Reports

Rod and Cone Pathways in the Inner Plexiform Layer of Cat Retina

Abstract. In cat retina, rod bipolar terminals do not synapse on ganglion cells but on two types of amacrine cell (types I and II). Cone bipolars synapse directly on ganglion cells and on type I amacrines. The type II amacrine appears to play a special internuncial role between bipolars and ganglion cells in the rod system.

The connections of rods and cones with bipolar and horizontal cells demonstrate remarkable specificity in the outer plexiform layer (OPL) of mammalian retinas (1). A single type of rod bipolar and several types of cone bipolar have been identified in cat and monkey by their connections with rod spherules and cone pedicles, respectively (1). On the other hand, very little is known about the specific connections of rod and cone bipolar terminals in the inner plexiform layer (IPL) where they synapse on amacrine and ganglion cells (2, 2a).

Golgi-impregnated rod bipolars in the cat, as in other mammals, have simple club-shaped endings that terminate in the inner half of the IPL and close to the ganglion cell somata (1) (Fig. 1B). Cone bipolars, on the other hand, have irregular, branched, laterally spreading terminals found primarily in the middle (Fig. 1A) and outer (Fig. 1C) thirds of the IPL. Despite their partial overlap, the arborizing processes of the various bipolar cell types maintain consistent differences in the level of their terminations within the IPL. In electron microscopic study of ser-

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ially sectioned, aldehye-fixed retinas (3), we were able to trace the dendritic processes of several rod and cone bipolars to their photoreceptor contacts. Marked cytoplasmic differences in the perikarya of rod and cone bipolars, and the rela-



tive ease of following bipolar processes to their synaptic terminals in the IPL, allowed the determination of their synaptic connections. In addition, we were able to establish morphological criteria distinguishing among two types of amacrine cell processes and ganglion cell dendrites in electron micrographs of the IPL.

Typical of dendrites in the central nervous system generally, ganglion cell dendrites (D in Fig. 2a) are recognizable as pale profiles containing regular arrays of microtubules, smooth and rough endoplasmic reticulum, and groups of small mitochondria. They are the only neuronal processes in the IPL which have no synaptic vesicles. The very numerous type I amacrine cell processes (A I in Fig. 2a) are often as pale as ganglion cell dendrites, but with fewer microtubules and larger mitochondria. Characteristically they contain synaptic vesicles and make the vast majority of "conventional" synapses in all parts of the IPL (2, 2a, 4). The type II amacrine cell has not previously been distinguished from other amacrines. Its cytoplasm is significantly more electron-

Fig. 1. Golgi-Kopsch-Colonnier-impregnated rod and cone bipolars, amacrine and ganglion cells in appropriate laminar and sublaminar relationship. (A) Invaginating cone bipolar. The terminal arborization of its centripetal process is found primarily in the middle third of the IPL. (B) Rod bipolar. Its centripetal process traverses the entire IPL. (C) Flat cone bipolar. The terminals are confined to the outer third of the IPL. (D) Narrow-field, bistratified, type II amacrine cell. Its dendritic tuft branching in the inner half of the IPL receives synapses from rod bipolars. Cone bipolar terminals contact its middle region by means of gap junctions. The large lobular appendages in the outer third synapse on ganglion cell dendrites and type I amacrine cell processes. (E) Narrow-field, tufted, unistratified ganglion cell in area centralis. Dendrites of such cells in the outer third of the IPL are probably contacted by the large lobular appendages of type II amacrine cells, by type I amacrine cells, and by cone bipolar terminals. [Bar = 30 μ m] (F) Schematic diagram of major rod and cone pathways through the IPL. Presynaptic processes contain synaptic vesicles. A break in the long AI process indicates that A I processes are presynaptic to all elements, but that the specific pathways connecting rod bipolars to ganglion cells through A I processes have not yet been found. Gap junctions have been found between processes of the same A II cell (5), as well as between cone bipolar terminals and A II processes, both illustrated as thick lines joining two processes. In (F) C = cone bipolar; R =rod bipolar; A I = type I amacrine; A II =type II amacrine; and G = ganglion cell.

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dense (A II in Fig. 2a) than that of type I amacrines and contains few microtubules, some rough endoplasmic reticulum and characteristic large mitochondria. Synaptic vesicles are scarce in type II amacrine cell processes except in the vesicle-filled presynaptic lobular appendages (Fig. 2c). The connections of bipolar cells with these three types of processes are described below.

In no instance have we observed rod bipolar terminals to make a synapse directly on ganglion cells, either on their dendrites or on their cell bodies. On the other hand, cone bipolar terminals often make ribbon synapses directly onto ganglion cell dendrites (Fig. 2a). Rod bipolars make ribbon synapses with amacrine cell processes only. Most often one of these is a type I amacrine cell process which always synapses back onto the bipolar in reciprocal fashion (2, 2a, 4) (Fig. 2a). The other member of a typical rod dyad is never a ganglion cell dendrite, but is instead the process of a type II amacrine cell (Figs. 1D and 2a).

Partial reconstructions of type II amacrine cells from serial sections (5) show their morphological similarity to a small, narrow-field amacrine cell seen in Golgi preparations (Fig. 1D). This narrow-field amacrine has a number of lobular appendages which emerge on thin stalks from the perikaryon and apical dendrite. These appendages are profusely segmented, but are confined to the outer third of the IPL. The secondary dendrites produce a tuft of irregular dendritic branches which ramify in the inner half of the IPL. Although the type II amacrine cell's dendrites contain scattered synaptic vesicles, they have never been observed to be presynaptic in the inner half of the IPL, but are instead postsynaptic to rod bipolars and type I amacrines. In contrast, the lobular appendages, while both pre- and postsynaptic to type I amacrine processes, are primarily presynaptic to ganglion cell dendrites on which they make distinctively small synapses (Fig. 2c). Thus the lobular appendages of each type II amacrine cell appear to provide a highly specialized and stratified pathway for transmission to ganglion cells of information received from a small cluster of rod bipolars in the inner half of the IPL (Fig. 1F).

A special feature of the type II amacrine cell is that it forms spatially extensive "gap" junctions (6) with dendrites of similar cells and with the terminals of cone bipolars (Fig. 2, a and b). Type I amacrines also form gap junctions, but these are small "macular" junctions 1000 to 1500 Å in diameter, which connect type I amacrine processes with each other exclusively. The function of these several types of gap junctions is unclear at present. A more thorough evaluation of these junctions will be presented elsewhere (5).

In the course of this study it has become evident that there are distinct pathways for rods and cones in the inner as well as the outer plexiform layers of the cat retina (Fig. 1F). The most striking difference between these two pathways is that cone bipolars make ribbon synapses directly onto ganglion cell dendrites whereas rod bipolars do not. Apparently, the only pathway from rod bipolars to ganglion cells involves the interpolation of amacrine cells (Fig. 1F). In particular, a specialized "type II" amacrine cell has been found which preserves a narrow-field, vertically organized pathway for the rod system in the IPL (7). This amacrine cell appears to conduct information from rod bipolar terminals in the inner half of the IPL toward the ganglion cell dendrites that end in the outer third of the IPL (5). Thus ganglion cells such as the narrow-field, tufted, unistratified cell of Fig. 1E, could receive rod input through the lobular appendages of the type II amacrine cell, but ganglion cells whose dendrites do not reach the outer third of the IPL would be inaccessible to rod influence via the type II amacrine. Such ganglion cells may receive rod input, however, via polysynaptic, type I amacrine cell pathways.

Synapses from cone bipolars directly onto ganglion cell dendrites occur fre-



Fig. 2. Electron micrographs from serial sections of cat retina. Paracentralis. (a) A cone bipolar (CONE BP) makes two ribbon synapses (r) with a ganglion cell dendrite (D) and two pale amacrine processes (A I). In addition, the cone bipolar makes an extensive gap junction with a type II amacrine cell process (A II) between the open arrows. A rod bipolar terminal (ROD BP) makes a ribbon synapse on the type II amacrine and a type I amacrine in a typical dyad. The type I amacrine makes a reciprocal synapse (closed arrow) (\times 33,000). (b) Septilaminar gap junction between a cone bipolar and a type II amacrine. The "gap" is about 30 Å wide. Wide arrows indicate where gap is most evident (\times 250,000). (c) Lobular appendage of a type II amacrine cell (A II) makes a small "punctate" synapse (open arrow) on a ganglion cell dendrite (D). At the synapse parallel membranes are separated by about 180 Å. Vesicles are clustered about a simple presynaptic conical density (open arrow). Little postsynaptic density is seen. A symmetrical punctum adhaerans (closed arrow) is adjacent to the synapse; m = mitochondrion (\times 100,000).

quently on ganglion cells that branch in the middle third of the IPL, as well as on those branching in the outer third. Indeed, neurophysiological studies have indicated that, while all ganglion cells seem to have rod inputs, both rod and cone pathways converge on many ganglion cells (8-10). If, as reported in the cat (10, 11), some ganglion cells do not receive input from cones, it is likely that their dendritic ramifications occur in the inner third of the IPL.

It has been proposed that bipolar cells convey sustained and simple center surround properties to ganglion cells, while amacrine cells are responsible for transient activity in ganglion cells, as well as complex receptive field properties, including directional selectivity (2a, 12). It has been suggested further that a high ratio of amacrine to bipolar synapses in the IPL (2a, 12) and on individual ganglion cells (13) is the substrate for the "complex" behavior of ganglion cells in submammalian vertebrates, as well as lagomorphs and some rodents.

In the rod-dominated retina of the cat most of the ganglion cells receive both rod and cone input (9, 10). We have shown that in the cat, rod bipolars require internuncial amacrines, while cone bipolars synapse directly on ganglion cells. One might then expect that a change from light-adapted to darkadapted conditions would result in a corresponding shift in ganglion cell responses to more transient activity and to more complex receptive field properties. Actually, the receptive field surrounds of ganglion cells are diminished, if not absent, in the dark (9, 10). Moreover, under the same conditions the sustained component of their responses becomes more prominent (14). Of possible importance in this regard is the recent discovery of sustained amacrine cells (15).

Thus, in the dark-adapted eve. amacrine cells of the cat must not only permit an increase in sustained activity but also convey to ganglion cells simple receptive field "center" properties. We suggest that the type II amacrine cell, because of its narrow-field morphology and stratified connections, is a good candidate for conveying dark-adapted receptive field center properties to ganglion cells in the retina of the cat. HELGA KOLB

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- We thank Julia Lohr for preparing the serial sections and Peter Gouras and Ralph Nelson 16. for help with the manuscript.
- 31 May 1974

Earthquakes and the Rotation of the Earth

Abstract. A correlation exists between long-term variations in the length of the day, Chandler wobble amplitudes, and global seismic activity. These variations may be partially due to climatic changes and ultimately to explosive volcanic activity.

The cause of the long-term (~ 10 years) variations in the length of the day are still unknown, but they are generally attributed to processes in the core (1). Short-term and seasonal variations can be confidently attributed to variations in zonal wind velocities (2). These shortterm variations are generally of the same order of magnitude as the long-



term ones-the so-called decade variations in the length of the day-so it is not out of the question that long-term climatic variations may also be responsible for the decade variations in the rotation rate of the earth. In this report I would like to point out an interesting correlation between the length of the day, Chandler wobble amplitudes, and the incidence rate of great earthquakes (Fig. 1). In particular, the large deviation in the length of day around the turn of the century correlates well with the worldwide increase in global seismic activity at the same time. Smaller peaks in the length of day and seismic activity occur in the 1830's and 1940's (Fig. 1). There is, as yet, no indication of increased seismic activity associated with the upswing in length of day starting about 1960.

The correlation coefficient between earthquake energy and length of day is 0.78 for unlagged 5-year means and 0.90 for sliding 20-year means taken at 5-year intervals. The correlations with volcanic activity and global climatic

Fig. 1. Changes in rotation rate of the earth $(\Delta \omega / \omega)$, Chandler wobble amplitudes, and 5-year means of earthquake energy (E_8) or moment (M_0) (10).