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Quantification of Responses From Proprioceptive Neurons in the Limbs of the Crab, *Cancer magister*

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ABSTRACT In the limbs of crustaceans, proprioception is monitored by chordotonal organs. One in particular, MC1, is arranged in a manner that is accessible for single unit recording of primary sensory neurons while simulating joint movement. The movement-sensitive cells are of two types, those sensitive to relaxation or to elongation of the chordotonal strand which corresponds to flexion or extension of the meropodite-carpopodite joint, respectively. A statistical method for the quantification of these movement-sensitive proprioceptive neuronal responses was implemented. This statistical index, eta^2, should allow neuronal responses recorded in different laboratories to be easily and quantitatively compared. In addition, an eta^2 value can be assigned to individual cells which represents a cell's consistency and degree to which the response is related to the stimulus. We found some cells to have a high eta^2 and to be consistent in their activity while other cells had a high degree of variability with low eta^2 values. *J. Exp. Zool. 284:629–636, 1999.* © 1999 Wiley-Liss, Inc.

Walking legs of crabs have six joints, each of which has a proprioceptive chordotonal organ. These joint receptors consist of an elastic strand into which are inserted the sensory endings of neurons, the neurons that signal movement, the direction of movement, and static position of the joint (Wiersma, '59; Bush, '65). Chordotonal organs that monitor joint movements are ubiquitous throughout *Crustacea* and *Insecta* (Mill, '76). Chordotonal organs in crustaceans are named by which joint they monitor (Alexandrowicz, '67); for instance, MC1 is an organ at the meropodite-carpopodite joint.

The MC1 chordotonal organ in the crab leg is of particular interest since the elastic strand forms a semi-planar sheet proximally. This shape apparently allows recruitment of subsets of sensory neurons for a differential response to the multi-directional forces generated during joint movement.

Because their cell bodies are large (10–40 µm in diameter) and located close to the organ that they monitor, the MC1 sensory neurons are easily identified and readily accessible for electrophysiological recordings. Within MC1 the proprioceptive neurons are arranged in a particular anatomical pattern; the static position-sensitive cells are separated from the dynamic movement-sensitive neurons. This allows the functional activity of individual dynamic movement-sensitive neurons to be assessed by recording from the large soma of single cells with the use of suction electrodes. Since the site of spike initiation is distal to the soma, the action potentials are easily recorded with an extracellular focal electrode placed on the soma.

We found it difficult to compare the responses of movement-sensitive neurons measured in our laboratory with other crustacean studies reported in the literature. Either the responses were not analyzed sufficiently quantitatively or multi-unit recordings were reported which did not allow for single cell analysis. Only one previous study recorded responses from single cells within a crustacean chordotonal organ while displacing the strand in order to assess individual neuronal function (Hartman and Boettiger, '67).

The purpose of this study is to more fully describe the functions of single neurons within a proprioceptive organ. In addition, we introduce a statistical method for the quantification of proprioceptive neuronal responses. This statistical index, eta^2, should allow neuronal responses re-

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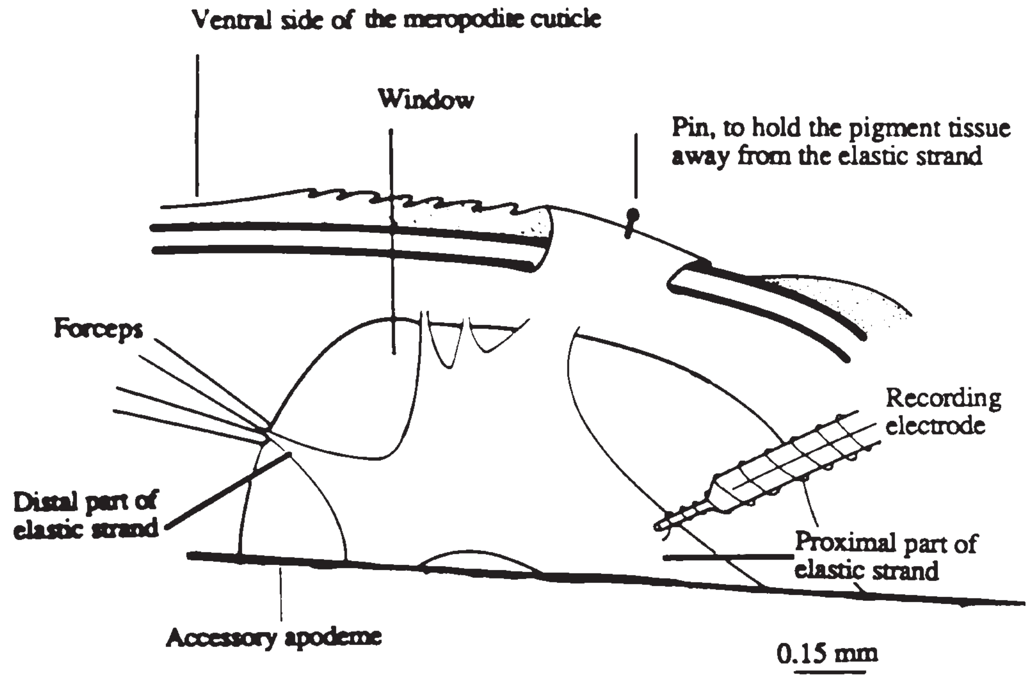
corded in different laboratories to be easily and quantitatively compared. Eta^2 is used commonly in psychology (Cohen, '65) and has a meaning similar to that of the coefficient of determination (the square of r). The difference between the index of eta^2 and r^2 is that eta^2 is not restricted to linear relationships (Mattson, '81). As described in earlier works (Cohen, '65), eta^2 is an index of correlation whose limits are zero and one and is thus analogous to, but not identical to, r^2. It describes any form of relationship involving a continuous dependent variable, while r^2 indexes linear relationships between two continuous variables.

MATERIALS AND METHODS

Male *C. magister* crabs, measuring 13–15 cm across the carapace, were used in this study. To expose the MC1 chordotonal organ the ventral connective tissue that articulates between the meropodite and the carpopodite was severed. The distal attachment of the MC1 strand is located at a slight indentation along the medial side of the cuticular ridge. To expose the MC1 strand fully, cuts were made longitudinally along the ventral midline and medially along the cuticle for the entire length of the meropodite at a level just dorsal to the medial condyle. The exoskeleton outside these two cuts was removed and discarded. The flexor tendon and muscle were removed, care being taken not to stretch the main leg nerve. The removal of the extensor tendon was accomplished by cutting the connective tissue between the tendon and its cuticular attachment, making certain not to detach the accessory tendon. To prevent damage to the MC1 strand and its neurons, it is easiest to find where the MC1 nerve bundle branches from the main leg nerve before cutting the nerve bundle. After the nerve branch was located it was cut on the proximal end to obtain the longest nerve bundle possible. With this approach there is no pulling on the MC1 neurons when removing the extensor tendon and main leg nerve. Each preparation was pinned to the Sylgard in the same position. The dissections were made based on consistent markings in the cuticle. The position of each pinned preparation was such that the elastic strand was in its normal position, midway between the extremes.

It is not possible to record from individual cells while moving the entire joint through the whole range of their normal excursions because of the large displacements of the entire preparation. To overcome this problem, the distal end of just the elastic strand of each chordotonal organ was stretched and relaxed over its normal in situ excursion range by a fine pair of forceps mounted to a modified AR4 25.4 cm loudspeaker (Fig. 1A). The forceps were attached to the base of the magnet in the center of speaker so they moved in and out as the speaker moved. Flexing of the meropodite-carpopodite joint causes elongation in the MC1 elastic strand, whereas extending the joint results in relaxation of the elastic strand. Measurements of intact chordotonal organs, made through a dissecting microscope with a calibrated eyepiece while moving the joint, provided the ranges to use for stretching and relaxing the in situ strand. The forceps were placed on the most distal end of the elastic strand and held so that the strand would be at a midrange of the displacement, as within the joint. This precaution helped to reduce variation of the recordings in each preparation. A servomechanism driven by waveform inputs from a Hewlett-Packard 3300A Low Frequency Function Generator controlled the elastic strand movements similar to that described previously (Wiersma and Boettiger, '59). The servomechanism was triggered by a pulse delivered at preselected intervals from a Grass S88 Stimulator. The 1 mm experimental displacements were driven by triangular waveforms with durations of 1, 2, and 4 sec, thus resulting in the rate of displacements at 1 mm/sec, 0.5 mm/sec, and 0.25 mm/sec respectively. This results in the time of relaxation and elongation to be equal in duration over the same excursion of displacement. These rates of displacement were chosen because they are similar to the animal's own movement rates. Permanent records of the trigger pulse, servomechanism waveform output, and neural output were stored on separate channels of video VHS tapes with a bandwidth of DC-10 KHz. The MC1 elastic strand is planar, with the distal part narrowing to an elongated flat strip

Fig. 1. **A:** The experimental arrangement for stretching the distal end of the chordotonal organ and recording from a neuron is indicated. The articulating membrane and cuticle on the ventral surface of the meropodite is removed exposing the accessory apodeme and the MC1 chordotonal organ. The forceps, mounted on a speaker, are placed on the distal attachment of the chordotonal organ for displacing the strand. **B:** Ventral view of an MC1 chordotonal organ within the first right walking leg of *Cancer magister*. The regional differences in neuron type are illustrated in the movement-sensitive cells being located in the proximal region of the organ whereas the static position-sensitive cells are located along the length of the organ on the medial edge. The movement-sensitive neurons with a clear center are relaxation-sensitive cells. Small cells within movement-sensitive nerve, not spotted, are stretch-sensitive cells.



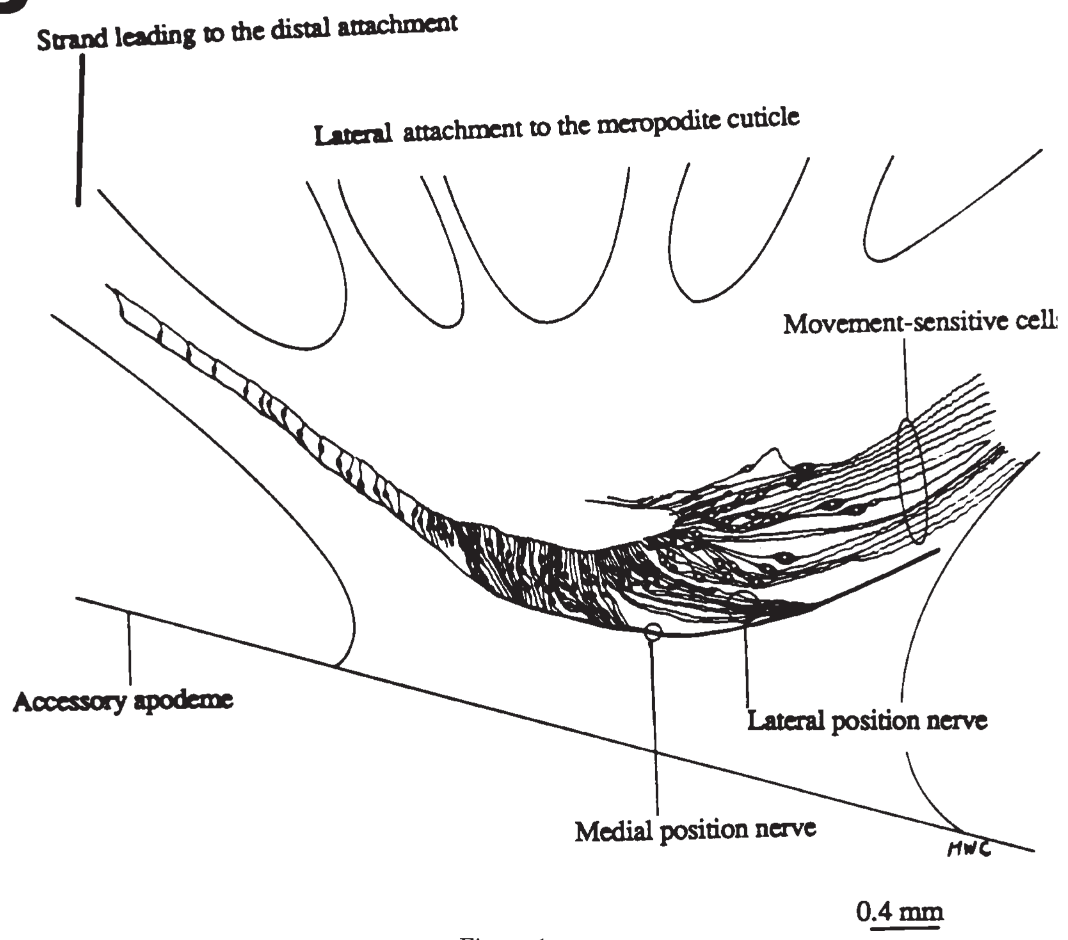


Figure 1.

that attaches to the cuticle. As a consequence, the proximal part of the strand is not displaced as much as the distal part during joint movements. The proximal movement is small enough to allow recording from the cell bodies of individual proximal region neurons during servomechanism-driven joint movement.

We have found that physiological saline diluted 50% with *C. magister* hemolymph provided a very stable bathing medium to maintain the chordotonal preparations for up to 6 hr without significant alteration in its response to movement (Cooper and Hartman, ’94). Whole blood was obtained by cardiac puncture from living crabs caught at the Point St. George Fisheries, Port Orford, Oregon. Blood pooled from many crabs was cooled in an ice bath to form a clot. The clot was discarded and the serum filtered through a Whatman sharkskin filter. It was placed in vials and stored at –80°C until needed.

Glass suction electrodes, with fire polished tips of final diameters of 10–30 µm and filled with the bathing medium, were used for recording spikes from cell bodies or axons (Hartman and Boettiger, ’67). The recordings from the cell bodies easily identified responses to individual cells. Five preparations were used for data analysis.

Data on VHS tapes were retrieved for analysis with the use of a Macintosh and the MacADIOS A/D converter. The data were acquired at a rate of 5.2 KHz. The spike trains were divided into a set number of bins, the number of bins depending on the rate at which the joint displacements were given. The length of each bin is one sixteenth of a second, regardless of the displacement rate. For each neuron, the same rate and magnitude of displacement was given 10 consecutive times with 10 sec between runs.

In order to convert to eta^2 values, data were placed into tables (as shown in Table 1), with each row representing one trial, and each column representing a time bin of 1/16 of a second in width. For a 1-second displacement (1 mm/sec) of the elastic strand repeated 10 times, there would be 16 bins (columns) in each row and 10 rows in a table to be analyzed. For a 2-second displacement (0.5 mm/sec) there would be 32 bins, and for a 4-second displacement (0.25 mm/sec) there would be 64 bins in each row. With this set number of bins for each rate of displacement, the bin width was kept constant at 1/16 of a second.

As indicated in Table 1, there were 10 trials at each rate of displacement. The ‘a’ represents the trial number where as ‘b’ represents the time bin.

TABLE 1. The data array in which eta^2 is calculated[1]

	Fraction of displacement	
	First 1/16th bin	Sixteenth 1/16th bin
Trials (a)	$Y_{a=1,\, b=1}$	$Y_{a=1,\, b=16}$
	$Y_{a=1,\, b=10}$	$Y_{a=10,\, b=16}$
	$\bar{Y}_{wb} = \sum_{a=1}^{a=10} Y_{ab/10}$	$\bar{Y}_{wbb} = \sum_{a=1}^{a=10} \sum_{b=1}^{b=16} Y_{ab/160}$

[1]d.f.: The d.f. between fractions of displacement is 15. The d.f. within fractions of displacement is 144.

Sum of squares: Between fractions = $SS_{bf} = 10\sum_{b=1}^{b=16}(Y_{wb} - \bar{Y}_{wbb})^2$

Within fractions = $SS_{wf} = \sum_{b=1}^{b=16} \sum_{a=1}^{a=10} Y_{ab} - \bar{Y}_{wb})^2$

Eta squared: $\text{eta}^2 = \dfrac{SS_{bf} / \text{d.f.}}{SS_{wf} / \text{d.f.}} = \dfrac{SS_{bf} / 15}{SS_{wf} / 144}$

The value of ‘b’ will range from 1→16 for a 1-sec displacement (1 mm/sec), 1→32 for a 2-sec displacement (0.5 mm/sec), and 1→64 for a 4-sec displacement (0.25 mm/sec). Table 1 represents a data set for a 1-sec displacement (1 mm/sec). The value within each bin, ‘Y’, represents the number of spikes recorded from the neuron. The mean number of spikes within bins of time is calculated for each time bin and is represented by the notation $\bar{Y}_{wb}$, whereas the notation $\bar{Y}_{wbb}$ represents the total mean within and between bins. The degrees of freedom (d.f.) for sixteen bins will be 15 (31 for 32 bins and 63 for 64 bins) between the fractions of displacement. The d.f. within the fractions is the total number of bins minus the number of time bins for that particular rate of displacement (160–16 for 1 mm/sec, 320–32 for 0.5 mm/sec, and 640–64 for 0.25 mm/sec). After the data is placed in a tabular form, the sum of the squares between fractions (SS_{bf}) and the sum of the squares within the fractions (SS_{wf}) can readily be calculated. Further calculation of the variance between the fractions and within fractions is accomplished by division of the associated d.f. value. The ratio of the variance between fraction and within fractions provides the index of eta^2 (Table 1). This type of index and tabular description has been successfully applied to activity recorded from respiratory neurons (Orem and Dick, ’83).

A high value of eta^2 indicates a strong relationship between analogous bins of the displacement for each trail. The eta^2 not only indicates the consistency of the response from trial to trial, but it will also quantify the degree of activity for a given

displacement of the elastic strand In other words, the eta^2 index allows one to know to what extent a movement-sensitive cell is movement-sensitive. In addition, the eta^2 allows a measure of magnitude to be assigned to the responses from particular proprioceptive neurons, which can be quantitatively compared to other neurons within a preparation and to identical neurons in different preparations.

The responses of 10 trials were averaged to obtain impulses-per-second of the movement-sensitive cells with bin widths of one-sixteenth of second. The averaged response was then converted to impulses-per-second and plotted as frequency versus real time. When the recording period was over, the anatomical arrangement of each preparation was determined by methylene blue staining. Anatomical drawings were made with a camera lucida attachment to a Wild dissecting microscope (Model M7A).

RESULTS

Location and function of the movement-sensitive neurons within the MC1 strand were characterized. It was determined that the movement-sensitive neurons are of two types, those responsive to relaxation or to elongation of the elastic strand. Staining of these neurons revealed that those with large somata (30–40 μm diameter) respond to relaxation of the strand; neurons with smaller somata (20–30 μm diameter) respond to elongation of the elastic strand. A representative preparation is shown in Figure 1B indicating the relative locations of these types of movement-sensitive cells. Cell bodies of movement-sensitive neurons are always found proximally in the elastic strand. Static position-sensitive cells, however, are arrayed in a line, starting in the middle of the strand and extending toward the distal end of the strand. These static position-sensitive cells send their axons to the medial and lateral position nerves (Fig. 1B). The responses from static position-sensitive cells have not been included in this study, so will not be further discussed.

Thirty-two movement-sensitive neurons from five MC1 preparations were analyzed. The frequency of responses to the three different displacement rates induced in the strand are plotted in Figure 2A. This plot is of the responses of the relaxation-sensitive cell shown in Figure 2B. This neuron maintained its firing frequency for the majority of the duration of the relaxation displacement. The firing frequency increases as the rate of displacement increases from 0.25 mm/sec to 1 mm/sec, but at each rate of displacement, the firing frequency is relatively constant. In comparison, a small percentage of movement-sensitive neurons did not maintain a constant firing frequency during a displacement. These types of neurons are considered to be responsible for the

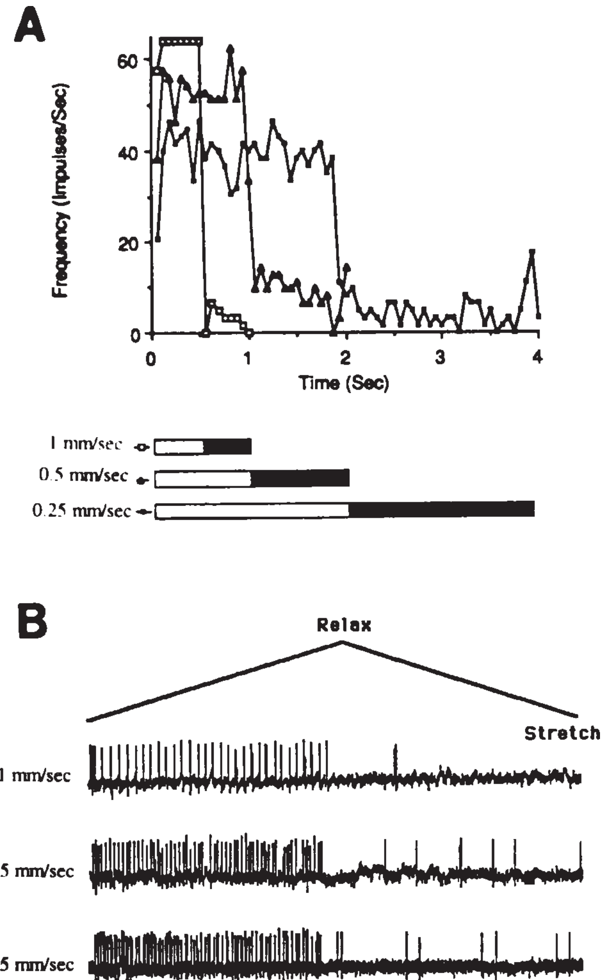


Fig. 2. The frequency plots and activity profile for a relaxation movement sensitive cell. **A:** As the rate of displacement is reduced from 1 mm/sec to 0.25 mm/sec, the firing frequency of the cell is also reduced. Note during the relaxation movement the cell maintains a relatively constant frequency. The open rectangles signify responses while relaxing the strand, while the closed rectangles represent stretching. The numbers next to the rectangles are the rate at which the strand was displaced. Each plot is derived from an average of 10 consecutive runs at each of the displacement rates indicated and the number of spikes were converted to impulses per second or frequency for each of the sixteenth-of-a-second bins. **B:** A typical response recorded from a relaxation-sensitive cell. The 1 mm displacement is shown at the top. The first train of spikes is from a 1-sec displacement (1 mm/sec) of the elastic strand. The middle tracing is from a 2-sec displacement (0.5 mm/sec). The bottom response is from a 4-second displacement (0.25 mm/sec).

range-fractionation of a movement that is observed (Hartman and Boettiger, '67).

Some neurons showed consistent responses during each of the 10 displacements, indicating that adaptation did not occur during the trials. Figure 3 shows the responses from trial 1, trial 2, and trial 3 of 1 mm/sec rate of displacement. The eta^2 value of 0.91 indicates that the responses were very similar for each trial. The recording shows responses from a stretch-sensitive cell and a relaxation-sensitive cell, but only the former was used to calculate eta^2. As shown, this neuron was responsive only to stretching of the strand. A cell in which the responses were not consistent among the 10 trials is shown in Figure 4 and, as expected, the eta^2 value is low, 0.38.

The data obtained for three different displacement rates of 32 movement-sensitive cells, taken from five different preparations, indicate that the consistency of activity is dependent on the displacement frequency (Table 2). As the displacement rate is reduced from 1 mm/sec to 0.25 mm/sec, the eta^2 value decreased in 30 out of 32 cases. This occurred in both relaxation- and stretch-sensitive cells. In Table 2 each cell is classified as either relaxation-sensitive (RSC) or stretch-sensitive (St).

To observe the degree to which eta^2 values change with the displacement rate, the eta^2 values from one representative cell in each prepara-

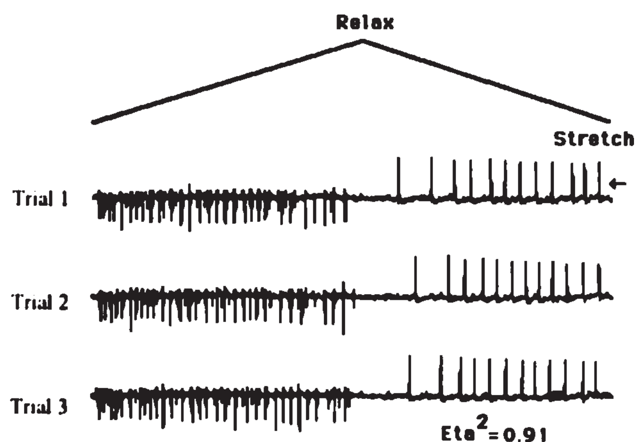


Fig. 3. Responses from movement-sensitive cells during three consecutive 1 mm/sec displacements of the elastic strand. Only the stretch-sensitive cell was analyzed for eta^2. This cell had consistent responses in each of the 10 trials. Activity from a neighboring relaxation-sensitive neuron is seen with the spike polarity in the opposite direction. This reversed polarity is due to differential recording of events outside the rim of the suction-electrode. The arrow represents the level used for the window discriminator.

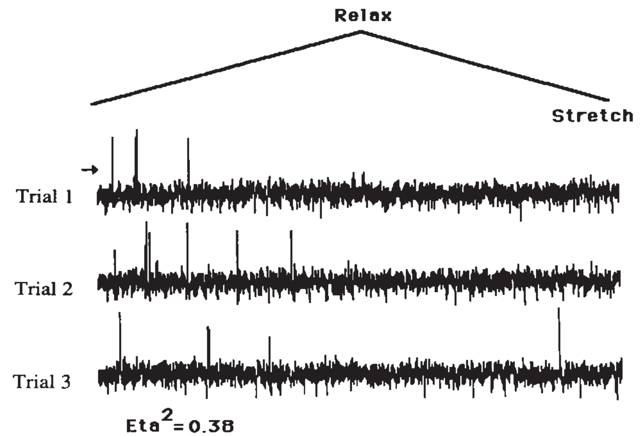


Fig. 4. A representative relaxation-sensitive cell did not show a consistent activity pattern in each of the ten displacements. The arrow represents the level of the window discriminator.

tion were plotted against displacement rate as shown in Figure 5. The increased number of degrees of freedom at lower rates of displacement (Table 1) is incorporated into the eta^2 measure. The change in degrees of freedom is the same for each cell as the rate of displacement is altered, but the eta^2 values did not change to the same degree for each cell. This indicates that some neurons are more sensitive to a change in the rate of movement than others. Similar graphs for each preparation indicated the same trend. To determine if there is any correlation of the consistency of a response to anatomical location of the sensory neurons in the chordotonal strand, the eta^2 values were listed for the cells in a figure drawn for each preparation. No relationship could be determined between eta^2 and cell location.

DISCUSSION

By quantifying the responses from single neurons, we have shown that a value can be assigned to individual cells which represents a cell's consistency of activity and degree to which the response is related to the stimulus. The stimulus, in this case, is directly correlated to joint movement. This analysis has shown that responses from proprioceptive neurons can be quantified and thus compared, with the use of the eta^2 index. Future studies measuring responses from proprioceptive neurons can be compared quantitatively if this eta^2 index is applied.

Responses with high eta^2 values have a high degree of consistency; for instance, the responses of a relaxation-sensitive cell with an eta^2 of 0.9

TABLE 2. Eta[2] values of movement-sensitive neurons

Cell	1.0 mm/sec[1]	0.5 mm/sec[1]	0.25 mm/sec[1]	Type[2]
Prep. 1				
1	0.81	0.75	0.42	RSC
2	0.83	0.82	0.79	St
3	0.38	0.11	NA	RSC
4	0.92	0.17	0.14	St
5	0.90	0.76	0.60	St
6	0.96	0.90	0.79	RSC
7	0.91	0.71	0.36	St
8	0.89	0.87	0.75	RSC
9	0.88	0.80	0.12	St
Prep. 2				
1	0.89	0.82	0.70	RSC
2	0.62	0.43	0.58	RSC
Prep. 3				
1	0.78	0.79	0.76	RSC
2	0.61	0.72	0.57	RSC
3	0.56	0.37	NA	St
4	0.53	0.45	0.28	RSC
5	0.55	0.32	0.11	RSC
6	0.51	0.37	0.32	RSC
Prep. 4				
1	0.77	0.53	0.26	RSC
2	0.64	0.44	0.25	RSC
3	0.57	0.39	0.32	RSC
4	0.74	0.85	0.56	RSC
5	0.89	0.82	0.69	RSC
6	0.89	0.86	0.71	RSC
7	0.69	0.19	0.13	RSC
8	0.46	0.19	0.13	RSC
9	0.80	0.45	0.34	RSC
10	0.31	0.22	0.13	RSC
Prep. 5				
1	0.89	0.67	0.30	St
2	0.76	0.69	0.65	RSC
3	0.91	0.74	0.36	St
4	0.65	0.74	0.59	RSC
5	0.84	0.58	0.10	RSC

[1]Rate at which the elastic strand was displaced.
[2]The type of response observed. Activity during relaxation of the strand, RSC, or during stretching of the strand, St. NA, no activity.

are more reliably coupled to relaxation than a relaxation-sensitive cell with an eta^2 of 0.4 at a rate of 1 mm/sec displacement. Eta^2 values above 0.5 occurred in 30 out of the 32 movement-sensitive neurons. As the rate of relaxation and stretch is decreased to 0.25 mm/sec for the same range of displacement, the eta^2 value decreased. This could be an indication that the neurons can not detect slow movements (0.25 mm/sec) with as much accuracy as at 1 mm/sec rate of displacement. A *Cancer magister* crab (14°C) walks within the range of displacement rates that were imposed in this study. Comparison of eta^2 values of proprioceptive neurons among Crustacea adapted to different rates of locomotion is underway.

We have shown how an eta^2 value for a proprioceptive neuron can vary depending on the rate at which a joint is moved. If different eta^2 values are to be compared among a variety of proprioceptive organs within crab limbs, the variables of bin width and the magnitude of displacement, as well as the rate, need to be controlled. We have analyzed some of the proprioceptive neurons in other chordotonal organs (MC2, CP1, and CP2) of *Cancer magister* to obtain eta^2 values; the trends are similar to those observed for neurons within the MC1 organ (Cooper, '89).

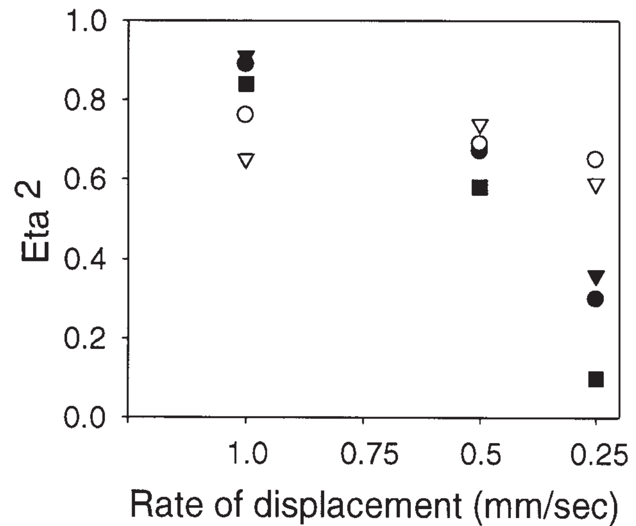


Fig. 5. Plot of eta^2 values for a given cell at the various displacement rates. There are five representative different neurons shown as indicated by the symbols that were displaced at the three rates (1 mm/sec, 0.5 mm/sec, and 0.25 mm/sec).

Relaxation-sensitive cells that maintained their firing frequency over the entire relaxation phase had eta^2 values similar to relaxation-sensitive cells that decreased their firing frequency during the relaxation phase. This indicates that even though the firing of a neuron might last over only a fraction of a displacement range, its frequency is consistently the same for each displacement. As one may expect, neurons displaying range-fractionation would likely be very consistent if they are to inform the CNS of the precise range and rate of a movement.

The original purpose of calculating this statistical index was to determine if there is an anatomical relationship among neurons with various eta^2 values within a chordotonal organ. No such anatomical relationship could be observed. Instead, we found that the eta^2 index is useful in the quantifying of neuronal responses and in determination of the degree to which responses from

proprioceptive neurons are altered by various conditions such as the presence of neuromodulators. In future studies, the eta^2 may prove valuable in the study of reflex arcs in coordinated locomotion, in kinesthetic computer modeling, and indexing regenerating sensory neurons (Cooper and Govind, '91; Hartman and Cooper, '94).

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LITERATURE CITED

Alexandrowicz JS. 1967. Receptor organs in the coxal region of *Palinurus vulgaris*. J Mar Biol Ass (UK) 47:415–432.

Bush BMH. 1965. Proprioception by chordotonal organs in the mero-carpopodite and carpo-propodite joints of *Carcinus meanas* legs. Comp Biochem Physiol 14:185–199.

Cohen J. 1965. Some statistical issues in psychological research. In: Wolman BB, editor. Handbook of clinical psychology. New York: McGraw-Hill. p 95–121.

Cooper RL. 1989. Joint and tension receptors in the limbs of the Dungeness crab, *Cancer magister*. PhD dissertation. Lubbock, TX: Texas Tech University Health Sciences Center.

Cooper RL, Govind CK. 1991. Axon composition of the proprioceptive PD nerve during growth and regeneration of lobster claws. J Exp Zool 260:181–193.

Cooper RL, Hartman HB. 1994. Responses of the bender apodeme tension receptors in the Dungeness crab, *Cancer magister*. J Comp Biochem Physiol 109A:479–486.

Hartman HB, Boettiger EG. 1963. The functional organization of the propus-dactylus organ in *Cancer irroratus* Say. Comp Biochem Physiol 22:651–663.

Hartman HB, Cooper RL. 1994. Regeneration and molting effects on a proprioceptor organ in the Dungeness crab, *Cancer magister*. J Neurobiol 25:461–471.

Mattson DE. 1981. Statistics: difficult concepts, understandable explanations. St. Louis: CV Mosby Co.

Mill PJ. 1976. Chordotonal organs of crustacean appendages. In: Mill PJ, editor. Structure and function of proprioceptors in the invertebrates. London: Chapman and Hall.

Orem J, Dick T. 1983. Consistency and signal strength of respiratory neuronal activity. J Neurophysiol 50:1098–1107.

Pasztor VM, MacMillan DL. 1990. The actions of proctolin, octopamine, and serotonin on the crustacean proprioceptors show species and neurone specificity. J Exp Biol 152:485–504.

Wiersma CAG. 1959. Movement receptors in decapod Crustacea. J Mar Biol Ass (UK) 38:143–152.

Wiersma CAG, Boettiger EG. 1959. Unidirectional movement fibers from a proprioceptive organ of the crab, *Carcinus maenas*. J Exp Biol 36:102–112.