Dynamic and Static Hysteresis in Crayfish Stretch Receptors*

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Abstract. This report calls attention to the magnitude and pervasiveness of hysteresis in the coding from length to afferent discharges in crayfish stretch receptor organs (SRO's). The influence of previous lengths on the rate that corresponded to a particular length L was manifest by a substantial excess of that encountered when L was arrived at from a shorter value over that when arrived at from a longer one. Hysteretic loops were present under dynamic conditions when length was modulated quasi-sinusoidally in the length vs. rate Lissajous plots of both the slowly and the fast-adapting organs (SAO, FAO), either not perturbed or perturbed. Loops became narrower with increasing frequency (except for when 1 to 1 locking appeared, Diez Martínez and Segundo, 1983). Hysteretic loops were present under static conditions when length changes were step-like, and fully adapted rates were noted in the SAO and in the perturbed FAO.

Earlier reports suggest that hysteresis reflects jointly at least mechanical and electrogenic factors in the "length-to-local dendritic effects" and in the "generator potential to discharge" stages.

Several models, either mechanical or mathematical, reveal hysteretic behavior. Detailed analysis has not been performed except for one instance (Chua and Bass, 1972) where, for example, loop-narrowing at higher frequencies occurs only with certain weighting functions whose physiological significance is as yet obscure.

Hysteresis may be more widespread than suspected in sensory (and perhaps other) systems: it involves a multi-valuedness that raises the issue of how central mechanisms infer stimulus magnitude retrospectively from the discharge.

Introduction

This report describes the hysteresis in the coding from length to afferent discharges in crayfish stretch-receptor organs, discussing mechanisms, implications and modeling attempts. It thus stresses a clear-cut feature that, though reported occasionally in the extensive earlier work on the organ, has received relatively little attention (e.g., Borsellino et al., 1965; Brown and Stein, 1966; Buño et al., 1978, 1984; Chaplain et al., 1971; Diez Martínez, 1981; Diez Martínez et al., 1983; Eyzaguirre and Kuffler, 1955; Krnjevic and van Gelder, 1961; Nakajima and Onodera, 1969a, b; Vibert and Segundo, 1979).

Materials and Methods

Experiments were on the 8th thoracic segment stretch-receptor organs (SRO's), fast-adapting (FAO) and slowly adapting (SAO), of Procambarus Clarkii of either sex in June, July, and August; the specimens, of 9–14 cm, had SRO's 4–12 mm in length. Dissection, mounting in about 14 °C van Harreveld solution, sensory stimulation, recording and data storing procedures are described elsewhere (e.g., Diez Martínez et al., 1983; Vibert et al., 1979). After measuring the 3.5–4 mm physiological range of SRO length changes (Diez Martínez et al., 1983), the SRO's caudal end inserted to the first abdominal segment was immobilized by anchoring the latter to the paraffin. Stimuli were length variations imposed by displacing a forceps that clamped the organ between its sensory innervation and cephalic insertion, and was moved by a Ling Electronics 102A electromagnetic shaler whose input was the output from a Wavetek 133 signal generator. The following stimuli delivered by the stretching device were considered within physiological ranges and are referred to as "clean or non-perturbed." The shaker followed sine waves with periodic, approximately sinusoidal, modulations, which were measured by a Grass *FTO3C* force-displacement transducer: frequencies of 0.2, 1.0, 3.0, and 10 cps were used predominantly. Depth of 0.06–0.75 mm, roughly 1–10% of total receptor length and 2–20% of physiological changes, were adjusted through the microscope. Also steps were imposed upon the shaker, and it responded with a quasi-step plus some over- or undershoot and ringing before stabilizing: our interest centered on the stationary

or fully adapted periods. Steps were of about 0.030 mm; successive ones, separated by approximately 60 s, carried the length throughout ranges of about 0.300 mm, followed in a regular cycle from the shortest to the longest and then back to the shortest, or vice versa. The "background" length, i.e., the minimal distance between the caudal insertion and the forceps, was set to a "resting" length corresponding approximately to an intermediate abdominal flexion in the intact animal.

In certain instances, sine waves and steps entered the shaker mixed with a Gaussian band-limited white noise whose cut-off was around 200 cps and whose amplitude remained 95% of the time under two-thirds of the peak-to-peak sine and the step amplitudes. The noise per se produced displacements that, though fast, irregular and difficult to predict, had a lower cut-off and more marked frequency peaks. The resulting mixed stimuli are referred to as "perturbed," "noisy" or "jittery" (Buño et al., 1977, 1984; Diez Martínez and Segundo, in preparation; Vibert and Segundo, 1979). The "noise", "jitter" or "dither" is meant to represent perturbations that are practically unavoidable in the natural receptor operation.

Primary afferent discharges of action potentials (AP's) were recorded extracellularly with a hook electrode from the cut dorsal nerve. The FAO did not discharge spontaneously, and its spikes were generally larger than those of the SAO; when smaller or similar, interference was avoided by silencing the SAO by freeing or damaging it. Individual records at a particular frequency or length lasted from 10 to 1000 s; each sample had at least 1000 AP's. A between-stimulus interval of about 10 min was allowed to minimize interactions which, though very real, were analyzed only for step-stimuli.

The data, stored on analog tape, were analyzed later on a DEC PDP 8E computer. Each AP train was divided into adjacent identical "bins" of, say, 1000 ms: the number of spikes in each divided by its width gave the "bin-rate," i.e., the rate in ips averaged within that bin. The bin-rate was displayed as a "running" rate, i.e., as a function of ongoing time. Stationary segments were identified as those where the peak-to-peak fluctuation in the sinusoidal series showed no trend, or by testing for the null hypothesis of no trend (Kendall, 1970) at a 95% significance level when steps were used. The cycle histograms of discharges during periodic modulations were constructed using bin-widths of 1/10 the average period. Length variations, on the other hand, were transformed into impulse trains at very high rates using a voltage-to-rate converter, and their cycle histograms were constructed. Finally, Lissajous figures of discharge intensity vs. stimulus magnitude were constructed, displaying the average rate in the ordinate and the corresponding average length in the abscissa and keeping tract of the order of their generation. In addition, the standard deviations (SD) and coefficients of variation (CV = SD/average) were calculated for each bin.

When length-steps were used, overall average rates were measured in each fully adapted, i.e., stationary trend-free region. Displays involved plots of lengths vs. average rates with points numbered in the order of their experimental generation.

Results

This section will concentrate on the highlights relevant to hysteresis, since the effects of sinusoidal modulations and the strong influences of background length, depth, modulation frequency and noise were described elsewhere (Diez Martínez, 1981; Diez Martínez et al.,

1983; Segundo and Diez Martínez, 1985; Vibert and Segundo, 1979).

Most characteristics, including the modulation of the afferent discharge at the stimulus frequency, showed an across-frequency gradient. The peak-to-peak swing was greatest along the first cycles, then declining to a stationary level (Diez Martínez et al., 1983). Cycle-by-cycle following ceased at the higher frequencies, with cut-off values around 5 cps for the SAO and beyond the 100 cps tested for the FAO. The usual average Lissajous rate vs. length plot had a flat extension to the left (at the shorter lengths) and a loop to the right (Figs. 1 and 2). A loop implies two rates for
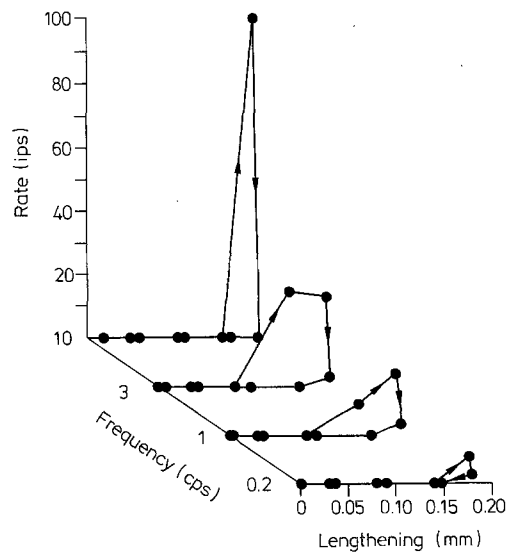
Fig. 1. Lissajous displays of length on abscissae vs. rate on ordinates during sinusoidal length modulations. Fast-adapting organ. Modulation frequencies: 0.2, 1, 3, and 10 cps. Depth: 0.18 mm. Resting length: 6.0 mm. In all figures, arrows indicate the succession with which points were generated experimentally
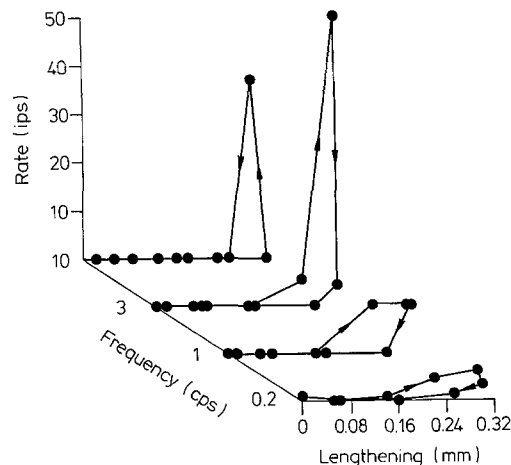
Fig. 2. Lissajous displays of length on abscissae vs. rate on ordinates during sinusoidal length modulations. Slowly-adapting organ. Modulation frequencies: 0.2, 1, 3, and 10 cps. Depth: 0.30 mm. Resting length: 6.0 mm

each length (double-valuedness), one while increasing, another while decreasing. Both the portion of the loops with increasing lengths and that with decreasing ones had one intermediate bin each, or occasionally two or more. In the FAO and in the SAO, usually loops with 0.2 and 1.0 cps were ellipse- or folium-like; with 3.0 cps, folium-like or triangular with the base on the abscissae; and with 10 cps, triangular with a narrow base on the abscissae (Figs. 1 and 2).

Loops usually developed clockwise, the rate leading the length by about 1/10 of the stimulus period or one bin (Figs. 1 and 2). In the FAO, for example, when the frequencies of the stimulus were 0.2, 1.0, 3.0, and 10.0 cps, clockwise predominance decreased through 95, 82, 74, and 71% (sample sizes 17–23); the proportion of counter-clockwise loops increased correspondingly. Most commonly, the rate led the length with 0.2 cps and 1.0 cps (1 bin lead), and was in phase with 3.0 and 10 cps; lags became the rule with the higher frequencies, e.g., 50–100 cps. In the SAO, loops developed generally clockwise (leads) with 0.2 and 1.0 cps and counter-clockwise (lags) with 3.0 and 10 cps; figures-of-eight were rare, resulting from an additional smaller and oppositely developing loop with 10 cps, or clockwise in another.

The openness of the rate vs. length loops decreased as the stimulus frequency augmented (Figs. 1 and 2; this became, frankly, more evident when plots were normalized, as in Fig. 6 of Diez Martínez et al. (1983). Clearcut exceptions to this appeared when, at over 3 cps, stimuli and discharges locket at a constant phase with at most one AP per cycle and, as a consequence, there were two very separate values at all frequencies.

The "flat extension" to the left corresponds to the no-discharge periods during shortening and elongation, implying a lower-limit saturation. In the majority with clockwise loops and leads, firing starts during elongation at a smaller length than where it stops during shortening: the extension thus coincides with the no-discharge period during elongation. As the stimulus frequency increased, more of each cycle was silent, and flat extensions became longer. With jittery sine stimuli, the tendency was for flat extensions to be smaller or absent, and for loops to move upwards, becoming more elliptical and narrower (Diez Martínez, 1981).

The following description of step-effects (Fig. 3) holds for either unperturbed or perturbed SAO's and for perturbed FAO's. i) Each step lengthening causes a transient acceleration that adapts down to a rate faster than the pre-step rate. ii) Each step shortening causes a transient slowing that adapts up to a stationary, "fully adapted," rate slower than the pre-step rate. iii) In the length vs. fully adapted rate plot (Fig. 3), some points that correspond to successive steps in a particular
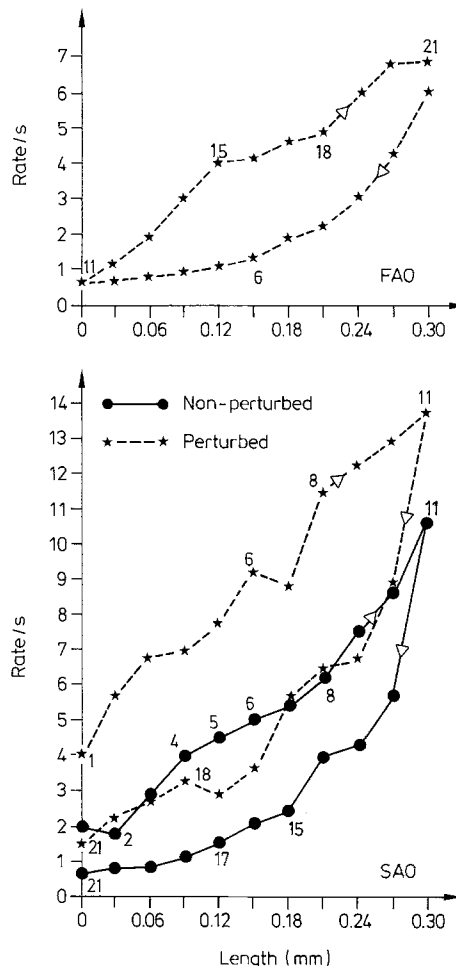

Fig. 3. Length on abscissae vs. rate on ordinates during fully-adapted periods in fast- (FAO) and slowly- (SAO) adapting organs

sense (e.g., all lengthenings) may fall close to a straight line (e.g., non-perturbed SAO points 4–8, 8–11, 15–21). Since, however, lines differ in slopes and/or intercepts from one succession to the other, the overall curve is linear at best in a piece-wise manner. iv) Slopes were usually positive, with the smaller (even zero) ones occurring at the shorter lengths (lower-limit saturation). v) Two rates corresponded to each particular length, the greater one during the lengthening sequence, the lower one during the shortening one. The separation between the two was around 30–75% of the larger one (e.g., non-perturbed SAO points 5 and 17). vi) When a full cycle was completed (in the sense that the initial and final lengths were identical) and the points were joined in order, a clockwise loop appeared, not necessarily closed because the initial and final rates might not coincide. vii) In the SAO, the perturbed loop was displaced upwards relative to that in the unperturbed condition. The separation between identical length points remained approximately of the same order. viii) The unperturbed FAO simply responds to

the steps (and perhaps the subsequent ringing), and then lapses into its silent, fully adapted state (e.g., Brown and Stein, 1966; Buño et al., 1978; Chaplain et al., 1971; Eyzaquirre and Kuffler, 1956; Krnjevic and van Gelder, 1961; Nakajima and Onodera, 1969a, b; Terzuolo and Washizu, 1962).

Discussion

"Hysteresis," according to Webster's Dictionary (Babcock Gove, 1981), is "a lagging of a physical effect on a body behind its cause (as behind changed forces and conditions)," "the influence of the previous history or treatment of a body on its subsequent response to a given force or changed condition," and "the changed response of a body that results from this influence." The concept applies either to dynamic phenomena when the forcing function fluctuates, or to static ones when changes are spaced and step-like. Though frequent in the inanimate world of forces and stresses, magnetizations and inductions, or polarizations and intensities, its physics is understood poorly. Also living matter, in particular the length-to-rate transduction in SRO's, exhibits features that fit within these definitions (e.g., Figs. 1–3) (Buño et al., 1977, 1984; Diez Martínez, 1981; Diez Martínez et al., 1983; Krnjevic and van Gelder, 1960; Vibert and Segundo, 1979); similar features are reported explicitly, or suggested by illustrations, for other mechanoreceptors (e.g., Mountcastle et al., 1963; Vidal et al., 1971). Hysteresis, which includes the double-valuedness, may in fact be more widespread in sensory systems than has been recognized. It relates closely to an asymmetric sensitivity to stimulus velocity (e.g., Diez Martínez and Segundo, 1983; Vidal et al., 1971). This raises the question of how central mechanisms infer stimulus magnitude retrospectively from afferent discharges, a point that is important but has been discussed extensively elsewhere (e.g., Fujita et al., 1968).

Mechano-electrical transduction involves transformations cascading across SRO length, neuronal deformations, generator potentials (GP's) and afferent discharges (e.g., Chaplain et al., 1971). The sequence of events is (Teorell, 1971): "*mechanical stimulus, displacement* (of length), change of tissue and membrane *tension*, effect on intra "cellular" *pressure*, change of transmembrane *hydrostatic pressure* gradient, *water flow* and change of membrane *conductance*, unstable damped membrane potential, i.e., *generator potential, local currents, conductance* changes, *action potentials* (propagating)." The context in which these transformations should be conceptualized is outlined appropriately by the electrokinetic model of Teorell (1971).

The present experiments do not shed light as to the individual contributions, but certain conjectures seem pertinent. Indeed, the following findings suggest that hysteresis reflects jointly at least mechanical and electrogenic factors in the "length-to-local dendritic effects" and the "generator potential-to-discharge" stages.

i) The length-to-tension conversion shows static hysteresis (Krnjevic and van Gelder, 1961). A dynamic character hinted at by a dependence on the steepness of the ramps (see also Terzuolo and Washizu, 1962) was confirmed because sinusoidal elongations reveal quasi-elliptical length-tension loops, i.e., dynamic hysteresis (associated with flat extensions to the left) (Chaplain et al., 1971); proportionality exists only for small (e.g., 0.05 mm) amplitudes. Because of our ignorance of the phenomena affecting dendrites, as well as of their mechanical properties, tension changes across them cannot be calculated reliably from those measured across the entire organ. Mechanically the SAO and FAO are similar, not obeying Hooke's law. Because the FAO is substantially thicker, however, it must have a lower coefficient of elasticity; also, because of this property and its geometry, it requires much greater elongations to create the same tension change per unit area. Suggested models have two components, a "non-linear spring" (whose tension-related length is sensed by the dendrites), and a "spring and dashpot"; in one model (Nakajima and Onodera, 1969b), the components are in series, the mixed one having the spring and dashpot in parallel; in the other (Chaplain et al., 1971), the components are in parallel, with the mixed one having the spring and dashpot in series (Chaplain et al., 1971).

ii) Though not explored deliberately, published data indicate that at least static hysteresis may be a feature of the GP-to-discharge transformation, an hypothesis likely even a priori since a simple leaky integrator model with a voltage-dependent active state favors depolarizations (Hartline, 1976). Nakajima and Onodera (1969a), in a thorough study including step shifts in clamped potential found many similarities between SAO and FAO. The one major discrepancy was that constant currents induced sustained discharges in the SAO and brief ones in the FAO: slow decreases and/or increases in the conductances for Na^+ and K^+, respectively, or an electrogenic pump feed-back that favors faster adaptations at greater lengths could be involved (see also Fischer and Michaelis, 1981). This silent condition of the FAO could be interrupted by brief hyperpolarizations, however, a finding which, added to the sustained discharge during a noisy stimulus (Buño et al., 1978), indicates a predominant sensitivity to the derivative of the stimulus with respect to time (as in Pacinian corpuscles, Alvarez Buylla and Ramírez de Arellano, 1953). Nakajima and Onodera (1969a) analyze the influence of

depolarizing currents up to intensities causing cessation of firing: their Fig. 9 illustrates for both SRO's that there are intermediate values for which discharges are present when reached from lesser depolarizations but not from the other side. Granit et al. (1963) showed that, if a current step is passed into a rat motoneuron, the discharge increases in the sense of less inward, more outward currents: their Fig. 1 illustrates that the two stationary portions at 10.1 nA differ, with that arrived at by depolarization from 8.2 nA having a higher rate and closer packed spikes than that arrived at by hyperpolarization from 12.8 nA. All this suggests that the discharge depends not only on the present current value but also on how it was reached.

iii) With sinusoidal SAO stretching (Figs. 1 and 2), the discharge modulation remains acceptably sinusoidal only sometimes and at best for about half a cycle when it fires (Brown and Stein, 1966; Chaplain et al., 1971; Diez Martínez et al., 1983; Vibert and Segundo, 1979). Hence, the consensus is that linear system analysis cannot provide exact results, except for cozily restricted domains (e.g., Borsellino et al., 1965; Sydness and Walløe, 1980). Using length inputs, Buño et al. (1984) found that a Gaussian noise raises the SAO mean rate and increases its static gain: the latter was true also within the bounds of the present experiments. Furthermore, the symmetric waveforms that crossed the resting length during lengthenings or shortenings had non-symmetric effects. For example, their influences upon the intervals they occupied differed: while lengthening zero-crossings advanced the next AP and were most effective early in the interval, the shortening ones delayed the AP and were most effective later. This is another sign of the asymmetric sensitivity, lengthenings being more effective as accelerators than shortenings as decelerators.

The repetitive firing of several sensory neurons under different conditions (i.e., step and sinusoidal stimuli) was modeled successfully by Fohlmeister and others (Fohlmeister, 1977; Fohlmeister et al., 1977a, b); a time and voltage dependent parameter improves the fit. The cycle histogram for the leaky integrator shown in their Fig. 1 is asymmetric around its midpoint, i.e., reveals hysteresis. Model-experimental discrepancies were particularly apparent when each AP was followed by modifications of the encoding, i.e., spike initiating, mechanism: such feedback is very real, carrying over from one interval to the next and being affected by successive arrivals. Conceivably, further complexities will be introduced by membrane inhomogeneities, either in the encoder region itself or over the entire neuron (Fohlmeister, 1979; Grampp, 1966).

The first-order afferent, or any neuron for that matter, argues Teorell (1971) compellingly, can be approached in terms of non-linear oscillation theory as a membrane system with intimate coupling between electrical, chemical, and mechanical forces and joint occurrence of changes in all spheres; this analog gains more and more credence as experimental evidence accumulates (e.g., Tasaki, 1982). The neuron would be a bag filled and surrounded by fluid whose membrane is porous, passing ions and water (containing fixed charges, it exhibits electro-osmosis), is visco-elastic opposing distension, and has a built-in current source producing polarizing currents (fuel-cell-like): in short, a leaky elastic balloon subject to filling by electro-osmosis and to externally induced deformations. These notions are formalized in a set of unavoidably non-linear differential equations derived from classical electrokinetics and non-linear mechanics. They imply a metastability whereby it can be triggered into oscillation by chemical, electrical or mechanical stimulation. Generator, postsynaptic, and action potentials are in fact membrane oscillations, less or more damped, respectively. Stretches or displacements lead to tension changes that provide the primary stimulus: the tension effect depends both on the amplitude and the velocity of the stretch or relaxation in a typical derivative-sensing process. The transmembrane pressure is the ultimate link in a mechanical-to-electrical concatenation; it is not clear, however, how tension then leads to electrical responses.

A mathematical model of systems characterized by hysteresis proposed by Chua and Bass (1972) relates the variables $x(t)$ and $y(t)$ by the differential equation:

$$\frac{dy}{dt} = W \circ \left[\frac{dx(t)}{dt} \right] h \circ [y(t)] g \circ [x(t) - fy(t)].$$

It provides static and dynamic hysteresis. Loops either widen, narrow, or do not change with increasing frequency, determined by the piece-wise linear function W that depends upon stimulus velocity. This model serves for the FAO including the static and dynamic hysteresis loops, the narrowing with stimulus frequency, and the flat extension observed with all frequencies. Loop widening with increasing stimulus frequency is common (e.g., when stretching skeletal muscle); narrowing, on the other hand, is rare. It happens in incandescent lamps because during each cycle, while at low frequencies the filament temperature and resistance follow, leading to a looped volt-ampere characteristic, at high ones the current varies so fast that there is not sufficient time for the filament to cool off. In fluorescent lamps the volt-ampere characteristics depend on the ionization state of the gas column: at low frequencies, the ionization lags as the current increases, creating a large voltage, and as it decreases the excess ions attenuate the voltage drop; at high frequencies the ionization tends to remain close to its average and the lamp behaves like a resistor with a high power factor.

The model of Chua and Bass (1972) serves for the FAO and SAO because it includes the static and dynamic hysteresis loops, the narrowing with stimulus frequency, and the flat extensions at all frequencies. However, it is difficult without further experimentation to correlate functional and structural characteristics with their non-linear functions.

References

Alvarez Buylla, R., Ramirez de Arellano, J.: Local responses in Pacinian corpuscles. Am. J. Physiol. **172**, 237–244 (1953)

Babcock Gove, P.: Third new international dictionary of the english language – unabridged. Springfield, MA: Merriam 1981

Borsellino, A., Poppele, R.E., Terzuolo, C.A.: Transfer functions of the slowly adapting stretch receptor organ of crustacea. In: Cold Spring Harbor Symposium on Quantitative Biology. **30**, 581–586 (1965)

Brown, M.C., Stein, R.: Quantitative studies on the slowly adapting stretch receptor of the crayfish. Kybernetik **3**, 175–181 (1966)

Buño, Jr., W., Bustamante, J., Fuentes, J.: White noise analysis of pacemaker-response interactions and non linearities in slowly-adapting crayfish stretch receptor. J. Physiol. **350**, 55–80 (1984)

Buño, W. Jr., Fuentes, J., Segundo, J.P.: Crayfish stret-receptor organs: effects of length-steps with and without perturbations. Biol. Cybern. **31**, 99–110 (1978)

Chaplain, R.A., Michaelis, B., Coenen, R.: Systems analysis of biological receptors. I. Quantitative description of the input-output characteristics of the slowly-adapting stretch receptor on the crayfish. Kybernetik **9**, 85–95 (1971)

Chua, L.O., Bass, S.C.: A generalized hysteresis model. IEEE Trans. CT-**19**, 36–48 (1972)

Diez Martínez, O.: Fast adapting stretch-receptor. Periodic and steady-state stimulation with and without perturbation. University of California, Los Angeles. Doctoral Thesis, 1981

Diez Martínez, O., Kohn, A.F., Segundo, J.P.: Pervasive locking, saturation, asymmetric rate-sensitivity and double-valuedness in crayfish stretch receptors. Biol. Cybern. **49**, 33–43 (1983)

Eyzaguirre, C., Kuffler, S.W.: Processes of excitation in the dendrites and in the soma of single isolated sensory nerve cells of the lobster and crayfish. J. Gen. Physiol. **39**, 87–119 (1955)

Fischer, W., Michaelis, B.: Frequency domain analysis of the dynamic properties of the encoder in the slowly-adapting crayfish stretch receptor neuron. Acta Biol. Med. Ger. **37**, 1665–1680 (1978)

Fohlmeister, J.F.: Excitation parameters of the repetitive firing mechanism from a statistical evaluation of nerve impulse trains. Biol. Cybern. **34**, 227–232 (1979)

Fohlmeister, J.F., Poppele, R.E., Purple, R.L.: Repetitive firing: a quantitative study of feedback in model encoders. J. gen. Physiol. **69**, 815–848 (1977a)

Fohlmeister, J.F., Poppele, R.E., Purple, R.L.: Repetitive firing: quantitative analysis of encoder behavior of slowly adapting stretch receptor of crayfish and eccentric cell of Limulus. J. Gen. Physiol. **69**, 849–877 (1977b)

Fujita, Y., Rosenberg, J., Segundo, J.P.: Activity of cells in the lateral vestibular nucleus as a function of head position. J. Physiol. **196**, 1–18 (1968)

Granit, R., Kernell, D., Shortess, G.K.: The behavior of mammalian motoneurones during long-lasting orthodromic, antidromic, and transmembrane stimulation. J. Physiol. **169**, 743–754 (1963)

Hartline, D.K.: Simulation of phase-dependent pattern changes to perturbations of regular firing in crayfish stretch receptor. Brain Res. **110**, 245–254 (1976)

Krnjevic, K., van Gelder, N.M.: Tension changes in crayfish stretch receptors. J. Physiol. **159**, 310–325 (1961)

Mountcastle, V.B., Poggio, G.F., Werner, G.: The relation of thalamic cell response to peripheral stimuli varied over an intensity continuum. J. Neurophysiol. **26**, 807 (1963)

Nakajima, S., Onodera, K.: Membrane properties of the stretch receptor neurones of crayfish with particular reference to mechanisms of sensory adaptation. J. Physiol. (London) **200**, 161–185 (1969a)

Nakajima, S., Onodera, K.: Adaptation of the generator potential in the crayfish stretch receptors under constant length and constant tension. J. Physiol. (London) **200**, 187–204 (1969b)

Segundo, J.P., Diez Martínez, O.: Stretch receptor responses to sinusoidal stimuli depend strongly on modulation depth and background length. Biol. Cybern. (in press)

Sydness, G., Walløe, L.: Transfer properties of the slowly-adapting stretch receptor of the crayfish abdomen. Acta Physiol. Scand. **109**, 439–445 (1980)

Tasaki, I.: Physiology and electrochemistry of nerve fibers. New York: Academic Press 1982

Teorell, T.: A biophysical analysis of mechano-electrical transduction. In: Handbook of sensory physiology, Vol. I. Loewenstein, W., ed. Berlin, Heidelberg, New York: Springer 1971, Chap. 10

Terzuolo, C.A., Washizu, W.: Relation between stimulus strength, generator potential and impulse frequency in stretch receptor of crustacea. J. Neurophysiol. **25**, 56–65 (1962)

Vibert, J.F., Segundo, J.P.: Slowly-adapting stretch-receptor organs: periodic stimulation with and without perturbations. Biol. Cybern. **33**, 81–95 (1979)

Vidal, J., Jeannerod, M., Lifshitz, W., Levitan, H., Rosenberg, J., Segundo, J.P.: Static and dynamic properties of gravity-sensitive receptors in the cat vestibular system. Kybernetik **9**, 205–215 (1971)

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