is 0.2–0.6 msec. The value is in good agreement with that obtained in other monosynaptic pathways[11]. It is, therefore, concluded that the SN-evoked IPSP in the thalamic cells were produced monosynaptically.

The threshold stimulus intensities for producing IPSPs in the cells studies were measured at various stimulating sites in and around SN. The positions with the lowest threshold, which ranged from 0.05 to 0.3 mA, were distributed in a localized area from the middle to the lateral part of SN; this corresponded approximately to the pars reticulata of the substantia nigra.

The histological locations of the impaled neurons were determined on serial frontal sections of the thalamus and summarized on the representative plane illustrated in figure 2. 10 cells which received monosynaptic EPSPs from BC, but without SN-evoked IPSPs, were located dorsally within the thalamus a location corresponding to VL. On the other hand, 18 cells which received monosynaptic IPSPs from SN and were not activated by BC stimulation, were located in an area ventral to VL, corresponding to the ventromedial (VM) nucleus of the thalamus.

It is agreed by many authors that the nigrothalamic pathway originates in the pars reticulata of SN[4,5,7]. That VM is an area in which the nigrothalamic projection terminates has been suggested with reservation by Rinvik[7] and more firmly by Mehler (personal communication). Our results show that the nigro-VM-pathway is inhibitory in nature and that VM-neurons which receive the inhibition from SN do not receive converging inputs from the cerebellum, indicating that cerebellar and nigral influences do not converge directly on single thalamic neurons[12].

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Response time constants in snail neurones[1]

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Summary. Neurones of *Helix aspersa* were excited and strength/duration curves plotted for an active and a silent cell. Experimental response latencies were longer than predicted by the theoretical relationship at low currents. The time constant of excitation was longer in the silent than the active cell.

The time constant of the molluscan neuronal soma, as calculated by measuring the electrotonic response of the cell to the application of a square current pulse[2–5], varies between 20 and 250 msec. This is 3–50 times longer than the time constants of mammalian neurones of different kinds measured in the same way. The time constant value, τ, calculated from strength/duration curves, obtained when motor neurones are depolarized and excited, is smaller than expected because of the effect of a subliminal local response[6–8]. When plots of strength/response time were made in snail neurones, we found that much longer, rather than shorter, response time constants were obtained. Furthermore, there was a deviation of the experimental values from the predicted curve.

Isolated brains from *Helix aspersa*, the common snail, were perfused with a physiological saline containing 80 mM NaCl, 4 mM KCl, 5 mM $MgCl_2$, 7 mM $CaCl_2$, 5 mM Tris-Cl corrected to pH 7.8, 10% glucose, 50 units/l each penicillin and streptomycin (Gibco), 0.4 ml/l 10× conc. amino acids for MEM Eagle and 0.2 ml/l 100× conc. vitamins for MEM Eagle (Gibco). 2 cells were chosen, one of which was active and the other silent. These were penetrated with glass microelectrodes containing 1 M potassium acetate at pH 6.8 with tip resistance of 5–30 MΩ. Signals were recorded via a conventional cathode follower and Wheatstone bridge circuit through which graded square-wave current pulses could be passed. Current amplitudes of 0–4 nA were injected into the cell soma, and the response time of action potentials was recorded. The membrane potential of each cell was adjusted to 5 ± 0.3 mV below the threshold of firing. The capacitative properties of the recording system gave it an inherent time constant of about 0.5 msec.

At low currents the response time of the cell tends towards infinity[9]. The minimal current required for a response, obtained by extrapolating the lower limits of a strength/duration curve, is the Rheobase (I_0). Values, as measured from curves for the active and silent cells, are given in the table. The current applied, I, is obtained from the equation

$$I = I_0 \cdot \frac{1}{1 - \exp(t/k)} \qquad (1)$$

where t is the duration of depolarization and k is a factor of dimension [T] The value of k cannot be derived directly from the results of this experiment, since it depends on a number of properties of the cell membrane, including its capacitance and space constant[9]. However, k can be obtained from equation 1. If I becomes $2I_0$, the equation simplifies to

$$k = \frac{t}{\ln \cdot 2}. \qquad (2)$$

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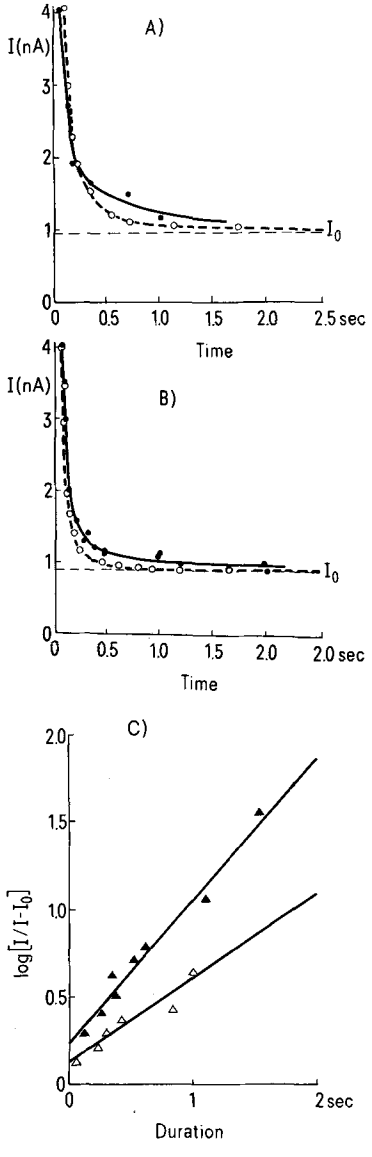
Comparison of numerical values measured from strength/duration curves in the active and silent cell

Neurone	I_o (nA)	Time constant for excitation (msec)
A (active)	0.965	580
B (silent)	0.92	800



Strength/duration curves for active and silent neurones in *Helix* brain. Results *A* from a cell which displays spontaneous APs at resting potential (average firing rate 0.7 sec^{-1}). *B* Results from a cell which displays no potentials. ●—●, experimental values of action potential latency from the start of the stimulus at different currents. Curve drawn to project the trend to infinity on the time axis. Asymptosis of this curve is the Rheobase (I_o), marked by horizontal broken line. ○—○, the calculated values of I for durations up to 2 sec from equation 1. Chronaxie, or duration of stimulus required to give response to a current of $2I_o$, is marked by the vertical broken line. *C* Calculation of τ from a plot of equation 3 for the 2 cells. Log I/I– I_o is plotted against stimulus duration for the active cell (△) and the silent cell (▲). Computed straight lines of best fit are drawn in. Gradient = τ.

The experimental curves (figure, a and b) show a marked deviation from equation 1 plotted for each cell. For just suprathreshold currents (i.e. those giving response times longer than chronaxie), the action potential appears later than predicted. The effect becomes insignificant for current values greater than twice threshold. Equation 3[8] may be used to obtain a time constant, τ, for the cell soma.

$$\frac{I_o}{I} = 1 - \exp\ (-t/\tau) \qquad (3)$$

When data is plotted as the function log $I/I - I_0$ against t (figure, c), a straight line of gradient τ is obtained (table).

Values of τ obtained by the strength/duration method are of the order of 5 times larger than those calculated from electrotonic responses in molluscan neurones[3,4] (unpublished observations). This would suggest that some property other than the true time constant of the soma membrane is detected by this type of experiment. A modified Hodgkin-Huxley model excluding a capacitance term reproduces molluscan excitation phenomena faithfully as if the slow time constant effect is mimicked by some other process[10]. Previous strength/duration experiments in squid giant axon[11] have provided evidence for long-term anomalies where the effect of a slow inward current may lead to the delayed responsiveness for long durations. A candidate for such a current in snail neurones might be the slow calcium current, reported for certain neurones[12], whose slow rise and decay time become most prominent for small depolarisations. The experimental values suggest a cumulative process which significantly affects the latency for excitation at times longer than about 200 msec. When a strong current is applied, the response latency is too short to be influenced by it. In the active and silent cells, Rheobase values were compatible. This suggests that, in the narrow range of stimulus intensities used, the current/voltage relations are similar. However, from the curves, a longer time constant for excitation (τ) is expressed by the silent than by the active cell, implying a more prominent effect of the factor prolonging growth of the membrane potential towards the firing threshold. Both values are longer than can be explained by the electrotonic spread of current. This phenomenon probably accounts for the delayed responsiveness of cells at low input currents, such as might be expected under physiological conditions when current increments result from the synaptic input.

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