visual fixation of standing targets, or hand-eye tracking of moving ones, or the inspection and detection of the visual cues themselves, even though our

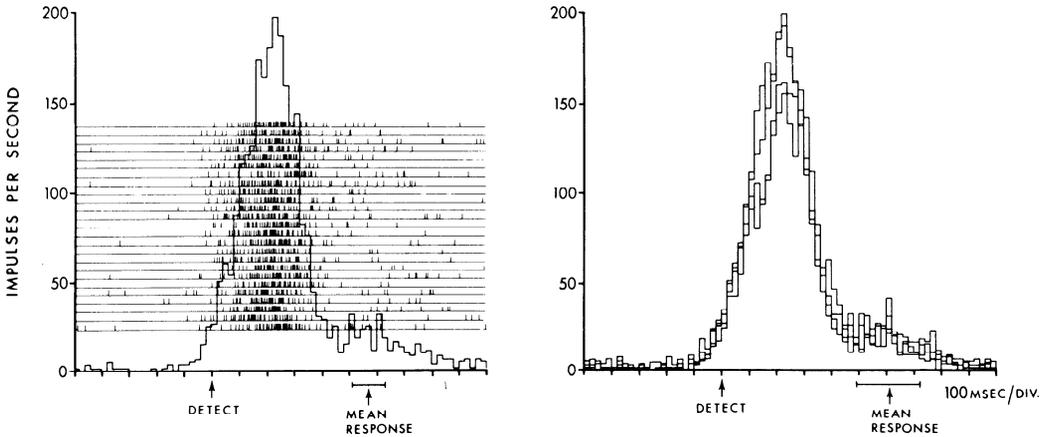


FIG. 9. Results of study of a projection neuron. In this experiment the animal was required to detect a 30-Hz mechanical sinusoid delivered to the glabrous skin of the right hand, and on detection to project his left arm to pull the lighted one of two target switches placed  $32^\circ$  apart, at arm's length, to earn a reward. Replicas of original records and averaged histograms of all results in this run are shown to the left. Each horizontal line is the time course during a single trial; each upward stroke, the instant in time at which a nerve impulse occurred; only a portion of trials averaged in the histogram are shown. Histogram bins = 20 ms. Records are aligned at the instant of detection; the arrow indicates the average response time; the bar =  $\pm 1$  SD. The four histograms to the right show the average time course of neuronal activity during four classes (each with many trials) determined by combinations of two different foreperiods, 500 and 1,500 ms, and the two target positions. The experiment shows: 1) that the activity of a projection neuron is independent of the sensory channel transmitting activity that initiates the behavioral act of projection, and 2) that neither the period of waiting nor the specific trajectory of the arm projection appears to influence the pattern of neuronal activity. Neuron 39-3, layer III, area 5, right hemisphere.

control tests showed them to be insensitive to visual stimuli per se. We have tested this hypothesis in another way by substituting somesthetic for visual stimuli as detection cues. Animals were trained to detect a vibratory stimulus delivered to the hand ipsilateral to the hemisphere under study, and thereupon to project the contralateral arm forward to contact a lighted panel switch, the target. The results of such a study are illustrated in Fig. 9. We observed for this neuron, as we did for the entire subset of projection neurons studied using vibratory stimuli as cues (26% of the total), no difference in the properties or discharge patterns which could be correlated in any way with the difference in the sensory channel used. We have never studied the same single neuron in both of these experimental paradigms. Thus the possibility exists that completely separate sets of parietal neurons are active, depending on the sensory channel used. This is unlikely, however, for each of the neurons studied with vibratory cues was first tested with visual ones, by inducing the animal to reach for parcels of food placed within arm's reach. The properties of these cells appear to be identical whether visual or somesthetic cues are used. We have used the following control, especially when recording from area 7, to differentiate between projection neurons and those of the several visual classes described later. The animal is first allowed to view the target toward which he desires to reach, be it food or lighted switch, but is forced to delay the projected movement. When his view of the target is occluded during that waiting period, the projection of the arm, when

allowed, occurs swiftly and accurately, and the associated discharge of the projection neurons is similar to that which occurs when the animal's view of the target is clear.

We conclude that the activity of the parietal projection neurons is independent of the modality of the sensory cuing signals and of continued visual guidance of the projected movement.

*Properties of hand-manipulation neurons.* These neurons are classed with projection neurons because the two resemble each other in their general properties. Hand-manipulation (HM) neurons are not activated by passive stimulation of the skin or the deep tissues of the hand or by gentle rotation of its joints. They are active selectively during certain types of exploratory behavior. There is a furious discharge, for example, when the animal manipulates within a small box to obtain a parcel of food ("winkling"). The activity is undiminished on trials in which the animal's view of the target is occluded before arm release. Tables 2 and 6 show that HM neurons occur in both areas 5 and 7, as do projection neurons. They are more likely to be encountered in penetrations somewhat more laterally placed than those in which arm-projection neurons are found, but there is considerable overlap.

Table 5 shows that many HM neurons are active when the animal manipulates with either hand, and a few with ipsilateral manipulation alone. Neurons related to the ipsilateral hand in either way are 4-5 times more common in area 7 than they are in area 5.

TABLE 5. *Distribution of projection and hand-manipulation neurons by laterality and by cortical area*

	Total Population			Area 5 Population			Area 7 Population		
	HM	Pro	Total	HM	Pro	Total	HM	Pro	Total
Contralateral	67	91	158	30	48	78	37	43	80
Contralateral and ipsilateral	15	17	32	2	1	3	13	16	29
Ipsilateral	2	5	7	1	3	4	1	2	3
Totals	84	113	197	33	52	85	51	61	112

Distribution of projection and hand-manipulation neurons of area 5 and area 7 by laterality and cortical area. Laterality definition was clear for 197 of the 218 neurons of this class identified in area 5, of which 179 were in histologically identified penetrations. HM = hand-manipulation neurons; Pro = projection neurons.

Hand-manipulation neurons differ from projection neurons in one important respect. Their activity is, in many cases, not restricted to operations aimed at obtaining food or drink or actions on surrogates which lead to those rewards. Many HM neurons are active during the act of grooming, a typical motor pattern of monkeys which apparently brings pleasure to both groomer and groomee. These same neurons, however, are not active when a monkey makes an aggressive movement of the hand, as in pinching. We have observed on a few occasions such a neuron to be active when the traction reflex of Denny-Brown (19) was elicited, and during tactually guided, searching movements of the hand. Hand-manipulation neurons were not activated by any passively delivered mechanical stimulus which our animals would tolerate; we have not tested the effect of noxious stimuli of greater intensity.

#### *Properties of neurons of area 7*

**GENERAL CHARACTERISTICS.** The neurons of area 7 differ from one another in their functional properties, so they can be classified as shown in Table 6. They are neither motor nor sensory, in the usual sense. Our results suggest that they are related to manual or to visual explorations of extrapersonal space, in a conditional not an obligatory fashion. The "visual" neurons of area 7 discharge at very low rates when the animal rests quietly; those rates increase sharply when he initiates visual exploration of his environment in the special ways described below. The projection and the hand-manipulation classes of neurons of area 7 resemble in al-

most every way similar ones of area 5; they differ only in that a greater proportion are related to actions of both upper extremities or to the ipsilateral one alone (see Table 5).

We wish to describe in more detail the properties of the visual neurons of area 7, particularly the visual fixation and visual tracking neurons.

**VISUAL FIXATION (VF) NEURONS OF AREA 7.** The discharge rates of cells of this class increase abruptly when the animal fixates certain objects. The object must, to be effective, be of interest to the animal, such as food when hungry or liquid when thirsty. The effect of such an object is maximal if it is located within arm's reach, and the associated discharge on fixation decreases with object distance. If the object is more than 1-2 m from the animal's head, the discharge associated with fixation habituates in the first few trials. Fixation of other, even novel, objects presented within arm's reach may be associated with brief periods of increased activity, but this declines with repeated presentations. Similarly, color photographs of food or of other monkeys projected on a screen within the animal's reach may be associated with increased activity on first presentation and visual fixation, but little after repeated displays. VF neurons are not activated: *a*) by visual stimuli not fixated, whether objects of interest or not; *b*) by passive mechanical stimulation or peripheral tissues; *c*) during random, exploratory movements of the limbs; *d*) by auditory stimuli; or *e*) during projection of the arm toward or manual exploration of targets previously identified by visual fixation, if

TABLE 6. *Classification of neurons of cortical area 7*

	Histologically Identified		Total	
	No.	%	No.	%
Projection and hand manipulation	124	32.9	128	26.7
Visual space	49	13.0	75	15.9
Visual tracking	49	13.0	88	18.6
Visual fixation	129	34.2	155	32.9
Special	19	5.0	21	4.4
Joint neurons, passively activated	7	1.9	7	1.5
Totals	377	100.0	474	100.0

Classification of the neurons studied in area 7, given as numbers and percents, for the total population and the subset of neurons in histologically identified penetrations. 49 of 61 penetrations in area 7 were identified; 100 neurons were studied quantitatively in computer-controlled runs.

vision is occluded before arm projection is permitted. The particular nature of the object fixated, and the presumed motivational drive it evokes in the animal, appear to be requirements for the associated activity of VF neurons. Such a cell may, for example, be completely silent as the animal explores his environment visually, fixating in sequence experimenter, instruments, books, etc., to be followed immediately by intense discharge on fixation of a food object presented within arm's length. That discharge increases as the target is moved closer to the animal's face, but ceases abruptly if the line of gaze is blocked or if the animal exhibits saccades away to another object.

Perhaps the behavioral act most effective for the associated discharge of VF neurons is one very characteristic of monkeys, the visual inspection of a parcel of food held in the monkey's hand, close to his mouth, before eating. Frequently, partially chewed or pouch-stored food parcels are taken from the mouth and inspected in this way before eating. The associated discharge of VF neurons during this act ceases if the line of gaze is blocked, even if the act of eating is not interrupted. This suggests that it is the visual fixation and inspection, not smelling or eating, that is important for the associated discharge of VF neurons.

In the trained animal the appearance of a light, which he has learned he must attend closely in order to perform successfully for liquid reward, is associated with a discharge that recurs with each trial, until satiation. An example is given in Fig. 10.

The results illustrated in Figs. 10 and 11 were obtained as a monkey worked in the paradigm of Fig. 1, with head fixation and microelectrode recording methods described earlier, but with a different test apparatus from that of Fig. 2. In this case the animal sat facing at 57 cm a frosted-glass tangent screen, 36° square. A target light spot (a laser beam) could be positioned at any location on the tangent screen, and moved in any direction at speeds up to 360°/s, for any distance within the screen area. The intensity of the light and its movements were under computer program control; movements were accomplished by mirrors mounted on moving coil galvanometers. DC electrooculograms were recorded via Ag-AgCl electrodes chronically im-

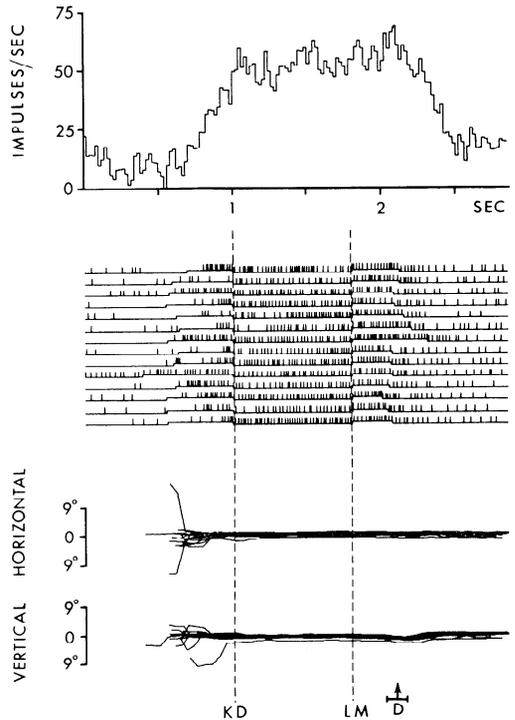


FIG. 10. Results of one part of a study of a visual fixation neuron of area 7. The monkey worked at a task in which he was required to fixate a target light (laser beam, 2 mm diameter) that appeared directly ahead in the central line of gaze on a frosted-glass tangent screen placed 57 cm from his eyes, to detect a slight dimming of the light for a reward. Sets of records, from below upward, are: 1) vertical electrooculograms; 2) horizontal electrooculograms; 3) replicas of the impulse discharges for a sample of trials; each line of these records is the time course during a single trial, each upward stroke the instant at which an impulse was discharged; the successive small upward and downward displacements of the line signals, for that trial, light on, closure of the signal key (KD), dimming of the light (LM), and its detection; average detect time is at  $D \pm 1$  SD; 4) a histogram averaging rates of impulse discharges during all trials. For the histogram, bin size = 20 ms; parabolic smoothing, 5 bins. Records and histograms show the increase in discharge rate with onset of the light and continuing discharge during its steady fixation until detection and reward. The rate of discharge then declined even though, as shown by the electrooculograms, eyes remained fixed on the site from which the light disappeared at the instant of detection. Neuron 65-89, area 7, right hemisphere, *M. mulatta*.

planted in small holes placed appropriately in the bone of the orbital rims. A complete description of these methods will be given at a later time, together with the results of quan-

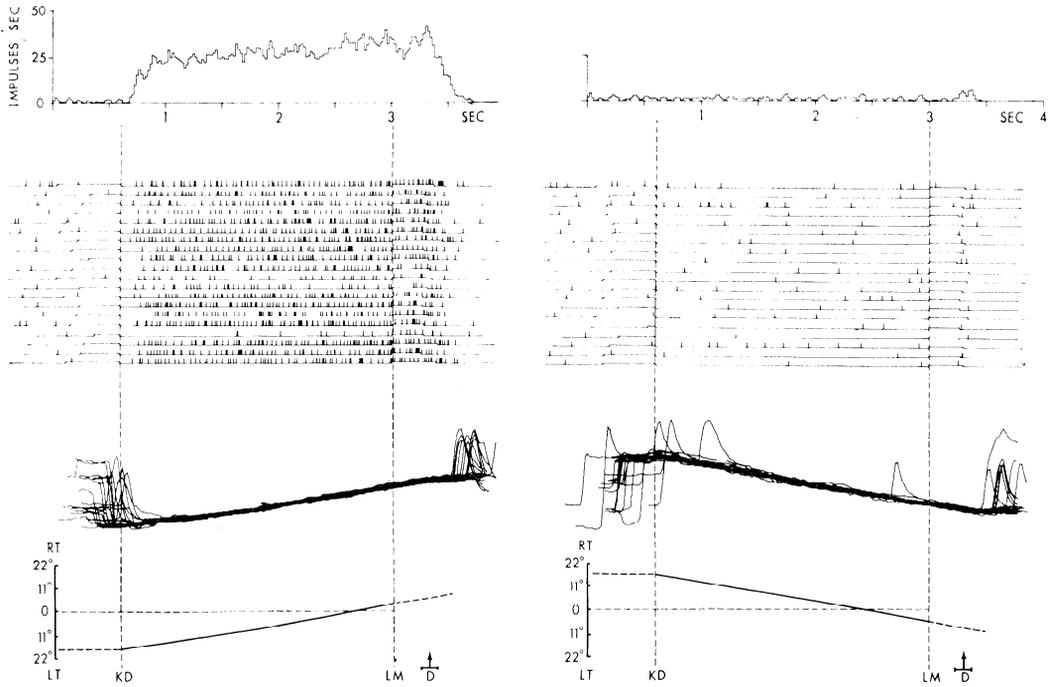


FIG. 11. Results of study of a visual tracking neuron in area 7 of the left hemisphere of a waking monkey, *M. mulatta*. The animal worked in a task in which he was required to pursue closely a small spot of light (laser beam, 2 mm diameter) moving across a frosted-glass tangent screen placed 57 cm from his eyes, to detect a slight dimming of the light, and release a key for reward. *Left column*: the light comes on 18° to the left of the midline, in the horizontal meridian of gaze; movement of the light begins when the animal closes the signal key (KD), and continues left to right at 9°/s for 22°, dimming at LM. The average detection latency of the animal is shown by the arrow at D; the horizontal line = 4 SD of the mean detection time. Light movement is indicated by the lowest line. Next above are superimposed horizontal electrooculograms, one for each of a number of trials; up = right, down = left. They show the guessing and searching movements of eyes as a trial begins, the quick saccade to target when the guess was wrong, the smooth pursuit movements, and the quick saccade breakaways after reward. Next above, for the same sample of trials, are replicas of impulse discharges. Each line represents the time course of one trial; each upward stroke, one impulse. Small displacements indicate, successively: light on, closure of key and onset of light movement, dimming of the light (LM), and key release (D). There is little or no activity during the search saccades or during the steady fixation; activity begins well before gaze is locked into a smooth pursuit of the moving target, and continues at a high rate during movement, as shown also by the histogram at the top; for the histogram, bin size = 20 ms, parabolic smoothing, 5 bins. Records to the right were obtained in a similar way, except that movements are in the opposite direction, right to left. The directional orientation of this neuron was almost complete.

titative studies of the visual neurons of area 7. We have confirmed, in those studies, the functional properties of VF and VT neurons described here, and discovered other classes of area 7 visual neurons related to target-directed saccades.

The electrooculograms and the replicas of the impulse discharges shown in Fig. 10 reveal that the neuron under study increased its activity abruptly with fixation of the target light, and continued to discharge at a high rate during steadily maintained fixation of the light. Other studies of this and other VF neurons have shown that the

steady discharge during steady fixation is powerfully suppressed during target-evoked saccadic movements, following which activity gradually increases during steady fixation at the new position. That activity may decline during continued steady fixation of the locus, after a reward is earned (see Fig. 10), or be interrupted abruptly if a break-away saccade occurs, which is not shown in Fig. 10.

The discharge of VF neurons does not depend uniquely on the particular direction of gaze, though the majority are more active when gaze is directed into the contralateral

half-field. This is itself further evidence that VF neurons are not "visually driven" in the sensory mode, for certainly the same sets of foveal receptors and the central neurons to which they are linked are activated when the object is fixated in two different lines of gaze. The discharge of VF neurons commonly persists during smooth pursuit of the object fixed if it is moved, independently of the direction of visual tracking.

**VISUAL TRACKING (VT) NEURONS OF AREA 7.** Neurons of this class do not discharge during static visual fixations; they are active when the animal pursues smoothly with his eyes an object moving through his visual field, with the further contingencies that the object is one of interest, such as food when hungry, and that it be within arm's reach. Otherwise the neuronal discharge associated with smooth visual tracking ceases after a few (two to six) trials. In the trained animal, activity occurs as he tracks a moving target light, as in the experimental design of Fig. 1. An example is given by the sets of records of Fig. 11. They are, from below upward: the path of the target light on the tangent screen; superimposed horizontal electrooculograms for a number of trials; replicas of the impulses discharged by the neuron under study, in area 7 of a monkey's left hemisphere, during those same trials; and a histogram averaging the impulse discharges for all trials in the run, only a few of which are replicated below. The records to the left were obtained during smooth pursuit tracking from left to right, those to the right for tracking in the opposite direction. The records to the left show that the neuron is virtually silent during the search saccades that precede and follow onset of the target light (being different for different trials) and during the steady fixation prior to depression of the signal key (KD). Activity begins as eye movement is smoothly locked onto the target path; it persists during movement of the light, its dimming (LM), and key release (D). It ceases as the light goes out and gaze breaks away. The records in the right-hand column show a very low rate of discharge when the eye is tracking in the opposite direction.

The frequencies of the directional sensitivities of the VT neurons are shown in

TABLE 7. *Directional properties and laterality relations of visual tracking neurons of area 7*

	Right Hemisphere	Left Hemisphere
<b>Direction</b>		
Left → right	19	10
Right → left	9	14
Up → down	5	10
Down → up	0	4
Vergence	6	7
Totals	39	45
<b>Side of extrapersonal space</b>		
Contralateral	26	11
Ipsilateral	1	17
Contra- + ipsilateral	12	8
Totals	39	36

Classification of visual tracking neurons of area 7 by directionality and laterality. 84 directions were identified for 75 neurons; 66 neurons were active during movements in only one direction, 9 during two.

Table 7. Information was available concerning this property for 75 of the 88 VT cells identified in area 7; 66 were active when a smooth pursuit occurred, in one direction only. Nine were active during tracking in either of two directions; they were reciprocal in four, irreciprocal in five. Table 7 shows that the VT neurons in each hemisphere possess, as populations, all the directional sensitivities tested, save for the "down-up" category for the right hemisphere. Undoubtedly with a larger sample it too would be represented. The number of directions identified and the small sample we have studied suggests that these statements on population distributions be regarded tentatively.

**VISUAL SPACE NEURONS OF AREA 7.** Neurons of this class are preferentially activated when visual stimuli are presented just lateral to the maximal lateral deviation of gaze, with head fixed. Many discharge with the rapid saccade to the full lateral position, while others discharge steadily as the animal maintains a full lateral deviation of the eyes, which does not bring the object into foveal fixation. A small number are preferentially active during a maximal vertical deviation of gaze aimed at a target placed just beyond range. Under the conditions of the present experiments we could

not specify further the properties of these cells. They may, of course, be related to maintained full lateral deviation of the eyes or to the head turning that under normal circumstances accompanies direction of gaze to the full lateral (or vertical) position.

We have identified the laterality property for 40 of the 75 neurons of this type we studied; 28 were activated by stimuli presented on the contralateral side, 5 responded only to stimuli presented ipsilaterally, and 7 responded in either case. Cells of this type are not activated by passive manipulation of the limbs, by auditory stimuli, or by projection of the arm and hand toward a target.

#### *Neurons of areas 5 and 7 with special properties*

We have observed 35 neurons in areas 5 and 7 with unusual properties, in combinations that differed greatly. We have classed them together because of their rarity for until larger numbers have been studied, we do not conclude that any one represents a major class of parietal neurons. We provide a brief description of some of them because of their intrinsic interest.

Eighteen of these neurons were functionally related to the coordination of the visual fixation of and arm projection toward desired objects in immediate extrapersonal space. They were all located in the posterior bank of the intraparietal sulcus, in the most anterior portion of area 7; 17 of the 18 were located in the right hemispheres of five different animals. This is a highly significant lateralization compared to that of our total sample (left, 567; right, 884, see Table 1). Nevertheless, any conclusion concerning hemispheric specialization of this nature must await study of a much larger sample of such neurons.

These hand-eye coordination, or summing, neurons usually showed an increment in activity during visual tracking or fixation of desired objects, and in some cases a minimal but in others no change in activity during projection of the hand toward or manipulation of such a target, previously identified visually, without visual guidance. It was the combination of these two events which was associated with the most intense activity. We did not design a task that required arm projection in the

absence of visual guidance, but in many individual tests for each of these neurons, blind reaching toward targets previously identified visually was observed not to be associated with any increase in discharge. Our sample of neurons of this type is too small to determine whether they are segregated by cortical layers, though we think not for we have identified them in layers III, IV, and VI.

Other types of cells with special properties were observed much less commonly. Five otherwise unremarkable visual tracking neurons could also be activated by passive stimulation of the skin (three cases) or by passive joint rotation (two cases); three of these were in area 5—and thus exceptional for visual neurons; and two in area 7—and thus exceptional for mechanoreceptive neurons. We observed five cells in area 5 that resembled a group described by Sakata et al. (73); they were active when the animal assumed a quiet resting posture, right arm and hand folded over the left forearm. They were not activated by passive manipulation of the arms nor during any other behavioral act. Dissolution of the posture was accompanied by virtual cessation of discharge. The properties of the 10 other special cells differed markedly, and each type was observed rarely.

*"Undrivable" cells.* We observed a number of neurons in areas 5 and 7 that we could not affect in any way. They did not respond to somesthetic, visual, or auditory stimuli, nor did their rates of discharge increase during any of the behavioral acts associated with the tasks we used. We could discover no other distinguishing features of these cells. They were, for example, about equally divided between those with initially negative and those with initially positive action potentials. The depth and areal distributions of these cells are shown in Table 8, which indicates a significant but small differential likelihood (as compared with the differential due to sampling bias) of such cells appearing in layer III of both areas 5 and 7. These cells are, as percentages of the total populations of identified neurons, about 3 times more common in area 7 than in area 5. Undrivable cells were not segregated and appeared singly, or sometimes in small groups, in the course of penetrations in which readily identified cells were found immediately above and below them. We have noted that some of these cells were encountered and tested during periods in which the animal was drowsy or inattentive, and we have observed other cells to become undrivable when drowsiness super-

vened. Nevertheless, we do not believe that the undrivability of all of these cells can be accounted for on this basis.

*Correlation of spatial distribution of neuronal populations with cytoarchitectural area and cortical depth*

The spatial distribution of cortical neurons with different functional properties is of interest with regard to *a*) whether it reveals discontinuities at cytoarchitectural boundaries, and *b*) whether the distributions in the various cortical layers may reveal something of intracortical processing mechanisms. It is difficult to make accurate estimates of the spatial distribution of different neuronal populations using the method of single-neuron analysis. The likelihood that at any given locus the electrical signs of the impulse discharges of one cell will be "isolated" from those of others, and thus allow identification and study of functional properties, depends on the size and input impedance of the microelectrode, the damage it has produced by its passage through the cortex, the sizes and packing density of the neurons in the immediate region, and the certainty with which the investigator can evoke the activity of the neurons under study. The one important factor which is measurable is the distribution of sampling; i.e., the total millimeters of microelectrode travel into different cortical loci or through different cortical layers. In that which follows (see Figs. 13 and 14) we compare the distribution of neuronal populations ob-

served with our own highly biased distribution of sampling, and conclude that the differential distribution of the neurons isolated and studied is largely determined by the sampling bias (see Table 9).

DISTRIBUTION OF CLASSES OF POSTERIOR PARIETAL NEURONS IN AREAS 5 AND 7. The majority of our microelectrode penetrations were made in a mediolaterally restricted band of the parietal cortex, extended in the anteroposterior dimension to allow sampling of areas 5 and 7, and particularly of the cortex lining the banks of the intraparietal sulcus. The reconstructions of Figs. 12, 15, and 16 show that we have only partially sampled those deep areas of cortex. For the present analysis of spatial distribution we have located each neuron by its distance from the depth of the intraparietal sulcus, which in the mediolateral zone we have explored marks the transition between areas 5 and 7; the measurements were made as described in METHODS. Neurons were classed by that distance in millimeters anterior or posterior to the depth of the fissure; these classes form the abscissas for the histograms of Fig. 13. In a similar way we have measured the sampling of the cortex as a function of anteroposterior position. In each reconstructed penetration, the midpoint of each 500- $\mu$ m segment was projected and measured as described in METHODS. The solid-bar histogram of Fig. 13, upper left, shows the resulting distribution of sampling; i.e., the total number of

TABLE 8. *Distributions of undrivable cells*

Layer	Area 5			Area 7		
	No. cells	% Cells	% Sampling	No. cells	% Cells	% Sampling
I	1	2.3	5.2	2	2.1	9.7
II	2	4.6	9.2	13	13.8	14.6
III	26	60.7	50.0	52	55.4	42.6
IV	2	4.6	14.1	11	11.7	13.1
V	3	7.0	9.5	9	9.6	10.8
VI	9	20.8	12.0	7	7.4	9.2
Totals	43	100.0	100.0	94	100.0	100.0
	$\frac{43}{676 + 43} \times 100 = 6\%$			$\frac{94}{341 + 94} \times 100 = 21.6\%$		

Distribution by cytoarchitectural area and layer of neurons that were spontaneously active, and which showed no relation to any sensory stimulus or behavioral act. The figures below show the percent of these undrivable cells in the total populations studied; this property is more common for area 7 cells than for those of area 5.

TABLE 9. *Depth distributions of sampling distances and neuronal population*

Layer	Samp Dist	Total Pop	R + HM	Joint	Deep	Skin	Others
Area 5							
I	5.3	0.6	0	0.2	4.2	0	0
II	9.2	7.1	8.6	6.7	6.9	11.7	0
III	49.7	43.4	44.1	48.2	33.3	31.7	22.8
IV	14.2	22.9	20.2	26.9	13.9	13.3	14.3
V	9.5	15.1	6.8	10.6	22.3	33.3	42.9
VI	12.1	10.9	20.3	7.4	19.4	10.0	20.0
Totals	100.0	100.0	100.0	100.0	100.0	100.0	100.0
<i>n</i>	156 mm	676	74	435	72	60	35

Layer	Samp Dist	Total Pop	R + HM	VF	VS	VT	Others
Area 7							
I	9.7	0.9	0.9	0.9	0	0	4.5
II	14.6	21.7	19.7	20.9	28.9	21.3	22.7
III	42.6	43.3	55.4	40.9	35.6	31.8	36.5
IV	13.1	17.9	19.7	19.1	4.4	25.6	13.6
V	10.8	8.6	1.7	9.1	13.3	17.0	9.1
VI	9.2	7.6	2.6	9.1	17.8	4.3	13.6
Totals	100.0	100.0	100.0	100.0	100.0	100.0	100.0
<i>n</i>	115 mm	341	117	110	45	47	21

Distribution in depth by cytoarchitectural layers in areas 5 and 7 of microelectrode sampling, the total population of neurons studied, and of several subsets identified by their qualitative natures. There appear to be no significant differential distributions of these subsets as regards depth, although study of greater numbers might establish statistical validity for some of the differences suggested in this table; e.g., the apparent difference in the depth distribution of the projection neurons of area 5 and that of the same subset in area 7. R + HM = rotation and hand manipulation, VF = visual fixation neurons, VS = visual space neurons, VT = visual tracking neurons.

millimeters of fresh brain traversed by a microelectrode for each anteroposterior millimeter segment of the cortex.

The hatched-bar histogram of Fig. 13, upper left, shows the distribution of all neurons isolated in the penetrations of areas 5 and 7 subsequently identified histologically and reconstructed. The congruence of the two histograms suggests that the highly biased distribution of the neurons isolated is largely determined by the distribution of sampling; i.e., the likelihood of isolating a neuron in any given segment is a function of the total sampling within that segment. That conclusion appears equally certain for the distributions of the subpopulations shown in the other three histograms of Fig. 13. Other factors that might influence the likelihood of isolating neurons account for a small part of the differential distributions.

The two histograms to the right of Fig. 13 reveal a remarkably sharp segregation of

the passively activated joint neurons to area 5 and of the several classes of visual neurons, here summed together, to area 7. It appears that over a transitional region of no more than 1–2 mm extent in the cortex lining the base of the intraparietal fissure, there is a sharp change in both the cytoarchitecture and in the functional properties of some large classes of cortical neurons. This functional transition is not, however, true for all classes of neurons, as shown by the histogram at the lower left of Fig. 13 for the population of projection and hand-manipulation neurons. This distribution, when corrected for sampling, is a flat one, which shows that the neuronal mechanisms determining the properties of this class of cells are present on both sides of the fissure, in two zones of cortex that differ cytoarchitecturally.

DISTRIBUTION OF POSTERIOR PARIETAL NEURONS IN DIFFERENT CORTICAL LAYERS. The distri-

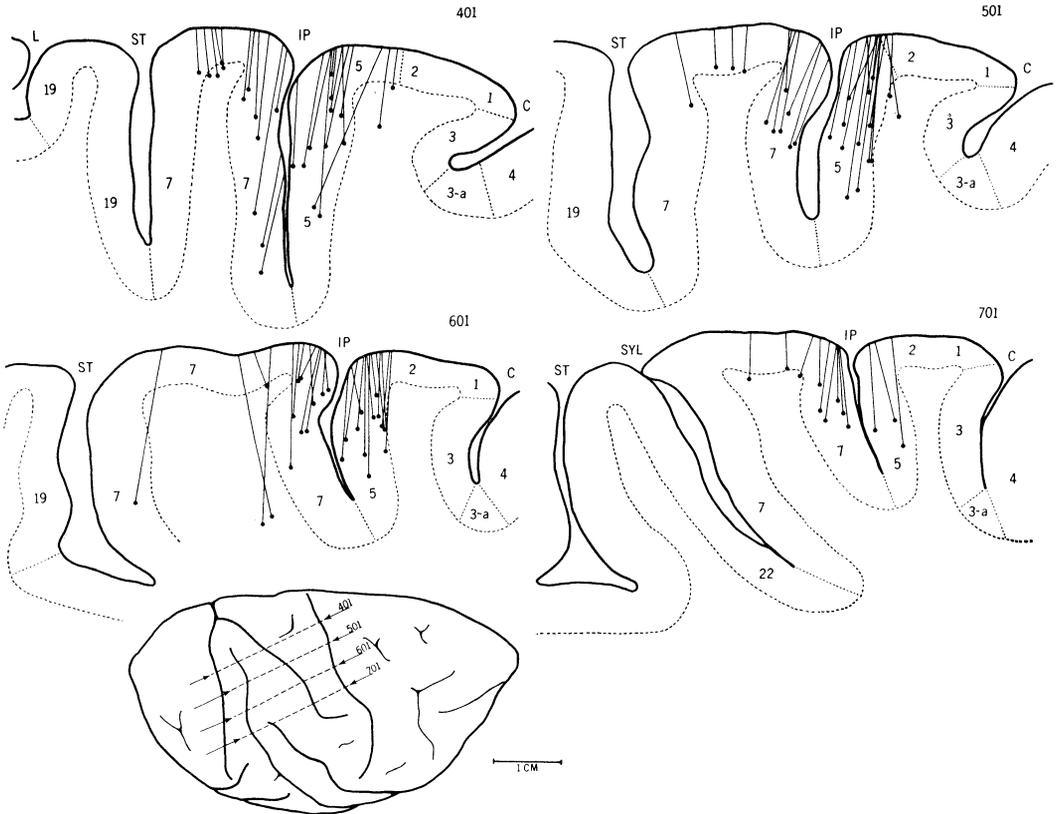


FIG. 12. Representation of reconstructions of all penetrations made in areas 5 and 7 that were identified in serial sections. Each reconstruction treated as if in the right hemisphere, and fitted to one of the four standard section drawings indicated by section numbers 401, 501, 601, and 701 of the standard brain chosen for the illustration. Cytoarchitectural areas indicated by arabic numerals. L, ST, IP, C, and SYL are lunete, superior temporal, intraparietal, central, and sylvian sulci, respectively.

butions of the identified classes of neurons between cortical layers of areas 5 and 7 are given by the hatched-bar histograms of Fig. 14. In each histogram cell a parallel solid column indicates the sampling density for that particular cortical layer. It is apparent that the differential distribution in depth of neurons can be accounted for in large measure by the bias in the sampling distribution. The exception is layer I, where few neurons exist and few were isolated. The depth distributions of sampling, of the total neuronal population and of the subpopulations by classes, are given in Table 9. It can be seen there that only rarely are depth distributions of the subpopulations significantly different from that of the parent population. There is some tendency for cells of the projection and hand-manipulation class to be segregated differentially in layers II, III, and IV of area 7 and in the

deeper layers of area 5, but the differential is too small to warrant any conclusions. In general, our results indicate that the cells of each of the classes can be found in any of layers II through VI, and that differential segregations by layer are not remarkable.

An analysis of variance (75) was performed on the anteroposterior and layered distributions of Figs. 13 and 14. In area 5, the difference in the total number of neurons in each of the 12 1-mm slabs of tissue in front of the depth of the intraparietal fissure is almost wholly accounted for by the distribution of sampling; i.e., the total amount of electrode passage within each of those slabs. The differences that could not be accounted for in this way amounted to 1.07% of the total variance. An F test showed that this is not significant. In area 7, the differences between the total number of neurons isolated in each of the 12 1-mm slabs of tissue posterior to the fissure were almost totally due to the difference in sampling.

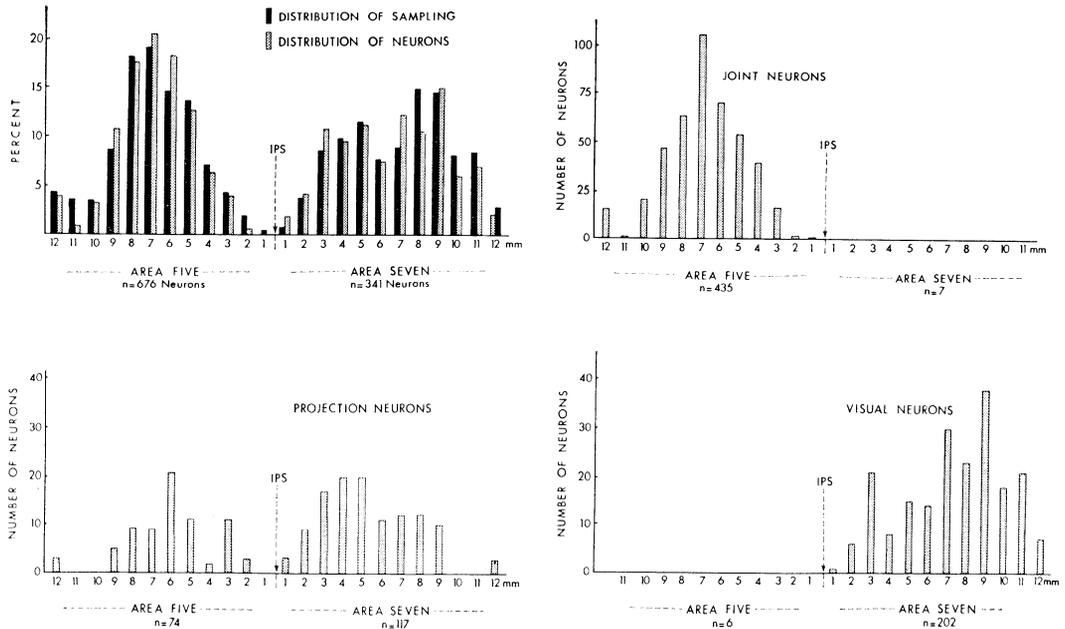


FIG. 13. Histograms that show in millimeter slabs of tissue the distribution of locations of neurons studied in areas 5 and 7 in the anteroposterior dimension relative to the depth of the intraparietal fissure. *Upper left*: cross-hatched bars compose distribution of the total population; solid bars, the distribution of sampling; i.e., the total distance of microelectrode passage within each millimeter slab. The biased distribution of neurons appears to be wholly determined by the distribution of sampling. Methods of localization and measurement and statistical analysis are given in the text. *Upper right*: distribution of joint neurons; they are restricted to area 5. *Lower right*: distribution of visual neurons (all classes together); they are restricted to area 7. *Lower left*: distribution of arm-projection and hand-manipulation neurons; they are found in both areas 5 and 7.

Only 0.24% of the total variance could not be accounted for in this way, and this was not significant.

The differences between the total numbers of neurons isolated in each of the layers of area 5 that could not be accounted for by the distribution of electrode sampling amounted to 18.9% of the total variance. This is significant (F test;  $P < 0.001$ ). The differences in the area 7 distributions that could not be accounted for by the distribution of sampling was only 4.7%, but this too was significant (F test;  $P < 0.01$ ).

**PATTERN OF FUNCTIONAL ORGANIZATION IN PARIETAL ASSOCIATION CORTEX.** Earlier studies of the primary sensory cortex of the postcentral gyrus provided preliminary evidence that the plan of functional organization of that cortex is a vertical one, an arrangement of neuronal circuits in columns extending across the cortical layers, composing the basic input-output chain of cortical operation (64, 71). These observations were confirmed in studies of the postcentral gyrus of waking monkeys as they performed a sen-

sory detection task (12). The results of each set of experiments suggested that the columnar arrangement on the exposed surface of the postcentral gyrus may shift to one of elongated slabs oriented anteroposteriorly, in the cortex lining the bank of the central fissure. A number of elegant investigations have produced evidence that this vertical mode of organization obtains in the primary visual cortex (43-45), in the precentral motor cortex (2, 72), and in the auditory cortex (61). One aim of our present study was to determine whether this mode of organization exists also in the association cortex of the parietal lobe. Our observations indicate that this is the case, but they are still insufficient for an unequivocal statement. They suggest, in addition, that a second and more dynamic or conditional mode of organization may be superimposed on a basically columnar one during certain behavioral states.

Figures 15 and 16 reproduce reconstructions of 21 of the 94 identified penetrations

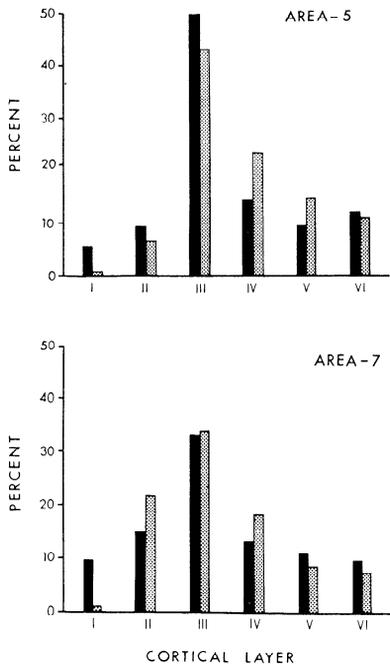


FIG. 14. Dotted bars show the distribution in depth by cytoarchitectural layer (roman numerals) of neurons identified in area 5 ( $n = 676$ ) and area 7 ( $n = 341$ ). Solid bars show the distribution of sampling; i.e., the total distance of microelectrode movement in each layer. Except for layer I, which contains few neurons, the biased depth distributions are largely accounted for by the biased distribution of sampling. Method of measurement and statistical analysis given in text.

we have made into areas 5 and 7; three made into the postcentral cortex (no. 1, 2, and 3 of Fig. 15) are added for comparison. The results shown here are representative of all we have made, and suggest the following. Firstly, when penetrations are made into the exposed surfaces of areas 5 or 7, the results resemble those in studies of the primary sensory cortex and support the idea of columnar organization. Thus, in penetrations normal to the cortical surface, the neurons encountered during electrode descent possess similar functional properties; e.g., see no. 4 and 5 of Fig. 15 and no. 8-11 of Fig. 16. Secondly, changes in functional properties occur, in slanting penetrations, in an en bloc not a random fashion; e.g., see no. 6-14 of Fig. 15, and no. 1-7 of Fig. 16. All of the classes of neurons identified in the two areas conform to this pattern, except those called "special," including particularly the conditional special neurons,

that are active only in certain ways when highly motivated acts of a certain kind are emitted by the animal. Thirdly, if one traces the penetrations of Figs. 15 and 16 into the banks of the intraparietal sulcus, the en bloc reversals between classes of neurons encountered become more common as the angle of electrode penetration to the neuronal columns becomes less acute, as would be expected on the basis of columnar organization. In some penetrations, however, long passages occur in which neurons of only a single class are encountered, as in no. 12 and 13 of Fig. 15 and no. 1 and 2 of Fig. 16, which suggests the "slab" mode of organization thought to obtain in the post-central bank of the central fissure.

Inspection of Figs. 15 and 16, however, suggest to us that all of the observations cannot be accounted for in the context of columnar organization. In penetrations within the banks of the intraparietal fissure, in the midst of blocks of cells otherwise of a single class, we commonly encountered neurons with different features that appeared singly, and these were usually of the projection and hand-manipulation class or of the special type. Each of these "out of place" neurons is indicated by a horizontal bar to the right in Figs. 15 and 16. We do not believe that all of these exceptions to the prediction of columnar organization can be accounted for on the assumption that the electrode in its passage across one column touched a small segment of an adjacent one that contained, commonly, but a single cell. The frequent occurrence of these exceptions in the cortex of the banks of the fissure, and the fact that these exceptions were almost always neurons of the conditional classes, leads us to the suggestion that there is within these regions of cortex a basic plan of columnar organization for function and that there is superimposed on it, from time to time, an additive one that is conditional in nature.

#### DISCUSSION

The major conclusion we draw from the observations described above is that there exist within the posterior parietal association cortex sets of neurons which function as a command apparatus for the behavioral acts of manual and visual exploration of

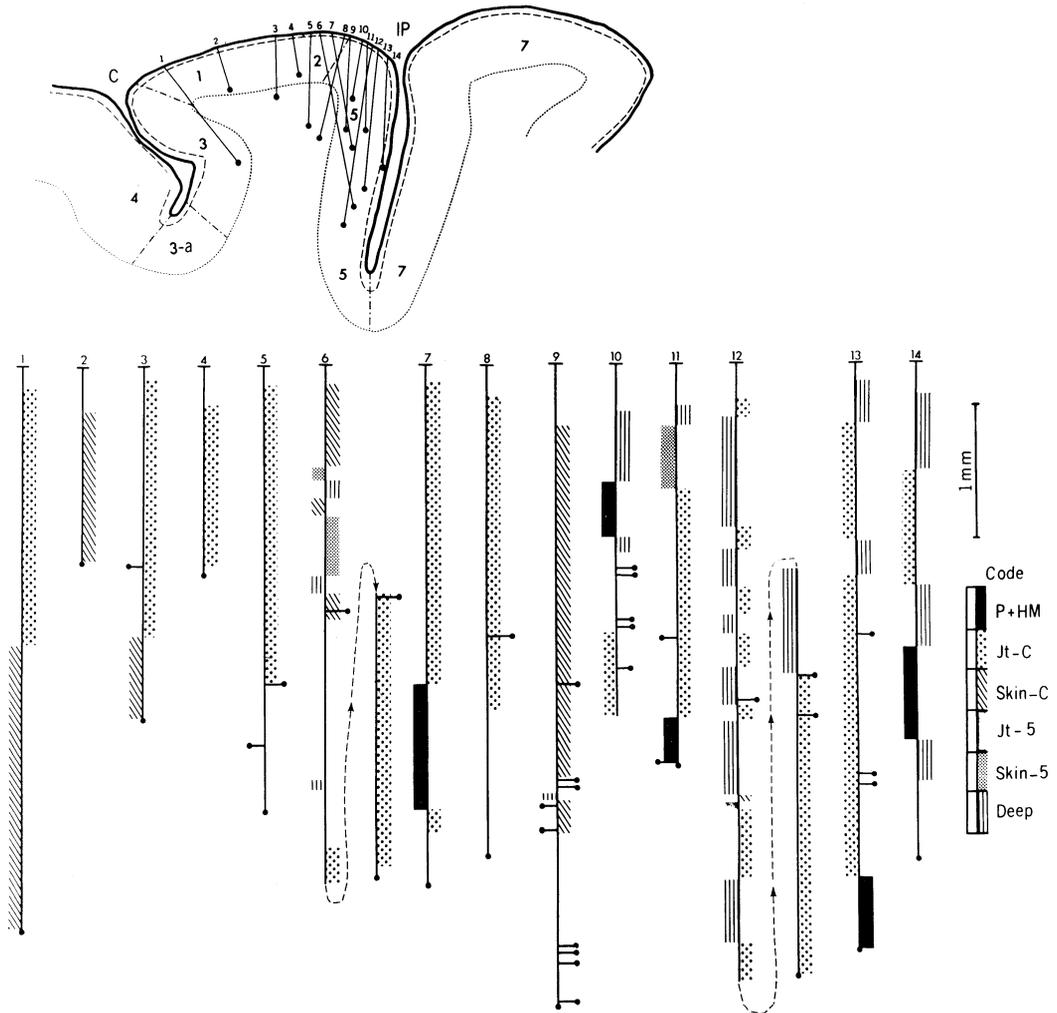


FIG. 15. A sample of reconstructions of microelectrode penetrations made into the postcentral gyrus of waking, behaving monkeys, in the present experiments. Code at lower right indicates the type of neurons encountered, both for single neurons isolated and for multiunit recordings: P + HM, projection and hand-manipulation neurons; Jt-C, joint neurons with contralateral receptive fields; skin-C cutaneous neurons with contralateral receptive fields; Jt-5 and skin-5 refer to joint and cutaneous neurons with the area 5 properties that are defined in the text; deep, neurons activated by stimulation of deep tissues other than joints (see Table 2). The horizontal bars indicate loci at which single neurons were isolated that were out of place with regard to the en bloc pattern of columnar organization; those to the left indicate passively driven neurons, those to the right indicate out of place active projection and special neurons, the latter those dynamically related to the behavioral acts emitted. This suggests the superimposition of a dynamic mode of organization on a passive one of columnar organization.

the immediately surrounding extrapersonal space. We first discuss these results in relation to the experimental method used to obtain them, then explore to what extent our observations on sensory neurons of areas 5 and 7 fit the association model; i.e., whether the properties of these cells suggest successive steps leading to perception,

particularly as regards spatial orientation and the percept of the body form. We then compare our interpretation with other alternatives, as regards validity, and examine to what degree the properties of the command and the sensory classes of parietal neurons suggest a positive image of the defects in behavior that occur in monkeys

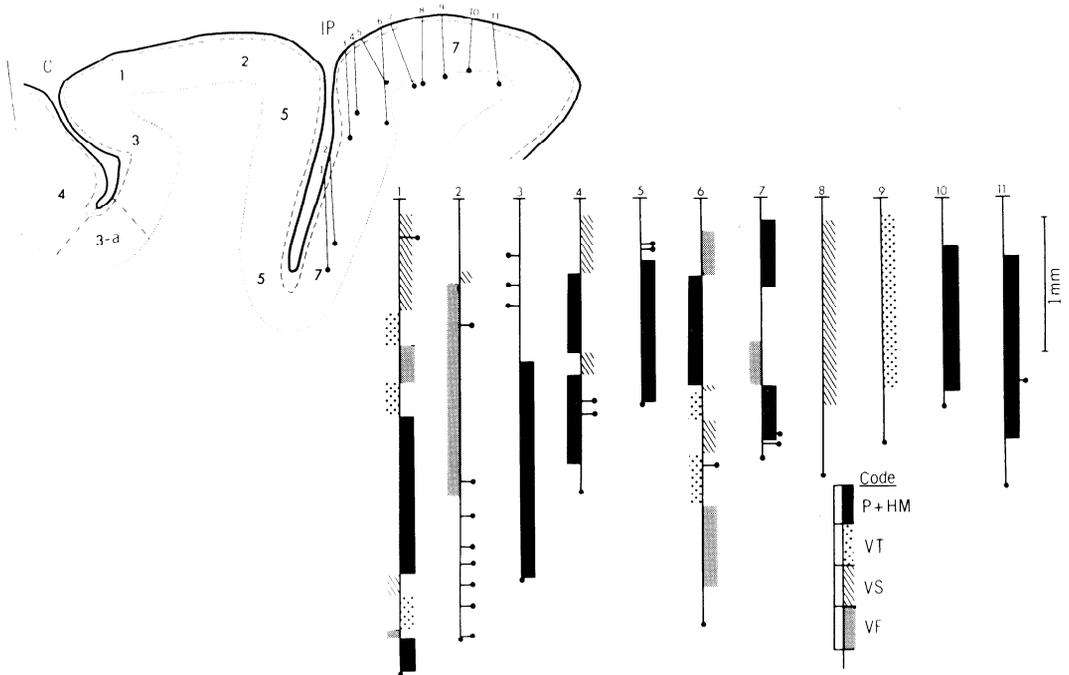


FIG. 16. A sample of reconstructions of microelectrode penetrations made into area 7 of waking, behaving monkeys in the present experiments. Code to lower right indicates classes of neurons encountered: P + HM, projection and hand manipulation neurons; VT, visual tracking neurons; VS, visual space neurons; and VF, visual fixation neurons. The horizontal bars indicate loci at which single neurons were isolated which were out of place with regard to the en bloc pattern of columnar organization; they are all neurons of the active and special classes and suggest that a dynamic mode of organization is at times superimposed on that of columnar organization.

after removal of areas 5 and 7. Finally, we consider to what extent the observations made in these areas can be accounted for on the basis of a columnar plan of functional organization, and suggest that a second, dynamic one is from time to time conditionally superimposed, depending on motivational set.

*Combined behavioral-electrophysiological experiment*

The experiment in which one controls and measures the behavior of animal or human subjects and records signs of the cerebral events thought relevant for that behavior has been used in studies of sleeping and waking, while recording the electroencephalogram, and in studies of the slow potential changes evoked by sensory stimuli, while the behavioral contingencies of the latter are varied. It was Jasper et al. (48) who first showed it feasible to monitor the activity of single cortical neurons in a

stable and reproducible fashion in a waking, behaving animal; in their case as a monkey developed a conditioned, differential avoidance response to noxious stimuli. The method was further developed by Hubel (42) and by Evarts (27-29). It has great power and raises several technical and conceptual problems.

The first is the choice of the appropriate behavioral task. The range of choice is clear for studies of the motor and sensory areas, but not obvious for other cortical areas whose neurons are not so clearly linked to particular peripheral events. Clues to the choice of task may come from: a) the thalamic and cortical connections of the area, b) preliminary microelectrode studies of the region in waking but naive animals, and c) the changes in behavior which follow removal of the area. We first explored areas 5 and 7 in naive animals and discovered the conditional nature of the activity of projection neurons and of

the visual fixation and tracking neurons. We confirmed that after removal of these areas monkeys are reluctant to project the contralateral arm into extrapersonal space and that when, after a time, they can be induced to do so, they make large errors. These observations suggested the tasks outlined in Fig. 1 and the apparatus illustrated in Fig. 2.

The results of our preliminary experiments bear also on another question. That is, to what extent were the observations made influenced by the prolonged training of our animals? It is an important question in itself whether the properties of neurons in the association areas can be readily modified by training. The experiments of Held (40, 78) suggest that this is the case, for infant monkeys and humans only learn with visual guidance and with practice to direct their hands and arms accurately into extrapersonal space. In the present context, we believe it is important that we did not observe sets of neuronal properties in our trained animals that we had not also observed in naive ones. We have no way of knowing whether training influenced quantitative relations between the activity of parietal neurons and the behavioral tasks.

The time relation between certain behavioral acts and the discharge of parietal neurons is critical for our interpretations. How strong is an inference of causality derived from the observation of simultaneous variation? The case would be strengthened if groups of neurons of the type we term "command" sets of a particular type exist only in the parietal cortex. So far, they have not been observed by those who have studied the association cortex of the frontal (31, 53) and temporal lobes (34), but more extensive surveys must be made before such a negative assertion can be made with confidence. Moreover, if our ideas are correct about the link between the holistic command sets of parietal neurons and the executive mechanisms of the motor cortical fields, sets of neurons with intermediate properties (between those of the parietal and the motor cortex) should exist in the premotor fields to which areas 5 and 7 project (49). The case for causality would be strengthened also if the item of behavior

thought causally related to the discharge of parietal neurons were irretrievably lost after removal of the posterior parietal association cortex. Some weeks after such a removal, however, ungainly and inaccurate projections of the arm and hand reappear that, poorly directed as they remain, achieve on repetition the biological end of target contact and retrieval. Undoubtedly the brain is, in this case, as in many others, capable of adapting to the effects of lesion, and in time accomplishes through other neuronal mechanisms an important biological objective, though less efficiently.

In sum, the causal relation between the activity of command sets of parietal neurons and the conditional operations of the hands and eyes in the immediate extrapersonal space remains a logical inference and requires further strengthening by evidence obtained in different but convergent types of investigations.

#### *Central image of body form and spatial orientation*

A central mechanism that integrates afferent signals originating in the joints could provide neural images of the static and dynamic relations of the body parts. Correlation of these dynamic neural images of the body form with information concerning its orientation with respect to gravity and to objects in surrounding space could specify the orientation and movement of the body in space. This is, as we perceive it, the traditional idea of sensory association. Defects in spatial orientation and in stereotactic exploration of the immediate bodily surround appear in primates after lesions of the parietal association cortex. In our present experiments we searched for evidence of somatic and visual convergences that might represent the initial step from the identification of sensory quality to the perception of orientation in space.

Area 5 contains large numbers of joint neurons which, like those of the postcentral sensory area, are related to single joints on the contralateral side of the body. This population can provide information concerning joint position and the direction and speed of joint rotations. It is uncertain whether there are two separate representa-

tions of the body form as regards the joints, one in area 2 and a second in area 5, or whether a single pattern extends over both. Our experiments were not sufficiently detailed to answer that question. The facts that the major corticocortical input to area 5 is from area 2, and that the thalamic source of direct afferents to area 5, the *n. lateralis posterior*, is not itself known to receive afferent signals originating in joint receptors, suggests that the joint neurons of area 5 are activated via projections from the postcentral somatosensory cortex, most likely area 2. This fits with the observations made by Sakata et al. (73) and by us that a small proportion of the joint neurons of area 5 receive an intramodal, spatial convergence. They may be related to two or more contralateral joints or to joints on both sides of the body. Some are preferentially activated by reciprocal movements or postures of opposing limbs. A few of these are active only during complex body postures that in the limit appear to involve the entire body. In sum, the intramodal spatial convergence that is the first requirement of the association model for spatial orientation has been observed rarely in area 5. Only further study can reveal whether that convergence is a more common property of area 5 neurons than presently appears likely, or whether the few complex cells observed represent an initial step in such a convergence that is carried further at another stage of corticocortical projection and association.

The association model for the construction of a percept of spatial orientation requires next an integration of visual information with that relating to body position and movement. We have observed in area 7 a small number of neurons ( $n = 18$ ) which may illustrate such a convergence, for they are active maximally during combinations of arm projection and visual fixation/tracking. We have interpreted these to be a special class of command neurons, but the possibility remains that they are of a special sensory nature, sensitive to a particular set of activity in complex joint neurons but only when it is conjoined with a particular type of conditional visual input. Our experimental arrangements did

not allow us to determine whether cells of areas 5 and 7 are sensitive to changes in the position of the body in the gravitational field.

In summary, there is little evidence to support the successive association model for the neural construction of the perception of the orientation and movement of the body in space, in the posterior parietal cortex, for the number of neurons observed with the requisite properties is too small to be convincing. This suggests that they may constitute a preliminary stage in an association completed at another level of cortical processing, perhaps in the cortex that lines the depths of the superior temporal sulcus, which receives an efferent projection from area 7.

Lesions that produce disorders of spatial orientation in humans almost always involve parts of the supramarginal and angular gyri, thus these signs of parietal lobe disease in man cannot be attributed with certainty to the loss of function of areas 5 and 7 alone. No humans with lesions restricted precisely to these areas have ever been identified and studied.

MOVEMENT FACILITATION OF AFFERENT NEURAL REPLICATION OF MOVEMENT. Many of the joint neurons of area 5 that are relatively insensitive to passive joint rotations are intensely active when those same movements are executed by the animal. There are several candidate explanations of this "activation" phenomenon. Firstly, peripheral joint afferents might be more efficiently excited during active as compared to passive movements because muscle contractions tense joint capsules, etc.; i.e., the activation phenomenon may reflect a change in peripheral sensitivity. If this were so, the phenomenon should appear for all joint neurons at all levels of the somatic system, which is not the case. Secondly, the "active joint neurons" of area 5 might not be joint neurons at all, but cells driven after relay by activity in some other set of primary afferents. Indeed, Duffy and Burchfiel (10, 23) identified and we have observed also that a small number of neurons of area 5 appear to be activated by stimulation of the spindle organs of muscles. Confusion of

joint with spindle driving appears unlikely, but confusion could arise if this set of neurons is driven by a relayed projection from the tendon organs of muscle. The latter are differentially sensitive to active tension as compared to passive stretch. The only observation against this proposition is that activation occurs during joint rotation and not when the animal contracts a muscle across a fixed joint. If these credible, but we believe unlikely, explanations are eliminated by future experiments, the possibility will remain that the movement-enhanced activity of the active joint neurons of area 5 results from a change that is wholly central. Such a change in the excitability of an afferent system would, on this idea, be evoked by neural activity occurring in parallel with efferent commands for movement; e.g., those from the motor cortex. This corollary or parallel activity would light up by synaptic facilitation that particular topographic sector of the system through which the incipient movement will take place. It seems unlikely that this shaping-facilitation occurs at any low level of the system, such as the dorsal column nuclei, for it is not a common property of joint neurons of the postcentral somatosensory cortex.

*Parietal command functions for manual exploration of surrounding space*

The projection and hand-manipulation neurons of the parietal cortex appear to be neither sensory nor motor in nature, but to stand in a selective command relation to movements of a particular sort. We wish to consider to what degree the evidence might be interpreted to support or deny three alternative interpretations.

The first is that the projection neurons are, in fact, joint neurons of the passive set. It was this possibility that caused us to make half of our experiments in the gentle and tractable *M. arctoides* (*speciosa*), for in this animal we could test repeatedly for driving of cortical neurons by passive manipulation of peripheral tissues. We are convinced that the projection and manipulation neurons are not passively driven.

The second alternative is that these are joint neurons of the active set, discussed above, but that the synaptic links between

periphery and the parietal lobe are, for this class, too insecure to allow cortical activation by passively evoked afferent activity. These neurons would thus differ from the active joint neurons only in the decreased degree of afferent synaptic security. There are two arguments against this alternative. The first is that neurons of this conditional nature have never been observed in the postcentral sensory cortex under the same experimental conditions (12). Such a facilitation of a subthreshold afferent input could only be effected at neural relays that project on areas 5 and 7 without traversing the sensory cortex. The n. lateralis posterior of the thalamus is one candidate source of such a projection, but it is not known to contain or to receive the detailed representation of the body form that this mechanism requires. The second constraint is that this mechanism would itself need be conditional in nature and be set in motion only during certain classes of movement, and not others.

The third alternative is that what we have observed in the posterior parietal cortex is a corollary discharge. On this supposition, the projection class of parietal neurons is activated by efferents that leave the premotor fields and project directly on areas 5 and 7, via well-known pathways, with no direct engagement of the somatic afferent system. There is no evidence that allows us to reject this hypothesis unequivocally. Such a corollary discharge would need, in this case, to be conditional. The fact that a considerable number of the projection and hand-manipulation neurons are active with movements of either arm appears less compatible with a corollary discharge than with the command hypothesis, but this is not a completely telling argument.

On the basis of the present evidence, therefore, it is not possible to reject absolutely these alternative explanations of our observations. We believe that the latter fit best with the command hypothesis, and we wish to explore its explanatory value as the basis of the abnormalities of function that follow removal of the parietal lobe.

POSITIVE IMAGE OF AMORPHOSYNTHESIS. There is no a priori reason to suppose that the defects in behavior that follow removal

of a cortical area will reflect precisely the functional properties of the neurons lost. The complex interactions of cortical and subcortical regions suggest a greater subtlety of defect, perhaps in changes in function of connected areas far removed from that destroyed (68). Nevertheless, it is of heuristic value to compare the properties of cells of areas 5 and 7 with the defects in behavior that follow their removal.

The most obvious changes in behavior of a monkey without parietal association cortex is his reluctance to move the contralateral limbs or to project them into extrapersonal space, and the errors he makes when he does so. We infer that these defects reflect the loss of a particular source of commands for movement. What results is a deficit of volition or motivation, not a motor paralysis.

Held and his colleagues (40, 41, 78) established that human infants achieve visually guided projection and grasping at about 5 mo. The rate of development of this skill can be modified by environmental deprivation or enrichment. Held raised infant monkeys in such a way that they never from birth viewed one hand and arm, which were otherwise free. This limb persisted in its infantlike, pawing motions, while the viewed limb followed the usual rate of development to a state of efficient, accurate, visually guided grasping and prehension. When the previously unseen hand was first viewed by the young monkey, he treated it as a foreign object, a depersonalization reminiscent of one sign of parietal lobe disease in man. In Held's experiment the monkey regained the capacity for skilled direction of the previously unseen arm and hand over a period of days or weeks and, in time, control of the limb was identical to that of the one viewed from birth. These findings suggest that at birth the connections through which the parietal neurons initiate arm projections and manipulations are incompletely developed, and that during maturation these connections are sensitive to modification by behavioral experience.

The failure to project the contralateral limbs after parietal lesion and the maintenance of catatonic postures can, we believe, be understood in terms of the loss

of the set of projection neurons in that cortex, coupled with the loss of the joint neurons that replicate body position and movement.

Removal of the parietal association cortex produces some deficits in the capacity of monkeys to make tactile form and shape discriminations in the dark (25, 26, 62, 63), which resembles the astereognosis of humans with parietal lobe disease. In recent experiments we have found that animals with removal of areas 5 and 7 show no impairment for detecting mechanical sinusoids (30 Hz) delivered to their hands nor in discriminating between such stimuli of different amplitudes (54). We have observed only rarely in areas 5 and 7 that cross-modal convergence between input from the glabrous skin and the intrinsic joints of the hand which, on the association model, might serve as a neural basis for stereognosis. We suggest, therefore, that these areas are intermediate stages, and that a further convergence and integration may occur at the next level of corticocortical projection. On that hypothesis, the astereognosis after lesions of areas 5 and 7 may be regarded as a cortical disconnection syndrome.

Denny-Brown (19) has interpreted the reciprocal release of tactile avoiding after parietal lesions and of tactile following after removal of the supplementary motor area, in monkeys, as examples of release phenomena. If excessive tactile avoiding is interpreted as due to loss of the action of the projection and manipulation command neurons, our observations fit with this hypothesis. The release of one cortical region after removal of another appears explicable only on the hypothesis that it upsets a balanced inhibition between the two which normally governs the ebb and flow of manual exploration of and withdrawal from the surrounding environment.

*Parietal command functions for visual exploration of surrounding space: directed visual attention*

The sets of parietal cells that we call "visual fixation" and "visual tracking" neurons have in common the property that their discharge is, to a considerable degree, conditional on the quality of the object fix-

ated and tracked. They appear to direct visual attention to objects of interest and motivational power, and to issue commands for maintaining directed fixation of the object when it is stationary, and to track it if it moves. They differ in that the VF neurons are active during both steady fixations and smooth pursuits, independently of direction, while VT neurons are active only during movement, and are directionally oriented. The activity of either set is abruptly interrupted by saccadic movements.

The loss of these sets of neurons could account for a salient feature of the parietal lobe syndrome in monkeys and in humans; namely, the visual inattention and neglect of the contralateral half-field of space that may occur without visual-field defect. The loss of the visual tracking neurons could result in the deficiency in slow pursuit movements, an oculomotor apraxia, which appears in some patients with lesions of the parietal lobe. In them, full eye movements may be executed at random, but the eyes cannot follow in slow pursuit when the patient's attention is alerted (14). The defect is for movements into the ipsilateral half-field; the slow pursuits are replaced by repeated saccades, a cogwheel movement (51). A congenital syndrome has been described in which the voluntary horizontal smooth pursuit movements are absent or defective in both directions, with full and normal random eye movements (1). Nothing is known of the cerebral lesions that produce it. Some bilateral injuries of the parietooccipital region in man result in a syndrome of "psychic" paralysis of visual fixation, optical ataxia, and disturbance of visual attention (Balint's syndrome) (36). It appears likely that a bilateral loss of the mechanisms for directed visual attention that we have observed in the inferior parietal lobule could result in deficiencies of this sort. We have made no observations that bear on the nature of the mechanisms for directed visual attention. The efferent projections from area 7 that reach the cortex of the frontal lobe, the thalamus, the basal ganglia (50, 69), and the superior colliculus, allow a number of hypothetical schemes. The fact that visual inattention

and neglect is a transient sign following frontal lobe lesions in both monkeys (55) and humans indicates the importance of the reciprocal connections between area 7 and area 46 of the frontal lobe, and suggests that visual neglect and inattention may, in some cases, be a disconnection syndrome.

The nature and the place of the neuronal processing between primary visual input and the activation of these command sets of parietal neurons is unknown. We have repeatedly observed that the VF and VT sets of neurons are not "driven" by visual stimuli presented outside the line of gaze or when the animal fixates uninteresting objects. Thus the action of these sets of parietal cells is not explicable in terms of sequentially arranged processes identifiably visual in nature; e.g., one leading from the visual cortex to such a highly specific type of conditional output, such as that observed in area 7. It is as if the parietal command neurons are thrown into action (are "released") by a completely preprocessed set of signals. There is some uncertainty whether area 7 receives a corticocortical projection from the prestriate visual fields, areas 18 or 19 (49, 67). If not, we can only surmise that the processing of visual input leading to the efferent commands for directed visual attention, for fixation and tracking, culminates in the pulvinar and n. lateralis posterior of the thalamus, and may be independent of the geniculostriate system (33, 36).

#### *General nature of command function*

We wish to emphasize the following: that our concept of command centers explicitly assumes that there exist within the central nervous system many sources of commands to the motor apparatus. The source of the command and its nature will differ remarkably in different behavioral reactions, even though the peripheral musculature engaged in the different acts may be virtually identical. The persistence of full random eye movements, in spite of the loss of the capacity for smooth pursuit tracking, in patients with lesions of the parietal lobe, provides an example of this principle, for in this case there can be no question but that the peripheral muscle

active in different classes of movement are identical.

*Functional organization of posterior parietal association cortex*

There is reasonably good evidence that the sensory and motor areas of the cerebral cortex are organized for function in a columnar manner; that the elementary, multicellular, functional unit of the cortex is a group of neurons distributed vertically across layers II–VI, within which inter-neuronal connections are very dense in the vertical direction and sparse horizontally, i.e., between columns (64, 71). This generalization is based on knowledge of the static properties of cortical neurons that differ in different sensory systems but include, among others, the modality type, the location and orientation of receptive fields, ocular dominance, directional sensitivity, etc. Moreover, more than one organizational pattern can exist in the same cortical region, as witness the interlocking and superimposed orientation and ocular dominance columns of the visual cortex discovered by Hubel and Weisel (44, 45). These findings do not imply an isolated function of the vertically oriented chain of cortical neurons. Indeed, evidence for intercolumnar interactions already exist; e.g., the intercolumnar, cross-modal inhibition observed in the somatosensory cortex of the monkey (65) and the cross-columnar projection thought to account for the binocularity of visual cortical neurons some synapses removed from the terminations of geniculocortical fibers; the first postsynaptic cortical neurons are monocular only (44, 45). Complex integrations also occur within columns. For example, successive convergence is thought to account for the increasing receptive-field complexity observed at successive stages of intracolumnar processing in area 17 of the monkey (44, 45). A dynamic integration is illustrated by the appearance of directional sensitivity for neurons of layers III and V of the postcentral gyrus, a property not possessed by cells of layer IV (79). Obviously, an important problem in cortical physiology is to elucidate the neuronal processing mechanisms that intervene between the input to and the output from this ele-

mentary unit. It is equally important to discover whether this mode of organization is a general property of all neocortex or a special characteristic of the sensory and motor areas.

Concerning the latter, we believe that our results provide evidence that the basic plan of columnar organization pertains also to the eulaminate cortex of the parietal association areas. Neurons of each of the classes are arranged there in columns which extend across the cellular layers in a vertical direction. In our present experiments, our mapping parameter was that of neuronal class only, so that we are uncertain concerning the degree of intracolumnar processing that exists, and its nature. We have no evidence, however, that the complex properties of the conditional classes of neurons result from the intracortical convergence or integration of cells with simpler properties. We cannot imagine, for example, any combination of these latter that might account for the properties of the projection and hand-manipulation neurons. Moreover, some of our observations suggest the possibility that another mode of organization is from time to time superimposed on the basically columnar pattern, and that this additional set formation is dynamic and conditional in nature. We observed when a monkey projected his arm to obtain an object he desired, that projection neurons within columns became active; in addition, others of more complex natures also became active. These latter appeared to be located, sometimes in complete isolation from others like them, in columns that in the passive behavioral state were found to contain only neurons with passive properties of a single class. These out of place neurons were observed too frequently, we believe, to be dismissed as due to experimental error. They never appeared to be neurons with passive properties that suddenly displayed conditional ones during the motivationally driven behavioral acts we studied. This exception to the pattern of columnar organization appeared commonly in the case of the most complex cells we studied, those that are active only during combined hand and eye tracking of desired objects. The evidence is so far too

tenuous to allow us to formulate in more precise terms what this superimposed, dynamic form of organization may be. It suggests that in different behavioral states, and at different times, neurons of the association cortex may be formed into different patterns of organization. These patterns may differ in different association areas. We did not observe any dynamic exceptions to the pattern of columnar organization in our earlier study of the postcentral gyrus, in waking, behaving monkeys (12).

In summary, the posterior parietal association cortex appears on the basis of our preliminary evidence to be organized in a columnar manner like that of the koniocortex of the postcentral gyrus and of the visual cortex. It may differ from those regions in that an additional, dynamic mode of operation appears under certain circumstances.

#### SUMMARY

Experiments were made on the posterior parietal association cortical areas 5 and 7 in 17 hemispheres of 11 monkeys, 6 *M. mulatta* and 5 *M. arctoides*. The electrical signs of the activity of single cortical cells were recorded with microelectrodes in waking animals as they carried out certain behavioral acts in response to a series of sensory cues. The behavioral paradigms were one for detection alone, and a second for detection plus projection of the arm to contact a stationary or moving target placed at arm's length. Of the 125 microelectrode penetrations made, 1,451 neurons were identified in terms of the correlation of their activity with the behavioral acts and their sensitivity or lack of it to sensory stimuli delivered passively; 180 were studied quantitatively. The locations of cortical neurons were identified in serial sections; 94 penetrations and 1,058 neurons were located with certainty.

About two-thirds of the neurons of area 5 were activated by passive rotation of the limbs at their joints; of these, 82% were related to single, contralateral joints, 10% to two or more contralateral joints, 6% to ipsilateral, and 2% to joints on both sides of the body. A few of the latter were active during complex bodily postures. A large proportion of area 5 neurons were

relatively insensitive to passive joint rotations, as compared with similar neurons of the postcentral gyrus, but were driven to high rates of discharge when the same joint was rotated during an active movement of the animal. We believe this phenomenon is most likely the result of a central facilitation in which that portion of the central, topographical representation of the body form in which a movement is about to occur is "lighted up" by a central discharge paralleling that which leads to movement itself.

Ten percent of the neurons of area 5 were activated by passive stimulation of the skin. Of these, 91% were related to continuous, contralateral receptive fields, 3% to ipsilateral ones, and 7% to fields on both sides of the body. As compared to those of postcentral cutaneous neurons, area 5 neurons subtend large receptive fields that frequently, unlike those of postcentral neurons, contain both hairy and glabrous skin. The majority were particularly sensitive to moving as compared to stationary stimuli, and 16% showed directional orientation.

An even smaller number of area 5 cells was activated by muscle stretch (3%). Neurons on which there appeared to be cross-modal convergence were observed with even greater rarity (1%).

The most novel class of neurons of area 5 (11%) is found also in area 7 (33%); we term them arm projection and hand-manipulation neurons. They are not activated by sensory stimuli, but discharge at high rates when the animal projects his arm or manipulates with his hand within the immediate extrapersonal space to obtain an object he desires; e.g., food when he is hungry, or to touch a lighted switch he has learned means liquid when he is thirsty. These cells are not active during other movements in which the same muscles are utilized. Their discharge is conditional in nature, and we suggest that they compose holistic commands for action for the manual exploration of surrounding space. These commands are not detailed instructions for muscular contraction, for the patterns of discharge vary little with large variations in the direction or speed of the movement executed to attain the target. Those patterns are independent of the period of waiting be-

tween sensory cue and projected action and of the particular sensory channel over which the cues arrive, whether visual or somesthetic.

Other than that set of projection neurons, almost all the other cells of area 7 are visual in nature. They fall into three classes, of which the first two appear to function in command roles. Cells of the first of these (34% of all area 7 neurons studied), the visual fixation neurons, are active when the animal fixates visually an object he desires, such as food when he is hungry, and the discharge continues during smooth visual pursuits of the object, if it moves, independently of direction. The discharge of these cells, like that of the projection neurons, is conditional on the nature of the object, the motivational set of the animal, and the location of the object. The associated discharge habituates rapidly if the animal is satiated or if it is presented beyond arm's reach. They are not directionally oriented. The second of these classes, the visual tracking neurons (13% of area 7 neurons), is active only during smooth visual pursuits of desired objects moving within arm's reach; they are directionally oriented. In all other properties they resemble the interested fixation of gaze neurons.

A small number of cells of area 7 (5%) is active during combined hand and eye tracking of moving objects.

We conclude that area 7 contains large sets of neurons that function in a command fashion, directing visual attention to and exploration of the immediately surrounding extrapersonal space.

Analysis of the results in terms of the location of neurons of the different classes suggests that the columnar pattern of organization, previously found to exist in primary sensory and motor cortical fields, applies also to the parietal association cor-

tex. However, the number of exceptions to that pattern, which occur most commonly in the depths of the intraparietal fissure and for neurons of the active command sets, suggests that when the parietal cortex transits from its passive to its active mode of operation, an additional pattern of organization is superimposed on the columnar one. The details of that second pattern are unknown.

We have only rarely found evidence in the parietal association cortex for the intra- and cross-modal convergence and interaction that we assume to be required by the traditional idea of sensory association.

We propose that several of the abnormalities of function that occur in humans and in monkeys after lesions of the parietal lobe can be understood as deficits of volition, of the will to explore with hand and eye the contralateral half-field of space, a deficit caused by the loss of the command operations for those explorations which exist in the parietal association cortex.

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