Dynamic properties of mechanoreceptor neurons mediating the defensive gill-withdrawal reflex in *Aplysia*

JOHN H. BYRNE

Division of Neurobiology and Behavior, Departments of Physiology and Psychiatry, College of Physicians and Surgeons of Columbia University, New York, N. Y. 10032 and Department of Physiology, School of Medicine, University of Pittsburgh, Pittsburgh, Pa. 15261 (U.S.A.)

(Accepted May 24th, 1976)

It has now become possible to analyze the cellular basis of behavior in a variety of different vertebrate and invertebrate preparations and to correlate the activity of individual identified cells with specific behaviors and behavioral modifications. But the ultimate test of how well a given neural circuit describes a behavior is to model the various transformations taking place within the neural circuit, to simulate and synthesize the circuit and test to see how well the synthesized circuit accounts for the behavior. One of the few behavioral responses for which a complete neural circuit has been proposed is the gill-withdrawal reflex to weak tactile stimulation of the siphon in the marine mollusc *Aplysia*. As a first step in performing a quantitative analysis of this behavior I have begun to examine the dynamic properties of its mechanoreceptor sensory neurons and have utilized the techniques of systems analysis to obtain an empirically derived transfer function which relates the mechanoreceptor discharge frequency to punctate stimuli delivered to the skin.

A number of different techniques of systems identification have been utilized to specify the dynamic properties of mechanoreceptors. These include step response analysis, frequency response testing with sine waves of various frequencies, and the use of wide-band noise. The choice between various techniques is to some extent dependent on the particular experimental situation and system under investigation but there is in general no rule for determining the optimal identification scheme. In these initial experiments step response analysis was utilized since it is most closely associated with classical stimulus–response techniques used in sensory physiology, is easy to implement and is preferable with a system like the *Aplysia* mechanoreceptor neurons which are slow in reaching a steady-state firing level.

Fig. 1A illustrates the typical intracellularly recorded response of an *Aplysia* mechanoreceptor to a 4 sec controlled force step stimuli (see ref. 3 for experimental arrangement). Part B is a poststimulus time (PST) histogram of the neural discharge obtained when 30 such stimuli were delivered. Here a 50 msec bin width was selected. After a time delay or latency of approximately 400 msec due to propagation delay, the impulse discharge increases rapidly to a peak within the first 100 msec. It then
Fig. 1. Dynamic response of mechanoreceptor neuron. A1: actual force waveform of punctate stimulus (probe diameter = 0.5 mm) delivered to the siphon skin with a feedback controlled electromechanical stimulator. A2: intracellularly recorded resultant discharge to force stimulus from a mechanoreceptor neuron cell body located in the abdominal ganglion. B: poststimulus time (PST) histogram obtained when 30 stimuli identical to A1 were delivered to the skin /1 min. Bin width = 50 msec.

decays at first rapidly and then more slowly over several seconds to an apparent steady-state firing level. Removal of the stimulus results in an off-response which is typical of moderate stimulus intensities but is usually absent with weaker ones. The general shape of the histogram indicates that it may be approximated by a series of exponentials. Initially a two exponential equation was selected but to obtain a better fit it was expanded to include a third exponential term. This expression given in equation 1 contains one exponential rising with a short time constant and two falling exponentials, one with a short time constant and the other with a time constant considerably longer.

\[
\text{Resp} = 3.8 - 111.8e^{-\frac{t}{0.025}} + 99.95e^{-\frac{t}{0.075}} + 8.05e^{-\frac{t}{1.09}}
\] (1)

The various parameters of equation 1 were estimated using the technique of ‘peeling’
exponentials\cite{1,23} but an index of their accuracy is not available due to the inherent limitations of this estimation scheme.

The ideal mathematical description of a dynamic system should not only be able to fit the data from which it was derived but also predict the response to any general input waveform. Clearly one then requires the differential equations relating the input to output of the dynamic system under study. Linear systems analysis offers a simple and straightforward means of obtaining this relationship. With the mechanoreceptor properties assumed both linear and time invariant\cite{3,5,6} a transfer function relating an arbitrary force input stimulus at the skin to the neural discharge of the mechanoreceptor can be realized by taking the Laplace transform of the empirical exponential expression and dividing by the Laplace transform of the input force waveform. Although the actual force input is the sum of two step inputs one positive step at time zero and another negative step at the end of 4 sec, the force input can initially be considered as a single positive unit step at zero time, since an apparent steady-state response occurs before the arrival of the negative step.

The transfer function describing the linear dynamic characteristics of the mechanoreceptor was thus determined as:

\[
\frac{\text{Resp}}{\text{Fin}} = \frac{(3.8) (0.389s + 1) (4.33s + 1)e^{-0.4s}}{(0.025s + 1)(0.075s + 1)(1.09s + 1)} \tag{2}
\]

The \(e^{-0.4s}\) term accounts for the time necessary for the nerve impulses to propagate from the skin to the recording site in the ganglion.

In initial simulations using the simulation language CSMP\cite{12} the simulated data points fit the experimental data well for the first 4 sec of the response but a large negative response was obtained with the removal of the stimulus. This is not surprising, however, since it is precisely what one would expect from a linear system. Clearly the assumptions concerning the mechanoreceptor linearity must be modified. Some of these non-linear effects may be attributed to the fact that as the stimulator probe withdraws after the step force indentation it becomes uncoupled from the skin. The mechanoreceptor is, however, still excited since some discharge appears to be synchronized with the negative step. A similar phenomenon in the pacinian corpuscle was attributed to pressures produced when energy stored in the elastic elements of the corpuscle during a positive step displacement was released with the negative step\cite{13,17}. Thus due to the geometry and elastic properties of the corpuscle the negative step produces a positive pressure pulse which of sufficient magnitude could cause distention of the mechanoreceptor membrane and lead to excitation. Although the fine structure of the \textit{Aplysia} mechanoreceptor terminals is unknown it seems reasonable that the mechanism generating the off-responses in \textit{Aplysia} bears some similarity to those in the pacinian corpuscle. As a first approximation the linear model presented was adjusted to simulate these effects by summing the normal positive simulated response with the absolute value of the negative response exceeding some preset value. The step response of the adjusted model is given by the dotted lines in Fig. 2A and a good fit to the experimental data for the entire duration of the discharge is obtained.

To further test the model experiments were performed to obtain the mechano-
receptor response to another force input waveshape. An input stimulus 4 sec in duration with a 1 sec rise time and 20 msec fall time was arbitrarily selected. Fig. 2B shows a histogram which was generated when 21 such stimuli were presented to another cell. The dotted lines superimposed on the histogram represent the simulated response scaled to match the steady-state level of the neural discharge. The simulated and experimental responses are in good agreement. Better fits might be achieved by applying modern techniques of systems identification (for review see ref. 10) and by accounting for additional non-linearities such as threshold and saturation. While preliminary, the results support the utility of performing similar analyses on the additional transformations taking place at the central and effector elements mediating this behavior. By the proper interconnection of these transformations it may then be
possible to synthesize the entire behavior and test to see how well the known neural elements account for the behavior and its capability for short- and long-term modifications.

Supported by NIH Grants MH-13579, NS-03076-01 and NS-09361-05.

4 Byrne, J., A feedback controlled stimulator that delivers controlled displacements or forces to cutaneous mechanoreceptors, IEEE Trans. bio-med. Engng., BME 22 (1975) 66–69.