BRIEF COMMUNICATION

DYNAMIC PROPERTIES OF THE ACTION POTENTIAL ENCODER IN AN INSECT MECHANOSENSORY NEURON

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ABSTRACT A variety of sensory receptors show adaptation to dynamic stimuli that can be well characterized as fractional differentiation of the input signal. The cause of this behavior is unknown, but because it can be represented by linear systems theory, it has been assumed to arise during early linear processes of transduction or adaptation, rather than during the nonlinear process of action potential encoding. I measured the action potential encoding properties of an insect mechanoreceptor by direct electrical stimulation of the sensory cell axon and found a dynamic response that is identical to the response given by mechanical stimulation. This indicates that the fractional differentiation is a property of the encoder rather than the transducer.

Sensory receptors often display adaptation where the response to a changing stimulus is much greater than the response to a steady stimulus. Mechanoreceptors are usually classified as rapidly or slowly adapting, terms that cover a range of behavior, from those receptors that respond transiently to a change in stimulus to those that continue to fire action potentials for as long as the stimulus is maintained. In a pioneering study, Pringle and Wilson (1952) examined the rapidly adapting behavior of an insect mechanoreceptor, the cockroach femoral tactile spine, and found that its adapting response to a step displacement could not be fitted by a single time constant, but instead required the summation of at least three exponential processes. It was later shown that the step response of the tactile spine (Chapman and Smith, 1963) and carotid body receptors (Landgren, 1953) could be well fitted by a power law relationship of the form

$$y(t) = g \cdot t^{-k}, \tag{1}$$

where $y(t)$ is the rate of action potential firing as a function of the time, t, after the step. This model requires only two parameters, k, the fractional exponent of time, and g, the rate of firing after 1 s. It is now well known that Eq. 1 describes a system that performs fractional differentiation of its input signal (Oldham and Spanier, 1974) such that

$$y(t) = \mathrm{d}^k x(t)/\mathrm{d}t^k. \tag{2}$$

Such systems may also be analyzed in the frequency domain using sinusoidal or random stimuli. In this case, the amplitude of the response increases with the kth power of applied frequency and the response leads the stimulus with a phase advance of $90k^0$ (Chapman and Smith, 1963).

Step responses and frequency responses of the fractional differentiator type have now been observed for a wide range of receptors, including arthropod cuticular receptors (French et al., 1972; French and Kuster, 1981; Bohnenberger, 1981), insect multipolar receptors (Kuster and French, 1983), crustacean stretch receptors (Brown and Stein, 1966), primate touch receptors (Mountcastle et al., 1972), *Limulus* eccentric cell photoreceptors (Biederman-Thorson and Thorson, 1971), and vestibular afferents in mammals (Tomko et al., 1981) and birds (Landolt and Correia, 1980). However, no satisfactory explanation for the behavior has emerged. Thorson and Biederman-Thorson (1974) reviewed the range of receptors that had been shown to give fractional differentiation at that time and discussed the models that had been proposed to explain it. The behavior appears to be linear in the sense that a sinusoidal input gives rise to a sinusoidal output of the same frequency that differs only in amplitude and phase. This idea has led to an emphasis on the use of linear mechanisms to account for fractional differentiation. However, linear physical systems that produce such behavior are comparatively unusual. The function could be approximated over a restricted frequency range by a cascade of exponential filters, but some sensory receptors have now been observed over a range of four or five decades of frequency without deviating from the power law (French and Kuster, 1981; Bohnenberger, 1981; Chapman et al., 1979), which makes a cascade model unlikely. Distributed processes such as heat conduction and diffusion can lead to semi-differentiation where the exponent $k = 0.5$. Similarly distributed mechanical processes have been suggested for the first stages of transduction in the tactile spine (French and Sanders, 1981) where the exponent is usually close to this value. Thorson and Biederman-Thorson (1974) proposed an alternative system of distributed exponential

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processes in which the output is a summation of many parallel pathways. However, this also breaks down when the behavior is observed over a wide frequency range, unless a similarly wide range of time constants is available and the outputs are summed in the correct proportions. Brown and Stein (1966) proposed a simple nonlinear mechanical model for the crayfish stretch receptor in which a nonlinear elastic component was connected to a linear viscous component, again concentrating upon the earliest stages of transduction.

The emphasis in the literature on linear models for fractional differentiation obscures the possibility that nonlinear processes that occur during action potential encoding could also be involved. Adaptation has been demonstrated during encoding in the Pacinian corpuscle (Mendelson and Loewenstein, 1964), in the crayfish stretch receptor (Nakajima and Onodera, 1969), and in mammalian muscle spindles (Poppele and Chen, 1972), so it might also occur during encoding in insect mechanoreceptors. I recently examined the dynamic behavior of the receptor potential in the cockroach tactile spine and could find no evidence for adaptation during transduction (French, 1984), even though this is a rapidly adapting receptor with a fractional differentiator response. This finding suggests that current theories that locate the behavior in the early stages of transduction are unlikely to be true; instead, the action potential encoding step is a more probable candidate. The experiment illustrated in Fig. 1 was therefore designed to test this theory.

A microelectrode was positioned adjacent to the axon and just below the cell body of the sensory neuron in the tactile spine. When a negative voltage was applied to the microelectrode, current flowed out through the axonal membrane, which simulated the depolarization caused by the receptor current during mechanical stimulation. When the microelectrode was moved up and down in the spine, one position was always found close to the bottom of the spine where the threshold for the production of action potentials was lower than elsewhere. It is not known at present whether this position represents a low threshold region of the axon or if results from the geometry of current flow through the axon as the axon penetrates the base of the spine.

The dynamic relationship between the current flowing through the microelectrode and the resultant action potentials monitored in the axon was identical to the relationship that has been described for the transformation of displacement into action potentials (French et al., 1972; French and Kuster, 1981), whether the applied stimulus was a step function, a sinusoid, or white noise. Fractional differentia-

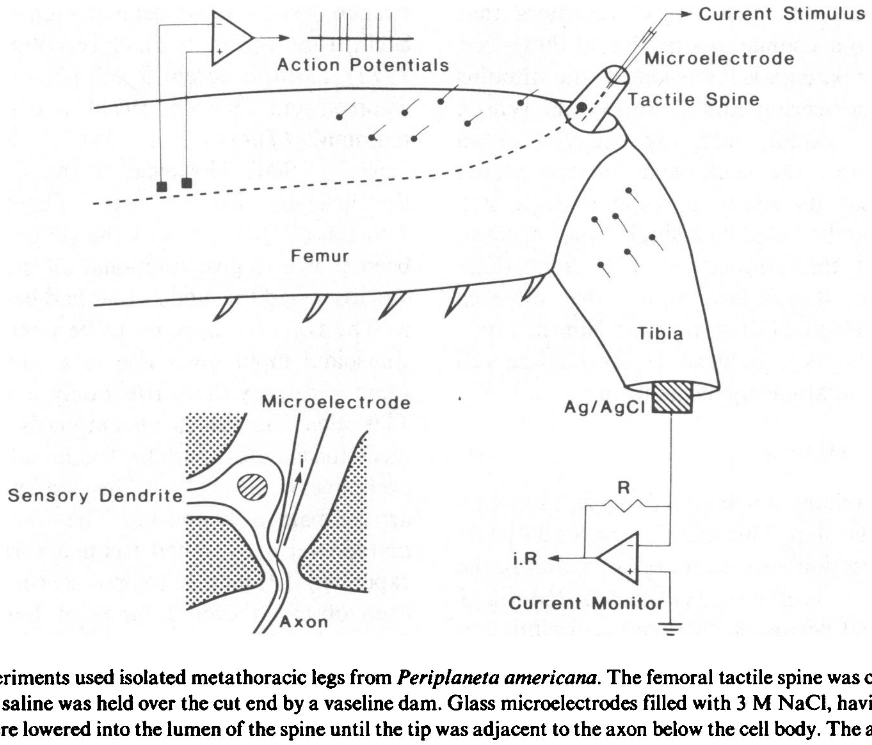

FIGURE 1 The experiments used isolated metathoracic legs from *Periplaneta americana*. The femoral tactile spine was cut above the sensory neuron and a pool of saline was held over the cut end by a vaseline dam. Glass microelectrodes filled with 3 M NaCl, having resistances in the range 30–40 MΩ, were lowered into the lumen of the spine until the tip was adjacent to the axon below the cell body. The approximate position of the electrode is shown in the inset. The morphology of the spine and sensory neuron were described by French and Sanders (1981). The microelectrode was connected to the stimulating circuit by a Ag/AgCl electrode and the ground return was connected via another Ag/AgCl electrode through the lumen of the tibia. Current through the spine was monitored via a virtual ground amplifier as illustrated. Action potentials in the sensory axon were monitored by two insect pins passed through the femur ~3 mm from the spine and connected to a differential AC amplifier. The most sensitive position for stimulation was determined by passing a sinusoidal current through the spine while adjusting the position of the electrode, and was usually near to the point at which the electrode touched the base of the spine, causing a rise in electrode resistance.

tion was obtained in each case. Fig. 2 illustrates two types of experiments in which this can be seen. With a randomly fluctuating suprathreshold current the frequency response function was well fitted by a fractional exponent of frequency. Only the gain of the response is shown, but the phase data was equally well fitted after accounting for the conduction delay between the spine and the recording electrodes. For 15 experiments, the exponent was k = 0.30 ± 0.07 (mean ± SD), which is in the middle of the range reported for mechanical displacement of the spine measured over a wide range of displacement amplitudes (French and Kuster, 1981).

By increasing the amplitude of a sinusoidal current until it was just below the threshold for producing action potentials, it was possible to measure threshold current vs. stimulus frequency. This relationship was well characterized by fractional integration and was of the same form as the threshold obtained by mechanical stimulation (Fig. 2). The exponent for current stimulation was $k = -0.34 \pm 0.10$ ($n = 15$), whereas that for mechanical stimulation was $k = -0.39 \pm 0.09$ (French, 1984). Therefore, the threshold experiments gave the same values for the exponent as were given by the frequency response measurements, although the threshold experiments were conducted with much smaller stimuli and without the occurrence of action potentials. These results show that the dynamic behavior of this mechanoreceptor can be demonstrated entirely by action potential encoding in the membrane of the sensory neuron. This eliminates distributed-parameter mechanical models that have been proposed to account for fractional differentiation in cuticular mechanoreceptors (French and Sanders, 1981), as well as distributed-conductance models (Thorson and Biederman-Thorson, 1974).

Simple models of neuronal encoding such as the leaky integrator (Rescigno et al., 1970; Stein et al., 1972) do not show adaptation of the type found in many receptors. Neither do the more elaborate Hodgkin-Huxley models (Hodgkin and Huxley, 1952; Holden, 1976). However, it is

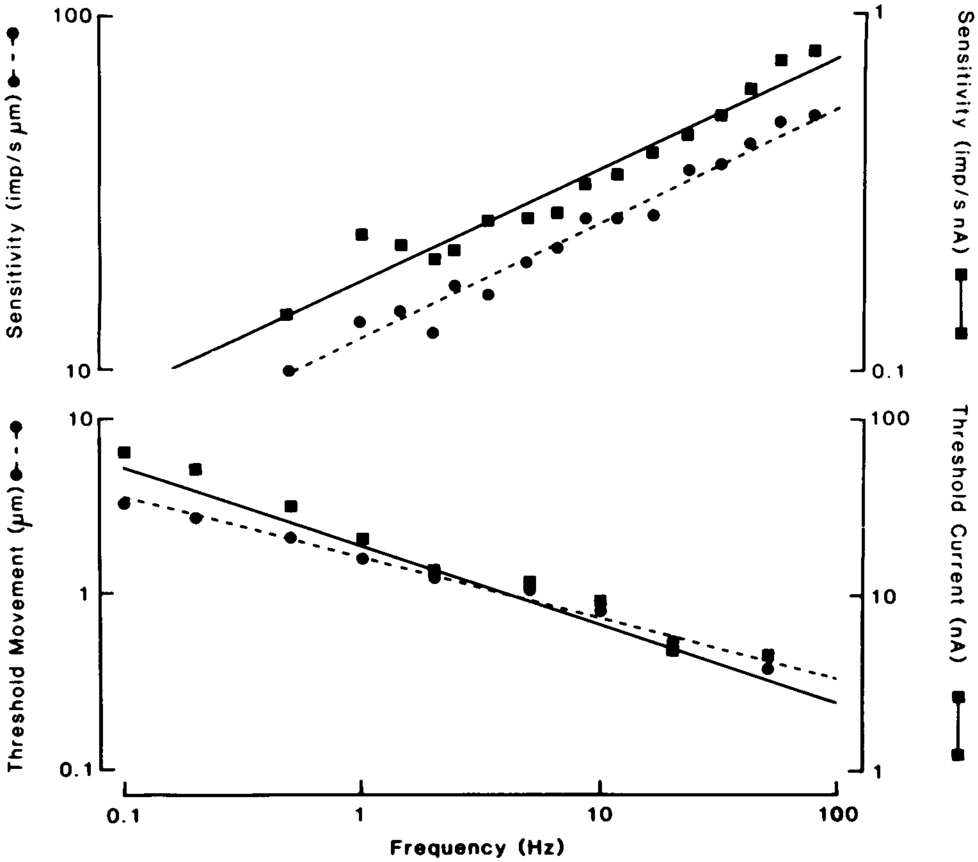

FIGURE 2 The upper graph compares the frequency response function of transduction in the tactile spine obtained by mechanical stimulation with that obtained by electrical stimulation. The experimental procedures for mechanical stimulation and the details of random signal generation, data gathering, and frequency domain analysis procedures are given by French and Kuster (1981). The frequency response function for mechanical stimulation was well fitted by a power law relationship (dashed line) with exponent $k = 0.32$, which is typical of values published previously. The electrically stimulated experiment gave $k = 0.31$ (solid line). The lower graph compares the thresholds for producing action potentials with mechanical and electrical stimulation over the same frequency range. In this case the slopes were well fitted by $K = -0.34$ (mechanical stimulation, dashed line) and $k = -0.46$ (electrical stimulation, solid line). For both the frequency response functions and the threshold measurements a typical experiment has been shown rather than averaged data because varying sensitivities cause different results to be separated vertically along the ordinate. Average values are presented in the text.

possible to construct modified versions of these models that do show realistic adaptation. Poppele and Chen (1972) found that adaptation in the muscle spindle could be fitted by the leaky integrator model if the membrane time constant was allowed to vary as a function of receptor firing rate. The leaky integrator model was generalized by allowing variation of the time constant to account for nonlinear membrane conductances (Fohlmeister, 1973) and could demonstrate tonic to strongly adapting behavior by variation of a single parameter. With feedback from the action potentials changing the input current, the variable time constant model was able to account for adaptation in the crayfish stretch receptor and the *Limulus* eccentric cell (Fohlmeister et al., 1977*a*,*b*).

Several factors have been suggested to account for adaptation in experimental preparations that could produce feedback to the encoder. Slow inactivation of the sodium current or the activity of an electrogenic sodium pump have been linked to adaptation in crayfish stretch receptors (Nakajima and Onodera, 1969; Sokolove and Cooke, 1971) and accommodation to a slowly rising depolarization has been related to slow sodium inactivation in myelinated axons (Vallbo, 1964). Addition of a slow sodium inactivation term can cause adaptation of the Hodgkin-Huxley encoder (Michaelis and Chaplain, 1973). More recently, the influx of calcium ions during action potential firing (Ito and Komatsu, 1979) has been coupled with the widespread calcium-activated potassium conductance to account for adaptation in *Aplysia* neurons (Lewis and Wilson, 1982) and crayfish stretch receptors (Ottoson and Swerup, 1982).

Although mechanisms of adaptation in sensory receptors are emerging from experimental and model studies, there is not yet a clear explanation of how fractional differentiation is produced. The present work shows that fractional differentiation in the cockroach tactile spine arises during encoding rather than in the transduction stage. How this superficially linear phenomenon is produced by the nonlinear encoder remains to be elucidated, but the adapting mechanisms that have already been discovered are likely to play an important role.

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