quencies of A and B, and the physiological parameters of C; its threshold, and the amplitude and duration of its synaptic potentials. This expression shows that the coincidence-detecting neuron C produces an average output spike frequency which is proportional to the product of the average input spike frequencies from neurons A and B, provided that the spike trains from A and B are statistically independent. Thus a coincidence-detecting neuron can function as a multiplier.

The analysis is checked in two ways. Results of computer simulations confirm the derived expression, and in addition demonstrate that increasing the jitter in the input spike trains decreases the jitter in the output spike train of the multiplier neuron. Thus, increasing the neural noise in the input to the multiplier actually improves its operation by making its output more regular.

We then use experimental spike trains from an eccentric cell in the compound eye of *Limulus* to define the input to the proposed multiplier, and demonstrate that the amount of jitter present in real spike trains is adequate for proper operation of the proposed scheme for multiplication. This test also verifies another prediction of the analysis, namely that the performance of the proposed multiplier is not adversely affected by the presence of correlations between interspike intervals of a given input train.

Finally, the operating characteristics of the multiplier are examined in the light of published behavioral and physiological data on the optomotor response in insect visual systems. We show that the proposed scheme for multiplication is a particularly attractive candidate for optomotor mechanisms.

This study brings out three points that are relevant, in our opinion, to experimental research in neurophysiology. a) It demonstrates that coincidence-detecting neurons can, in principle, operate as multipliers. Examination of experimental data on neurons from this point of view could provide a new insight into their role in specific nervous systems. b) It provides a reasonable hypothesis for the mechanism of multiplication in insect optomotor systems. c) In a broader perspective, the study describes one way in which nervous systems could usefully employ the noise that is inherently present in them.

Analysis of Coincidence Detector

There are three steps in the following analysis. We first determine the temporal resolution of the coincidence-detecting neuron in terms of its threshold level, and the amplitude and time constant of the EPSP's induced in it. We then use this information to construct a paradigm to find the output spike train of the neuron. Finally we derive an expression for the average output spike frequency, using the paradigm.

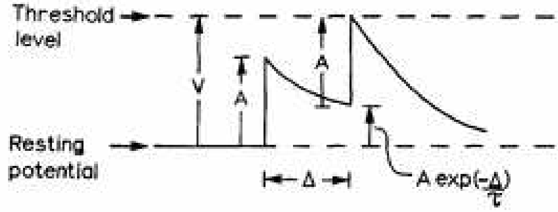

Fig. 2. Determination of temporal resolution Δ of coincidence detector neuron. The figure shows two EPSP's, each assumed to be an exponential of peak amplitude A and time constant τ, being summed in the neuron. Δ is the maximum separation in time that the two EPSP's can have to cause the generator potential to exceed the threshold level V

(a) Temporal Resolution

We define temporal resolution as the maximum separation in time, Δ, that two EPSP's can have for the generator potential of the coincidence detector neuron to exceed the threshold level V (see Fig. 2). Assuming an exponential waveform of peak amplitude A and time constant τ for the EPSP's, we obtain the following equation relating Δ to the neural parameters V, A, and τ:

$$A \exp\left(-\frac{\Delta}{\tau}\right) + A = V$$

which can be solved to yield the temporal resolution of the coincidence detector:

$$\Delta = \tau \log_e \left(\frac{1}{\frac{V}{A} - 1} \right). \tag{1}$$

Thus, neuron C of Fig. 1 will produce a spike whenever it receives two presynaptic spikes that arrive within Δ sec of each other, and will operate as a coincidence detector provided that the conditions of Fig. 1 are satisfied. These conditions may now be stated more precisely in terms of the variables of Eq. (1) and Fig. 2.

i) The condition $V/2 < A < V$ ensures that a spike is triggered in C only by a pair of input spikes and not by a single spike. This corresponds to condition (a) of Fig. 1.

ii) The smallest interspike interval in each of the input spike trains should be larger than Δ. This ensures that C does not detect false coincidences through temporal summation of the EPSP's induced