to stimulation of the nondeprived eye fall into group 5; and neurons equally responsive to stimulation of either eye fall into group 3. Cells in groups 2 and 4 are binocular but their responses are dominated by either the deprived or the open eye, respectively. In addition, each neuron was assessed qualitatively for orientation selectivity. "Selective" neurons were defined operationally as those that did not respond to a nonpreferred orientation; "biased" neurons responded to all orientations, but the response to the nonpreferred orientation was detectably weaker than the response to the preferred orientation; "aspecific" neurons responded to all orientations without any clear preference. See also W. Singer, *Exp. Brain Res.* **47**, 209 (1982).

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Conduction Velocity Variations Minimize Conduction Time Differences Among Retinal Ganglion Cell Axons

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The visual system is able to accurately represent the spatiotemporal relations among the elements of a changing visual scene as the image moves across the retinal surface. This precise spatiotemporal mapping occurs despite great variability in retinal position and conduction velocity even among retinal ganglion cells of the same physiological class—a variability that would seem to reduce the precision with which spatiotemporal information can be transmitted to central visual areas. There was a strong negative relation between the intraretinal and extraretinal conduction time for axons of individual ganglion cells of the X-cell class. The effect of this relation was to produce a nearly constant total transmission time between the soma of a retinal X cell and its central target site. Thus, the variation in the conduction velocities of retinal ganglion cell axons may ensure that, regardless of the constraints imposed by retinal topography, a precise spatiotemporal central representation of the retinal image is maintained.

OUR VISUAL SYSTEM ENABLES US TO perceive both the spatial and temporal aspects of a constantly changing visual world. The temporal relationships between the elements of a moving retinal image, therefore, must be preserved in the central structures responsible for visual perception. These relationships are maintained despite a number of sources of variability that can obscure the timing between retinal ganglion cell signals in the pathway from the retina to central visual areas. Two primary factors influence the time that it takes the signal from a retinal ganglion cell to reach its central target—the cell's axonal conduction velocity and position in the retina. The axons of retinal ganglion cells comprise two segments. These axons are unmyelinated as they course across the retina from the cell soma to the optic disk; at the optic disk they are invested with myelin and leave the retina to form the optic nerve. Conduction velocity is quite slow in the intraretinal, unmyelinated segment of the axon and increases considerably in the myelinated extraretinal segment. In the cat, there are a number of classes of ganglion cells (*1–4*) but, even within a single physiological class, there is a wide range of axonal conduction velocities both within the retina and in the optic nerve and tract (*4–6*). Because of the slow intraretinal conduction velocities of these cells, the distance between a ganglion cell and the optic disk greatly influences the time required for the signal from that cell to travel across the surface of the retina. Intraretinal conduction time is also a function of the position of a retinal ganglion cell relative to the area centralis. Conduction velocity within the retina is a function of axon caliber (*7*), which increases with retinal eccentricity (distance from the area centralis). These sources of variability lead to an apparent paradox. How is the visual system able to encode spatiotemporal information, the precise direction of movement of an object, for instance, when variations in axonal conduction velocity, and differences in retinal location, can apparently obscure the temporal relationships among ganglion cell signals in the pathway from the retina to the central visual areas of the brain?

To answer this question, we have analyzed the conduction characteristics of a sample of retinal ganglion cell axons from the cat in vivo. All of these data were obtained from retinal X cells, the ganglion cells in the cat that have, among other physiological characteristics, small receptive fields, predominantly linear spatial summation of visual stimuli, and a sustained response to standing contrast (*8, 9*). After we had investigated their physiological properties with an intraretinal microelectrode, these cells were intracellularly injected with horseradish peroxidase (HRP) and were found to have the morphological characteristics ascribed to the anatomically recog-

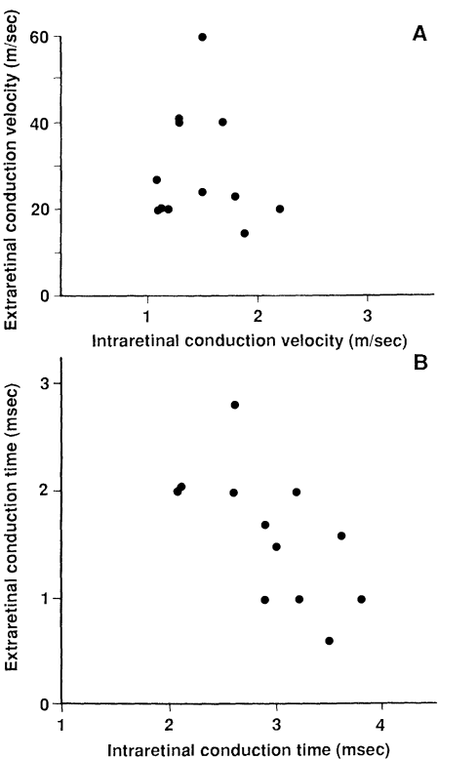

Fig. 1. (**A**) Conduction velocity across the retinal surface (intraretinal conduction velocity) plotted as a function of conduction velocity within the optic nerve and tract (extraretinal conduction velocity) for twelve retinal X-cell axons. There was no obvious relation between these two measures. (**B**) The relation between intraretinal conduction time and extraretinal conduction time for the same X-cell axons as in (A). There is a negative relation ($r = -0.62$, $P < 0.013$) between the time that it takes an action potential to travel across the surface of the retina and the time in which that same signal travels through the optic tract.

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nized β cells (*1*). β Cells in the cat have medium-sized somata and axons and small, densely branched dendritic arbors. The details of the physiological preparation, anesthesia, and anatomical analyses are described in (*4*).

For twelve retinal X cells from nine cats we were able to achieve antidromic activation of their projection axons from two stimulating sites: at the optic chiasm and at a site in the optic tract below the dorsal lateral geniculate nucleus (LGN_d) of either the contralateral or ipsilateral side. The depth of the optic chiasm electrodes was chosen by recording the potential evoked by the flash of a strobe light into the eyes. The electrodes were cemented in place at the depth that produced the strongest evoked response. The two pairs of optic tract electrodes were cemented in place at the depth that produced the maximum short latency (≤0.5 msec) response evoked by electrical stimulation of the optic chiasm electrodes. The three pairs of stimulating electrodes were then cemented together, as a unit, on the surface of the skull. This allowed us to measure the distance between the stimulating electrodes, after perfusion of the animal, while still maintaining the spatial relationships among the three electrode pairs as they had been during the recording session. Since each ganglion cell was injected with HRP, we could also measure the distance of the cell from the optic disk. Because the conduction velocities of ganglion cell axons within the retina are very slow, this measurement was critical to ensure the accuracy of the subsequent calculations. The distance and latency measurements were used to calculate both the intraretinal and extraretinal conduction velocities for each of the X cells and the conduction time through both the myelinated and unmyelinated segment of each axon. In all of these analyses we considered the distance from the optic chiasm to the LGN_d to be 19 mm (from our measurements in a number of animals) and the distance between the optic chiasm and the optic disk to be 21 mm (*10*). These distances probably underestimate the total axonal conduction time to the LGN_d, because the axons of retinal ganglion cells do not follow a straight course from the optic chiasm to the LGN_d. Because it was impossible to predict the exact course of any single axon, however, no attempt was made to correct for this error. There is no evidence that would suggest that the underestimation should affect some cells in our sample more than others. Also, these measures do not take into account any change in conduction velocity that may occur after the axon branches to form its terminal arbor in the LGN_d.

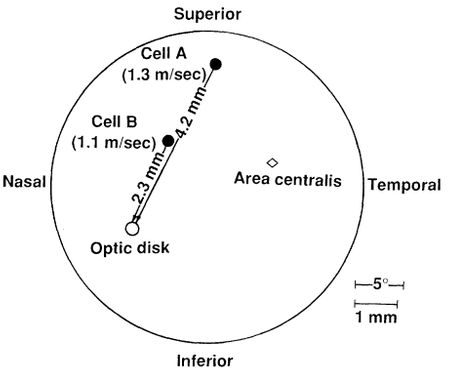

Fig. 2. Schematic representation of the positions of two labeled X cells relative to the area centralis and the optic disk. The scale of this drawing, both in degrees of visual angle and in distance along the retinal surface, is at the lower right. Both of these ganglion cells were injected at similar retinal eccentricities and had similar intraretinal conduction velocities (intraretinal conduction velocity is a function of axon size, which increases with increasing distance from the area centralis). Cell A (11.9° eccentricity; intraretinal conduction velocity, 1.3 m/sec), located 4.2 mm from the optic disk, had an intraretinal conduction time of 3.2 msec. The signal from cell B (10.8° from the area centralis; intraretinal conduction velocity, 1.1 m/sec), because it was only slightly more than half as far from the optic disk, took only 2.1 msec to travel across the surface of the retina. Cell A had an extraretinal conduction velocity of 40 m/sec (total conduction time, 4.2 msec); cell B traveled at a rate of only 20 m/sec after leaving the retina (total conduction time, 4.1 msec).

The largest cat retinal ganglion cells have, on average, the largest axons and the fastest axonal conduction velocities, and, within any class of cat retinal ganglion cell, conduction velocity decreases as soma size and axon caliber decrease (*7*). Because it seemed reasonable to assume that the relation between soma size, axon size, and axonal conduction velocity is maintained in the optic nerve and tract, we were surprised to find no obvious relation between extraretinal and intraretinal conduction velocity among our sample of labeled X cells (Fig. 1A). Because we had a reasonably accurate measure of the distance that an action potential traveled in both the intraretinal and extraretinal segments of these axons, we determined the degree of correlation between the conduction time within the retina and the conduction time within the optic nerve and tract. The relation between intraretinal and extraretinal conduction time for each retinal X cell was much higher ($r = -0.62$; $P < 0.013$) than that for conduction velocity alone (Fig. 1B). Thus, if the signal from any individual retinal X cell takes a relatively long time to travel across the retinal surface (in the unmyelinated axon segment), the time that it takes to conduct the signal through the myelinated segment (the optic nerve and tract) is proportionately shorter. This results in little cell-to-cell variability in the total axonal conduction time within this sample of projection neurons (mean total conduction time, 4.56 msec; SD, 0.52 msec).

An example of the temporal compensation we have described here (and an illustration of the complexity of the interactions between retinal topography and the morphological and physiological characteristics of individual retinal ganglion cells) is shown in Fig. 2. Other data obtained in these experiments showed that the morphological dimensions of retinal X cells (including axon diameter) increase in size with increasing distance from the area centralis. As mentioned above, conduction velocity in the unmyelinated segment of these axons is a function of axon caliber (*7*). The intraretinal conduction velocity of cat retinal ganglion cells, therefore, increases with increasing retinal eccentricity. However, the time that an action potential takes to reach the optic tract is a function not only of the conduction velocity of the axon but also of the distance of the retinal ganglion cell from the optic disk.

Because the area centralis in the cat retina is located temporal and superior to the optic disk, it is possible for two retinal ganglion cells at similar distances from the area centralis (and therefore similar axon diameters) to be located at significantly different distances from the optic disk (Fig. 2). We labeled two retinal X cells at comparable distances from the area centralis (11.9° and 10.8°) that had similar intraretinal conduction velocities (1.3 and 1.1 m/sec, respectively). Both of these X cells were located in the nasal hemifield, but one X cell (cell A) was injected 5.5° nasal and 10.5° superior to the area centralis; it was positioned, therefore, 4.2 mm from the optic disk. The other X cell (cell B) was 10.5° nasal and 2.5° superior to the area centralis. This cell was only 2.3 mm from the optic disk. Since the two retinal X cells had comparable intraretinal conduction velocities, the difference in retinal position resulted in a substantial difference in intraretinal conduction time between the two cells. An action potential generated at the axon hillock of cell A took 3.2 msec to travel across the surface of the retina; the intraretinal conduction time for cell B was only 2.1 msec. We found, however, that the conduction velocity within the optic tract of cell A was 40 m/sec (extraretinal conduction time, 1.0 msec), while the extraretinal conduction velocity of cell B was 20 m/sec (extraretinal conduction time, 2.0 msec). The complementary intraretinal and extraretinal conduction times of these two retinal ganglion cells resulted in the signal from both cell A and cell B having similar total conduction times between their somata

and the LGN_d (4.2 msec for the cell at 11.9° eccentricity and 4.1 msec for the cell at 10.8° eccentricity). This finding suggests that the variability in conduction velocities between cat retinal ganglion cells may have a functional basis; the variability may reflect a mechanism that ensures that visual signals arising from different areas of the retina reach their central target nuclei (in the case of X cells, primarily the LGN_d) in the same amount of time. The result, therefore, is a characteristic latency for all of the visual input arriving at the LGN_d through the X-cell pathway.

By recording simultaneously in the retina and the LGN_d, Cleland *et al.* (*11*) showed that there were latency differences in the input to the LGN_d among different classes of cat retinal ganglion cells. The mean latency between an action potential recorded in the retina and one recorded in a postsynaptic LGN_d sustained (X) cell was approximately 4.8 msec (*12*). These results are in reasonable agreement with ours when one considers that their mean latency also included the synaptic delay between the retinal ganglion cell axon and the generation of an action potential in the postsynaptic LGN_d neuron. The range of X-cell latencies that they reported was larger than ours, but this difference could be due to a number of factors. For example, their retinal recordings were obtained both from ganglion cell somata and, in some instances, from ganglion cell axons between the soma and the optic disk. The postsynaptic "jitter" that occurs in the responses of LGN_d neurons to electrical stimulation of their retinal afferents (*13*) would also increase the variability in the latencies reported by these investigators.

Our data pertain only to one (the X-cell pathway) of a number of parallel information streams between the retina and the visual areas of the central nervous system (*8*). For each of the physiological types of retinal ganglion cell, there may be a characteristic latency such as we have demonstrated for retinal X cells.

Since visual perception is a function that is presumed to occur at a central site or sites that do not receive direct retinal input, it is difficult to predict the degree of spatiotemporal precision necessary to accomplish these higher order visual functions in the central visual pathways beyond the LGN_d. Nor can we determine if, in fact, the temporal relations between retinal ganglion cell signals described here are preserved as this information is relayed along more central pathways. A scheme of retinal organization in which each pathway has a characteristic conduction time, however, could provide two relevant aspects of the timing of the visual signals relayed by retinal ganglion cells—the temporal relation among the responses of different cells in the same pathway to a changing stimulus and, on a larger scale, the relations among the visual signals from two or more parallel pathways. The maintenance of these temporal relations, both within and among these parallel information channels, may be necessary for maintaining an accurate central representation of the spatiotemporal aspects of a visual scene.

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Heritability at the Species Level: Analysis of Geographic Ranges of Cretaceous Mollusks

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Geographic range has been regarded as a property of species rather than of individuals and thus as a potential factor in macroevolutionary processes. Species durations in Late Cretaceous mollusks exhibit statistically significant positive relationships with geographic range, and the attainment of a typical frequency distribution of geographic ranges in the cohort of species that originated just before the end-Cretaceous extinction indicates that species duration is the dependent variable. The strong relation between geographic ranges in pairs of closely related species indicates that the trait is, in effect, heritable at the species level. The significant heritabilities strengthen claims for processes of evolution by species-level selection, and for differential survivorship of organismic-level traits owing to extinction and origination processes operating at higher levels.

EVOLUTION BY NATURAL SELECTION can occur at any level of biological organization if three prerequisites are satisfied: for a given focal level within the hierarchy, a trait must exhibit variation, its interaction with the environment must result in differential birth or death, and the trait must be heritable, that is, offspring must significantly resemble parents for the trait in question (*1, 2*). Evolutionary research has focused primarily on the level of individuals within populations, but recently a number of authors (*1–3*) have suggested that certain traits, such as geographic range or genetic population structure, can be regarded as species-level properties subject to processes of selection and drift at that level as well (*4*). For Late Cretaceous mollusks, geographic range does meet all three prerequisites for evolution under selection: there is variation among species that gives rise to differential species survivorship, and that variation is heritable (as defined above) at the species level.

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The Gulf and Atlantic Coastal Plain of North America contains one of the most diverse and best-preserved molluscan faunas of the latest Cretaceous (Campanian-Maestrichtian stages). Geographic ranges and temporal durations of bivalve and gastropod species were calculated on the basis of my own and museum collections and the published literature with a series of 2 million year (m.y.) increments within the last 16 m.y. of Late Cretaceous marine deposition; species distributions were mapped on the approximately 5000-km discontinuous outcrop belt to a precision of ±20 km (*5, 6*). Sampling is inevitably incomplete, and so recorded geographic ranges should be regarded as proportional to original distributions rather than as absolute and complete measurements (*5*). Species pairs used in heritability analysis were delineated primarily on the basis of cladistic assessment of published statements (*7*) regarding evolutionary relationships. Not all speciation events are recognizable in the fossil record, but the necessary use of species distinguishable on the basis of observable morphology