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16. Abstract

Work in this laboratory has suggested that the effects of psychoactive drugs on visual performance may best be understood, and/or predicted, by studying differential effects of the drugs on functionally differentiated sets of neurones in visual projection systems in the brain. This study demonstrates that the nucleus rotundus, an avian posterior thalamic visual relay nucleus homologous to parts of the mammalian lateralis posterior/pulvinar complex, is divided into at least three functionally distinct neurone subsets. The "posterior" rotundal cells respond to any moving retinal image. Ventral rotundal cells respond preferentially to intensity modulation of moving or stationary stimuli. Anterior rotundal neurones respond preferentially to such abstract properties of moving stimuli as size, velocity, and direction of movement. All subnuclei may be further subdivided by function. The findings reinforce current theories which suggest that pattern vision results from cortical integration of the outputs of many classes of pattern selective visual projection system neurones. Preliminary findings are also presented suggesting that effects of psychoactive drugs, such as ethanol, can indeed be predicted or understood by studies on differential effects on neurones in this model system.

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FUNCTIONAL LOCALIZATION IN THE NUCLEUS ROTUNDUS

I. Introduction.

Recent work of Benowitz and Karten (1) has shown that the projections from the optic tectum to the nucleus rotundus in the pigeon are spatially organized with specific regions or layers of the optic tectum projecting to specific, anatomically defined areas of rotundus. The present study, in part a reexamination of previous data, was initiated to see whether regional differences in rotundal functions could be correlated with the anatomical areas defined by Benowitz and Karten (1).

II. Methods.

Extracellular unit recordings were taken from rotundal neurones in urethane-anesthetized white Carneau pigeons. Projected spots of light or black cardboard targets were moved against a light-gray tangent screen to elicit visual responses in spontaneously active cells. The tangent screen was mounted vertically, parallel to the parasagittal plane, at a distance of 1.5 m from the pigeon's left eye. Absolute room illumination levels varied but were usually in the low photopic range. Although more elaborate data reduction techniques, such as poststimulus time histograms, were used, most data were taken as subjective evaluations of the unit firing frequency heard on the audio monitor (2, 13). A five-point intensity scale was used; strong, moderate and weak excitation, no effect, and inhibition. Recording techniques and equipment and electrode localization procedures were conventional (10).

The sampling procedures were such that only spontaneously active neurones were selected for detailed study, because the general procedure was to advance the electrode until a spontaneously active unit was found and then examine its characteristics. In 20 tracks we simply advanced the electrodes in 50-μm increments and tested at each point to see if unit activity was evokable. The data suggested that only one in three of the visually driven neurones was spontaneously active. For the most part the evoked responses of "active" and "quiet" neurones were similar, though it is quite possible that "active" and "quiet" neurones represent functionally distinct populations. More than 600 units or small clusters of units were examined in 62 electrode penetrations. The tracks sampled activity in rotundus throughout its rostrocaudal and dorsoventral extent. However, some bias was present; the central, lateral, and dorsal areas of the nucleus were sampled more extensively than medial and ventral zones.

For each isolated unit or cluster of units we determined field size, directional responses for each of a wide range of target configurations, responses to changes in ambient illumination, and responses to stationary diffuse or discrete light flashes.

III. Results.

A. Qualitative Description of Response Characteristics

Much of this material has previously been reported (15, 16, 17) and what
follows is, for the most part, a review and summary. About 80 percent of the
rotundal units had very large visual fields, ranging from 100° to 175° (15,
18). Most of the units with smaller fields were seen in the ventral quarter
of rotundus or as occasional units with large, long-duration spikes mixed
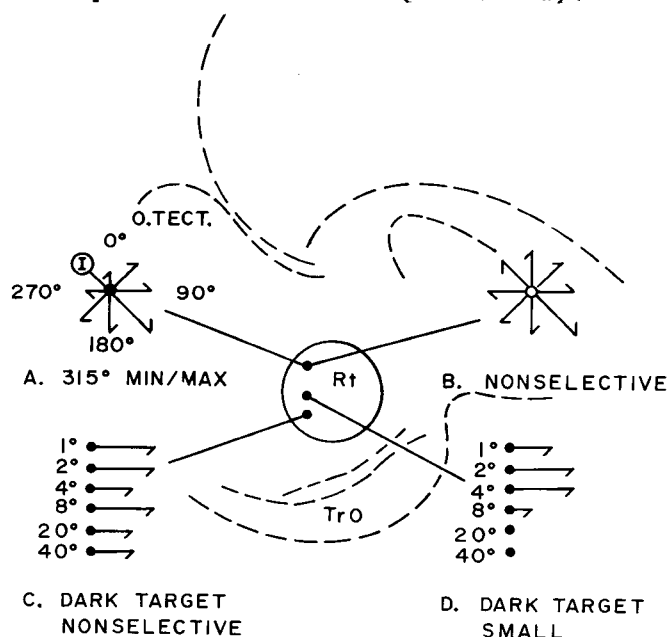with other units in the posterior rotundus (see below).

Figure 1. An illustration of some neurone response patterns found in the
nucleus rotundus. For each diagram the length of the arrow represents
response magnitude, the direction of the arrow indicates the direction of
stimulus movement. A circled I signifies an inhibition of spontaneous
activity. The uppermost neurone was interrogated with two stimuli, a small
dark cardboard target (A) and a projected spot of light of the same size (B).
In (A) a movement along the 315° axis produces an inhibition of ongoing
activity while the opposite movement, in the 135° direction, produces a
maximum response. This defines a "315° min/max" axis for this neurone. How-
ever, little directional sensitivity is apparent when this unit was tested
with a projected spot of light (B). This unit was also tested with dark
targets of various sizes (C). As shown, there is little variation in
response correlated with stimulus size. Responses to horizontal (90°) move-
ment are shown for simplicity though this class of cells simply does not
discriminate target size, whatever other selectivity characteristics the cell
may demonstrate. In (D) is shown response characteristics of a cell that
responds only to relatively small targets. Abbreviations: O. Tect. = Optic
Tectum; Rt. = Nucleus Rotundus; Tr. O. = Optic Tract; GLV = Lateral
Geniculate nucleus, pars ventralis.

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Figure 1 diagrams the most common types of responses seen in the nucleus rotundus. In each diagram, the length of the vector indicates response magnitude and the direction of the vector indicates the direction of movement of the target on the tangent screen, $0°$ being vertical and $90°$ being anterior. Figure 1A shows the variations in response seen as a target is moved in various directions. Clearly, the maximum response is seen at $135°$. The circled I at $315°$ indicates that movement in this direction caused an inhibition of spontaneous activity of the neurone. Thus, a "$315°$ min/max" axis is defined. This pattern was elicited by a $2°$ diameter, 3-mm-thick, black cardboard target. Such targets were commonly the most "efficient" visual stimuli in that they usually elicited the largest amplitude and most parametrically selective responses seen in any given rotundal unit. Thus, Figure 1B shows the response elicited in the same cell by a projected white spot of light, also of $2°$ diameter. Clearly, the response to the moving light spot is not so directionally selective as the dark-target response. Figure 1C shows amplitudes of the responses of the same neurone to horizontal movements of targets of the indicated sizes. This unit is nonselective for size; that is, the response intensity is independent of target size. The response pattern of Figure 1D shows a "size selective" unit, so called because the response intensity is clearly a function of target size.

The smallest targets used subtended 4 min of arc. About 10 percent of the units tested responded weakly or moderately, to this stimulus; this response suggests an ultimate angular threshold for this system of less than 2 min of arc. The two most common rotundal response patterns were the combinations of the configurations in Figures 1A and 1D (directionally selective for small dark targets) and those in Figures 1B and 1C (nonselective for anything but movement).

About 40 percent of the directionally sensitive cells also show a dead zone in their response pattern; that is, a unit will respond to an appropriate stimulus only if the stimulus moved in a straight line through a distance of more than $2-10°$ of arc. This is not a latency phenomenon, because the size of the dead zone is not a function of stimulus velocity, and the stimulus may be moved within the dead zone in any manner and for any length of time without affecting the firing of the unit. The diameter of the dead zone was, as indicated, always in the range of $2-10°$ and, for any given unit, of constant size. Surprisingly, dead zones were seen in units selective for large targets as well as in those selective for small stimuli.

The neurones selected for examination in these studies showed little adaptation to repeated presentation of a stimulus. However, about 10 percent of all rotundal units encountered do show some kind of adaptation phenomena. About a third of these are directionally selective cells requiring priming; that is, after a rest period of more than 5 min, during which there was no movement in the visual field, the initial 1-3 s of stimulation evokes only generalized, nonselective response patterns. The selective response patterns develop rapidly after this initial lethargy and remain stable and consistent

throughout the remainder of the examination. The other units show complex patterns of adaptation, usually a function of the stimulus parameters, that have not been examined in detail (17) but are generally similar to those described for tectal units by Woods and Frost (20).

Although rotundal responses have been categorized to some extent in the preceding paragraphs, these categories are neither complete nor mutually exclusive. Indeed, it seems as if every possible combination of size, directional, and brightness response preference has been seen. Figure 2 shows some of the various response patterns that can be seen during one electrode penetration. Figure 2A shows a cluster of three units that have the "common" pattern. Figure 2B is similar but the min/max axis is rotated 45°; there is no inhibitory response to movement and there are equal responses to small dark and small light targets.
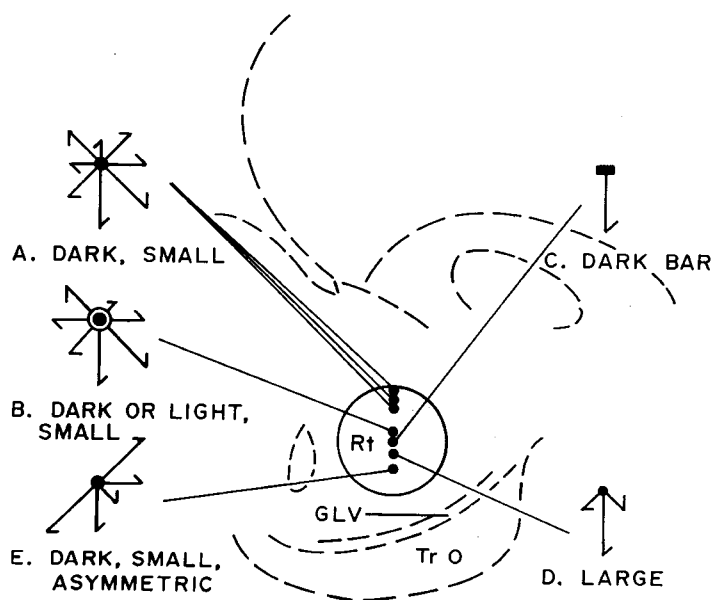

Figure 2. An illustration of typical response patterns seen in the course of single electrode penetration. The first three units in sequence responded only to small dark targets with some directional sensitivity (A). The next unit (B) was similar but with different directional preferences, and it responded to either dark or light spots. Neurone (C) responded only to a dark bar (8° x 1°) moved downwards. Cell (D) responded only to a very large dark target, greater than 30°, moving downwards. Unit (E) is similar, again, to (A) and (B).

Figure 2C shows a very sharply tuned response to an 8° x 1° dark bar. Figure 2D is similar but the response is only to targets greater than 20°, while Figure 2E is a common variant on the Figure 1A response. More complex

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response patterns are also seen. One type, the "left turn" neurone, responds only if something the size and shape of a human stands more than 1 m from the bird and pivots or turns sharply to the left (five units) or right (two units). These and other equally whimsical cells occur chiefly in the most lateral and anterior part of the rotundus. Furthermore, some of our very first unit studies suggested that excitability as well as size and directional preferences could be affected by substantial changes in ambient illumination (3) or by electrical stimulation in brain stem areas traditionally associated with the "reticular activating system" concept (unpublished observations). Because, say, directional selectivity can also be affected by such things as dark vs. light stimuli (Figure 1), it is apparent that the response characteristics of rotundal neurones depend, to an uncomfortable extent, on the minutiae of the experimental arrangements.

B. Regional Distribution of Responses

Perhaps the simplest categorization of rotundal cells is: directionally selective vs. not selective. In Figure 3 we have plotted, for each cell in each of 10 tracks, whether it was directionally selective. A 10-track subset of the total was used to keep Figure 3 fairly simple. The two different classes of directionally sensitive cells were plotted because they differ pharmacologically, but they should be considered as one group here.

DIRECTIONAL RESPONSES OF ROTUNDAL
WIDE-FIELD NEURONES

* NO DIRECTIONAL PREFERENCES
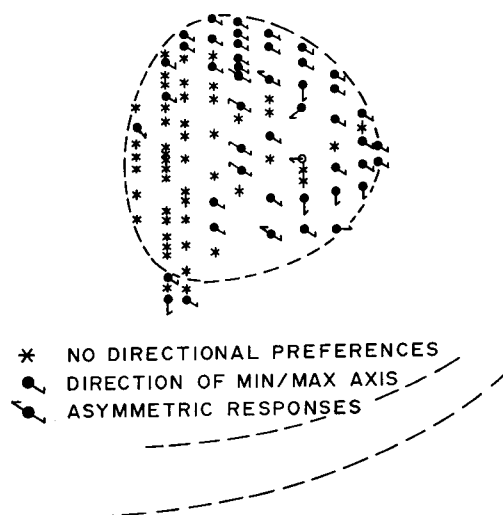DIRECTION OF MIN/MAX AXIS
ASYMMETRIC RESPONSES

Figure 3. Visual response patterns seen in 10 selected electrode tracks are plotted against a diagram of a sagittal section through the center of the nucleus rotundus. The neurones were classified according to their responses to different directions of stimulus movement as described in Figures 1 and 2. There is a clear tendency for units without directional selectivity or preferences to cluster in the posterior third of rotundus.

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Clearly, the cells showing no directional preferences tend to cluster in the posterior third of the nucleus.

There is a good deal of overlap between categories, but the distribution does suggest that the posterior third of rotundus differs from the remainder. In six tracks in dorsal anterior rotundus the min/max axis of successive directionally selective units rotated clockwise as the electrode was advanced along the usual dorsoventral axis. This rotation of response axis, taken together with the "left turn" cells, for example, suggests a high degree of functional localization in rotundus, though the complexity of the responses, the limited number of test patterns used, and the paucity of data on any given neurone response pattern make verification impossible now.

Rotundal units also differ with respect to the size of their preferred stimulus. So, in Figure 4, we have plotted size preferences seen in rotundal units. We again used a 10-track subset of the total for simplicity but sampled 10 tracks different from those used in Figure 3. Again, as in Figure 3, the nonselective units, the ones fired by anything moving, tend to be grouped in the posterior third of rotundus. There is a sampling error here, though. Were all tracks plotted, the separation, though still clear, would not be as sharp as it appears in this figure. In eight tracks preferred stimulus size increased as the electrode advanced through the dorsal half of anterior rotundus. This increase suggests, again, that there may be a much higher degree of functional organization within rotundus than that suggested in Figures 3 and 4, based, as they are, on quite simple categorizations.

Although posterior rotundal responses have been described in terms of single-unit responses, what occurs is, in fact, rather complex. Spontaneously active single units are fairly easy to isolate in this area, at least in deeply anesthetized animals. In "posterior rotundus" the probability of finding spontaneously active neurones increases with depth of anesthesia, though the rate for any given unit does not increase with an increase in anesthesia depth. The presence of a moving stimulus induces a characteristic 30-100 Hz rhythmic high frequency activity in the local EEG and also causes virtually every neurone in the area of the electrode to fire at rates of up to 250/s. There is some tendency for the neurone firing to cluster on the positive-going slope of the EEG waves. This evoked multiunit activity usually makes it difficult to discern whether the spontaneously active unit shares its neighbor's excitement over the stimulus, though this is usually the case. This pattern of activity is unique to posterior rotundus.

There are also pharmacological differences between anterior and posterior rotundal neurones. For example, ethanol inhibits anterior rotundal spontaneous activities at very low doses, while posterior rotundal cells show a complex, dose-dependent inhibitory-excitatory-inhibitory sequence of changes (Revzin, in preparation). Nonvisual dorsal thalamic neurones are usually inhibited by ethanol, but the threshold doses are three to five

IV. Discussion.

As we have seen, the available data suggests that nucleus rotundus is functionally differentiated. Neurones in posterior rotundus tend to respond to any image movement on the retina, whereas anterior rotundal responses tend to be selective for such abstract qualities of the moving stimulus as size, direction, contrast, velocity, etc. Ventral rotundal responses are similar to anterior response patterns, but these cells seem more concerned about brightness than the others. These are broad, even crude, distinctions. There is evidence that suggests far more precise and complex localizations. In some penetrations a series of "315° min/max" units would be followed by a series of units that are not directionally selective but, say, size selective. Further, in some penetrations a systematic variation in size or directional selectivity of the units was seen as the micropipette moved ventrally. Lastly, Benowitz and Karten (1) reported an anatomical parcellation that was rather more complex than the functional parcellations seen here.

Now, the characteristic response properties of rotundal units seem to be determined in tectum (4, 7, 8, 9, 14, 17) or in retina (14). This determination, taken together with the functional localization discussed above and the characteristic wide visual field of rotundal neurones (6, 17), suggest that the responses of all tectal neurones having some unique set of response properties are summed and sent to a specific and unique subarea of rotundus. That is, localization in tectum is a function of the spatial localization of the stimulus; in rotundus it is a function of the responses to some set of abstractions about the stimulus.

A good deal of recent research in mammalian visual function has suggested that form perception depends on a kind of parallel processing (5) in which the identification of the stimulus depends on an integration of the outputs of numbers of neurones or neuronal systems, each responding to a different subset of abstract stimulus qualities (19). In rotundus, each subset of neurones seems to respond preferentially in the presence of some defined set of stimulus qualities; that is, the firing of any given group of rotundal neurones signifies that a stimulus of defined properties exists somewhere in the visual field. This information is relayed to ectostriatal "core" (11), where the response patterns are very similar to those in rotundus (12). Ectostriatal "core," in turn, projects to ectostriatal "belt," as does the hyperstriatal visual area, the functional homolog, perhaps, of striatal cortex (11). Thus, the major area of integration of information from two major avian visual projection pathways may be the ectostriatal "belt," which thus may also be a major center controlling form and motion perception in the bird.

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