

others are euphoric and ludic (a term introduced by Piaget (1951) to describe the play, imitative, and dramatic aspects of the behavior of young children); some are angry and paranoid, and others are withdrawn and depressed. The disorders of consciousness include anosognosia (denial of illness), disorientation for place and time, reduplication (reduplicative paramnesia), confabulations, delusions, and other highly condensed metaphors. These findings suggest that the predominance of left-sided neglect is related to the development of hemisphere specialization, with particular reference to the more diffuse organization of sensory functions in the right hemisphere (Semmes et al. 1960) and the metaphorical and emotional aspects of speech [see also Corballis & Morgan: "On the Biological Basis of Human Laterality" *BBS* 1(2) 1978].

Hemi-neglect in man and monkey is not limited to parietal lobe lesions. It occurs as a result of pathology in the frontal and temporal lobes, thalamus, cingulate area, and other parts of the limbic-reticular system (Weinstein, Kahn & Slot 1955; Heiman & Valenstein 1972; Watson et al. 1974). Parietal lobe lesions are generally deeply seated, and hemi-neglect is infrequent after cortical ablations. It is common during clinical improvement for hemi-inattention to clear up, along with other disturbances of consciousness, while extinction persists.

The work of Mountcastle, Lynch, and their associates is of great significance, in that it demonstrates that the posterior parietal area selectively mediates attentional and motivational processes. It provides a neural basis for behavioral features hitherto regarded by many as "psychological" and not as integral components of hemi-neglect. One needs also to take into account cortico-limbic interactions and the role of hemisphere specialization.

**Note**

\*Professor of Neurology Emeritus, Mount Sinai Medical School, New York, NY 10029.

by V. B. Mountcastle, B. C. Motter, and R. A. Andersen

Department of Physiology, The Johns Hopkins University School of Medicine, Baltimore, Md. 21205

**Some further observations on the functional properties of neurons in the parietal lobe of the waking monkey\***

Dr. Lynch has referred in his target article to a third study of the inferior parietal lobule of waking monkeys that we have carried out during the last four years, only preliminary descriptions of this work have appeared (Yin & Mountcastle 1977; Motter & Mountcastle 1979; 1980; Andersen & Mountcastle 1980). It is therefore appropriate that we provide for this discussion a brief summary of these results; they will be described in detail in three forthcoming papers.

We have performed experiments in this new series in nineteen monkey hemispheres, we have identified 1,616 parietal neurons and studied 781 of them under conditions in which both the animal's behavior and the presentation of stimuli were controlled precisely. We used three different experimental arrangements sequentially in the series; these permitted us considerable flexibility in task selection and stimulus presentation. Our objectives were, first, to define precisely the properties of the light sensitive (LS) cells of the parietal cortex, and particularly to examine the effect of behavioral state upon their excitability. Second, we wished to examine again the properties of the other large classes of neurons of this region, previously defined, to determine whether, as Robinson, Goldberg, & Stanton (1978) suggest, all parietal neurons - whatever other complex properties they possess - are also excited directly by sensory stimulation of one kind or another, and, that all neurons active in connection with any form of visual behavior are directly related to visual receptive fields. We therefore adopted the categorization strategy that any neuron which, under any circumstance whatsoever, responded to a light stimulus, no matter what other properties it possessed, was classified as an LS neuron.

Table 1 shows that, on this criterion (which weights the case in favor of the designation of light sensitivity and in favor of the suggestion of Robinson, Goldberg, & Stanton), about 30% of parietal cells are light-sensitive, and about one-eighth of these have other complex properties as well. We have again determined the functional properties (described below) of other large classes of neurons within the inferior parietal lobule. In summary, our results have convinced us that the sweeping statements that all parietal neurons have direct sensory inputs, and that all "visual" neurons have visual receptive fields, are false. Our observations pertain to the area PG of the inferior parietal lobule, and not to the more anterolateral portions of the area studied by Hyvarinen and colleagues (Hyvarinen 1974; Hyvarinen et al. 1978).

**Properties of light-sensitive neurons.** The response areas of the parietal LS neurons are commonly very large, and two-thirds are distributed in both the contralateral and ipsilateral portions of the visual fields. There are two such classes of response area. Neurons of the most common type (60%) subtend very large and frequently bilateral response areas which exclude the immediate foveal and perifoveal zones of central vision - a phenomenon we term *foveal sparing*. The remainder of the neurons are related to response areas that do include the region of central vision; indeed, many are symmetrically distributed about, and maximally sensitive at, the fovea. These two classes of response areas are thus to some degree reciprocal to one another in spatial distribution.

The most striking dynamic property of these neurons is their sensitivity to the movement of light stimuli, and to the direction of that movement. Some are sensitive to velocities as high as 800°/sec., though most are related to very flat velocity sensitivity functions with broad peaks in the range of 30-90°/sec. The directional vectors point in opposite directions in the two halves of the visual fields, either towards (75%) or away (25%) from the central line of gaze. In many cases these vectors appear to be arranged in a radial manner with reference to the central line of fixation. We term this *opponent vector orientation*. The "visual" properties of these LS parietal neurons suggest that they could play roles in a number of behaviors that are disordered by lesions of the parietal lobe in primates: in visually-guided movements, particularly of the hands during fixation; in attracting visual attention; and in updating the central image of surrounding space and the position and movement of the organism within that space.

**The effect of state upon the excitability of the light sensitive neurons of the parietal lobe.** We have examined the sensitivity of LS neurons under three conditions: (a) as the animal intently fixates a target light whose dimming he must detect for reward; (b) as the animal looks into a uniform field awaiting the onset of that target light, during the (variable) intertrial intervals, and (c) as the animal sits quietly, performing no task, gazing into a uniform field. Analyses allowed us to extract from the data collected in states (b) and (c) the coordinates of

Table 1 (Mountcastle et al.) *Parietal neuron response characteristics:*

Unidentified	494 (30.5%)
Fixation (216) and Fixation Suppression (45)	262 (16%)
Light-Sensitive	494 (30.5%)
LS only	427
Fixation + LS	46
Fixation Suppression + LS	14
Manipulation + LS	7
Oculomotor	161 (10%)
Tracking	23
Saccade	59
Re-fixation	25
Veigence	50
Projection (126) and Manipulation (79)	205 (13%)
Total	1,616 (100%)

the instantaneous position of the eyes at the time of onset of a light stimulus - when the animal was fixating - but fixating no particular target. This coordinate of eye position, together with the spatial coordinates of the stimulus presented, made it possible to collect trials for each neuron in which stimuli were delivered within response areas previously defined in state (a), but now delivered in states (b) or (c). The results obtained were straightforward: under conditions (b) or (c) the large majority of parietal LS neurons do not respond, or respond much less vigorously, to lights that are potent agents for exciting these cells when the animal intently fixates a target light. We conclude from these findings that the excitability of the system linking the retina and the parietal lobe is sensitively affected by the behavioral state. In these two contrasting cases the states are defined as (a) *excentric fixation of a target in an otherwise uniform field*, and (b,c) *casual fixation into the uniform field, with no target*. The importance of this *state control mechanism* for maintaining a high level of excitability of this system during periods of intense fixation and occupation with "lovel work" is obvious, if this system is considered to provide signals leading to shifts of gaze and attention required by the sudden appearance of new stimuli eccentrically placed in the visual fields.

We have observed a second and powerful control of the excitability of LS neurons. Changes in the angle of gaze change the responses to stimuli delivered to identical retinotopic positions. This effect is so powerful that in one line of gaze it may completely suppress responses that would be of a very high intensity in another. The effect is clear for LS neurons whose response areas are organized in retinotopic coordinates. Experiments carried out in complete darkness give similar results. We have no evidence concerning the central neural mechanism of this effect.

**Fixation neurons.** A fixation neuron is one that, in our categorization, is active during fixation of an object (novel, or rewarding, or aversive) but cannot be activated by any light stimulus under any conditions. We have confirmed again the existence of a large class of such neurons in area 7 (28%), and we documented that they retain this property in total darkness. We confirm also the description of Sakata et al. (1980) of the three-dimensional distribution of the limited-gaze fields of these neurons.

**Oculomotor neurons.** We have observed again in this study, as in earlier ones (Lynch et al. 1977; Mountcastle et al. 1975), a relatively small class of neurons that we term oculomotor. This is a pleomorphic group, made up of different subclasses active during tracking, during saccades, upon re-fixation, and during vergence movements. The saccade neurons make up only about 4% of the parietal neurons identified in this study (7% in an earlier one), but they appear to have evoked considerably more disagreement between Goldberg and Robinson and Lynch (as the latter has expressed himself in this review) than their numbers justify. Our own conclusions concerning the saccade neurons differ somewhat from that of either party. They are as follows:

1. There does exist a small class of neurons in area 7 that is active before visually-evoked but not spontaneous saccadic movements of the eyes. We have observed again that these *strictly saccadic neurons* are insensitive to any light stimuli we could generate in any of three different test arrangements we have used. We add the observation, made so far in only a few cases, that strictly saccadic neurons are active before and during saccades made to locations in the visual field in which no target light exists.
2. A number of LS neurons are affected by saccadic movements, and these cells may be related to "saccade" fields that are much larger than their LS fields.
3. The majority of LS neurons are unaffected by saccades, but a relatively small percentage show the phenomenon of "enhancement" described by Goldberg, Robinson, & Stanton (1977) and Yin & Mountcastle (1977). Whether enhancement is an important and common or trivial and rare property of parietal LS neurons may be determined by the experimental conditions under which it is elicited. We observe, both with regard to our own experience and the published records of Goldberg and Robinson, that the changes called "enhance-

ment" are frequently small, and that the variability is so great that these small changes (in histogram profiles) require statistical validation. It seems likely to us that there exists a gradient in properties from those LS cells that are unaffected by saccades at one extreme, through LS cells with saccadic enhancement and LS cells with saccade fields, to strictly saccadic neurons at the other. This of course suggests that these sets of neurons lie in an intracortical processing chain leading from afferent input to outputs leading to action. The times of discharge of these various sets of neurons, related to onset time of a saccade target, fit with this interpretation, but there is no direct evidence for such a sequential processing.

The event-related activity of strictly saccade neurons, like that of LS cells, may also be under state control. We have observed that when a saccade is made under condition (b) - i.e., from a position of fixation into a uniform field without a target, to an eccentrically-placed target that suddenly appears - the activity of the saccade neuron may be greatly reduced, or absent, as compared to that associated with a saccade from one target light to another - that is, in condition (a). Care was taken to compare, in the two cases, saccades of the same size and direction. The implication of these observations is that both the activity of LS neurons and of at least one class of oculomotor neurons in the parietal lobe may be sensitively affected by state - in this case, one of attentive fixation.

**Projection and manipulation neurons.** These cells are active before and during the projection of the arm towards, or the manipulation of, a target; they make up 13% of the population of this current study. Neurons of these classes are also present in area 5. Are these neurons activated by sensory stimulation? We are certain that they are not sensitive to visual stimuli, for we have trained monkeys to reach and manipulate in total darkness, and we have studied a number of projection/manipulation cells in both light and darkness: the latter exhibited the same properties in the two conditions. They are, moreover, insensitive to projected visual stimuli delivered during task execution with visual fixation.

Are these cells sensitive to passive stimulation of the skin and deep tissues of the arm and hand? Anyone experienced with waking monkeys will recognize how difficult it is to answer this question with certainty, particularly when dealing with rhesus monkeys. It was just for this reason that, in our first study of the parietal lobe, we chose the tractable *M. arctoides* for study. In that study, as in the present one, *absence of response to passive mechanical stimulation of the tissues of arm and hand has been a defining characteristic of projection and manipulation neurons*. We have confirmed again in the present series that projection and manipulation neurons fitting this requirement are present (13%) in area PG of the inferior parietal lobule. In our studies, neurons active during projection and manipulation that were also sensitive to mechanical stimulation of the arm have always been classified as mechanoreceptive neurons or, rarely, as complex neurons. Cells of this type are exceedingly rare in area PG, but they are common in area 5 in front of the parietal fissure, and in the more anterolateral portions of the inferior parietal lobule studied by Hyvarinen and his colleagues (Hyvarinen & Poranen 1974; Hyvarinen & Shtepin 1979).

**Unidentified neurons.** A relatively large number of neurons (30%) observed in this study escaped clear identification, even though we examined them in every possible "clinical" way we could devise, and even though large numbers were tested extensively in controlled behavioral-test stimulus runs.

**On the classification of neurons in studies of the homotypical cortex in waking monkeys.** A major problem in experiments such as those carried out in several laboratories on the parietal cortex in waking, behaving monkeys is how to classify different sets of neurons that display different properties. It is our opinion that the differences that appear in different descriptions are due in part to different approaches to the problem of classification, rather than to differences in primary observations. In earlier work on the heterotypical cortex of the motor and sensory areas, the correlation between different methods of classification yielded important insights into cortical function.

## Commentary/Lynch: Posterior parietal cortex

The correlation between classifications made on the basis of physiological properties and anatomical facts has been particularly fruitful. It has not yet been possible to do this in studies of the parietal lobe, and all investigators have attempted classification on the basis of rather simple empirical observations. These classifications, and the proportions of neurons in the various classes, differ widely between different studies. This is so, we believe, for three reasons:

1. Qualitative identification of cell types by simple examination cannot be made with certainty in waking monkeys, and the use of this "clinical" method alone leads to consistent errors in identification - at least that is our own experience.

2. The controlled behavioral-task/test-stimulus sets that can be delivered in any particular experiment are limited in variety by the test apparatus used.

3. The different objectives of different investigators will inevitably bias the sample of neurons observed. This is true for the three successive studies from our own laboratory, for in them the proportions of cell types varied greatly, even though the major cell types identified remained the same.

We conclude from our own experience and infer from the published results of others that differences between the cell types identified and the proportions of different cell types tabulated in different studies are due to the variables listed above, and they provide no ground whatsoever for polemic controversy.

**Conceptual approaches to the study of parietal lobe function.** We observe with surprise that some students of parietal lobe function are content to conceptualize the problem at relatively simple levels, as if this large region of homotypical cortex and the widely distributed system of which it is a part could be classified as simply "sensory" or "motor" in function. It is with even greater surprise that we discover ourselves described as favoring the idea of a "motor" function for the parietal lobe. That statement of our views is false. The record shows that, in every publication from our laboratory dealing with parietal lobe function, we have taken care to indicate the several general hypotheses under consideration, and we have given reasons for favoring - in however tentative a fashion - one over another. No simple motor or sensory concept has ever been considered by us to be adequate, or ever stated by us to be so. For the evidence, see Mountcastle 1976, pp. 39-40; Mountcastle 1975, pp. 129-130; Mountcastle et al. 1975, pp. 898-904; Lynch, et al. 1977, pp. 385-386; and Mountcastle 1978, pp. 26-27. We accordingly wish to restate here the overall general hypothesis we use as a guide to studies of parietal lobe function.

Our general hypothesis is that the homotypical cortex of the parietal lobe, together with the distributed system of which it is a central node, generates an internal neural construction of the immediately surrounding space, of the location and movements of objects within it in relation to body position, and of the position and movements of the body in relation to that immediately surrounding space. The region appears in general to be concerned with continually updating information regarding the relation between internal and external coordinate systems. It is not "sensory" in the accepted meaning of that word, although it is linked to systems providing abstracted versions of sensory events and may play a role in perception, particularly spatial perception. It is not "motor" in the accepted meaning of that word, but it is linked via its output channels to the different mechanisms of the nervous system. Several lines of evidence indicate that it plays an important role in the initiation of certain actions into immediately surrounding space - e.g., in visually-guided manual operations, in the direction of visual attention, and so forth. That is what is meant by the "command function" (not "command neuron") of the parietal lobe (cf. Kuppermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978). We defined that term specifically to exclude the composition of closely linked motor programs. Almost certainly the parietal lobe receives information concerning initiatives toward action via centrally reflected "corollary discharges" (see Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man" *BBS* 1(1) 1978). Parietal lobe function appears to us to be far too complex to be labelled associative, if that term is defined either in the restricted anatomical sense of

Flechsig or in the more general sense of the associationistic psychologists.

These statements are of course too general for direct experimental testing, and for purposes of experimental design they are reduced to a series of intermediate level hypotheses.

Other investigators have of course generated their own hypotheses concerning parietal lobe function, based on their own experimental results. In general, they fall either into the category of association hypotheses or into an even more restricted category - that the parietal lobe is a higher-order visual processing area *per se*. We believe that there is some truth in each of these ideas, but that neither provides an adequate framework in which to study the complexities of parietal lobe function. We wish to include what is real about them in the more general concept given above.

**On future studies of the parietal lobe.** It is our opinion that the period of initial and general surveys of the functional properties of parietal lobe neurons, studied in waking monkeys, is now completed. The remaining differences concerning some observations, and particularly in the conceptualization of the problems, will undoubtedly be resolved in the light of the results of continuing and more precise studies. The method of successive approximations to reality will inevitably work its way. A major problem must now be solved before further progress of a fundamental nature can be made. This concerns the fact that the complex behavior in which the parietal lobe appears to play a role, in terms of central neural mechanisms, requires that equally complex forms of behavior be brought under direct experimental control, if one hopes to observe those neural mechanisms. This must be done in a way that is compatible with the electrophysiological aspects of the experiment. For example, how can one devise a behavioral task that reveals some aspect of spatial perception or spatial orientation - a task that a monkey will repeat hundreds of times during each day's recording session?

A second set of major problems has to do with the functional organization of the region. All investigators have observed the rather simple aspects of columnar organization in the parietal cortex, beyond that, little is known. It is our own opinion that the huge expanse of cortex we label the inferior parietal lobule contains a number of definable cytoarchitectural areas, and that these areas are likely to entertain different, if overlapping, extrinsic connections. Indeed, recent anatomical discoveries suggest very strongly that this is the case. Such a regional differentiation is compatible with the further parcellation of areas into functional modules, and with the idea that subsets of these modules may entertain subsets of the extrinsic connections of the area.

One working hypothesis worthy of testing is that each such functional module of area PG receives, among others, visual input, and leads, via intramodular processing chains, to outputs concerned with the direction of gaze, of visual attention, and so on. The testing of such an hypothesis is fraught with difficulties, whatever the experimental result. The search for causal relations between neural activity and such complicated behavioral events is always shadowed by the spectre that one observes parallel but independent events. Moreover, it may be that our window into the world of the function of the brain is far too small to reveal the overall working of such a large-numbered, specifically interconnected, yet adaptive system, involved in such varied and complicated operations as those the parietal lobe mechanisms are thought to govern. For the moment, a continued application of the method of single-neuron analysis in waking, behaving monkeys, with post-hoc reconstruction of population events, in experiments in which the behavior is controlled as precisely as possible, offers one feasible, even if limited, experimental approach to the study of the higher functions of the brain. Until better methods become available, we have no alternative but to pursue this one as energetically and rigorously as possible.

### Editorial note

In view of the central role of the work of Dr. Mountcastle's laboratory on the topic under discussion, he was given the opportunity to read all the other

commentaries in preparing this contribution. For this reason, there was insufficient time to make this commentary available to Dr. Lynch in the preparation of his response.

## Author's Response

by James C. Lynch

Departments of Physiology and Neurology, Mayo Clinic and Foundation, Rochester, Minn. 55901

### Parietal function: different aspects of the unified whole

The most common single theme that emerges in these commentaries concerns the question of whether the function of posterior parietal association cortex (and particularly of individual neurons within it) is basically sensory, basically motor, or basically something else. Hyvärinen, Mansfield, Schlag, and Stein address this question with particular directness.

Schlag suggests that the categories "sensory" and "motor" are not appropriate to the classification of neurons that are not relatively peripheral in the nervous system, and he describes his important finding that there are cells in the intralaminar nuclei of the thalamus that have activity time-locked to either sensory events or motor events, depending upon the conditions of the experimental situation.

Hyvärinen, in a very thoughtful and probing commentary, also questions whether an experimental approach that emphasizes the traditional sensory-motor dichotomy "is valid in the associative cortex in nonanesthetized, behaving animals or man." Hyvärinen goes on to say, "In such a system, neurons or neuronal ensembles are not merely sensory or merely motor; their essential role involves the integration of these aspects."

Stein provides an excellent discussion of the difficulties involved in talking about the "initiation" of a behavioral act. He observes that, on the one hand, the initiation of a movement can be defined in strictly sensory terms; on the other hand, it can be defined in terms of neural activity that is time-locked to actual muscle contraction, but that the usual meaning of "initiation" includes concepts that transcend either the simple sensory or motor definition. In fact, the complexities of the relation between the terms "neural activity involved in the initiation of behavior," "neural activity that commands movement," and "motor activity" permeate many of the commentaries. Mansfield points out that the traditional division of the cerebral cortex into separate sensory, association, and motor areas in itself carries certain implications regarding the processing of information by the nervous system, and that some of these implied processing relationships have been found to be very unlikely. He emphasizes the distributive and re-entrant nature of visual and visuomotor processing.

Three commentaries are primarily concerned with the contribution of neuroanatomical information to the understanding of the functional organization of posterior parietal cortex. Jones, Mesulam, and Pandya & Seltzer all provide new data and helpful observations that serve to clarify the cytoarchitectural and connective complexities of this area. Jones observes that while the posterior parietal cortex is relatively homogeneous from a cytoarchitectural viewpoint,

## Response/Lynch: Posterior parietal cortex

clear divisions between subareas can be observed when using connectivity as a criterion.

Jones expresses caution about placing too much importance on the parcellation of posterior parietal cortex into smaller and smaller subareas, but he also expresses the conviction that these regional variations in connectivity must be related to the relative proportions of different categories of columns and the differing connectivity patterns of the various types of columns. He suggests that if something similar to the columnar hypothesis should prove to be correct for the neural organization in posterior parietal cortex, it will be the connectivity of the individual columns that is the greatest interest, not their mere existence. (Both Chow and Mansfield point out that the isolated cortical slab method has great potential for the study of the intrinsic processing properties of cerebral cortex.) I agree with Jones completely on this point, and our laboratory, as well as others, is currently working on the problem of functional connectivity.

In this regard, Pandya & Seltzer make the interesting observation that there is now some evidence that, within a given cytoarchitectural region in posterior parietal cortex, cortical connections (demonstrated by autoradiography) are not distributed homogeneously but are arranged in discrete clumps or patches. In support of Jones's proposal that regional specializations in connectivity may be important, Pandya & Seltzer also have observed that area PF, but not PG, receives direct input from the postcentral gyrus. This finding coincides with Hyvärinen & Shelepin's observation (1979) that cells with somato-sensory properties are more common in the lateral portion of the inferior parietal lobule (PF) than they are in the medial portion (PG). However, in spite of the apparent anatomical specificity of several subregions within posterior parietal cortex, we are still left with the behavioral finding that destruction of individual subregions has not been correlated with specific behavioral deficits (Moffett, Etlinger, Morton, & Piercy 1967; Ridley & Ettliger 1975; Ungerleider & Mishkin, in press), and that the severity of the behavioral deficits is more directly related to the overall amount of cortex destroyed than to any other variable.

Chow mentions that some of the data relating to posterior parietal cortex is reminiscent of, if not totally consonant with, Lashley's concept of equipotentiality (Lashley 1949), and the similarity has occurred to me as well. Although Lashley's original hypothesis embraced the whole of the cerebral cortex, and has been shown conclusively to be incorrect in that context, perhaps some similar principle may hold within the limited confines of a cortical region such as posterior parietal cortex. There is also the possibility that as more exacting behavioral tests are used, and lesions are made that more precisely coincide with the subdivisions of connective specialization, some correlations between behavior and subregions of posterior parietal cortex may yet emerge. However, my own feeling is that although there is clearly some regional specialization of cortical connectivity within posterior parietal cortex, there is nevertheless such a large degree of overlap among the various specialized patterns of connectivity that it is unlikely that very many instances of clear dissociation of function will be demonstrated within the subregions of posterior parietal cortex (see, for example, Figure 1 in Hyvärinen & Shelepin 1979).

Both Jones and Mesulam mention the progressive connectivity of sensory and association cortex, which is indeed a striking and undoubtedly important feature of neural organization. All three of the anatomical commentators emphasize the relative remoteness of much of posterior parietal association cortex from the primary sensory areas. Mesulam addresses this point in particular detail. He suggests that the connections of area PG might be categorized as "sensory association," "limbic," "reticular," and "motor," and that the