XIX. NEUROPHYSIOLOGY[*]

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A. ON PROBABILISTIC LOGIC

Any logical statement of the finite calculus of propositions can be expressed as follows. Subscript the symbol for the δ primitive propositions A_j, with j taking the ascending powers of 2 from 2^O to $2^{\delta-1}$ written in binary numbers. Thus: A_1, A_{10}, A_{100}, and so forth. Construct a V table with spaces S_i subscripted with the integers i, in binary form, from 0 to $2^\delta - 1$. [Cf. column S_i of Table XIX-1.] Each i is the sum of one and only one selection of j's and so identifies its space as the concurrence of those arguments ranging from S_O for "None" to $S_{2^\delta-1}$ for "All." [Cf. column A_j of Table XIX-1.] Thus A_1 and A_{100} are in S_{101} and A_{10} is not, for which we write $1 \in 101$ and $100 \in 101$ and $10 \notin 101$. In the logical text first replace A_j by V_h with a 1 in S_i if $A_j \in S_i$ and with a 0 if $A_j \notin S_i$, which makes V_h the truth-table of A_j with T = 1, F = 0.

> Note that any symbol for any logical function of two of the δA_j, and these are the usual ones of symbolic logic, can be reduced to a single table V_r by the rules given in the Quarterly Progress Report of April 15, 1958, for operators with jots in x's. It is a special case of what we state here for any δ and for the likelihood, $0 \leqslant p_i \leqslant 1$, of a 1 appearing in S_i in a probabilistic logic in which these functions are uncertain.

Repeated applications of a single rule serve to reduce symbols for probabilistic functions of any δA_j to a single table of probabilities, and similarly any uncertain functions of these, etc., to a single V_r with the same subscripts of S_r as the V_h for the A_j. [Cf. V_r of Table XIX-1.] This rule reads: Replace the symbol for a function by V_k in which the k of S_k are again the integers in binary form but refer to the h of V_h, and the p'_k of V_k betoken the likelihood of a 1 in S_k. Construct V_r and insert in S_r the likelihood p''_r of a 1 in S_r computed by Eq. 1, in which $k^* = 2^\delta - 1$ of V_k. [See Example 1.]

$$p''_r = \sum_0^{k^*} p'_k \prod_{\substack{h \in k \\ r=i}} p_{ih} \prod_{\substack{h \notin k \\ r=i}} (1 - p_{ih}) \tag{1}$$

Table XIX-1.

A_j	S_i	$V_{h=1}$	$V_{h=10}$	V_h	V_k	V_r
None	S_0	p_0	p_0	None	p'_0	p''_0
A_1	S_1	p_1	p_1	V_1	p'_1	p''_1
A_{10}	S_{10}	p_{10}	p_{10}	V_{10}	p'_{10}	p''_{10}
A_{10} A_1	S_{11}	p_{11}	p_{11}	Both	p'_{11}	p''_{11}
A_{100}	S_{100}	p_{100}	p_{100}			p''_{100}
A_{100} A_{10}	S_{101}	p_{101}	p_{101}			p''_{101}
A_{100} A_{10} A_1	S_{110}	p_{110}	p_{110}			p''_{110}
All	S_{111}	p_{111}	p_{111}			p''_{111}

Example 1

Let V_h be $\delta = 3$, V_k be $\delta = 2$ (as in Table XIX-1), and write $q = 1 - p$ in Eq. 1, then we have:

$$p''_0 = p'_0 \; q_{0,1} \; q_{0,10}$$
$$+ p'_1 \; p_{0,1} \; q_{0,10}$$
$$+ p'_{10} \; q_{0,1} \; p_{0,10}$$
$$+ p'_{11} \; p_{0,1} \; p_{0,10}$$

$$p''_1 = p'_0 \; q_{1,1} \; q_{1,10}$$
$$+ p'_1 \; p_{1,1} \; q_{1,10}$$
$$+ p'_{10} \; q_{1,1} \; p_{1,10}$$
$$+ p'_{11} \; p_{1,1} \; p_{1,10}$$

$$p''_{10} = p'_0 \; q_{10,1} \; q_{1,10}$$
$$+ p'_1 \; p_{10,1} \; q_{1,10}$$
$$+ p'_{10} \; q_{10,1} \; p_{1,10}$$
$$+ p'_{11} \; p_{10,1} \; p_{1,10}$$

etc. to

$$p''_{111} = p'_0 \; q_{111,1} \; q_{111,10}$$
$$+ p'_1 \; p_{111,1} \; q_{111,10}$$
$$+ p'_{10} \; q_{111,1} \; p_{111,10}$$
$$+ p'_{11} \; p_{111,1} \; p_{111,10}$$

W. S. McCulloch

B. SPINAL-CORD TOUCH CELLS AND THEIR CONNECTIONS

The following is a summary of a paper that is being prepared for journal publication.

Skin primary afferent neurons and the cells on which they end in the spinal cord were studied in cats following spinal transection. The recordings were made with intracellular microelectrodes.

1. Afferent Fibers

a. Single fibers that respond to light touch of the skin or hair movement innervate a contiguous area of skin with an oval shape averaging 10 mm by 9 mm, irrespective of the position of the ending on the limb.

b. Pressure-sensitive fibers form a continuous group within which the threshold varies according to the fiber diameter. No justification can be found for making an arbitrary subdivision of these fibers into light-touch, deep-touch, and pain fibers. Within the single group, as the diameter decreases, the threshold increases; and the rate of adaptation to a maintained stimulus decreases.

c. The pattern of discharge in a single fiber is dependent on the intensity and duration of the stimulus and on the position within the sensitive area.

d. Some of the smaller fibers respond both to pressure and to temperature changes of the skin.

2. Primary Central Cells

a. Single central cells that respond to light touch are arranged in a marked lamina in the dorsal part of the dorsal horn. Within this lamina there is a topographic organization, with the peripheral part of the leg medial and the proximal part lateral. This region is also shown to be the termination of the fast fibers of skin nerves.

b. Each central cell responds to light touch in a contiguous oval area of skin with an average size of 63 mm by 32 mm, irrespective of the position on the limb.

c. The afferent fibers' projection shows no signs of a subliminal fringe, so that the peripheral area subserved by a single cell is unaffected by posttetanic potentiation, strychnine, asphyxia, small doses of barbiturate, or temperature changes.

d. The afferent fibers converging onto a single cell run together in a small microbundle in the dorsal root. Each dorsal rootlet contains many such microbundles from different parts of the leg.

e. All cells that respond to light touch show the slower rate of adaptation to continued stimulus — a fact that suggests that they are also innervated by fibers other than the large low-threshold fibers.

f. All cells that respond to light touch also respond to skin temperature changes.

g. It is suggested that fibers of many different diameters converge onto these cells, so that they respond to all modalities of skin sensation, but that the pattern of discharge differs with the nature of the stimulus.

P. D. Wall

C. FROG VISION

In this note we essay to show that the retina of the frog communicates to the brain in terms of three operations on the image in the eye. The neurons doing each of these three operations are distributed uniformly along the retinal surface, and all neurons of one operation come together in the brain to form a single layer of endings that continuously map the visual field. There are three such layers in registration at the visual brain of the frog, each quite separate physiologically, and each giving a map of the visual field in terms of one operation.

1. Anatomy of Frog Visual System

Between the rods and cones of the retina and the ganglion cells whose axons form the optic nerve lies a layer of connecting neurons (bipolars, horizontals, and amacrines). In the frog there are about 1 million receptors, 5-7 million connecting neurons, and half a million ganglion cells (1). The connections are such that there is a synaptic path from a rod or cone to several thousand ganglion cells, and a ganglion cell receives paths from several thousand receptors. Clearly, such an arrangement would not allow for good resolution were the retina to map a visual image in terms of light intensity point by point into a distribution of excitement in the optic nerve.

We sought to find whether or not the retina abstracts properties of an image in terms of distributed operations on overlapping areas, and we were able to establish a set of three operations beyond doubt. The three may be further subdivided later, and their descriptions somewhat modified, but qualitatively they are unlikely to change materially. Our discovery of these operations arose from anatomical study, and they, in turn, suggest a way of establishing some relations of form and function, as will be discussed in a later report.

There is only one layer of ganglion cells in the frog. They are half a million in number (as against a million rods and cones). The neurons are packed together tightly in a sheet at the level of the cell bodies. Their dendrites, however, which may extend laterally from $50\,\mu$ to $500\,\mu$, interlace widely into what is called the inner plexiform layer which is a close-packed neuropil containing the terminal arbors of those neurons that lie between receptors and ganglion cells. Thus the amount of overlap of adjacent ganglion cells is enormous in respect to what they see. Morphologically there are several types of these cells that are as distinct in their dendritic patterns as different species of trees, from which fact we would infer that they work in different ways. Physiologically, there are three gross subdivisions of these same cells, and it is appropriate, because of the dense packing and great overlap, to consider each subdivision as a separate and continuous sheet with respect to the operation it performs. It appears that these three interlaced operations are separated out at the level of the tectum where the optic axons

end, and there display themselves as three distinct parallel layers of terminals (which, so far, are established only physiologically). Each layer gives a continuous map of the visual field with respect to the function abstracted, all layers are congruent, and they are also aligned (that is, they are in registration one beneath the other). Extending into these layers are the dendrites of the receiving cells in the tectum and, on the whole, these dendrites are directed normal to the operational layers, so that any large branch samples the operations with respect to a particular small region of the retina. Although we have some data on the tectal cells we cannot yet say how they recombine the operations for the tectal output.

2. Physiology of the System

We had separated out the three operations by studies on the optic nerve, fiber by fiber. The fact that the same operations were physically separated at the tectum came as strong support to the validity of our notions. It is easier to discuss the fibers at the tectal level, where they are ordered, rather than in the nerve, where we have found that they are not only scrambled as to function but also as to region of origin. (The details will be presented in a forthcoming report.)

Hartline (2-5) and Barlow (6) had separated three parallel operations called "on," "on-off," and "off." Our fiber groups are grossly the same as theirs, by their classification, but the functions are described in multidimensional terms with a view to establishing what invariants in the visual image are abstracted. The first operation has not, to our knowledge, been described previously in any form, and it is only by elimination that we identify it with the continuous "on" group.

3. Operation A (Edging – Contrast)

In the most superficial layer of terminals at any point along the tectal surface are collected all those elements from a region in the retina (with a 10°-15° radius) that react to visual stimuli in the following manner. A fiber of this sort does not respond to a sharp step (up or down) of light intensity over its whole receptive field. Occasionally, a fiber will produce a spike in response to light or extinction of light, but the response is not constant. It does respond markedly to a step of light or dark made in a part of the receptive field and will continue responding; sometimes the response is sufficiently long that one might suppose it to be a continuous "on" or "off" fiber in the classification of Hartline, Barlow, Ruffler, Fitzhugh, and others. In fact, it signals a maintained contrast in its receptive field, and the laws governing its activity are best seen in the following description of an experiment.

A grey background much larger than the receptive field of a fiber is centered over that receptive field at a distance of 7 inches from the eye. A solid black circle called a target, or lure, is moved into and across the receptive field and provokes a burst of

activity. The target is again moved in and stopped at some particular place in the receptive field. Its inward movement is accompanied by discharges, and after it stops the fiber continues firing at a lower rate for some time (some axons go on indefinitely). If the illumination is now switched to absolute darkness for 1 sec and then on again while the target remains in place, the continuous firing is abolished. Sometimes it is re-established after a few seconds. If the dark interruption is longer, more fibers can be erased in this way. If the same maneuvers (i.e., passing through the receptive field with a target of fixed size and at a fixed velocity, or coming into the field and stopping with the edge of the target at the center) are made under different illuminations, the two varieties of response show little change in frequency or pattern throughout the range, from very little bright lighting to the point where the object is barely visible. The only difference that does occur is that the bursts accompanying movement become a little longer when the light is dimmer. Targets as small as 3' can be resolved. We have not tried to use smaller ones. Contrasts as small as those from shadows that are almost imperceptible to us provoke responses.

If a 7° target is made so that its center of about 3°-4° is quite black but shades off to the grey of the surrounding area at its edge, a burst in response to movement across the receptive field or to coming in and stopping can be obtained, but the burst is not as intense as it is for either a 7° or 3° solid circle with a sharp boundary. Furthermore, the sustained firing evoked by a target stopping within the field, no matter where stopping occurs, never approaches that evoked by either 7° or 3° targets having sharp boundaries. Thus the sharpness of the edge determines in part the strength of response. Again the action of the fiber is almost invariant under change of illumination.

If we now make a target consisting of an open circle of 7° with a thin black line as the edge, the responses are again markedly reduced. As the bounding line of the circle becomes thicker, the responses get larger until they approach the response to a solid black target.

Finally, if we examine the fine structure of the responses we find that for some fibers there is a measure of target size in that most of the well-spaced single spikes found with smaller targets become doubled when larger targets are used.

Some preliminary tests suggest that these axons are the slowest conducting (0.3 to 0.6 m/sec) and thus possibly the smallest unmyelinated ones. Their receptive fields vary from 3° to approximately 15°. In general, their response to a moving object is directly related to velocity (up to a certain maximum) and the size of target, and inversely related to the size of the receptive field.

In summary, these fibers measure a function of the sharpness and amount (up to some maximum) of a boundary between lighter and darker in their receptive fields. The function is weighted by the areas of the two phases. Some fibers show a size preference, the response dropping off if the target gets larger or smaller than optimum. It is

necessary to bring in the boundary by active movement to get the function. A stationary boundary excites only a few fibers. In those fibers requiring the bringing in of the boundary, the activity can be erased by 1 sec of absolute darkness. The responses so defined are almost invariant with respect to illumination and are not very much affected by contrast if the phases are homogeneous and sharply marked.

4. Operation B (Center Nulling — Front and/or Back Detectors)

The second layer of terminals from the optic nerve in the tectum comprises elements that at any point along the tectum make the following operation for the same region of the retina as is operated on by the homologous point in the first layer.

Single fibers of this group respond to the "on" and/or "off" of a spot or field of light with a burst of 1-5 spikes that are regularly spaced. All of those fibers coming from the same area on the retina respond to the "on" or "off" with the same spacing of discharge and are thus markedly phased when seen in the aggregate. Each fiber responds to the moving of a black target against a grey background within its receptive field, but cannot usually detect targets smaller than 3°, although some may detect targets as small as 1.5°. The response is cut off more sharply than it is turned on (using frequency only as a parameter) when an object moves through the receptive field, the field usually being approximately 12°-15° in diameter. The response occasionally depends on direction, but most often does not. It is usually larger when the target is larger, but some fibers show a size preference. The response increases as velocity increases to a certain optimum, beyond which there is a drop.

The fibers that show phasic "on-and-off" response to light also show a double response to movement across the receptive field. There is a center-null position for each of the fibers, such that the front and back of a target 7° or more in diameter produce sharp discontinuitues — the front, from maximum rate of firing to a pause; the back, from pause to maximum. Sensitivity to "on" and/or "off" is greatest at the center of this receptive field, then diminishes to the periphery, and goes over into inhibition of the center, as described by Barlow (6). These neurons can be distinguished from those of Operations A or C because they are the only ones by whose discharge one can count fingers as one moves his hand across the field. They operate by virtue of "on" at periphery inhibiting "on" at center, and "off" inhibiting "off" (6).

Seen in aggregate, the phasic "on," "on-and-off," and "off" fibers from one region act as a sharp front-and-back detector of a moving object in that region up to quite high speeds.

In summary, the fibers of this operation have no enduring response at all. They react to sharp changes of light locally or generally, and to movement within the proper region of the visual field. The response to movement has low resolution in size and speed, but the arrangement is such that the passage of a target past a certain point at

fixed speed causes a sharp drop or access in firing. A group coming from one region in the retina signal sharply the front and back of a moving target. These responses are invariant under change of illumination.

5. Operation C (Blobbing — Gross Movement Detectors)

We have studied these fibers most extensively of any because they are easiest to characterize. They give the deepest sheet of termini, which is in accurate registration with the first two sheets.

Each of these fibers responds to a step of darkness with a prolonged and almost periodic discharge. If the step is to almost complete darkness, some fibers will continue to respond indefinitely. All of these fibers are so much alike in this response that, when seen in aggregates of a pair up to several thousands, they bunch together with marked phasing, and they set up, in any situation where the activity can be integrated, oscillations of about 18 per second, with a $Q > 50$, but with a definite hiatus of response at the end of the first few waves. The Q depends on how long, up to several minutes, the light has been "on" before "off." The fibers are exceedingly sensitive to minute dimmings of general lighting. The "off" discharge is sharply inhibited by a step of "on" or by a movement through the field if there is still some light left. The "off" discharge occurs shortly if only one part of the receptive field is dimmed. Such a fiber measures average dimming (weighted by distance from the center of the receptive field) and so responds to movement of targets. The larger the target, the darker it gets in the receptive field, and the stronger is the discharge. It was a misinterpretation of this property that gave rise to the "centrifugal" fibers in the earlier reports by one of the authors (J.Y.L.). These fibers were defined by the response to a spot of light moved through the receptive field. Here, of course, as has been pointed out by the other author (H.R.M.), the slower the movement, the longer a spot would stay on center, and the longer would be the discharge on moving away; and so one would suppose the receptive field more or less constant, if large in size. Movement of the spot of light toward the center would inhibit the discharge. The response to a moving target varies little as the lighting is changed; if anything, the response increases with quick dimming.

In summary, these neurons measure the degree of average darkening of the receptive fields and exhibit the change with a long time constant. In the aggregate, the sensitivity to a downward change of total light in the receptive fields is quite large. The response to a moving target is almost invariant under change of illumination.

6. General Remarks

The operations are probably far from completely defined, although their characters seem clear. All of the responses to movement are almost invariant under simultaneously changing illumination of the target and background; that is, so long as the objects

in the field preserve their contrast. In Operation A there is a retinal memory of recent movement, the long duration of which preserves the event that something stopped at the stopping place. This combined discharge has an aggregate amplitude that decreases as the number of discharging fibers diminishes, for the fibers have a wide distribution of individual time constants. There is a sharp localization of a moving object by the excited region in the tectum, a measurement of size by both front and back determination and average darkening, and a measurement of velocity that is given by the distribution of a gross proportionality to velocity in the response of individual units. There is an additional memory of average darkening, which can be erased by a single movement.

That is how the matter presently stands. But there are indications that the three crude groups defined are further subdivided; that is, Operation A into two suboperations, and Operation B into three or four. We have found among individual fibers in the optic nerve some that are invariant under change of size of target and that measure only speed, others that measure neither size nor speed but simply signal movement, others that indicate size more than speed, others that show marked optima for a particular size and speed, others that show a marked directionality, and so on. One set of fibers, quite distinct from those of Operation C, measured inversely the degree of illumination of a field with neither overshoots on change nor accommodation. These occur somewhere in the Operation B layer.

What is very intriguing is that each of the operations is, in a sense, oscillatory. That is, suppose we are in the layer for Operation A at one point and are looking at about 6-10 afferent units simultaneously, and suddenly we bring in a sharp contrast. All of the fibers will discharge violently and then settle down to firing in bunched groups almost periodically. One fiber after another will drop out or fire sporadically, but its firing will occur more probably in a bunching so long as the bunching lasts (several seconds). The same process takes place in the other operations, but not with identical periodicity. That the oscillations are not under central control is shown in an optic nerve that has been severed from the brain. Although we cannot argue much about the provenance or purpose of these oscillations in the several operations, we can remark that they indicate a great uniformity of the ganglion cells involved in each operation.

The resemblance of these operations to those used by Oliver Selfridge in his letter-recognizing machine is obvious, and we are indebted to him for some of the terminology as well as the background of our concepts.

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D. INFALLIBLE NETS OF FALLIBLE NEURONS

Our Quarterly Progress Report of April 15, 1958, stated incorrectly that infallibility of nets of fallible neurons require $\delta > 2$ and degenerate diagrams. Tautology and contradiction can be computed error-free with $\delta = 2$ nondegenerate diagrams, although all of the component symbols are infected with probable jots. Nondegenerate $\delta > 2$ neurons with interaction of afferents yield infallible circuits when the number of jots appearing by chance in its symbols is nearly half the number of its blank spaces. For this we design the circuit to segregate errors. We have examined the extent to which threshold, signal strength, afferent interaction, and even synapsis, or connections, can be allowed to vary without loss of infallibility in the input-output function and have found the limits to be much greater than we had imagined. These findings and a further study of logically stable nets are being prepared for a technical report.

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