lage. Considerable knowledge might be gained about the effect of inflammation on the metabolism of human cartilage proteinpolysaccharides by comparing the amount, chemical composition, and turnover of this new component in normal and inflammatory synovial fluids.

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Direction-Selective Units in Rabbit Retina: Distribution of Preferred Directions

Abstract. *The preferred directions of 102 direction-selective ganglion cells in the rabbit retina have been determined. Cells of the "on-off" type form four nonoverlapping groups; cells of the "on" type fall into three groups. The on-off groups appear to correspond to the directions of apparent object displacement produced by contractions of the four rectus muscles. Each group of cells could, without further processing, provide the error signal for a visual servo-system minimizing retinal image motion.*

The vertebrate retina used to be regarded as a transducer of light into nervous impulses, but it has recently become clear that complex "editing" and selection of features from the retinal image are performed before any impulses are transmitted centrally. Individual nerve cells signal the presence of particular spatiotemporal features of the image, thus performing a primitive pattern-recognition operation. One important feature of the retinal image pattern is its movement, and certain retinal ganglion cells in frogs, rabbits, pigeons, and ground squirrels have been found to signal the direction of image movement (*1*). These cells respond maximally when the image moves in one particular direction, called the "preferred" direction, and not at all when it moves in the opposite, "null," direction.

This asymmetrical response is very striking, and when impulses from a single cell are recorded, the unit can be studied by simply moving a small hand-held target in different directions through the appropriate part of the visual field. The orientation of the preferred-null axis is a characteristic that can be determined in this way, and the distribution of these axes in the population of ganglion cells is of interest, especially since a single "direction-selective" cell could not signal direction of motion without ambiguity.

In the rabbit, these direction-selective cells have been further divided into two groups (*2*). Cells of the more common "on-off" type respond to small stationary light spots flashed in the receptive field with a discharge at both the beginning and the end of the flash. Cells of the second group, the "on" type, respond only at the beginning; they respond to slower movements and there is evidence that their mechanism is different. We report here the distribution of preferred directions of 79 "on-off" and 23 "on" type direction-selective ganglion cells from a total sample of 577 units isolated in the retinas of 21 rabbits. We excluded 48 direction-selective units from this study because they were insufficiently studied or were in the extreme periphery of the visual field.

Microelectrode recordings from ganglion cells, or their axons, were made by recently described methods (*3*). The preferred axis is not perturbed by a moderate amount of aberration (*4*), so it was permissible to use the rabbit's natural pupil to avoid vignetting of peripheral receptive fields by an artificial pupil. Receptive fields were plotted on a uniformly illuminated tangent screen (15 cd/m^2) placed 57 cm from the cornea and roughly normal to the pupillary axis. Since data from a number of animals were to be combined, it was necessary to relate the preferred directions to some observable retinal landmark whose position could be expected to remain fairly constant from animal to animal. For this purpose, we chose the large retinal blood vessels which travel a reasonably straight course over the band of myelinated nerve fibers. Two points on these blood vessels, 20° to 30° on either side of the optic disc, were projected onto the tangent screen with a reversible ophthalmoscope; these points established the reference line to which all data for that animal could be compared. A similar technique was used to determine the orientation of the blood vessels in six unanesthetized, but restrained, animals. The line of blood vessels is not horizontal, but has a mean rotation of $10.7° \pm 2.25°$ ($N = 6$) from the horizontal, with the anterior end lower.

Figure 1 shows the preferred directions of on-off direction-selective units from the superior visual field within 40° of the pupillary axis. The receptive fields have been superimposed and the preferred directions drawn relative to the horizontal and vertical of object space for the normally oriented animal (*5*). The distribution has four lobes, which may be designated anterior (35 units), superior (9), posterior (17), and inferior (18), but the group means are slightly deviated from the horizontal and vertical, especially the posterior group. These conclusions have been verified statistically, and this prompted us to search for an explanation in terms of the use that is made of the direction information provided by these cells.

When a substantial portion of the visual field is moved in one direction, the rabbit shows optokinetic eye movements, whose slow phase follows the stimulus very precisely (*6*). These movements reduce the sweep of the image over the retina, and one thus has evidence of an optical servo-stabilization system. Clearly, the corrective eye movements require error-signals that indicate which direction the image is slipping over the retina, and the on-off direction-selective ganglion cells could serve this function.

In man and many other animals, the superior and inferior rectus muscles

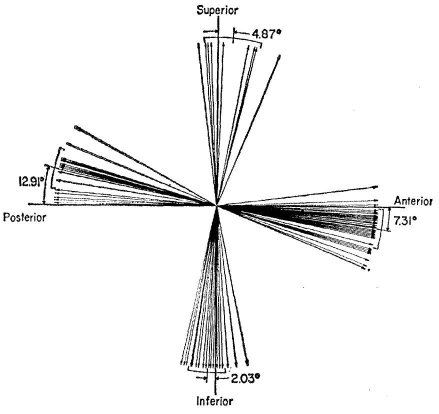

Fig. 1. Distribution of the preferred directions of 79 "on-off" direction-selective units. The axes are the horizontal and vertical in the visual field (*5*). The mean ± one standard deviation is indicated for each group.

produce torsion about the visual axis as well as elevation and depression. The superior and inferior oblique muscles contribute to movement of the visual axis as well as producing torsion, or counteracting the torsion caused by other muscles. In the rabbit, however, the extraocular muscles are arranged in a more straightforward manner; the superior and inferior obliques must produce almost pure torsion around the visual axis, leaving uncomplicated rotations about the other axes to the four rectus muscles. It is tempting to suppose that each of the four orientations of direction-selective units correspond to the directions of image motion that result from contraction of one rectus muscle and the relaxation of its antagonist. If they are correctly aligned, the pattern of neural connections required to minimize image movement would be very simple; the output from, say, the anterior group of direction-selective units should excite the anterior rectus and inhibit the posterior, and the other groups should make the appropriate excitatory and inhibitory connections.

To test this suggestion, we have dissected the rabbit's orbit carefully, and it is indeed true that the anterior and posterior recti insert a little below and above a horizontal line through the pupil. Thus the direction of motion will be twisted relative to the horizontal in the same way as the means of the groups are twisted in Fig. 1. The insertions of the superior and inferior recti are also displaced from the vertical, but it remains to be seen whether the details of the distribution of preferred directions will fit in with this explanation.

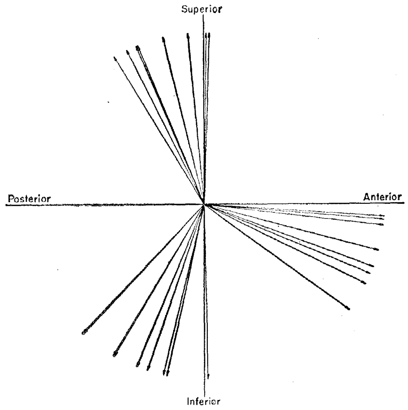

Fig. 2. Preferred directions of 23 "on" type direction-selective units. Other details are the same as Fig. 1.

The "on" type units have been recorded infrequently, and the number is still small. The distribution is shown in Fig. 2, and has an unmistakable tendency toward a three-lobed distribution. Our only comment is that three preferred directions are the minimum required to signal the full range of possible directions of motion. Two preferred directions would not be enough, since movement in the null direction could not be signaled effectively by a further reduction of the low spontaneous discharge of these cells. This distribution certainly makes an additional point of distinction from the "on-off" type (*2*), and it would be particularly interesting to know the central destinations of the information provided by each type.

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Synaptic Noise as a Source of Variability in the Interval between Action Potentials

Abstract. *The source of variability in the interval between action potentials has been identified in a class of cat spinal motoneurons. The observed random fluctuations in membrane potential (synaptic noise) together with an empirical description of spike generation accurately predict the statistical structure of variability observed to occur in the neuron's discharge.*

The marked variability characteristic of most neurons' steady-state output has been of considerable interest (*1*), because it has been believed to add uncertainty to the information transmitted by the neuron and because it may provide clues about the mechanisms underlying the transformation of input to output. Despite considerable investigation, the sources of variability in the interval between action potentials (the interspike interval) have not yet been clearly identified for any type of neuron. One obvious possible source is the haphazard fluctuations in membrane potential (*2*) seen even in the quiescent neuron. The question arises as to whether such input fluctuations (synaptic noise) can account for the output (interspike interval) variability. We have shown that synaptic noise, together with a simple model for spike generation, can indeed account for variability in the interspike interval in one class of cat spinal motoneurons.

Intracellular recordings (Fig. 1) from spinal motoneurons suggest a mechanism by which synaptic noise could produce variability in the interspike interval. During natural stimulation, or when a constant current is passed through the recording electrode, many previously silent spinal motoneurons discharged repetitively. Immediately after a spike the membrane repolarizes, and then the membrane potential rises approximately linearly to the firing level where another spike is generated (Fig. 1B). Superimposed upon this ramp-like approach of the membrane potential to the firing level, however, are random voltage fluctuations that look much like the synaptic noise of the quiescent neuron. These fluctuations in voltage appear to cause the membrane potential to reach the firing level at randomly varying times instead of at a fixed time, as would be the case if no fluctuations were present. According to this model then, synaptic noise produces variability in the inter-