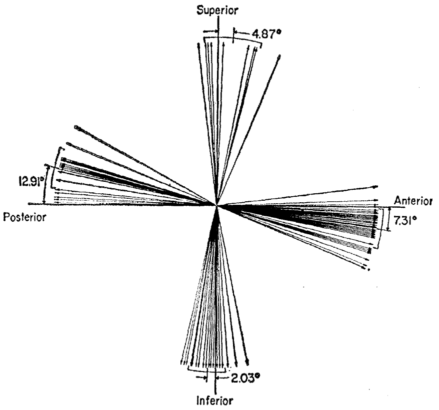

Fig. 1. Distribution of the preferred directions of 79 "on-off" direction-selective units. The axes are the horizontal and vertical in the visual field (*5*). The mean ± one standard deviation is indicated for each group.

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.

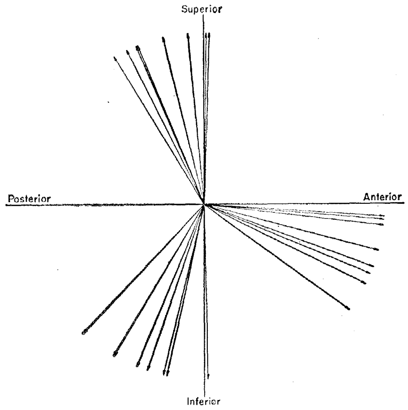

Fig. 2. Preferred directions of 23 "on" type direction-selective units. Other details are the same as Fig. 1.

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.

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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7. We are grateful to W. R. Levick for much valuable advice: the glass-insulated tungsten microelectrodes were designed by him. C.W.O. is a predoctoral fellow of the National Institute of General Medical Sciences, PHS, and the work was supported, in part, by PHS grant NB-05215.

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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-

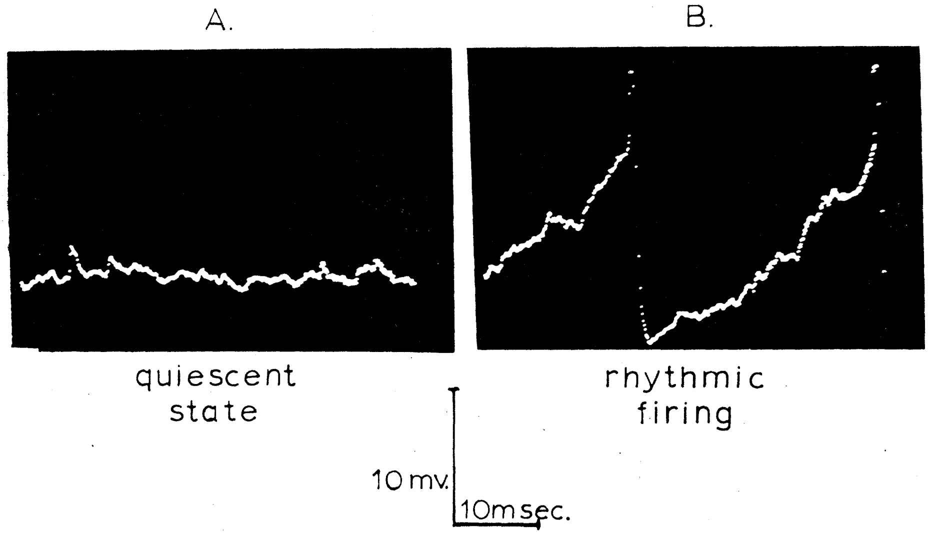

Fig. 1. Displays of membrane potential as a function of time showing synaptic noise in a quiescent motoneuron (A) and the ramp-like approach to the firing level with superimposed noise (B) when repetitive firing was induced by current passed through the membrane. Note that the action potentials are off scale in B. Because these records are displays of digitalized data from LINC memory, the separate data samples are visible as dots where the membrane potential was changing rapidly.

spike interval by causing variations in the time at which the membrane potential first crosses the firing level.

Although data from intracellular recordings are in qualitative agreement with our proposed model, only quantitative evidence can establish that more complicated assumptions are unnecessary. For example, it would be very difficult, on the basis of mere inspection of records, to say that some source of noise other than synaptic noise is not present, or that synaptic noise does not interact with the ramp generating processes instead of simply adding to the membrane potential as it approaches the firing level.

Specifically, then, we find that the statistical structure of variability in the interspike interval can be accurately predicted from the observed properties of synaptic noise together with a simple model of the spike-generating mechanism based on the assumption that the synaptic noise simply adds to a linear rise of the membrane potential to a firing level.

Our data are based on observations of lumbosacral motoneurons in cats lightly anesthetized with pentobarbital. Intracellular recordings were obtained with low-resistance (2 to 8 megohm) glass microelectrodes filled with either 2.8*M* KCl or 2.5*M* potassium acetate. Signals were led through a negative capacitance preamplifier, recorded on tape (frequency response flat from 0 to 5 khz), and finally played back into a digital computer (LINC) for analysis. Analog voltages were converted into eight-bit words with a sampling rate of 5 khz.

In the quiescent state all motoneurons exhibited the haphazard fluctuations in membrane potential termed synaptic noise (Fig. 1A). When current was passed through the recording electrode, the motoneuron fired repetitively (Fig. 1B), showing a ramp-like approach to the firing level and prominent, superimposed fluctuations in membrane potential which have the same appearance as synaptic noise seen in the resting neuron.

To analyze the interspike interval variability, we first compiled in the computer a list of intervals between successive action potentials and screened these lists for segments of statistically stationary data containing a minimum of 500 successive intervals. From about 100 neurons that at the time of the experiment appeared to yield stable intracellular recordings, we have selected four to report on here; seven segments of data from these four motoneurons were chosen for detailed analysis.

Specifying completely the statistical structure of a neuron's interspike-interval variability would require computation of the conditional probability of a particular interval length given the entire past history of that neuron's behavior. For our motoneurons, however, serial autocorrelograms revealed that an interval is independent of all preceding intervals; in this case, then, the interspike-interval histogram provides a complete specification of a neuron's interval fluctuations.

Cumulated interspike interval histograms from four lists of intervals yielded by two motoneurons are shown in Fig. 2. These plots are made on a probability scale so that a Gaussian interspike-interval histogram would give a straight line; histograms from cells not

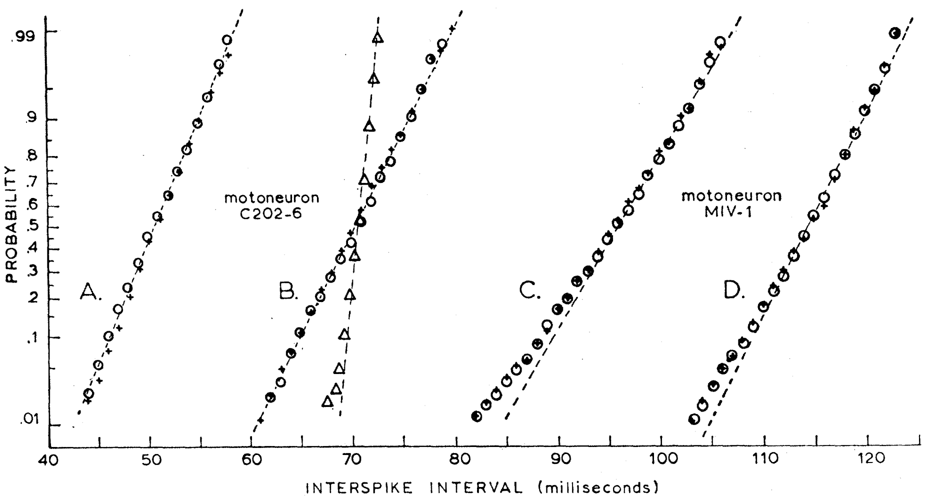

Fig. 2. Observed and predicted cumulative histograms of interspike intervals from two motoneurons. The ordinate is a probability scale on which a Gaussian distribution gives a straight line. Two sets of data from a motoneuron whose firing level increased linearly with time after a spike are shown (+) in (A) and (B), while results from a second motoneuron with a constant firing level are shown (+) in (C) and (D). Predictions made from synaptic noise and the observed characteristics of the spike-generating mechanism (open circles) are in good agreement with observed histograms; if the time dependence of the firing level in (B) is ignored and if a constant firing level is used for making the predictions, the predicted points (open triangles) deviate markedly from the observed. For clarity of the illustration, the points in (B) have been shifted 15 msec to the right along the time axis.

included in the illustration were also approximately Gaussian [as opposed to exponential, multimodal, and so forth (*1*)].

If the simple model of motoneuron behavior described earlier is accurate, we should be able to predict these observed interspike-interval histograms from measurements on the synaptic noise and on the average properties of the spike-generating mechanism by simulating motoneuron behavior with the digital computer. Simulation is preferable to the analytic approach employed earlier (*4*) because idealizing assumptions inapplicable to some neurons are thus avoided.

To make this simulation, a linearly rising "membrane potential" was generated in the computer, and synaptic noise was added to this membrane potential ramp. When the membrane potential plus noise first reached the "firing level," the length of time since the previous crossing of the firing level was stored, and the membrane potential was reset to begin the process anew. In this way, a sequence of "interspike intervals" could be generated, and their statistics could be compared with those of the observed neuronal behavior.

Simulating a specific neuron's behavior requires that parameters be selected for the deterministic spike-generation process and for the synaptic noise. The values for the ramp slope, starting point, and firing level were measured from records of membrane potential. "Synaptic noise" for the simulation was derived from one of two sources. In one instance the output of a commercial white-noise generator was filtered to produce noise with the same statistical structure (Gaussian probability density and exponential autocorrelation function) as that observed in the neuron. In the other cases, tape-recorded samples of synaptic noise from the quiescent cell were used. Whatever the source of the noise voltage, it was sampled at 5 khz and added to the "membrane potential" ramp generated within the computer. It must be emphasized that all parameters of the simulation were estimated from intracellular recordings from the particular neuron whose behavior was being examined and that a neuron's own synaptic noise was used in the simulation; no parameters were obtained from the interspike-interval histograms we wished to predict.

Predicted interspike interval histograms for two motoneurons are shown in their cumulated form in Fig. 2. The obviously good agreement between predicted and observed histograms was confirmed by Kolmogorov-Smirnov goodness-of-fit tests (*5*); for all motoneurons included in this report, more often than one time in five, two observed histograms generated by the motoneuron itself would differ as much as the observed and predicted histograms.

The sensitivity of this method to inaccurate assumptions is illustrated by one of the cells (C202-6) included in Fig. 2. Although the firing level was constant in some cells, it was observed to increase linearly with time from the preceding spike in others. If this systematic rise in the level was ignored—that is, if a constant firing level was adopted in the simulation—the predicted interspike-interval histogram had a much smaller standard deviation than that observed for the motoneuron (Fig. 2B). By arbitrarily increasing the amplitude of the synaptic noise in the simulation by about 100 percent, we could make the predicted and observed standard deviations of the interspike-interval histograms match; however, their shapes were different, the predicted histogram being negatively skewed. When the increase in firing level (approximately 50 μv/msec) observed in the motoneuron was included in the simulation, the synaptic noise seen in the cells gave an accurate prediction of the observed interspike-interval histograms (circles, Fig. 2, A and B).

Although synaptic noise appears well-established as the dominant source of interspike-interval variability in at least some cells, the question of whether additional noise sources make important contributions in other cells naturally arises. This is a difficult question to answer, however, since any failure to predict accurately the observed interspike-interval histogram does not imply that sources of variability other than synaptic noise were the cause of failure. For example, if the firing level depends in some complicated way on the entire history of the membrane potential path, that is, if voltage fluctuations that do not cross the firing level still have some effect on the state of the neuron, then our predictions will fail because the model of the (deterministic) spike-generating mechanism is inadequate and not because something other than synaptic noise is a major source of noise. To identify a second major noise source, then, it must be shown that including its observed properties in the stimulation leads to accurate prediction of the interspike interval histogram. In one cell, we found the slope of the membrane potential ramp to vary randomly from interval to interval. Since including this additional observed behavior in the simulation leads to accurate prediction of the interspike-interval histogram, we have discovered at least one instance where a source other than synaptic noise (presumably variability arising in the spike-generating mechanism) is important. It is interesting to note that we have not yet found neurons in which threshold variability has appeared to contribute significantly to the interspike-interval variability.

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3 January 1967

Honey Bees: Do They Use the Direction Information Contained in Their Dance Maneuver?

Abstract. *Direction communication experiments, when controlled against unilateral visitation of trained foragers at the experimental site, exhibited no evidence supporting the precision of communication suggested in the dance "language" hypothesis. Results compare well with those which might be expected on the basis of the geometric arrangement of the feeding dishes.*

A previous investigation demonstrated the importance of conditioned responses in the exploitation of food sources by honey bees (*1*). Experienced foragers were experimentally recruited to feeding sites, by means of odor stimuli, without their having gained information from the dance maneuver. That