BASAL JUNCTIONS AT SYNAPTIC ENDINGS OF TURTLE VISUAL CELLS

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It has been often assumed that the first synapse of the visual pathway is confined to the region where the visual cell ending is indented by processes of other retinal elements (4, 9, 15), identified as horizontal and bipolar cells (11, 16). In the vicinity of the indented area, the visual cells contain small vesicles similar to those found at other synapses (3, 13, 14), and dense lamellae are conspicuously placed between the branches of the indenting processes (9). This recessed junction has received considerable attention in the past, but recently the existence of other junctional areas between visual cells and second order neurons has been suggested in the primate and frog retinas (6, 7, 11). In those instances junctions were found at the basal surface of cone pedicles, and structures interpreted as filaments extending between both cell membranes were noted in the frog retina (6).

During the course of previous work on toad and rat retinas, I have also occasionally noticed the presence of opaque cross-bars in the intercellular gaps surrounding visual cell endings. These structures did not seem to be located within the area of the recessed junction, but the complex architecture of the toad and rat retinas made this interpretation

uncertain. A more favorable material is provided by the retina of the turtle, *Pseudemys elegans*, because of the simpler pattern of organization of its outer synaptic layer.

Most visual cells in the turtle retina are single and double cones; some visual cells which lack an oil droplet are likely to be rods (18). Since the synaptic endings of the rod cells have not been as yet identified, no further reference will be made to the possible duplex nature of the turtle retina.

The synaptic endings of turtle visual cells are bulky pedicles, about 5–6 μ in diameter, which lodge several branched terminals—each of them typically related to a synaptic lamella (Fig. 1). The basal (vitread) surface of the pedicles is concave, and makes contact with the tips of many fine cell processes (Figs. 1 and 2). The junctional nature of these contacts is immediately apparent, since the intervening gaps have a very regular width (about 160 A), and the cell membranes are underlined by a layer of opaque cytoplasm (Figs. 1, 2, and 3). These junctions, to be called basal junctions, occupy most of the basal surface of the pedicles; their location relative to the recessed type of junction can be seen in Fig. 2.

The symmetric layers of opaque material are the only cytoplasmic differentiations seen on either side of the basal junctions. Underlying the visual cell membrane there are sometimes focal accumulations of opaque cytoplasm, which resemble those found along presynaptic membranes at cerebral synapses (8). Although a few synaptic vesicles are present near the basal surface of the visual cell ending, they are never clustered close to the plasma membrane (6, 7) (Figs. 2 and 3).

Transverse sections of the basal junctions reveal the presence of an opaque substance within the intercellular gaps (Figs. 2 and 3). In suitably oriented sections, this substance appears as opaque cross-bars spanning the gap (Fig. 4). The cross-bars are regularly spaced (repeating period about 190 A), and appear slightly denser and thicker at the midpoint between the junctional membranes (Fig. 4).

Similar cross-bars are observed at septate junctions between invertebrate epithelial cells (1, 2, 12, 19, 20). In tangential section, these junctions show a hexagonal lattice interpreted as the frontal view of the gap substance (1, 10, 19). Lattice patterns are occasionally seen also at the region of the basal junctions, but here they appear to be formed by two sets of parallel lines intersecting at right angles (Figs. 5 and 6). The present evidence does not indicate whether this grid is located within the thickness of the gap, in the plane of the junctional membranes, or within the opaque material underlining the membranes. Since the spacing between parallel lines is the same as that between cross-bars, it seems likely that the grid reflects the organization of the gap substance.

The basal junctions link each pedicle to hundreds of cell processes. The identity of these processes has not been established and, therefore, little can be said about the functional role of the junctions. Their resemblance to invertebrate septate junctions may be of significance, since septate junctions are thought to be responsible for electrical coupling between epithelial cells (1, 19). Also of interest is the similarity of the basal junctions to cerebral axodendritic synapses, where the presence of cross-bars within the clefts has been reported (5, 17). In this instance, however, the observations have been limited to transverse sections of the synapses, and the similarity may be only superficial. One clear difference is that the axodendritic synapses display clusters of vesicles near the presynaptic membrane (8), while this feature is absent at the basal junctions of the visual cells.

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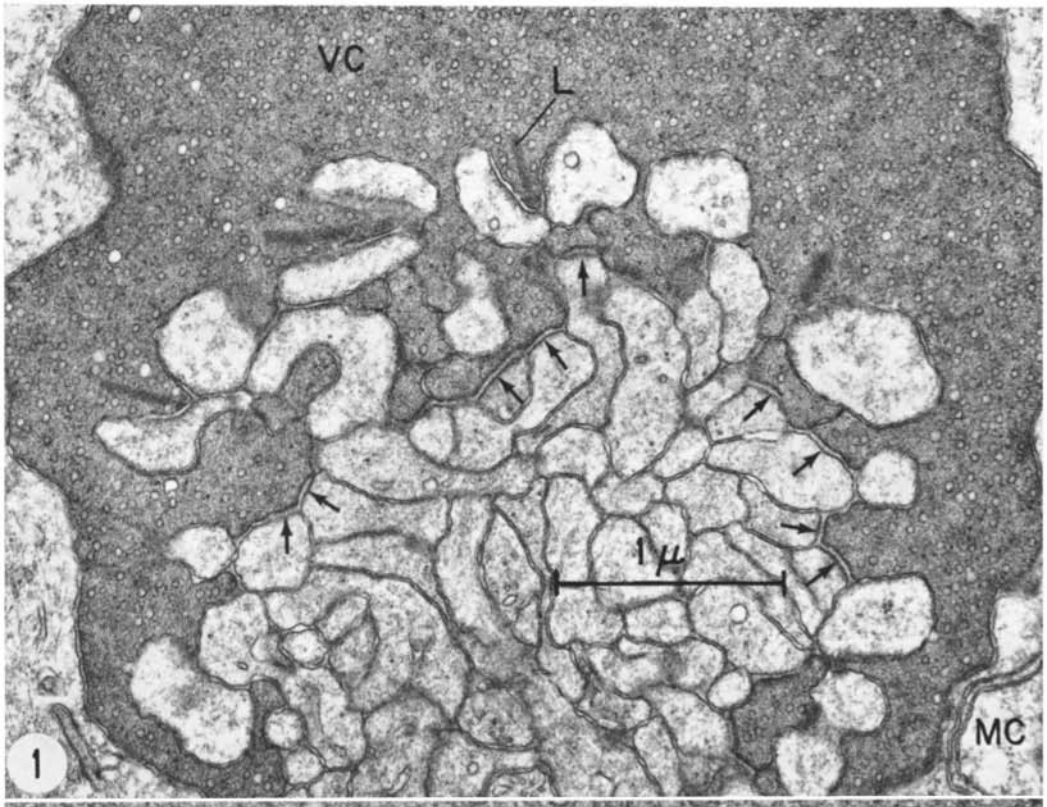
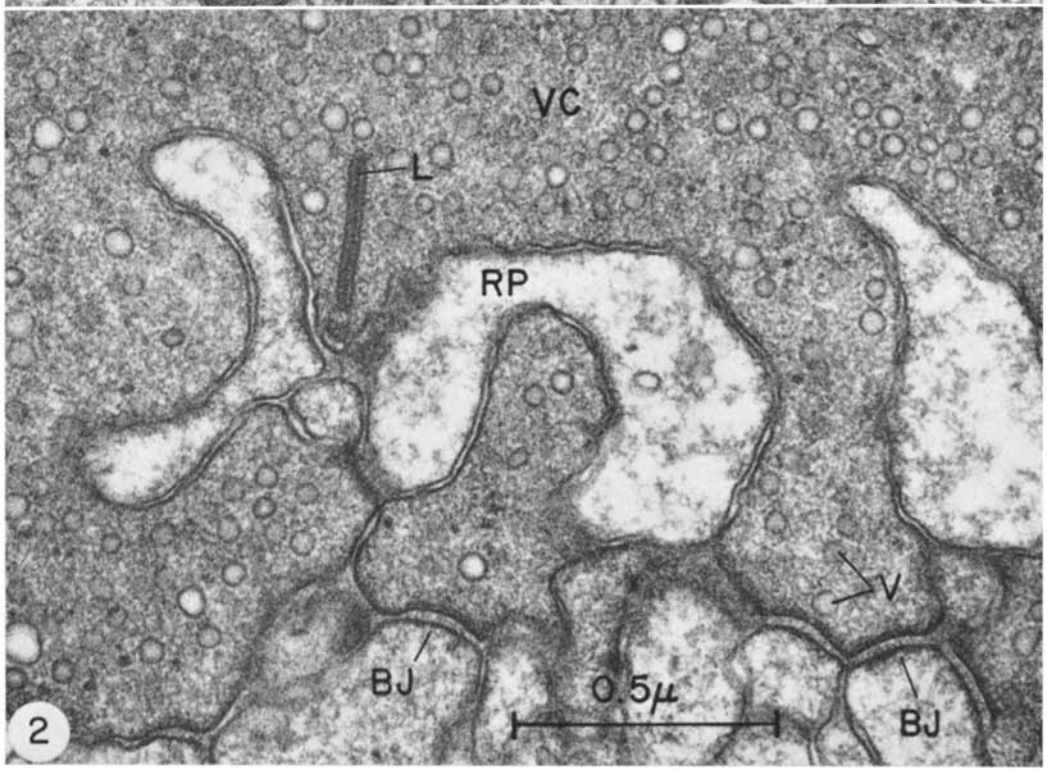
FIGURE 1 Electron micrograph of the synaptic ending of a turtle visual cell (*VC*). The arrows point to the basal junctions. Synaptic lamellae (*L*) mark the recessed junctions. *MC*, Müller cell processes. Fixed overnight in cold 2% glutaraldehyde in 0.1 M phosphate buffer (pH 7.5), and postfixed for 1 hr in 1% OsO_4 in the same buffer. The blocks were stained in buffered uranyl acetate, dehydrated in ethanol, and embedded in Epon. Section stained with uranyl acetate and lead citrate. × 30,000

FIGURE 2 Several basal junctions (*BJ*) are seen at the vitread surface of a visual cell pedicle (*VC*). The junctional gaps are occupied by an opaque material. A recessed junction is indicated by a synaptic lamella (*L*) between two cell processes (*RP*) lodged within an invagination of the pedicle. *V*, synaptic vesicles. Fixed and stained as for Fig. 1. × 70,000


VC
L
1 μ
MC
1


VC
L
RP
V
BJ
0.5μ
BJ
2

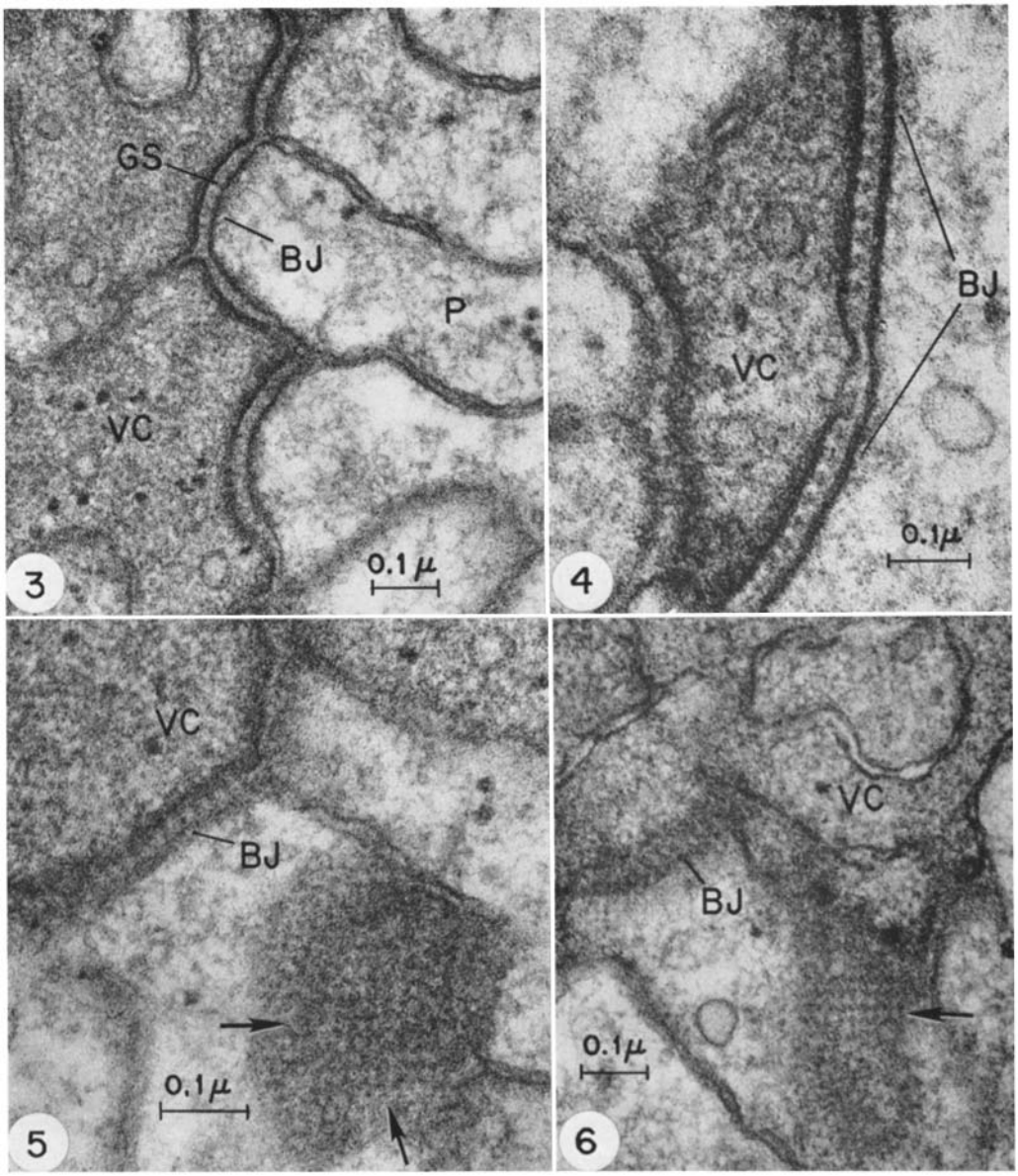


FIGURE 3 Several basal junctions (*BJ*) between a visual cell ending (*VC*) and the tips of fine cell processes (*P*). The junctional membranes are underlined by symmetrical layers of opaque cytoplasm, and the gap is occupied by an opaque substance (*GS*). No clusters of synaptic vesicles are observed near the junctions. Fixed and processed as for Fig. 1, except that staining of the block was omitted. × 90,000

FIGURE 4 Transverse section of a basal junction (*BJ*). Opaque cross-bars are seen spanning the intercellular gap. *VC*, visual cell ending. Fixed and stained as for Fig. 3. × 160,000

FIGURES 5 and 6 Lattice patterns (arrows) at the region of the basal junctions. Some basal junctions are seen in transverse or oblique section (*BJ*). *VC*, visual cell endings. Fixed and stained as for Fig. 3. Fig. 5, × 120,000. Fig. 6, × 90,000

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