The primate retina contains two types of ganglion cells, with high and low contrast sensitivity

(spatial vision/visual neurons/macaque monkey)

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ABSTRACT Previously, we discovered that the broad-band cells in the two magnocellular (large cell) layers of the monkey lateral geniculate nucleus (LGN) are much more sensitive to luminance contrast than are the color-sensitive cells in the four parvocellular (small cell) layers. We now report that this large difference in contrast sensitivity is due not to LGN circuitry but to differences in sensitivity of the retinal ganglion cells that provide excitatory synaptic input to the LGN neurons. This means that the parallel analysis of color and luminance in the visual scene begins in the retina, probably at a retinal site distal to the ganglion cells.

Contrast is an important characteristic of the visual world. It is the physical quantity that specifies the relative variation in luminance of a visual stimulus compared to its average level. The visibility and brightness of objects depend mainly on the contrast with their background. Previously, we have related the sensitivity for contrast to the functional significance of the organization of the monkey's lateral geniculate nucleus (LGN) into cellular layers: four dorsal layers of small cells (parvocellular) and two ventral layers of large cells (magnocellular). The contrast gain of cells in the magnocellular layers is about 10 times higher than that of the cells in the parvocellular layers (1, 2). This observation has been confirmed by several other investigators (3–8). Here we report that the monkey retina contains two types of ganglion cells, one with high and the other with low luminance-contrast sensitivity. The high contrast sensitivity type projects to the magnocellular layers, and the low-sensitivity type projects to the parvocellular layers. Thus, it is the retina, and not the pattern of connectivity within the LGN, that is responsible for the large difference in contrast gain between parvocellular and magnocellular geniculate neurons.

METHOD

We recorded in the LGN, with one electrode, the activity of retinal ganglion cells together with that of LGN neurons. Five adult macaque monkeys were used: three *Macaca fascicularis* and two *Macaca mulatta*. No difference was found between the two species. Surgery was performed under ketamine anesthesia, supplemented with intravenous injections of thiamylal (Surital). During the experiment the animals were lightly anesthetized with urethane (20 mg/kg per hr), paralyzed with Flaxedil (5–10 mg/kg per hr), and artificially respired. The eyes were protected with contact lenses and refracted for the viewing distance of 57 cm. Extracellular recordings were performed with saline-filled glass microelectrodes with tips of 2–4 μm and resistance of 10–20 M Ω . The visual stimuli were spots or gratings that were produced electronically on a Tektronix 608 CRT (white P4

phosphor), with a mean luminance of 100 cd/m². The contrast of the stimuli was defined as $(L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}})$, where L_{max} and L_{min} were the maximum and minimum luminances in the stimulus. The electronic visual stimulator (9) was controlled by a computer that accumulated PST histograms of the neural responses and Fourier-analyzed the averaged responses. The location of the cells (in the parvo- or magnocellular layers) was determined by changes in which eye excited the LGN neurons and by electrode depth reading and track reconstruction. Details of the procedure are given in ref. 2.

RESULTS

S Potential Recordings. We recorded S potentials (extracellularly recorded excitatory synaptic potentials) and LGN cell nerve impulses simultaneously. The S potentials are a quantitative index of retinal ganglion cell activity (10–12). It has been proven that the S potentials originate from action potentials fired by ganglion cells (11–13). For most recordings in the monkey's LGN, the S potentials appear to be from a single retinal ganglion cell: they are of approximately fixed amplitude with a fixed latency to electrical stimulation of the optic chiasm, and they do not overlap in time (cf. ref. 12). All of the data reported here were obtained from such unitary recordings. By triggering two comparators, one at the level of the S potential and the other at the level of the LGN spike, we discriminated the two events and studied the responses of the ganglion cell and its LGN target separately. Fig. 1 illustrates the electrical record of a typical pair: unitary S potential and its LGN target cell.

Response-Contrast Functions. We compared the dependence of response amplitude on stimulus contrast for magnocellular-projecting and parvocellular-projecting retinal ganglion cells. Fig. 2 shows the average response-contrast functions obtained from 36 S potentials recorded in the magno- and parvocellular layers of one rhesus monkey. The stimuli in these experiments were sinusoidal gratings near the optimal spatial frequency for each cell, drifting at a constant velocity such that the temporal modulation was at 4 Hz. The contrast ranged from 0.02 to 0.64. The response measure is the amplitude of the sinusoid that best fits the PST histogram (fundamental Fourier component). The response-contrast functions plotted in Fig. 2 were calculated by averaging responses from all units of a given type at each contrast. The average response-contrast function of magnocellular-projecting ganglion cells increases steeply with contrast and begins to saturate at contrasts of ≈ 0.08 –0.1. The responses of parvocellular-projecting ganglion cells increase much more gradually as contrast is increased and do not saturate with the highest contrasts used (0.64).

The slope of the linear portion of these response-contrast functions at low contrast is the contrast gain, the change in

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Abbreviations: LGN, lateral geniculate nucleus; S potential, excitatory synaptic potential.

FIG. 1. Extracellular recording from the monkey LGN. The small, slow potentials are the excitatory synaptic potentials (S potentials) elicited in a LGN cell by nerve impulses in a retinal ganglion cell. The large action potentials are fired by a LGN cell. The lower trace is a segment of a record shown with an expanded time scale. Note that in the lower record, the first LGN spike rises from an S potential.

response amplitude per unit contrast. Contrast sensitivity is the reciprocal of the contrast required to reach a criterion response.* Since the response-contrast functions have no threshold and are linear at low contrast, contrast sensitivity will be proportional to contrast gain. Fig. 2 shows that the magnocellular-projecting ganglion cells have a much higher contrast gain and consequently a much higher contrast sensitivity than the parvocellular-projecting ganglion cells.

Distribution of Contrast Gain. The linear, low contrast portion of the response-contrast function of each cell was fitted with a least-squares best-fitting straight line. The slope of this line is the contrast gain of the cell. Fig. 3 is a histogram of the contrast gains of 55 ganglion cells. They fall into two distinct groups: ganglion cells that terminate on parvocellular cells having a low contrast gain and ganglion cells that go to the magnocellular layers having a high contrast gain (and therefore high contrast sensitivity). There is a distinct gap in the distribution of contrast gains.

The low contrast gain of the cells projecting to the parvocellular layers was *not* caused by the fact that we used white stimuli. This conclusion follows from the results of experiments in which we interposed Wratten color filters between the monitor screen and the monkey's eyes. Red, green, or blue filters were used to make the stimulus spectral energy distribution have approximately the same wavelength peak as the spectral sensitivity of the ganglion cells. In about half of the parvocellular-projecting ganglion cells that were tested with more than one color, the response-contrast curves became somewhat steeper, but the slope remained well below that of the magnocellular responses. In the others there was no change.

The difference in contrast gain cannot be attributed to differences in dynamics between the ganglion cells going to the parvocellular or magnocellular layers. The stimuli used in these experiments were modulated at 4 Hz, close to the optimal temporal frequency for parvocellular neurons but a little below the optimal frequency for magnocellular cells (8).

DISCUSSION

Our results are relevant to an understanding of parallel processing of visual information in the primate. Parallel processing along separate neural channels from retina to

FIG. 2. Average response-contrast functions for 36 S potentials recorded from one rhesus monkey: 28 recorded in the parvocellular layers (●) and 8 recorded in the magnocellular layers (○). The stimulus was a sinusoidal grating of optimal spatial frequency for each cell, drifting at 4 Hz. The error bars are ± 1 SD. The smooth curves are derived from the Michaelis-Menten equation $y = ax/(b + x)$. The half-saturation value (b) was 0.13 for the magnocellular-projecting ganglion cells and 1.74 for the parvocellular-projecting cells.

brain has been found in every vertebrate that has been investigated (14). These visual streams have different functions, cell types, and organization. The two we focus on here—the color-sensitive channel (parvocellular-mediated) and the broad-band channel (magnocellular-mediated)—have been shown in anatomical, physiological, and psychophysical studies to be distinct and separate. In psychophysical experiments, Mullen (15) has found that the contrast sensitivity for chromatic, isoluminance patterns was lower than the one for isochromatic, luminance patterns. Hawken and Parker (5) and Blasdel and Fitzpatrick (6) reported that those cells in the visual cortex of the monkey that receive their input from the magnocellular layers (in layer IVc-alpha) have high contrast sensitivity, whereas those cortical cells receiving their input from the parvocellular layers (in IVc-beta) have low contrast sensitivity. Thus, the separation of the color-sensitive and broad-band channels, which was

FIG. 3. Distribution of the contrast gain (impulses per second/% change in contrast) for 55 ganglion cells from five monkeys. ■, Parvocellular-projecting cells; □, magnocellular-projecting cells.

*Note that this definition of sensitivity differs somewhat from the one used in psychophysics in that this physiological definition does not refer explicitly to signal/noise ratio.

observed originally in the LGN, starts in the retina and extends at least to the primary visual cortex.

The results we report here also explain some recent physiological measurements on the spatial frequency resolution of monkey ganglion cells. Lee *et al.* (16) report that the tonic and phasic monkey ganglion cells (presumably, the parvocellular- and magnocellular-projecting cells, respectively) have similar spatial frequency resolution, even though it is well documented that the tonic cells have smaller receptive fields (17), and previous work on cat visual neurons indicated that spatial frequency resolution is reciprocal to receptive field size (reviewed in ref. 18). The puzzle disappears if one recognizes that the spatial frequency resolving power of a cell depends on the size of its receptive field *and* on the contrast gain of the cell. The higher gain of the phasic cells is enough to account for their high resolution.

Previously, investigators have sorted ganglion cells in the monkey retina into functional groups characterized by the following properties: spectral organization of the cells, time course of response, spatial organization of the receptive field, conduction velocity of axons, and linearity of spatial summation (17, 19–21). Linearity of spatial summation is the same for the S potentials as for their LGN targets. Thus, most magnocellular-projecting ganglion cells sum visual signals in a linear manner, as do almost all parvocellular-projecting ganglion cells (cf. refs. 1, 2, 22, 23). Practically all of the highly sensitive retinal ganglion cells that provide input to the magnocellular layers have broad spectral sensitivity and were probably classified by previous investigators as phasic cells (17, 19–21). Monkey ganglion cells with low contrast sensitivity are either color-opponent or have a narrow-band spectral sensitivity. Probably there is also an anatomical correlation of ganglion cell shape with contrast sensitivity since retinal ganglion cells that project to the parvocellular layers have different morphology from cells that project to the magnocellular layers (24, 25). None of the previous studies of monkey ganglion cells has reported the large difference in contrast sensitivity described here. Consistent with our results, it was found previously that phasic, spectrally broad-band cells had a larger response to a given contrast and had a larger maximum response than tonic cells (19, 20, 26).

The correlation of contrast sensitivity with other cellular properties discussed above suggests that there is a visual, functional significance to the parallel projection from retina to brain. Presumably the high sensitivity ganglion cells function near threshold for isochromatic luminance patterns, and the low sensitivity cells are recruited at higher contrasts,

when the response of the high sensitivity group becomes saturated.

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