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Color-Opponent Responses in the Avian Lateral Geniculate: A Study in the Quail (*Coturnix coturnix japonica*)

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Extracellular recordings were made from cells in the ventral lateral geniculate (GLv) of the Japanese quail (*Coturnix coturnix japonica*), and their responses studied with chromatic stimuli. A total of 156 units were studied, and of these, 124 were found to be optimally responsive to changes in hue, and not to changes of contrast or motion of the stimuli in their receptive fields.

These chromatic responses can be characterized as follows: (1) they have large (average 15° × 15°) receptive fields; (2) these receptive fields are mostly located in the anterior part of the visual field; (3) the receptive fields are organized in a (rough) retinotopy in agreement with anatomical findings; (4) units exhibit a sustained response in the dark or under white illumination, which is strongly modulated by changes in hue of stimuli of equal illuminance; (4) the units have a complementary inhibitory response, thus exhibiting a color-opponent pattern of responses; (5) the inhibitory and excitatory areas of the receptive fields are uniform and superimposed; (6) there is a tendency of units of the same optimal chromatic responses to be clustered together in the GLv; (7) although units of all preferences are found, the population is dominated by units with preferences in the short wavelength end of the spectrum (48%).

This is the first report of a region in the avian brain where color-opponent responses are found in significant numbers, thus making it apparent that the difficulty of finding similar units in the optic tract, tectum, dorsal geniculate, or telencephalon, is not due to a lack of appropriate retinal afferents. The relationship between the present findings and other reports on the GLv's anatomy and physiology are discussed, as well as its possible roles in the generation of chromatic behavioral discrimination of birds.

INTRODUCTION

There is common agreement that birds are capable of sophisticated color discriminations. This view seems to be based on two sources of evidence. First, behavioral studies, especially in the pigeon, which show that these animals are capable of color discrimination quite similar to that of humans[2,16,33]. Second, the presence of photopigments of spectral sensitivities which are compatible with trichromatic vision[3,5,6,11,14], and perhaps, with tetra or pentachromatic vision due to the presence of ultraviolet photopigment and the peak-shifting effect of oil droplets[4,27,30].

In sharp contrast to these behavioral and photobiological studies, we know virtually nothing about the neuronal mechanisms in the avian retina and central nuclei that participate in the generation of chromatic behavioral discrimination. In fact, it is surprising to find in the literature only one incomplete description of chromatic fibers in the optic nerve[11]. Similarly, only incomplete descriptions exist of chromatic responses in the thalamus of the pigeon and chicken[8,12]. Color-opponent units have been found in the nucleus rotundus, the main projection of the optic tectum in its ascending pathway[15,34]. This finding corresponds well with the fact that the lesions in the nucleus rotundus lead to deficits in color discriminations[17], while those of the telencephalon (Wulst) do not[29]. When chromatic responses were sought for in the tectum, they were not found[20] although a significant number of tectal cells do respond to color substitution experiments[21].

Thus, in none of the major structures of the two parallel ascending retinofugal pathways of birds, the tecto-fugal (retina–tectum–nucleus rotundus–ectostriatum) and the thalamofugal (retina–n. dorsalis lateralis anterioris–hyperstriatum)[7,23], does one

easily find color-opponent responses. This situation in birds is distinctly different from the one found in mammals, where abundant numbers of cells with chromatic responses are normally found in optic nerve, thalamus and cortex, but not in the superior colliculus (for review see ref. 10). These differences between mammals and birds stand out as a fascinating puzzle in the comparative physiology of color vision.

Our purpose in the present article is to report that the ventral lateral geniculate nucleus of quail contains a substantial fraction of cells which can be classified as color-opponent. In what follows we shall describe their response, and discuss the possible role they play in the chromatic abilities of these birds.

The avian ventral lateral geniculate (GLv) is a bi-laminated diencephalic mass which receives retinal, tectal and Wulst inputs. The known projections of the GLv are to the tectum and some tegmental nuclei[7,19,23,32]. Thus, the GLv stands in a peculiar position in the visual projection of birds, as a bridge through which both major ascending pathways are interrelated (see Fig. 2). A recent study established that the topographic projections to the GLv from retina and tectum were in register. Also, there is a projection from GLv to tectum that appears to be in topographic register with the corresponding retino-rectal projection[9]. These connections make it plausible to think of the GLv as being comparable to the ventral geniculate of non-primate mammals. However, in another recent study of the response properties of the avian GLv, it was found that most of the GLv cells were movement- and direction-sensitive, and had wide receptive fields[28]. This seems to differ from the physiology encountered in the mammalian GLv[18,26,31].

Thus, although the connections of the avian GLv are fairly well established, its functional role and its homology to the mammalian GLv are far from clear. However, when one considers the questions of color-opponent responses in the ascending visual pathways, it seems so far, that the GLv is the only place where they have been found in abundance, thus shedding some light on the GLv operation, and making it clear that avian retinal ganglion cells do, in appropriate configurations, give rise to color-opponent responses.

MATERIALS AND METHODS

All observations were performed on the Japanese quail (*Coturnix coturnix japonica*), purchased from a local dealer. Animals of both sexes were chosen indifferently (46 and 54%). They were all adults (older than 6 months) and weighed between 100 and 180 g.

Determination of retinal and visual field coordinates

Receptive fields were mapped onto a translucent hemisphere carrying vertical and horizontal angular coordinates. The animal was put on a head holder so that the center of rotation passed through the middle of its head, and so that the optical axis of the eye coincided with the center of the hemisphere. At this position, the middle vertical plane of the animal made an angle of 30° with the diameter of the hemisphere (see Fig. 1a).

In order to align the position of the visual field with retinal points, the pecten was used as the major landmark, together with the edge of maximum curvature of the ocular globe. As reversible ophthalmoscopy is impracticable in these animals, a standard system of coordinates was established with freshly killed animals put in the recording position with the tissue behind the eye removed. Small (1 mm) holes were produced in the back of the ocular globe with a hot point at several positions. A portable laser beam of small diameter was directed through the opening from behind the eye, and the inverse projection of the beam was located on the hemisphere. This allowed an accurate correlation between visual fields and retinal points using the position of the pecten as a reference (see Fig. 1b).

Maintenance procedures and surgery

For the recording session animals were paralyzed (Tubocuranine, 0.1 ml/100 g b.w.) after being introduced into a plastic chamber from which only the head emerged through a rubber collar. A vacuum pump provided periodical negative pressures inside the chamber for the animal's respiration (90–100 ml/40–50 strokes/min). The bird's temperature was kept constant with a warm pad (42 °C), and the ECG was monitored continuously throughout the experiment. Eye movements were checked for on several occasions, and found to be absent when the animal was adequately paralyzed.

Surgery was carried out by putting local anesthesia on pressure points and under the head skin where the skull was opened with a dental drill exposing the telencephalic vesicles. A small pool of dental cement was built around the opening to cover the brain with warm Ringer solution, and then topped with a layer of mineral oil to prevent desiccation. The eye contralateral to the opened hemisphere was kept opened with a thread pierced through the lower eyelid. The cornea was protected with a thin layer of silicone.

This procedure allowed for stable recordings, and experiments usually lasting for 10–20 h. For the recording sessions the animal was placed in a stereotaxic headholder in the configuration recommended by Karten and Hodos[22].

Stimulation and electrical recording

The animal was stimulated by shining light from two identical 500 W tungsten filament slide projectors (Leitz Prado) onto the translucent hemisphere (60 cm in diameter), or onto a movable flat screen (70 cm × 70 cm). The projectors were fitted with movable wheels carrying sets of calibrated Kodak color interference filters (numbers K1–K7), Kodak Wratten gelatin filters (nos. 25, 15, 66, 38 A) and neutral density filters. Both projectors were mounted on universal joints, and could easily be adapted for projecting moving stimuli.

The transmission of the color stimuli was calibrated for equal intensity with a thermopile and a Gilson polygraph adjuster for microvolt readings. In this way calibration curves from the thermopile were combined with curves from the neutral density filters to produce a set of matching intensities. A Bausch and Lomb monochromator was used as a standard intensity source. In our stimulation conditions, stimuli had a luminance of 32 cd/m^2, and were delivered on a background intensity of no more than 4 cd/m^2.

Micropipettes filled with Woods metal and with tips plated with Pt black, were used as microelectrodes. They measured between 2–5 μm at the tip, and had a resistance of less than 0.4 MΩ after plating. The extracellular recordings were obtained through a high impedance cathode-follower, amplified, and relayed to a standard oscilloscope. With these electrodes, responses from GLv cells are readily distinguished from the responses of retinal, tectal and Wulst afferents, because cellular responses have a larger voltage and slower time course than fibers; in addition, fibers are triphasic while cellular responses are biphasic.

The cell responses, an audio monitor display of the spike frequency, and the ECG, were monitored throughout the experiment. Responses, stimulus parameters, and a voice commentary were stored on a magnetic tape for further analysis. Off-line analysis was carried out with a microcomputer (North Star) specially programmed for histograms of spikes over time with varying bin widths.

Histological procedures

Animals were anesthetized with ether and put on a perfusion table. Perfusion was carried out through the heart with normal saline, followed by formol, until neck ridgidity was apparent. The brain was taken out of the skull and left in fixative overnight for subsequent histological processing with paraffin embedding. The brain was sectioned every 20 μm at an orientation comparable to that used during the recording session, following the pigeon's atlas[22]. Sections were mounted serially and stained with cresyl-violet. Sequential sections were projected through a camera lucida and drawn every 100 μm for three-dimensional reconstructions. Similar procedures were used to locate lesion marks left during the recording sessions.

RESULTS

We report here the results of studying 156 units which responded to chromatic stimuli, as detailed below. This number of chromatic units corresponds to roughly half of the units encountered. Only a few of the non-chromatic units were studied in some detail, and thus are not included in the present description.

Location of the geniculate and retinotopy

All the units studied were located either in the external (GLve) or internal lamina (GLvi) of the GLv, although there was a tendency for the units to fall in GLve. Location of the nucleus could be determined by marking electrode positions and subsequent histological control, by stereotaxic coordinates, as well as by the fact that there was a sharp

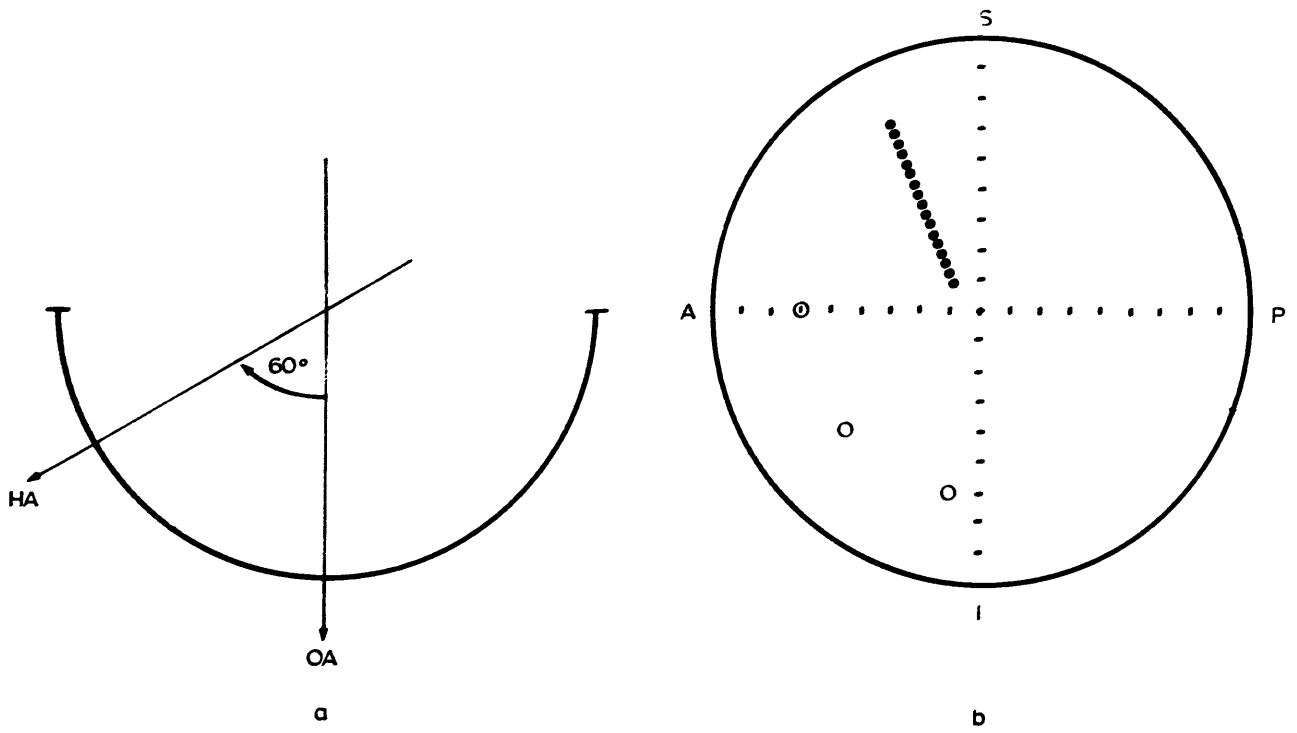


Fig. 1a: arrangement for visual receptive field determination. The retina of the quail's left eye was positioned in the center of a hemispherical dome, indicated by the semicircle. The optical axis of the eye (OA) formed an angle of approximately 60° with the main axis of the head (HA). b: the correspondence between retinal points and visual fields coordinates was determined through inverse projection of 3 retinal points with a narrow laser beam (see Methods). The pecten was used as a reference and is indicated in its visual projection by black dots. Coordinates in the visual field hemisphere are given by a standard set of meridians and parallels, which are only indicated here as they cross the horizontal and vertical axis, respectively (compare with Fig. 12). The open circles correspond to the position in the quail's retina under the edge of maximum curvature of the eye. A, anterior; S, superior; P, posterior; I, inferior.

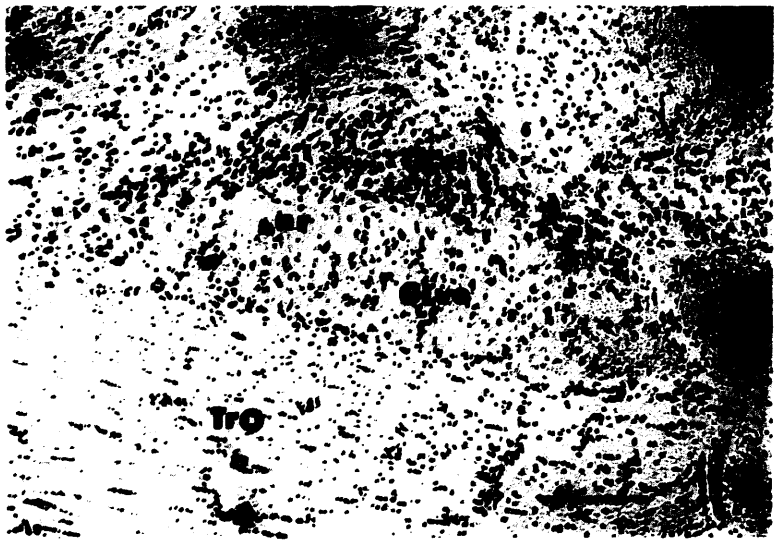
transition in the recording characteristics of GLv unit and optic tract fibers. Cells judged to be doubtful by these criteria, were excluded from further data analysis.

The GLv in the Japanese quail differs slightly in its location, relative to the stereotaxic coordinates, from the GLv of the pigeon, as specified by the atlas of Karten & Hodos[22]. The center of the nucleus was found to be at 3.00 A and 1.75 L, with anterior and lateral extensions shown in the diagram of Fig. 3, and at a depth of 7 mm from the telencephalic surface. This implies an overall reduction in size of about 30% of the quail's brain relative to the pigeon's brain.

Receptive fields from the units studied fell on the GLv surface on a rough retinotopy. In Fig. 4 we have reproduced two sets of successive penetrations in the nucleus and their corresponding receptive fields. As can be seen from this representative sample, there is an overall orientation for the changes of location in the nucleus relative to changes of location in the visual field.

In all the penetrations performed, it was a consistent feature that cells encountered successively had their receptive field in the same visual locus. However, a finer study of retinotopy than that summarized in Fig. 4 is not possible due to the relatively large size of the receptive fields (see below) and a variability in the exact direction of change in successive penetrations from one animal to the next. Thus, from our data, we are not able to define a fine grain retinotopy, but only to ascertain the fact that at least a rough retinotopy does exist, and that it corresponds basically to a double inversion (Fig. 5).

The observed retinotopy was not uniform with regards to the magnification factor, defined as the microns one needs to move on the GLv to achieve a constant displacement in the visual field. In Fig. 6 we have plotted all of the magnification factors found in the set of experiments performed, along the



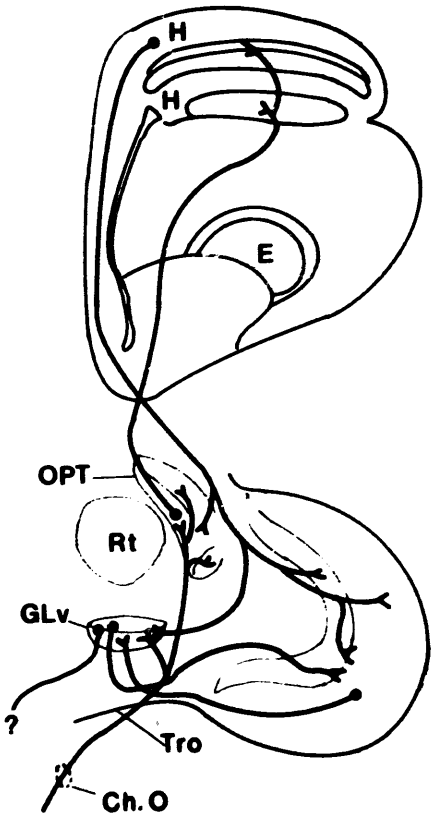


Fig. 2. The ventral lateral geniculate (GLv) is a bilaminated nucleus situated between the nucleus rotundus and the optic tract in the bird's diencephalon. It receives retinal afferents from the thalamofugal pathways, as well as from the tectum, and the hyperstriatum. It projects to the tectum and, apparently, to the tegmentum. A Nissl stain cross section of the GLv shows the internal magnocellular layer (GLvi) and the external parvo-cellular layer (GLve), comprising an intermediate neuropil (nr). Ch.O. optic chiasma; GLv, ventral lateral geniculate; H, hyperstriatum; E, ectostriatum; OPT, nuclei opticus principalis thalami, homologue to mammalian dorsal lateral geniculate; Rt, n. rotundus; TeO, tectum opticum; Tro, optic tract. Calibration 200 μm.

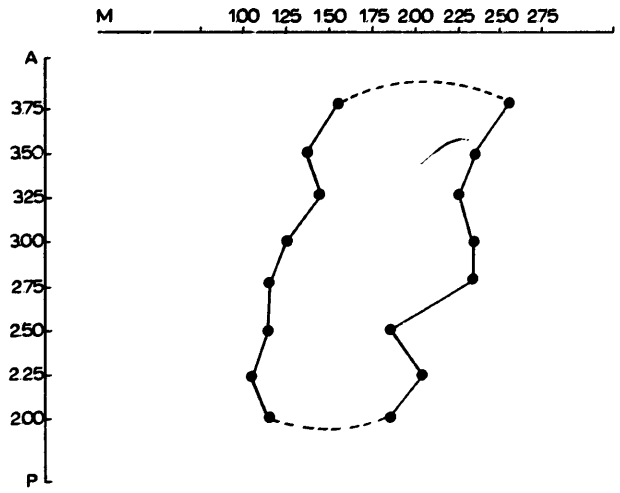


Fig. 3. A reconstruction of the GLv in the horizontal plane to show its stereotaxic position when the animal is positioned according to the conventions of the pigeon's atlas[22]. Note the slight lateral displacement of the nucleus in the anteroposterior axis. A, anterior; P, posterior; M, medial.

horizontal meridian and along the 10° anterior vertical meridian. As can be seen, both directions show a peak at the central portion of the visual field which, thus has a much larger anatomical representation in the GLv than the anterior or posterior areas.

Chromatic responses

Most of the units reported in this study could be easily detected because they had a sustained discharge either under illumination of the whole visual field, or also in the dim background light. This sustained discharge could be modulated by illumination of the receptive field with different wavelengths, and such modulation formed the basis for the chromatic characterization. The situation for all units is summarized in Table I.

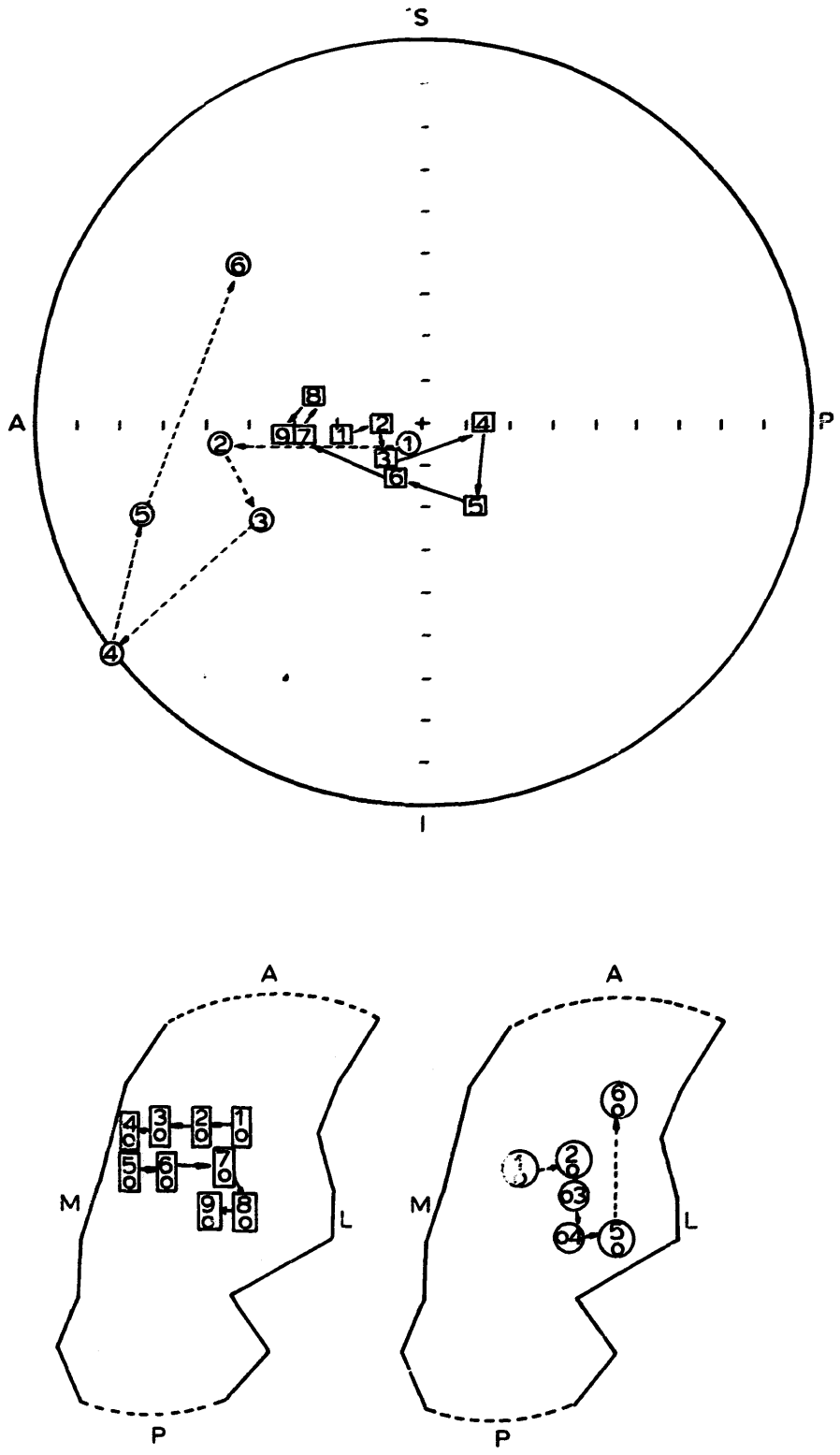


Fig. 4. Two series of electrode penetrations in two different animals; the GLv area is plotted here with its corresponding visual field coordinates. Only the center of the receptive field has been indicated to avoid clutter. These sequences of electrode penetrations give evidence of retinotopy, which is summarized in Fig. 5. Abbreviations as in Figs. 1 and 3.

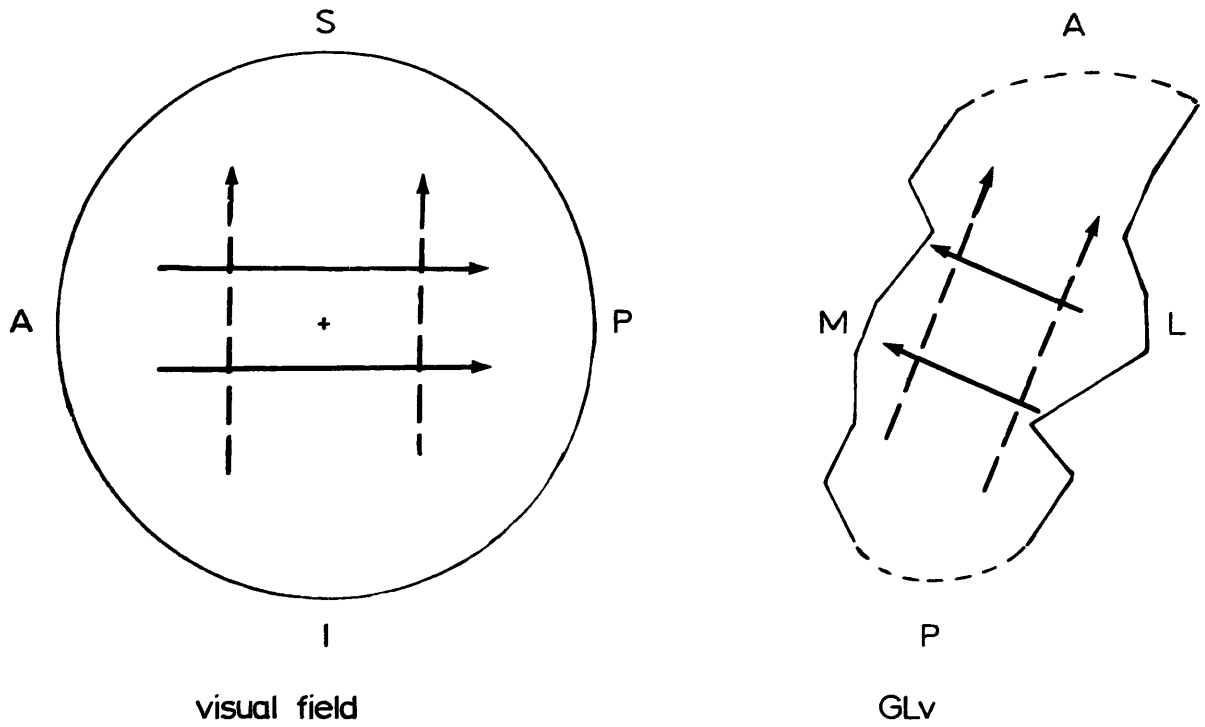


Fig. 5. Diagrammatic representation of the retinal projection upon the GLv on the basis of physiological observations (Fig. 4). A medial displacement in the GLv amounts to a posterior shift in receptive field, and an anterior displacement in the GLv amounts to an upward shift in receptive field. This retinotopy matches well the anatomical projection described for the chick by Crossland and Uchwart[9]. The posterior receptive fields are, however, much less represented in the GLv than the middle and anterior receptive fields (compare with Fig. 6 and 12).

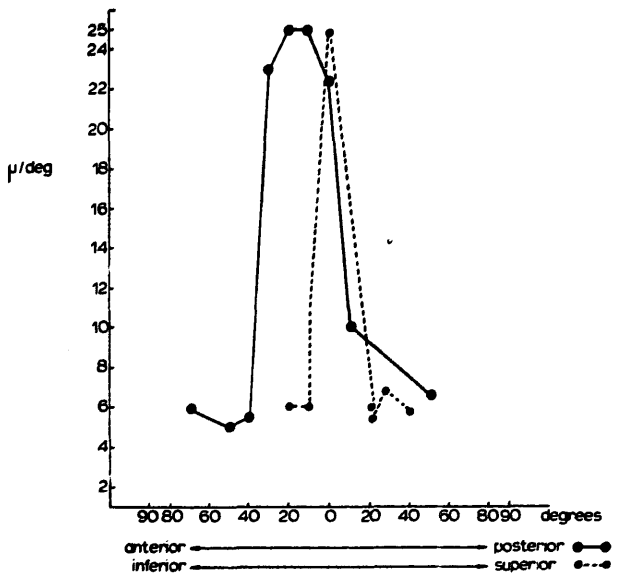


Fig. 6. Magnification factor in the retina-GLv projection measured in microns of distance in the GLv needed for a constant displacement in visual field coordinates. Plot is constructed on the basis of all the electrode penetrations which fell on the horizontal meridian (solid line), and along the 10° anterior vertical meridian (dotted line). It is evident that the magnification factor is not uniform and that it increases considerably in the anterior-superior quadrant, tapering off towards the periphery.

TABLE I

Chromatic responses in the quail's lateral geniculate

Wavelength of optimum response (nm)	*Number of units*
Class I: Units with only chromatic responses	
690	16
600	10
580	18
540	20
450	37
410	23
Class II: Units with transient responses with chromatic modulation	17
Class III: Units with variable preference or undefined receptive field	15
Total	156

Fig. 7 shows a clear example of a chromatic response in the GLv. Although this cell did not have a sustained discharge in light or dark background, only light from a very narrow band of the middle of the spectrum (580 nm) was capable of triggering in it

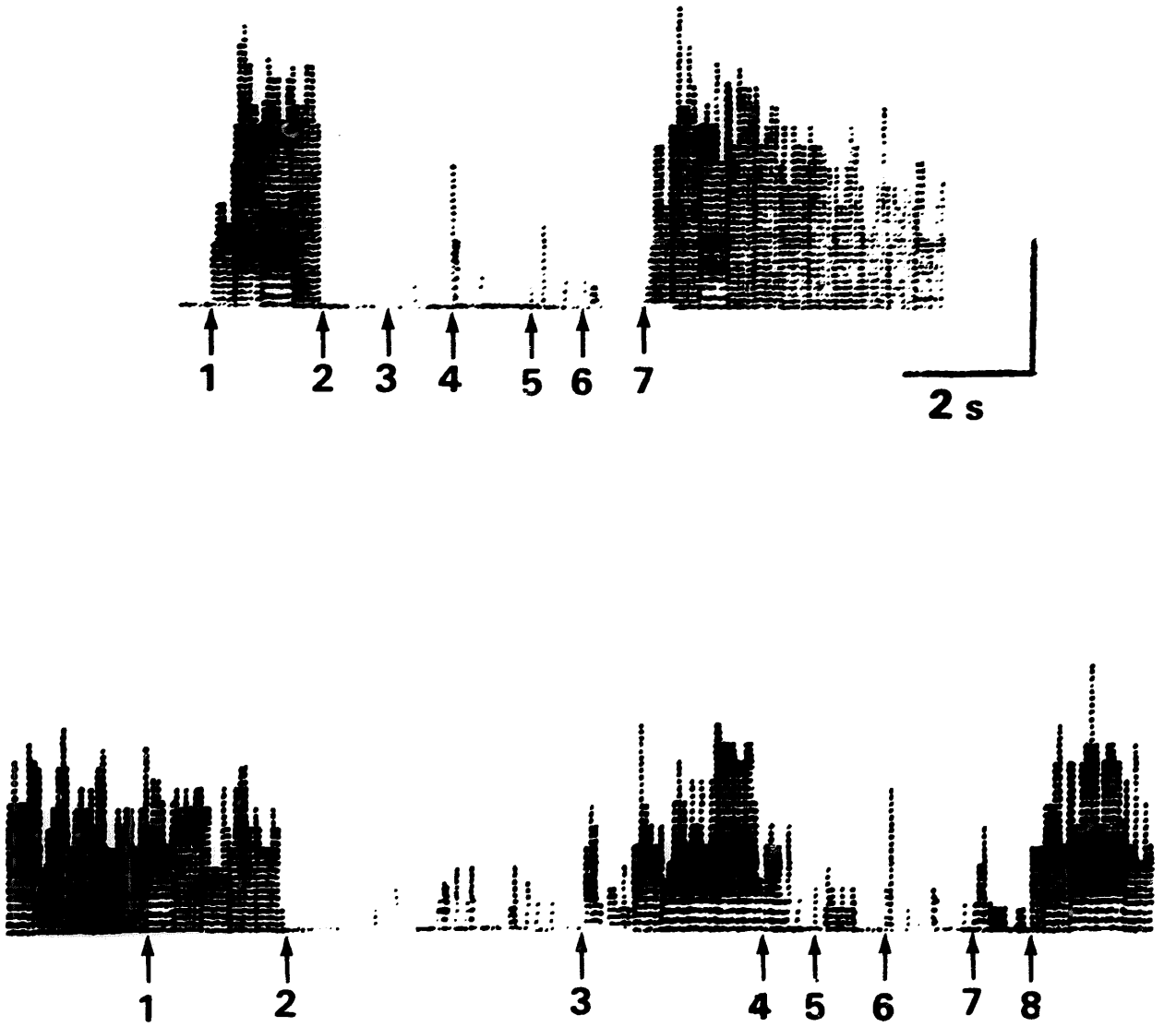


Fig. 7. Response of a GLv neuron to a monochromatic light which filled its receptive field (10° in diameter). The unit was monitored continuously as the light was changed at the points indicated by the arrows. The response here is shown as a computer produced histogram of spike frequency by an abrupt transition to another monochromatic filter held in a rotatory wheel in front of the projector (scale, 20 spikes/s; time bin, 300 ms). At (1) the unit was in the dark and a 32 cd/m² yellow (580 nm) light flooded its receptive field giving rise to a brisk response. At (2) the yellow light was replaced by white light of equal intensity, abolishing this response. A succession of equi-intensity monochromatic lights followed: (3) violet (410 nm); (4) blue (450 nm); (5) green (540 nm); (6) red (680 nm), and again yellow (580 nm) at (7). The lower record shows the response of the same cell to a more intricate chromatic situation: color shadows. At the beginning of the record the whole receptive field is illuminated with yellow light. At (1) a white light is superimposed on the yellow light with a second projector. At (2) the yellow projector is occluded and the cell is consequently inhibited. At (3) the yellow filter of the first project has been replaced with a violet filter, and a dark object has been interposed so as to produce a clear yellow color shadow on the cell's receptive field, at which it fires briskly. At (4) the shadow is kept in place but the first projector is changed from blue to yellow in (5), to green in (6), and to red in (7). Finally, the white light of the second projector is turned off and a pure yellow light is presented again in (8). It is quite evident that the response to the pure monochromatic yellow, this cell's unique preference, can also be elicited through contrast and edge relationships such as those involved in producing a color shadow.

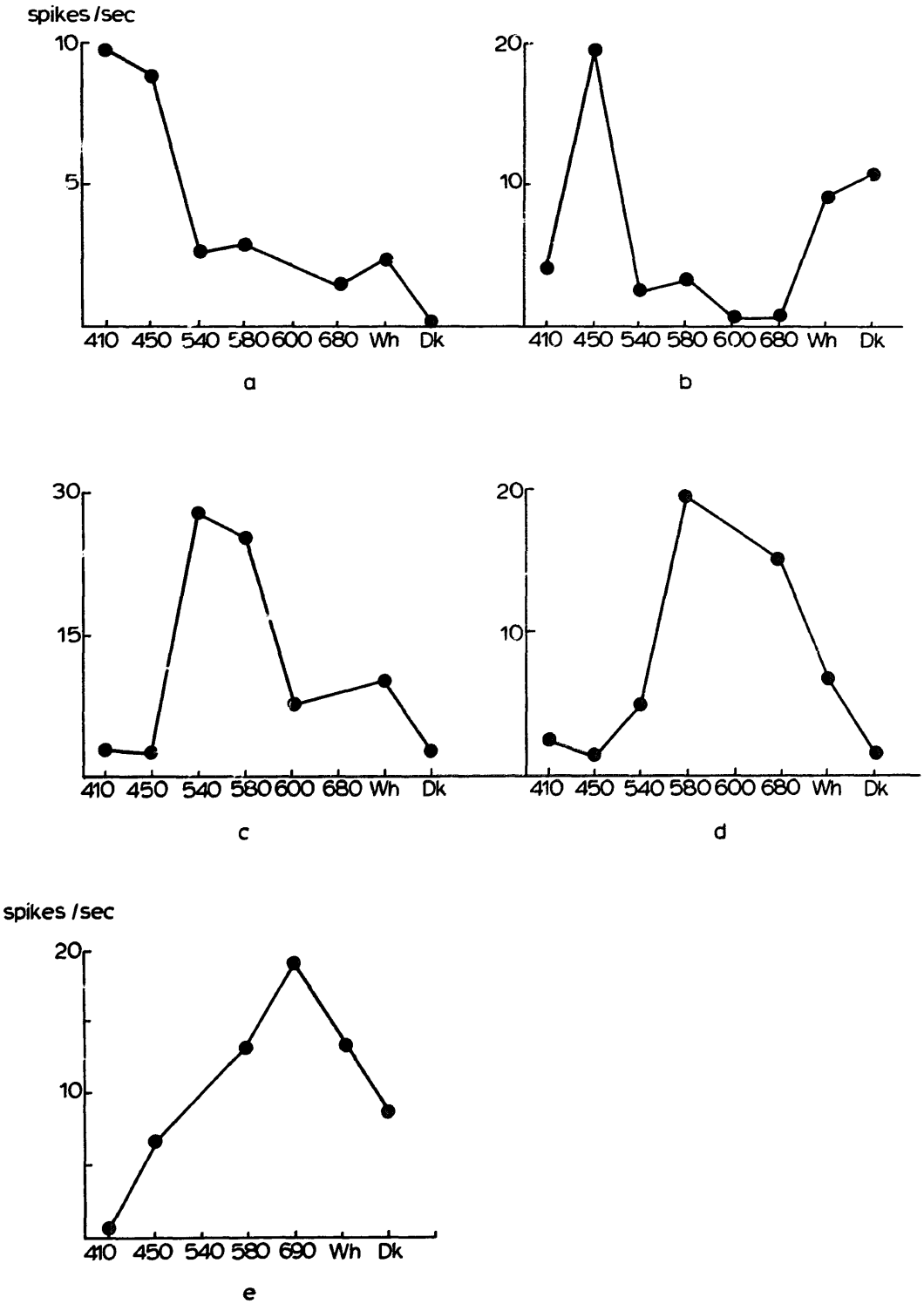


Fig. 8. Action spectra for a representative sample of GLv chromatic cells, drawn from spike frequency data such as shown on the previous figure. Notice that in many cases there is sustained discharge to both white light and dim background light. Also, that there are cells with a chromatic preference which matches every filter type used in these experiments. However, the relative proportions of such cells vary considerably, the short-wave class being by far more predominant (48%).

a discharge. As discussed below, these chromatic responses could be inhibited by a coincident illumination of the receptive fields with lights from either the shorter or longer end of the spectrum.

Action spectra were thus obtained on the basis of spike frequency and a representative sample from all groups are shown in Fig. 8. It should be mentioned that there seem to be cells with peak preference for all the filters used in this study, although there was clearly a numerical preference for units to be centered in the short wavelength of the spectrum (48% of class I cells), a subject to which we will return below. Cells with violet preference might also be able to respond to shorter wavelengths, in the ultraviolet region, as is possible in birds. We did not study this possibility.

Because of their clear color-opponent characteristics these cells are called chromatic in this study. They differ sharply in their mode of response from units which responded better either to the on–off of illumination or to motion[28]. Chromatic units have little, if any, transient responses, and do not show a

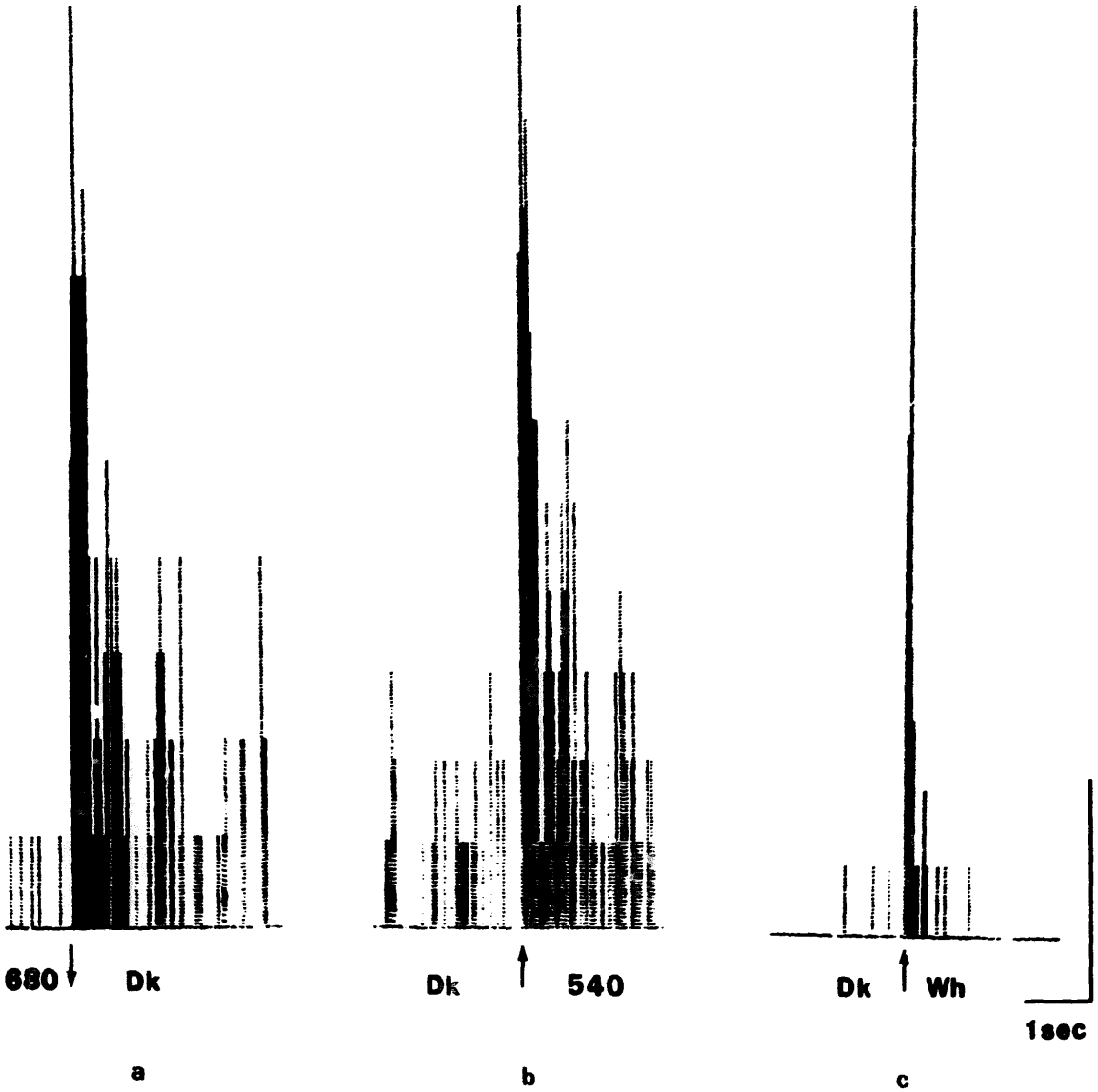


Fig. 9. Response of a GLv unit which combined motion and chromatic sensitivity. In all conditions the cell responds with a transient discharge which decays rapidly; however, this response can be induced at either the on or off of light depending on the wavelength of the light used (a and b). Thus, this cell behaved as a purely off cell for red, as a purely on cell for green, and also as purely on cell for white (c), although with a much weaker response. Cells which combine movement sensitivity and chromatic sensitivity are rare (11%), the most common case being either cells with a sustained response modulated by wavelength or cells with transient responses modulated by movement with independence of chroma. Time bin, 40 ms; scale, 75 spikes/s.

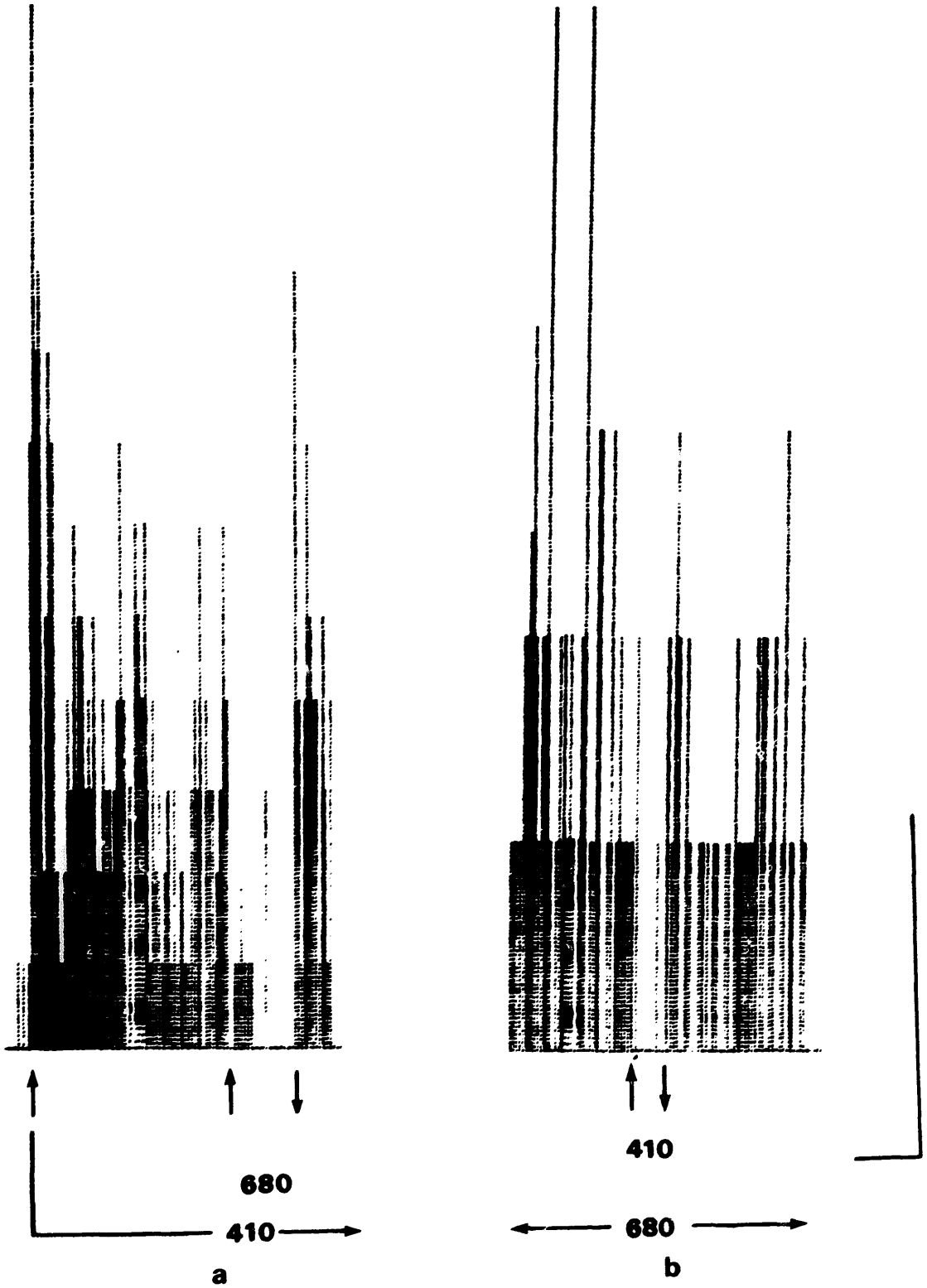


Fig. 10a: GLv cells responding preferentially to violet (on at the first upward arrow), but strongly inhibited by a simultaneous superposition of red (second upward arrow) while it is on (downward arrow). Scale, 200 ms; 10 spikes/s. b: GLv cells responding with the exact opposite configuration to excitation and inhibition. A sustained response to red is stopped while a violet light is turned on simultaneously in its receptive field (arrows). Scale, 180 ms; 25 spikes/s.

preference for either the on or the off transient response. However, there are some cases (11%) where we found a superposition of chromatic and motion (or transient) characteristics as illustrated in Fig. 9. By and large, however, these two cell types remained in clearly distinguishable classes.

Characteristics of the receptive field

Receptive fields of chromatic units did not show any sign of local differentiation. They were all uniform, and extended either in circular or oblong shapes for considerable distances. The average size was 15° × 15°, but some cells had fields as large as 40° × 40°. The receptive fields did not seem to have very sharp boundaries, and the effectiveness of light in eliciting a response seemed to diminish continuously at the edges. The inhibitory fields with opponent illumination had similar characteristics to the excitatory fields. Thus, excitatory and inhibitory contributions are superimposed in the geniculate chromatic cells in a uniform way, rather than in a center-surround configuration.

Every chromatic cell characterized by a particular wavelength preference, had an optimum inhibitory wavelength. This is illustrated in Fig. 10 showing two cells with opposite preference, and correspondingly, with opposite inhibitory preferences. Furthermore, this inhibitory chromatic effect was clearly dependent of the balance of illumination impinging on the total field. This is shown in Fig. 11 for the cell with the action spectra indicated in Fig. 8 (e). In Fig. 11 (left graph) we have plotted the change in response (number of spikes per unit time) in a cycle of turning on and off the optimum inhibitory light (violet, 410 nm). This difference in response is compared at 3 levels of illumination above and below the one normally used in the experiments. It is seen that while changes in white light alone do not alter the cell's response, they can condition the effectiveness of turning on and off the inhibitory com-

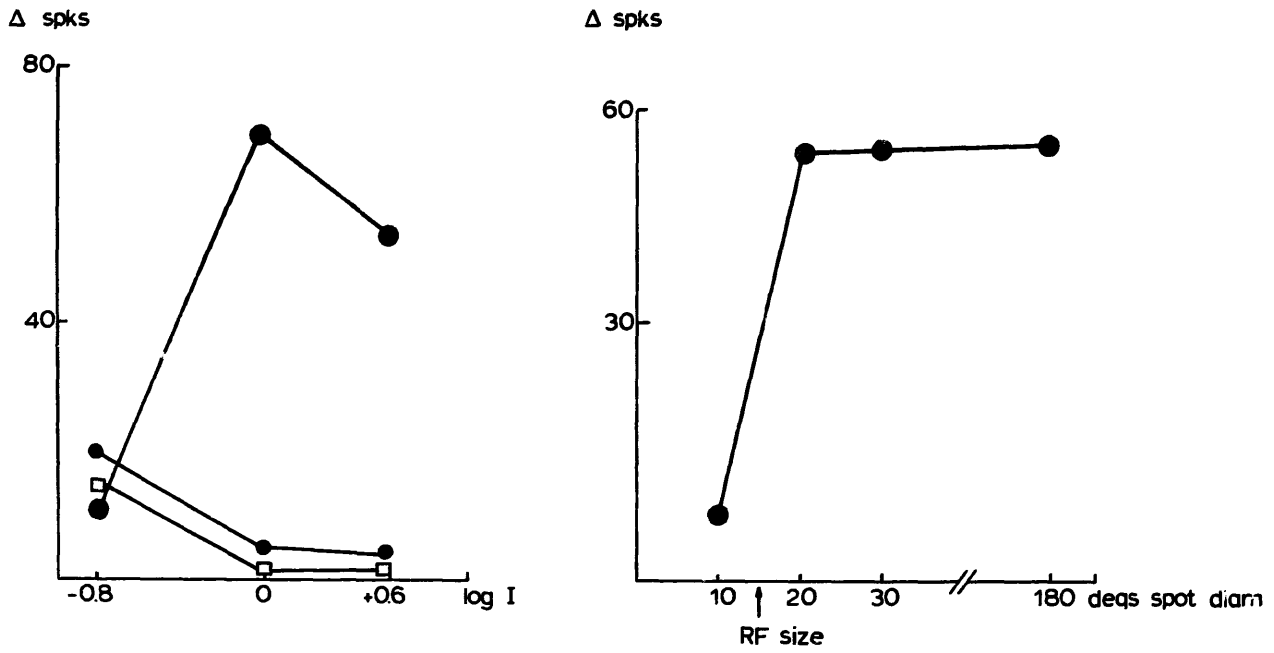


Fig. 11. Organization of the color-opponent process in the GLv units. The effectiveness of this inhibition could be modulated by the relative amount of violet and other illuminants in the field. This is shown in the left graph, where we have plotted the strength of the cell's response whose action spectra is shown in Fig. 8e, measured in terms of differences of the number of spikes to an on/off cycle, when its receptive field was illuminated by both violet and white of equal intensity. The large dots show the response of the cell when the violet light was attenuated 0.8 units below the standard intensity (taken here as 0), and brightened 0.6 units above it. It is evident that below a certain intensity relative to the surround illumination the inhibitory component is reduced. In contrast, a similar attenuation of the white light, shown in small dots, shows virtually no change. For comparison the response of cells to the same levels of illumination to white light alone, are indicated in squares.

At the right the strength of the cell's response relative to the total area covered by the violet light, is compared to the size of the receptive field determined with the preferred red excitatory component. It is clear that both the excitatory and inhibitory areas of the receptive field are superimposed and do not have a concentric organization.

ponent of the receptive field. This inhibitory effect is a function of the total area of the receptive field illuminated with the inhibitory light as shown in Fig. 11 (right graph).

For the receptive fields that fell in the binocular part of the visual field, ipsilateral contributions were looked for but not found.

Chromatic regions

Cells in adjacent geniculate regions found in one penetration were identical in their retinotopic projection. Surprisingly, they were also identical in their chromatic preferences. Furthermore, it was consistently noted that, when moving the electrode to a nearby position, although there was a change in receptive field, there was a tendency to maintain a type of chromatic preference. This was most clearly seen in the anterior part of the visual field, where virtually no units other than ones with preferences in the short wavelength region were found. In Fig. 12 a summary of locations and preferences is presented,

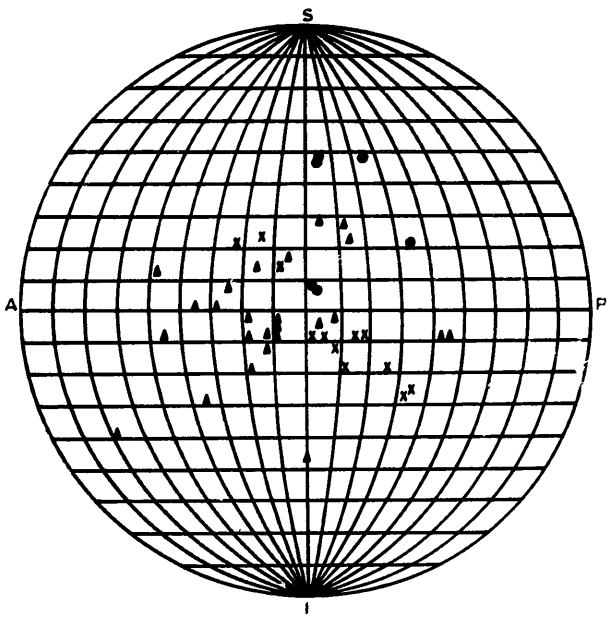


Fig. 12. Location of receptive field centers of every third unit recorded, plotted in 3 groups: short (410 and 450 nm, triangle), middle (540 and 580 nm, circles), and long (600 and 680 nm, crosses) wavelength. It is evident that locations in the middle region of the visual field predominate, in correspondence with the larger representation of the central retina. Also, there is a clear tendency for a clustering of units of the same chromatic group, most notably of the short wavelength range in the anterior receptive field. This clustering was evident in all recordings, in that units of similar chromatic type were always in the vicinity.

pooling data from every third unit to avoid crowding.

DISCUSSION

Previous findings on the geniculate

This study complements two recent reports that deal specifically with the lateral geniculate in birds (chicken); the anatomical study of Crossland and Uchwart[9], and the physiological analysis of Pateromikelakis[28]. We have found complete agreement with the anatomical findings of Crossland and Uchwart in the rough projection of the retina onto the geniculate with caudal-rostral and medial-lateral reversions. This stands in contrast to the findings of Pateromikelakis who found no evidence of retinotopy for contrast and movement sensitive units. One possible explanation for this difference, excluding species differences, is that chromatic and non-chromatic units might differ in this respect. In fact, we found that most chromatic units were located in the GLvi, while the tectal input stays mostly in the GLve. It is this tectal input which, presumably, is responsible for the receptive field characteristics of the geniculate units described by Pateromikelakis. Units in the GLvi could receive fibers from retinal axons which also enter mostly in the Glve, but also extend ramification into the GLvi, as seen in Fink-Heimer preparation (Maturana, Varela and Guiloff, unpublished observations).

Two further discrepancies with the study of the chick need explanation. First, Pateromikelakis found no units with fields located in the posterior hemifield. In contrast, in our study we found several cells that have posterior receptive fields. However, a similar tendency is noted in our data; while we found some cells that occupy fully anterior fields, we found only a few cells that occupy fields beyond the 30° posterior vertical meridian. This scarcity of cells in the posterior visual field is entirely in keeping with the finding that it contains less area of projection from the retina[9]. It also corresponds with the observation that the quail's retina contains a higher density of ganglion cells in two patches of the posterior retina with a correspondingly larger GLv representation much like the pigeon[13].

A second discrepancy with the reported physiology of the chick's geniculate is that only a small

fraction (less than 10%) of the units in the study of Pateromikelakis were movement insensitive and responded only to illumination changes. Such cells are the only candidates, in that study, to be similar to our chromatic cells. Excluding species differences, a plausible explanation at present for this discrepancy in the proportion of different kinds of cells between our and Pateromikelakis's studies, is the difference in technique for detecting the geniculate responses.

Possible role of the GLv in chromatic behavior

The results presented here show quite unequivocally that the retinal afferences have the possibility of connecting, at the thalamic level, in a manner that results in typical color-opponent responses. However, as pointed out in the Introduction, records of such color-opponent responses are notoriously scarce in studies of the optic tract, thalamus and tectum.

This demonstration of color-opponent cells in the GLv, however, does not by itself clarify how the retina and GLv participate in the generation of the domain of chromatic distinctions in quails (Kovacs, 1980). In fact, as described in the Introduction, the GLv occupies a peculiar position interconnecting the two major ascending pathways that project from the retina to the avian central nervous system (Fig. 2). Thus, the possible participation of this nucleus in the generation of chromatic behavior is certainly different from that of the mammalian GLv. This conclusion is strengthened when we consider the fact that half of the chromatic preferences are in the short wavelength end of the spectrum. This hardly seems compatible with the rich chromatic space that one might expect adequate for the diurnal, open field life of quails[25].

We are under the impression that this nucleus might play a double role with respect to chromatic behavior. On the one hand it could serve as a reciprocal modulator of the thalamic and tectal pathways by introducing chromatic bias according to different visual conditions. This possibility could be studied by recording from tectal units under GLv stimulation. On the other hand, the reported connection of the GLv to sub-thalamic areas[1], make it possible that the ventral geniculate in birds participates in processes, perhaps of neurosecretory nature, that are influenced by light changes.

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