APPENDIX

A SECOND TYPE OF MIDGET BIPOLAR CELL IN THE PRIMATE RETINA

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Electron microscopy of the retina shows that neural processes contact cone pedicles in two ways. They may penetrate into the cone pedicle in invaginations or make superficial contacts on the base of the pedicle. In the primate, three processes penetrate into each invagination and this arrangement has been called a triad (Missotten 1965). The central element of the triad has been identified as being from a midget bipolar cell, while the lateral elements have been shown to be horizontal cell processes. The neural processes making superficial contacts on the pedicle base are believed to be the apical dendrites of flat bipolars (Missotten 1965; Stell 1965*b*; Dowling & Boycott 1966).

The main paper develops and correlates these findings with the light microscopy of Golgi-stained retinae. For example, in the central area of the primate retina, the number of apical processes that can be counted on a midget bipolar dendrite closely matches the number of invaginations into a cone pedicle of the central area (p. 124). This suggests that a midget bipolar extends processes to the centre of every invagination of a single pedicle, which agrees with the findings so far obtained by electron microscopy.

To further our knowledge of the contacts in the outer plexiform layer of the primate retina, one of us (H.K.) has undertaken a study of Golgi-stained retinae of rhesus monkey by electron microscopy. For this purpose both the Golgi–Colonnier (Colonnier 1964) and the Golgi rapid triple impregnation (Stell 1965*a*) methods have been used (see methods in main paper p. 112). The results to date substantially confirm the above description and will be presented in full elsewhere (H. Kolb, in preparation). However, in the course of this work a new type of midget bipolar has been found and will be described here.

Polyak (1941) was the first to recognize the midget bipolar as a neuron exclusive to one cone, and described it as characterized by a single small dendritic terminal (bouquet) that exactly fitted, in size, the base of the cone pedicle. The present study now subdivides midget bipolars into two distinct types. The apical processes of the new type of midget bipolar make superficial contacts on the base of the cone pedicle. They never penetrate into the invaginations of a cone pedicle as do the processes of the previously described bipolar. This new cell will be called the flat midget bipolar to distinguish it from the previously described type of cell, which we shall refer to as an invaginating midget bipolar.

Figure 101, plate 45, is an electron micrograph of a rhesus monkey retina fixed with osmium tetroxide and shows the configuration of the triad of processes invaginating the cone pedicle with the associated synaptic ribbon and vesicles. Processes making superficial contacts on the cone pedicle are marked by arrows. Figure 102 shows an electron micrograph of a Golgi-stained process from a midget bipolar that was identified by light microscopy as a type with processes penetrating into the cone pedicle. By comparison, figure 103 shows a quite different situation. This is an electron micrograph of the terminals of two apical processes of a flat midget bipolar and it can be clearly seen that they lie at the

side of the central process of the triad and do not enter the pedicle. They make the superficial type of contact. Figure 104 again shows flat midget contacts, and, by comparison with figure 101 above it, clearly shows that the point of contact is superficial to the cone base, identical to the arrowed processes in figure 101.

Analysis of serial sections of the invaginating and flat midget bipolar terminations on the cone pedicle reveals that the invaginating midget bipolar has an apical process to fit in to every triad as the central element, whereas the flat midget bipolar has double the number of apical processes, all of which make superficial contacts. Both types of midget bipolar contact only a single cone pedicle. In most cases the flat midget bipolar endings lie adjacent to the point of entry of the invaginating midget into the triad (figures 103 and 104), but

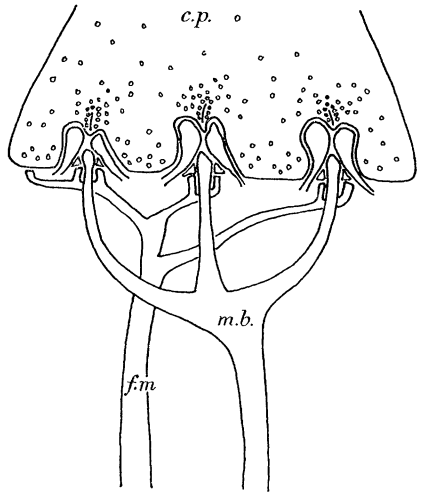


FIGURE 99. Diagram to illustrate that one kind of midget bipolar (*m.b.*) forms the central process of each of the invaginations into a cone pedicle (*c.p.*), while another midget bipolar (*f.m.*) makes only surface contacts onto the same cone pedicle base. The cone pedicle drawn is about 9 μm in diameter and would, therefore, contain about 25 triads; only three have been shown here (and clearly the diagram only be can approximately to scale). Each invaginating midget bipolar (*m.b.*) would, therefore, have as many contacts with the cone pedicle as there are triads. The flat midget bipolar (*f.m.*) has at least twice that number, and the points of contact are mostly on parts of the cone pedicle base between the points of entry of the invaginating midget bipolar processes and the horizontal cell processes. The lateral processes in the triads are of horizontal cells.

they may occasionally make contact at some distance from a triad. The apical processes of the flat midget are smaller in diameter than the conventional midgets, i.e. about 0·1 μm as compared with about 0·2 μm for invaginating midget processes.

Following discovery of the flat midget bipolar by electron microscopy, we tried to see if the two types of midget bipolar can be recognized by light microscopy. In both new material and that used for the preceding paper this has been possible; and from examination of over 300 cells at least one in every three midget bipolars could be identified as a flat midget bipolar. Figure 105, plate 45, shows a light micrograph of an invaginating midget bipolar. The dendritic terminal contains clearly defined apical processes. The cell body lies high in the inner nuclear layer and the axon passes straight down to terminate in the lower portion of the inner plexiform layer. By comparison, figure 106 shows a flat midget

bipolar situated within 500 μm of the invaginating midget of figure 105. The cell body lies lower in the inner nuclear layer and its longer dendrite passes up to the outer plexiform layer to form a flattened dendritic terminal. Individual apical processes cannot be resolved. The axon passes down to end just within the inner plexiform layer at a much higher level than the axon terminal of the conventional midget bipolar.

The shape of the dendritic terminal is the most obvious difference between the invaginating and the flat midget bipolars, see figures 107 to 112. Figure 107 is an invaginating midget bipolar (as are those of figure 15, plate 34, and figures 24 to 26, plate 35), and six apical processes can be distinguished in one plane of focus. Figures 108 and 109, plate 45, are of flat midget bipolars and show the flattened shape of the dendritic terminals. The main dendrite often branches at a lower level in the outer plexiform layer than does the main dendrite of the invaginating midget bipolar, and the subbranches all pass up vertically or obliquely to form a flattened or dome-shaped aggregation of processes that synapse with the same cone pedicle (figures 108 and 109). Electron microscopy shows that the branches subdivide into many small apical processes that turn to run horizontally under the cone pedicle. Individual apical processes can only rarely be distinguished by light microscopy. Electron microscopy of a flat midget bipolar, however, shows that there are about twice as many apical processes when compared with the processes on the invaginating midget bipolar. Also they are of a finer diameter. Thus the appearance of the terminal of a flat midget bipolar as a single mass under the light microscope is not surprising. Figures 111 and 112, plate 45, show different focusses of two cells, an invaginating midget bipolar and a flat midget bipolar, lying 5 μm from each other. In one plane of focus (figure 111) the invaginating midget dendritic terminal is clearly defined, and consists of distinct apical processes each of which corresponds to the central element of the triad in size (0·2 μm). Some of the apical processes (e.g. to the left of the arrow, figure 111, plate 45) subdivide, suggesting that they pass to two closely neighbouring triads, a fact often observed by electron microscopy. In the other plane of focus the flat midget terminal is to be seen and it appears as a solid mass with a few distinguishable horizontally running processes. In figures 107 and 111 part of the cell body of the invaginating midget bipolar is to be seen, whereas in none of the photomicrographs of the flat midget is it visible at the same level, again showing that the cell body of this type of midget lies lower in the inner nuclear layer for this type of cell. Figure 8, plate 34, of the main paper shows a typical flat midget bipolar cell at magnification $\times 800$.

The differences between the invaginating midget bipolar and the flat midget bipolar are summarized in figure 99, which is a diagram combining the electron microscope and light microscope findings just described.

The discovery of the flat midget bipolar raises the important question of whether some or all cones connect with more than one midget bipolar cell. On a few occasions we have observed by light microscopy two stained midget bipolars that overlap to such a degree that they are almost certainly innervating the same cone pedicle (figure 110, plate 45, and figure 11, plate 34). It is difficult to decide in such cases whether one cell is an invaginating midget bipolar and the other a flat midget bipolar, but this seems to be the likely inference. The different levels of the cell body and axon terminations (see figure 11, plate 34) are suggestive evidence that these are in fact an invaginating and a flat midget bipolar

contacting the same cone pedicle. The evidence is that there is no type of bipolar other than the invaginating midget that extends processes into the invaginations of the cone pedicle. Therefore, every cone pedicle in the primate must be connected to a conventional midget bipolar, but at present, we can only say with certainty that some of the cones

Description of plate 45

All the illustrations on this plate are from the retinae of rhesus monkey.

Figure 101. Electron micrograph of a portion of a cone pedicle showing the arrangement of the triads with associated synaptic ribbons and synaptic vesicles. Processes making superficial contacts are arrowed. Osmium-tetroxide fixation. × 22800.

Figure 102. Electron micrograph of a triad with a central process from an invaginating midget bipolar impregnated with Golgi stain. Golgi rapid triple impregnation method (Stell 1965*a*). × 22800.

Figure 103. Electron micrograph of a triad with the superficial contacts from apical dendrites of a flat midget bipolar impregnated with Golgi stain. The processes lie on either side of a process of an invaginating midget bipolar. Golgi rapid triple impregnation method (Stell 1965*a*). × 49000.

Figure 104. Electron micrograph of two triads and with Golgi-impregnated superficial contacts from a flat midget bipolar. Compare with figure 101. The arrowed stained processes correspond to the arrowed processes in figure 101. Golgi rapid triple impregnation method (Stell 1965*a*). × 24600.

Figure 105. Invaginating midget bipolar cell. The apical dendrite is approximately 6 μm in diameter. The cell was between 1·0 and 1·5 mm from the centre of the foveal pit. Golgi–Colonnier staining. × 1700.

Figure 106. Flat midget bipolar cell. The apical dendrite is approximately 6 μm in diameter and the cell was between 1·0 and 1·5 mm from the centre of the foveal pit. Golgi–Colonnier method. × 1700.

Figure 107. Dendritic terminal of an invaginating midget bipolar, showing the small distinct apical processes. Note the cell body is visible. Golgi–Colonnier. 1·0 to 1·5 mm from the foveal pit. × 3000.

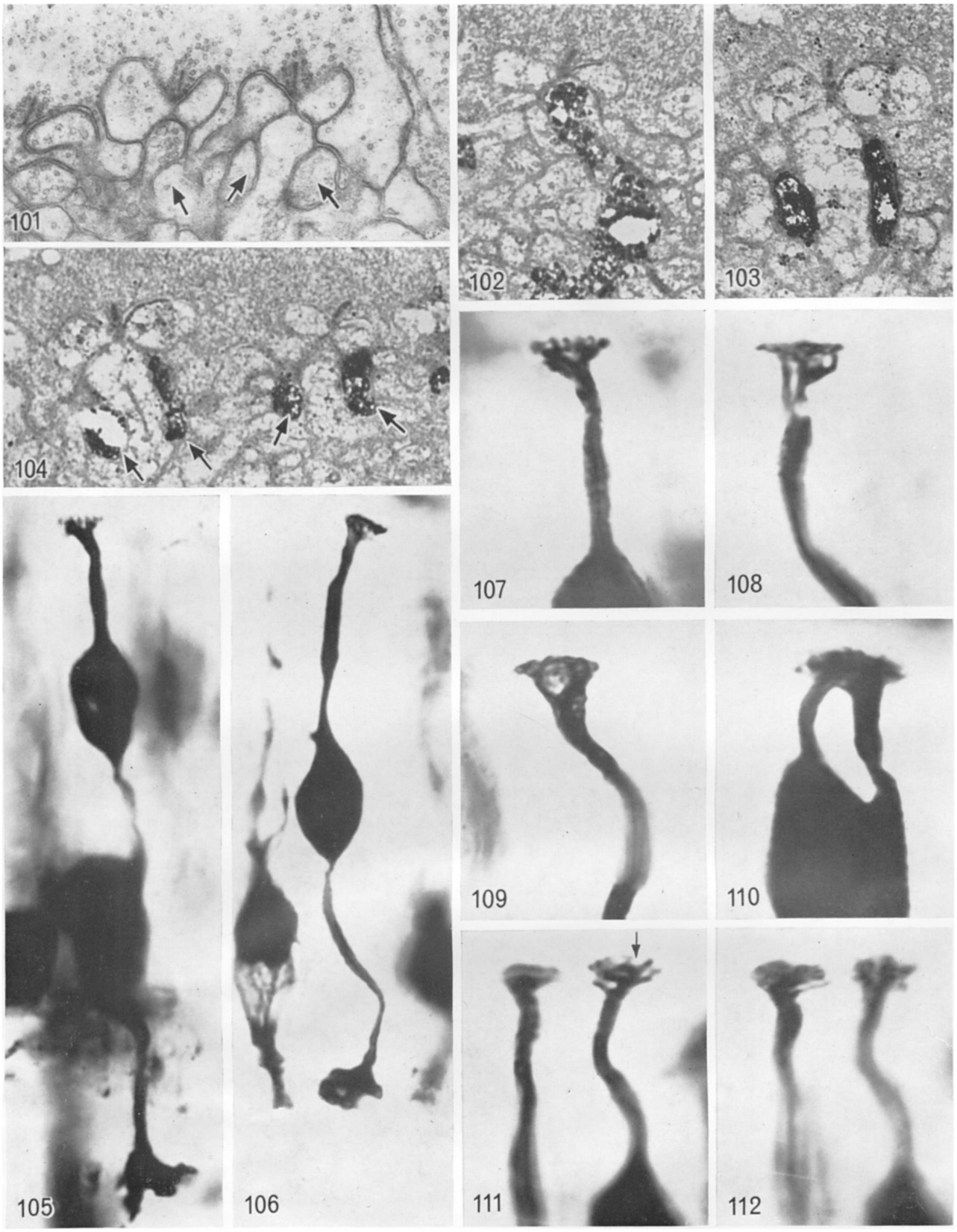
Figure 108. Dendritic terminal of a flat midget bipolar; its top arranged in line with figure 107 the perikaryon is not visible. Golgi–Colonnier method. × 3000.

Figure 109. Dendritic terminal of a flat midget bipolar lying within 1·0 mm of the foveal pit. Golgi rapid triple impregnation method (Stell 1965*a*). × 3000.

Figure 110. Two midget bipolars overlapping to such an extent that they must be innervating the same cone pedicle. Note the cell body of the one bipolar lies high and suggests that this one is an invaginating midget bipolar while the other one may be the flat midget bipolar type. This is an enlargement of the cells shown in figure 11, plate 34, of the main paper. Golgi–Colonnier method. × 3000.

Figure 111. An invaginating midget bipolar is in focus in this photo-micrograph while the neighbouring flat midget bipolar is out of focus. Note the distinct apical dendrites on the terminal and the branching into two of one of the processes to the left of the arrow. The view is slightly oblique. Golgi rapid triple impregnation method. × 3000.

Figure 112. The same field as the previous picture but the flat midget bipolar is now in focus. The cells are separated by 3 to 4 μm. Note the dense flat appearance of the dendritic terminal of this cell due to the lack of resolution of the processes. The cells are from within 1·0 mm of the foveal pit. Golgi rapid triple impregnation method. × 3000.



(*Facing p.* 180)

connect with the two types of midget bipolar cell. Whether all cones have such an arrangement or whether some cone pedicles connect with more than one flat midget bipolar cannot be decided at the present time. The different levels at which the axons of the two types of midget bipolars terminate in the inner plexiform layer may have some significance. Polyak (1941) noticed this and stated that the number of midgets with short axons was equal to the number with long axons but made no distinction of cell types in this observation. The two types of midget bipolar may be contacting two different types of ganglion cell, although midget ganglion cells whose dendritic trees end at a high level or a low level in the inner plexiform layer appear to be otherwise identical.

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