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Mapping the visual sensory onto the visual motor system

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Recording in the brainstem of the alert macaque revealed single units whose impulse rates vary with eye position with preferred directions that are neither horizontal or vertical nor do they correspond to the direction of activity of any of the twelve extraocular muscles. The facts that these units change firing rates well before the occurrence of changes of eye position and that they are located cranial to the third nerve nucleus suggest that they are supranuclear. It is shown how these units could function in the processes by which the sensory visual input is translated into the pattern of oculomotor organization demanded by the kinematic laws of eye movement.

In presenting some of our work on single units in the mammalian oculomotor system, we shall take our point of departure from a fundamental characteristic of the oculomotor system: the manner by which a steady-state eye position is achieved in the alert primate. It is doubtful whether this is a reasonable model of all motor control, and from perusal of the literature on muscular control one wonders whether it is worth the trouble to make any comparison at all between the general somatic motor apparatus and the eye musculature. At any rate, on the basis of some behavioral experiments in the human being and the then state of knowledge of physiology, one of us concluded twenty years ago that to each steady-state eye position there corresponded a graded set of steady-state innervations to the eye muscles. This was confirmed in three independent papers published in 1970. All showed that in the alert macaque the impulse rate in motoneurons leading to eye muscles is a unique and even almost linear function of eye position. The most usual kind of eye movement, the saccade, involves the simultaneous resetting of impulse rates in all concerned motoneurons to a new value. Because the impulse rates uniquely code for eye position, one may talk about the position-coded output of ocular motoneurons. In view of the con-
stant load on the muscles and the apparent absence of a functional stretch reflex,\(^5\) position coding of the lower motor neuron seems a reasonable way of obtaining a steady-state eye position uniquely. There are some transients during saccades and during tracking, but for the time being they may be regarded as second-order phenomena.

Since the totality of motor and sensory situations in a freely behaving animal is hopelessly large for an experiment, we have to eliminate at least a few interacting factors. It would be idle to deny the presence of important interaction; all we can hope is that, when the quarantine is lifted, the system studied under isolation continues to operate as in the experiment to at least a first order of approximation. To mention the positive side of our preparation first: It is a primate with an oculomotor apparatus indistinguishable in all essential structure and function from that of the human being; the animal is not anesthetized or paralyzed. On the other hand we have immobilized the head, so we cannot study that important confluence of neural activity by which head and eye movements are coordinated.\(^0\) In what we are going to say it is not crucial. For one thing, there is no reason to claim that unit activity related to eye movement is not related to other movement as well; for another, the voluminous literature on human eye movement and perceptual experiments, with which findings like ours may be correlated, was accumulated largely with experimental subjects whose heads were held steady, often in bite bars.

Suppose we have an alert primate, head fixed, no special vestibular input, who is looking around voluntarily. A panorama viewed from a distant mountain top would be an ideal stimulus, because binocular observation is not excluded so long as no special vergence effort is called for or executed.

During such an experiment, oculomotorneurons will behave as shown in Fig. 1. The question of the immediate supranuclear input that causes such behavior remains essentially unanswered. Here are some cells in the vicinity of the motor nuclei that may have something to do with it (Figs. 2 to 5). Rather than pursue in detail the manner in which each of these cell types fires, we would like to go to one kind of cell that is somewhat further removed from these immediate perinuclear regions (Fig. 6). Their discharge changes precede eye movements by about 20 msec, i.e., with plenty of time to participate in some sequence of events that sets into train the motoneuron firing changes. The location of the cells, about 1 to 2 mm cranial to the third nerve nuclei, is a hint, because internuclear organization seems to be located in the pontine reticular formation ventral to the nuclei and caudal to the third nerve nuclei. Another clue, and one that we shall be most concerned with, is that the firing patterns of the neurons (Fig. 6) are linked to eye position in a manner quite unlike anything found in the nuclei. There one finds activity that follows the mechanical direction of pull of individual eye muscles. What we have in Fig. 6, however, is an example of a unit that is position coded with eye position but in an oblique direction, in this case down and to the left. We cannot yet say much about the distribution of directions in the populations of such units, or even whether what we have seen is representative of a distinct population. One thing is clear, however: The direction of some of these units is not that of any particular extraocular muscle among the twelve. We must consider where such a unit might
Figs. 2 to 5. Single-unit discharges recorded from the brainstem of the alert macaque. These units are not located in the oculomotor nuclei, and may be supranuclear motor neurons. Traces are as described for Fig. 1. 2, Omnidirectional saccade-burst unit. 3, Unidirectional (up) saccade-burst unit. 4, Tonic position-coded saccade-stop unit. 5, Tonic position-coded saccade-burst unit.

Fig. 6. Tonic, oblique position-coded single-unit discharges recorded from the brainstem of the alert macaque cranial to the oculomotor nuclei. Traces are as described for Fig. 1.

be involved in the scheme of supranuclear control.

The eye moving in its orbit like a ball in a socket joint has in theory three rotational degrees of freedom. There is no difficulty conceiving of a rotation around a vertical axis (a purely horizontal movement) or one around a horizontal, fronto-parallel axis (a purely vertical movement). What happens when the eye is to be moved into a quadrant? If one were to use ordinary cartesian geometry, it would appear to be a simple matter to move the eye in the manner of a vector with independent horizontal and vertical components. Unfortunately, rotations are not simply vectors but are subject to other laws of operation. In particular, because the commutative law does not hold for rotations, the order in which two separate rotations are carried out is not immaterial. Thus, in general, if the eye started off from the straight-forward position and executed a certain horizontal movement followed by a certain vertical movement, it would end up in a different position than if it carried out the two rotations in the opposite order.

The origin and utility of position coding of motoneuron output now becomes clear: Functioning in the absence of position sense feedback, decisions concerning the exact rotations have to be made, and indeed are made, before the onset of any saccade in order to produce a unique eye position. To put this another way: Because of the noncommutative nature of rotations, specific sequences of operations have to be adopted to get the fovea to a given location uniquely. If the position error were measured, for example, in angles of longitude and latitude, then it would be necessary to make the movement corresponding to the longitudinal error first and then that corresponding to latitude. Since the adjustment is made in two dimensions simultaneously, the two errors have to be fed in and the correct rotation, meridian and eccentricity, computed ahead of time.

Ordinarily the eye uses only two of the possible three rotational degrees of freedom. This is summarized by Listing's well-known law, which is based on an organization in terms of meridian and eccentricity rather than of horizontal and vertical.
movement coordinates. Whether the latter are significant in their own right remains to be shown unequivocally, although stimulation studies, in particular those of Robinson and Fuchs in the cortex and the work from Bender's laboratory, as well as clinical conditions such as Parinaud's syndrome, seem to point to a segregation into horizontal and vertical movement channels at some supranuclear stage. The niche for our obliquely coded units, then, is more likely to be in the machinery by which a sensorily determined need to move the eye, say down and left, is translated into the mechanics of the movement. If, for example, there are horizontal and vertical movement channels, unit coding for a particular oblique direction would be connected with suitable individual weighting to these systems. The fact that their activity changes precede the beginning of a movement by 20 msec makes our units excellent candidates to issue the preliminary instructions for the saccades with those horizontal and vertical components which are needed to reach a fixation position neither in the sagittal nor in the horizontal plane.

Before proceeding to a discussion of the merits of this organization, here is a hint of complexities to come. These units do not seem to participate strongly in tracking movements. This may be because no tracking stimulus was given that happened to be in a narrowly defined preferred direction of activity during their availability for study. On the other hand, it has never been satisfactorily demonstrated that Listing's law holds during tracking movements. On the contrary, the only available data, those of Fender for rather small movements (30 min. of arc), suggest that it does not.

Given that the oculomotor apparatus is organized with only two instead of three degrees of freedom, it is again topical to ask why the system used is that described by Listing rather than another equivalent one. This was a favorite topic a hundred years ago. Helmholtz, Hering, Meissner, Nagel, and Wundt all addressed themselves to it. Of the then-current theories, the most reasonable is probably that of Hering. 10 It is worth presenting here because, like so many of Hering's theories, it is truly psychophysical, i.e., it spans the gap between physics and psychology, and there can be no greater aim for sensory physiology.

Suppose one has specified that an eye is to move to fixate a certain point, i.e., that the fixation line has been directed to that point and the latter imaged on the fovea. This information leaves open the question of what rotational orientation the eyeball is to assume around the fixation line. One tacitly presumes that this constitutes no problem, and indeed it does not if the fixated point lies in a vertical or horizontal plane through the straight-ahead direction of the fixation line. As soon as the fixated point lies inside the quadrants of the visual fields, there are several possible ways that the eye can be oriented. The way this actually works physiologically is the substance of a special study, that of the kinetics of the eye. 11 Important for our discussion is the consequence: The retinal image of a horizontal line above or below the horizontal plane of regard actually twists around the retinal horizontal meridian as the eye scans along such a horizontal line. Similarly, the retinal image of a vertical line not in the median sagittal plane of the eye turns with respect to the vertical retinal meridian as the eye looks up and down along the line. This apparent cyclotorsion does not, however, occur for any straight line in a fronto-parallel plane which passes through the straight-ahead position of the fixation line. As the eye looks along such a line, say from top right through the straight-ahead position toward down and left, the image of such a line remains on the same (oblique) retinal meridian. Other rotational axes can be designated, and are in fact used in various instruments and devices, but the eye happens to adhere to this particular schema. Helmholtz, 12 who did
not much believe in innate spatial organization of the visual system and, therefore, had to seek explanations for Listing's law in terms of what would come about most naturally with continued use, advanced a theory of minimal discrepancy of visual targets and retinal meridians. Hering, whose thinking is much more in tune with current concepts, insisted that the special virtue of the actual kinematic schema of the eye, as enunciated in Listing's law, is this particular direction congruence of elements of a long oblique line as the eye looks along it.

There thus might be a special place for units such as the one depicted in Fig. 6 in the sequence of excitation patterns that leads from sensory stimulation to motor output. If the organization of motor behavior expressed in Listing's law has its origin in the intrinsic characteristics of the sensory system, there is need for a recoding to take care of the translation into the code appropriate to the supranuclear motor centers, just as the code of the latter system has to be translated into the language appropriate to the direction of action of the twelve extraocular muscles.

All this deserves detailed discussion, but all we can do here is point to a phrase used in the above paragraph that transcends everything else in importance. In assigning to the units described here a place at the juncture of the sensory and motor systems, we suggested that they meet a condition set by the intrinsic characteristics of the sensory system, namely, a need to retain directional congruence in elements of long straight lines passing through the fixation points as the eye looks along such a line.

The demonstration of units in the visual cortex responding preferentially to short line segments of given orientation provides some substance to such a speculation, although we are talking about long lines in the visual field here. In this context, what is needed are cross-cortical connections of units in different parts of the field that share the same orientation and, perhaps even further, the connection of those units which together would constitute a single long line.

Is the call for such a system of connectivity reasonable? How compelling is the need for direction-congruence for radial lines going through the straight-ahead position of the fixation? Enough to use it as a primary organizing principle of the oculomotor system and to build in an intermediate recoding system? To go even further and deeper, how important are long straight lines in the make-up of the visual apparatus? In fact, what are straight lines?

Ordinary geometry teaches that a straight line is the shortest distance between two points. This statement retains validity even in non-Euclidian geometry. This is a somewhat unsatisfactory answer because the shortest-distance paradigm is bound up with metrical geometry, and there is no immediately obvious reason why one should examine visual space with a set of metrical axioms. On the other hand, the most general system of geometry, topology, is not more appealing, because one cannot do much with a body of theorems within which there is no difference between a cube and a sphere.

We are here driven up against one of the most profound questions that can ever be asked: What is the origin of the axioms of geometry? There is now no overwhelming reason to presuppose that Euclid's geometry or even the simpler non-Euclidian geometries represent fundamental properties of the universe. With this realization, out goes the rationalization of the preeminence of the straight line as the shortest distance between two points, for that implies a metrical bias that may not be a primary property of geometrical intuition. There have been fascinating attempts to approach geometry via postulates that are either entirely nonmetrical or introduce metrical relations only as particularizations. When one examines these and also when one looks over what Euclid actually had to say, one is struck by the fact that these attempts at axiomatic underpinnings of
all geometry have one thing in common: the tacit indefinability of a straight line.

Thus, Bertrand Russell:

Any two points have one relation, their distance, which is independent of the rest of space, and this relation requires, as its measure, a curve uniquely determined by those two points. I might have taken the bull by the horns, and said: Two points can have no relation but what is given by lines which join them and therefore there must be one line joining them which they completely determine.

And William James:

When we speak of the relation of direction of two points towards each other, we mean simply the sensation of the line that joins the two points together. The line is the relation.

And finally the first two axioms from Hilbert, the prototype of all axiomatics of geometry:

1. For each two points A, B there exists always one straight line which belongs to these two points.
2. For each two points A, B there exists never more than one straight line belonging to these two points.

If all this leads rather convincingly to the concept that the uniqueness of a straight line stems from its primacy in the human mind and/or nervous system, this is, of course, no more than an affirmation of Immanuel Kant's thesis of the synthetic a priori, i.e., the existence of pure intuitions or given judgments which may perhaps not appear without any experiential influence, but within whose framework our sensory input must nevertheless operate.

Kant was, in fact, quite explicit:

Geometry is founded on successive synthesis of the productive imagination in the creation of configurations. Its axioms express the condition of sensory intuition a priori under which alone can be generated the schema of a pure concept of external appearances; e.g., between two points only one straight line is possible; two straight lines cannot contain a space, etc.

While this relegation of a straight line to the place of a pure intuition a priori, i.e., a basic property of the human mind—express it if you will as a consequence of our neural connectivity, or as a characteristic of the apparatus for creating the externality within which we suppose we are embedded—is comforting to the mystic in all of us, it need not be a bar to further analysis.

For one thing, the virtue of the physiologic schema which led us to inquire into the intrinsic characteristics of a straight line is that it assures directional self-congruence of a line. This is a metric quality of a kind. There are other metric properties in visual space, perhaps not as succinctly stateable as Luneburg would have had it, yet congruence, inequality, curvature, distance are surely not all empty manipulative symbols. The researches in the neural, and whether we like it or not, philosophic, foundations of perception have some way to go. And the relevance of oculomotor studies was not only wisely appreciated by the organizers of this symposium but was distilled by Hering over a century ago in this beautiful language:

It is obvious that the motor apparatus of the visual organ has to fit the sensory apparatus as the shell does an egg. For, whether one assumes that they were set up according to a wise plan, or that they developed with each other and through each other in an inevitable way as the evolutionary series is traversed, in any case: the capabilities of the one have to correspond to the needs of the other.

If we wished for a motto for this afternoon’s discussion, this surely would be it.

REFERENCES


Discussion

Schiller: Do I understand from the implications of what you say that signals coming down from cortex tend to be organized according to a meridian, and transformations have to be made subsequently for the eccentricity?

Westheimer: We cannot as yet say how the signals coming from the cortex are organized, but we have given neurophysiologic evidence compatible with a meridian-eccentricity organization and have considered some of its implications.

Bishop: You are saying, are you not, that the information goes through several coordinate systems? First through a meridian-eccentricity one, then a horizontal-vertical one and then to the extraocular muscles?

Westheimer: That is the hypothesis we are considering.

Horbidge: I don’t think any of us would like to consider geometry as a product of our own perceptual or eye movement systems. It is worth saying that in the crab there are not six but nine eye muscles: Perception depends on a system with an hexagonal facet arrangement of the compound eye, but in the brain there appears to be in many arthropods an organization system which seems to have horizontal and vertical components but not control of eye rotation. There is something convenient about having horizontal and vertical control of eye position. Some crabs have in addition horizontal but no vertical eye tremor. It is not surprising to me that the vertebrate has the system you describe.

Westheimer: Thank you, Professor Horridge.

Mackay: I think that if we are going to talk about the geometry of space it has to do mainly with the number of degrees of freedom we find regardless of how many muscles we use. There are only a certain number of ways to move without repeating ourselves. I cannot see anything in the geometry of eye movements which would have any bearing on things like the three dimensions of space. Even a blind man would have these three dimensions.

Westheimer: We have based our discussion on a three-dimensional space. A rigid body in such a space has three rotational degrees of freedom, whereas eye positions can ordinarily be described fully with only two coordinates. This justifies, in fact demands, an examination of the perceptual implications of that particular coordinate system in which, to specify a position, two independent parameters suffice rather than three parameters with one degree of interdependence required by other equivalent systems. Moreover, it would be surprising if the organization of this unique two-parameter system arose fortuitously at the most peripheral motor level.