Representation of Touch Location by a Population of Leech Sensory Neurons

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Lewis, John E. and William B. Kristan, Jr. Representation of touch location by a population of leech sensory neurons. J. Neurophysiol. 80: 2584–2592, 1998. To form accurate representations of the world, sensory systems must accurately encode stimuli in the spike trains of populations of neurons. The nature of such neuronal population codes is beginning to be understood. We characterize the entire sensory system underlying a simple withdrawal reflex in the leech, a bend directed away from the site of a light touch. Our studies show that two different populations of mechanosensory neurons each encode touch information with an accuracy that can more than account for the behavioral output. However, we found that only one of the populations, the P cells, is important for the behavior. The sensory representation of touch location is based on the spike counts in all of the four P cells. Further, fewer than three action potentials in the P cell population, occurring during the first 100 ms of a touch stimulus, may be required to process touch location information to produce the appropriately directed bend.

INTRODUCTION

To transmit information to the neuronal networks producing behavior, sensory systems must represent this information in neural spike trains. The accuracy of sensory representation limits the accuracy that any subsequent processing stage can achieve, the final stage being the production of behavior. In some sensory modalities, the accuracy with which different stimuli can be behaviorally discriminated is better than the spacing of the individual sensory receptors, a phenomenon called hyperacuity (Churchland and Sejnowski 1992; Heiligenberg 1991). Hyperacuity is usually attributed to neural population coding, or ensemble coding. Because this form of representation combines the inputs from many neurons, a stimulus does not uniquely correspond to activity in any single neuron but rather is represented by population activity.

Three major factors determine the accuracy of representation by neural population coding (Abbott 1994). First is the nature of the neural spike trains of individual neurons. For example, the downstream networks might be sensitive either to the average spike count or the precise timing of individual spikes. Second is the specificity of the responses of individual neurons to different stimuli (i.e., the width of the neuronal tuning curves). Third is the variability of the neuronal response to identical stimuli. Some studies quantified all three factors for a subset of the neurons involved in processing a particular sensory stimulus (e.g., Miller et al. 1991; Wheat et al. 1995), but none have yet characterized an entire sensory system in this way.

We address these issues in a small network that maps the location of a touch to a directed motor output. This network underlies the local bend behavior of the medicinal leech (Kristan et al. 1982; Lewis 1997; Lockery and Kristan 1990a,b). The local bend is a withdrawal reflex elicited by a touch to the leech body wall. Coordinated contraction of the longitudinal body wall musculature results in a bend directed away from the touched site. The behavioral accuracy, as measured by the difference between the bend direction and stimulus location, is ~8% [root-mean-squared (RMS) error] (Lewis and Kristan 1998a). A stimulus that elicits a local bend activates two sets of mechanosensory neurons, T and P cells. Previous studies suggested that the T and P cells encode different aspects of a mechanical stimulus; the T cells are thought to encode the velocity of a moving mechanical stimulus, whereas the P cells are more likely to encode the magnitude of the stimulus (Carlton and McVean 1995).

We characterize the sensory representation of touch location to provide a sensory context for the measured behavioral accuracy. We show that a population code involving either the T cell or the P cell spike counts encodes touch location on the body perimeter with an accuracy better than 3% (RMS error). The accuracy of either population is sufficient to account for the behavioral accuracy. In fact, despite the ability of T cells to encode touch location more accurately than do the P cells, our behavioral measurements show that the P cells contribute the major information about touch location to the networks underlying the local bend. Remarkably, this information could be transmitted during the first 100 ms of stimulus presentation, when the population of P cells has fired less than three action potentials, and before muscle contraction begins.

METHODS

All experiments were performed on 1.5- to 2.5-g leeches, Hirudo medicinalis, obtained from Leeches USA (Westbury, NY). Animals were anesthetized in ice-cold leech saline. Surgical methods were similar to those described previously (Muller et al. 1981). The leech has a body plan consisting of 21 midbody segments (denoted MS1–MS21) with a corresponding segmental nerve cord (1 ganglion per segment). We used three variations of semiintact preparations consisting of a single innervated segment (ganglion–body wall preparation) depending on the requirements of the experiment: 1) whole segment preparation, in which all nerves in a single segment were intact, 2) lateral hemisegment preparation, in

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TABLE 1. Stimulus intensity and filament properties

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Force, mN</th>
<th>Filament Length, cm</th>
<th>Filament Material</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.35 ± 0.02</td>
<td>1.4</td>
<td>Tungsten (0.001 in.)</td>
</tr>
<tr>
<td>2</td>
<td>1.1 ± 0.3</td>
<td>0.9</td>
<td>Tungsten (0.002 in.)</td>
</tr>
<tr>
<td>3</td>
<td>11 ± 0.4</td>
<td>2.0</td>
<td>Nylon (2 200 µm)</td>
</tr>
<tr>
<td>4</td>
<td>22 ± 0.3</td>
<td>1.6</td>
<td>Nylon (2 200 µm)</td>
</tr>
<tr>
<td>5</td>
<td>37 ± 1.1</td>
<td>0.9</td>
<td>Nylon (2 200 µm)</td>
</tr>
</tbody>
</table>

The force is shown as means ± SD from 5 trials with each filament. Filaments of different material (cross-sectional diameter indicated by () and lengths were calibrated using a force transducer (Biocom, Culver City, CA).

which the right or left one-half of the body wall remained innervated to a single ganglion, and 3) dorsal hemisegment, in which the right and left dorsal posterior nerves remain intact, and all others were cut. These ganglion–body wall preparations allowed electrophysiological recording to be made from the nervous system while mechanical stimuli were delivered directly to the body wall (Kristan 1982; Nicholls and Baylor 1968).

Mechanical stimulation was performed as described previously (Lewis 1997; Lewis and Kristan 1998a). Briefly, stimuli (500-ms duration) were delivered to the body wall with a solenoid-driven push rod with various filaments attached to one end (Table 1). We used standard intracellular recording techniques (Muller et al. 1981) with sharp electrodes (20–30 MΩ) and the Axoclamp-2B amplifier (Axon Instruments, Foster City, CA). Neurons were identified on the basis of their physiology and location within the ganglion (Muller et al. 1981). Data were collected with Axotape 2.0 and Digidata 1200 PC-based data acquisition system (Axon Instruments). Off-line data analysis was performed with Axotape 2.0 and Axograph 2.0 (Axon Instruments), Systat 5.2 (Systat, Evanston, IL), and Microsoft Excel.

Body wall coordinate system

We define a coordinate system for the body wall perimeter as follows (see also Lewis 1997; Lewis and Kristan 1998a). The dorsal and ventral midlines correspond to the stimulus locations S = 0° and S = ±180°, and the left and right lateral midlines correspond to S = −90° and S = +90° respectively.

Intensity tuning

To assess intensity tuning of the local bend behavior, we measured the tension produced by longitudinal muscles as an indicator of local bend strength (Kristan 1982; Lewis 1997; Lockery and Kristan 1991). In ganglion–body wall (MS9 or MS10) preparations, we measured muscle tension evoked by mechanical body wall stimuli at the same location (S = 45°). Sutures (6–0, Ethicon, Somerville, NJ) were tied to the edges of the excised body wall (outside the innervated segment) and attached to force transducers (Biocom). Stimuli were given every 2 min. The response was quantified as the peak tension (subtracted from baseline) generated during a given trial. Similar experiments were performed while recording intracellularly from the mechanosensory neurons. Responses were quantified by the number of action potentials that occurred during a 700-ms period beginning at stimulus onset.

Spatial tuning of the mechanosensory neurons

We measured tuning curves for the sensory neurons as a function of stimulus location on the body wall perimeter. For these experiments, we used a 22-mN stimulus. This intensity has the advantage of being closer to the plateau part of the P cell intensity tuning curve (Fig. 6), and therefore any small fluctuations in stimulus intensity will result in relatively small changes in P cell response. In preparations consisting of multiple innervated segments, a stimulus could activate T and P neurons from neighboring ganglia through their respective secondary receptive fields (Muller et al. 1981). The 22-mN stimulus did not activate the secondary fields of P neurons and activated those of the T neurons to <10% of their maximum response (Lewis and Kristan 1998a). Typically, recordings from two neurons were made while mechanical stimuli were delivered at different locations in random order at an interval of 30–60 s. Although the local bend response can habituate to stimuli delivered at these intervals (Lockery and Kristan 1991), we found the responses of the mechanosensory neurons to be consistent for intervals as short as 15 s in preliminary experiments.

The responses of the mechanosensory neurons were quantified by counting the number of action potentials elicited during a 700-ms window after stimulus onset. Tuning curves were constructed by plotting the mean responses as a function of stimulus location. The tuning curves were fit to a cosine function (see RESULTS), and the quality of the fit was given by the R² value. The R² value indicates the proportion of the variance in the data that is accounted for by the regression curve. For the analysis summarized in Fig. 7, tuning curves were constructed for different encoding times (i.e., time from stimulus onset) by counting action potentials for different time windows (see RESULTS). To compare tuning curves for the different encoding times we plotted the mean normalized spike counts against one another and performed a linear regression. We then used an F test to determine whether the slope of the regression line was significantly different from one.

Spike train decoding

We estimate the accuracy of the sensory representation of stimulus location by using an approach described by Salinas and Abbott (1994). This approach involves using the population vector method for decoding the activity of a population of neurons (e.g., Georgopoulos et al. 1986). The population vector, in the context of this study, is the sum of the preferred stimulus locations of each neuron considered, weighted by the corresponding spike counts. The population vector method, when compared with other decoding methods, produces the smallest maximum decoding error when the preferred locations are uniformly distributed over the input space (Salinas and Abbott 1994). We use this method for convenience, as it is particularly appropriate for neural populations with cosine tuning curves. Although, for these purposes, a decoding method need not be physiologically realistic, it appears that the population vector method is actually implemented by the local bend network (Lewis and Kristan 1998b).

Monte Carlo simulations are performed such that in one iteration a set of integer spike counts is generated, based on the firing statistics for each neuron at a given stimulus location, S. In other words, the spike counts are drawn from a random distribution with mean and SD given by each neurons’ tuning curve and the corresponding neuronal variability (Fig. 4), respectively. Given the set of spike counts, an estimate of stimulus location, Ș_est, is made by using the population vector method. The error, unless otherwise stated, is defined as the distance between the estimate Ș_est and actual stimulus location S, expressed as a percentage of 360°. This process is repeated for 3,000 iterations (each iteration having a different set of spike counts) for a given stimulus location to obtain an estimate of the RMS error at that location.

The RMS error is a measure of accuracy and was previously related to the transformation, or mutual information, which quantifies information transmission between an input and an output (Theunissen and Miller 1991). The transformation can describe the amount of information about stimulus location that is encoded.
Spatial tuning: response as a function of stimulus location

To assess the ability of the T and P cells to encode the location of a mechanical stimulus on the skin, we first characterized their average response properties as a function of stimulus location around the body perimeter. Figure 2 shows tuning curves of normalized spike count versus stimulus location for the right T and P cells. These curves represent the averages over six different animals. Both T and P cells exhibit broad and overlapping tuning curves, with peaks distributed around the body perimeter. By using the common convention, we refer to the stimulus location that produces the maximum response for a given cell as that cell’s preferred location. The preferred locations serve to identify the different cells; $T_D$ and $P_D$ are activated most by dorsal stimuli, $T_V$ and $P_V$ by ventral stimuli, and $T_L$ by lateral stimuli.

The shapes of these tuning curves, along with the periodic nature of the dependent variable (i.e., stimulus location, $S$, on the body perimeter varies between $-180°$ and $+180°$), suggest that a cosine function might be an appropriate summary of the data from both cell types. We fit the means for each cell from each individual animal to the cosine function in Eq. 2

$$f(S) = \frac{R_{max}}{1 - A \{ \cos (S - S_0) - A \}}$$

This formulation was used previously (e.g., Miller et al. 1991) and is convenient because $R_{max}$ is the maximum re-

FIG. 1. Typical mechanosensory spike trains. Intracellular recordings from the T and P mechanosensory neurons during a 500-ms mechanical stimulus to the body wall (22 mN). The T cell exhibits rapidly adapting responses at both stimulus onset and offset, whereas the P cell shows a comparatively tonic response.

FIG. 2. Mechanosensory neuron tuning curves to stimulus location. Mean normalized spike count is plotted for different stimulus locations for the (A) 3 types of T cells and (B) 2 types of P cells (mean ± SE, 6 animals). The mean spike counts at the tuning curve peaks were 15.1 (T cells) and 7.2 (P cells).
response, $S_o$ is the preferred location, and $A$ is the threshold (associated with the width of the curve at the zero crossing). In all animals, the T-cell responses were well described by this function ($T_D$, $R^2 > 0.88$; $T_L$, $R^2 > 0.80$; $T_V$, $R^2 > 0.91$). The same was true for the $P_{TD}$-cell responses ($R^2 > 0.85$). The fits to the $P_V$-cell responses were not quite as good, with $R^2 > 0.77$ (except for one animal, where $R^2 = 0.64$). A potential source of this discrepancy is the apparent skewness toward the lateral midline in the average $P_V$ tuning curve (Fig. 2B). However, we found that the data from individual animals were not fit better by a skewed function (Batschelet 1981). By comparing the parameter values corresponding to the fits from all the data, we found that a simpler model might describe the tuning properties of these cells. The values for the parameter $A$ were close to zero and were not significantly different between cells ($P > 0.05$) in every case but one ($P_{TD}$ vs. $T_L$, $P < 0.05$; Dunn's multiple comparison, postest). Further, the values for the parameter $S_o$ were all close to those expected when each of the P and T cells have preferred locations evenly distributed around the body perimeter (±45 and ±135° for P cells and ±30, ±90, and ±150° for T cells). For these reasons, we tested whether the entire population of sensory cells could be described by identical cosine tuning curves distributed evenly around the body perimeter. We pooled the data from all cells by defining a relative stimulus location, $S^*$, as the difference between the actual stimulus location and the hypothesized preferred location for that cell (Fig. 3). A simple cosine function $f(\theta)$ fit these transformed data well (Eq. 2: $R_{\text{max}} = 0.9$, $A = 0$, $S_o = 0$; $R^2 = 0.80$), suggesting that the T and P sensory neurons exhibit cosine tuning curves with preferred locations at regular locations around the body wall, as suggested from previous qualitative studies (Nicholls and Baylor 1968).

### T- and P-cell response variability

In addition to a neuron’s average tuning properties, another important factor affecting stimulus encoding is the trial-to-trial variability of its response. We characterize the variability of the T- and P-cell—normalized spike count as in other systems (e.g., Miller et al. 1991) by plotting the SD versus the average response for a number of trials in a single cell (Fig. 4). There was a significant relationship between the SD and the mean for both cell types ($P < 0.001$). The dotted lines in each panel (Fig. 4, A and B) show the regression lines describing this relationship. The $y$-intercept was not significantly different from zero for the T-cell data ($P > 0.05$) but was significant for the P-cell data ($P < 0.001$). The slope of these regression lines (0.17 for T cells; 0.19 for P cells) provides a measure of the coefficient of variation in the responses. Most cortical neurons fire with coefficients of variation near 1 but in some cases can have values as low as 0.2 (Gur et al. 1997).

Another aspect of response variability with potential implications for stimulus encoding is correlated firing between neurons (e.g., Britten et al. 1992). The method we used to estimate encoding accuracy in the following section assumes that the responses of different neurons are uncorrelated. In our case, this is justified as we found no evidence for correlated responses between pairs of T or P cells during dual
Quantifying the accuracy of stimulus encoding

With the characterization of the T- and P-cell tuning curves (Figs. 2 and 3) and their response variability (Fig. 4), we used a previously described stimulus reconstruction method, the population vector method (Salinas and Abbott 1994), to quantify how accurately these sensory neurons encode stimulus location (see METHODS). Accuracy is given by the RMS error of the stimulus reconstruction. The preferred locations of cells within each group are uniformly distributed around the body perimeter, so decoding based on either T or P cells would be perfect (i.e., no error) if there were no variability in the cells’ responses. This is because stimulus location is accurately projected onto a set of coordinate axes (i.e., the preferred location vectors) by virtue of the cosine tuning curves and can thus be accurately reconstructed from this coordinate system.

Shown in Fig. 5A are the idealized tuning curves for all the cells used in the decoding process. The error bar in each panel is the SD (from Fig. 4) at the tuning curve peak. Figure 5B shows the decoding error as a function of stimulus location for each cell type. Decoding with P-cell spike trains results in an RMS error over all stimulus locations of 2.9% (i.e., 10°). The error is smaller than average for stimuli near the preferred location of each P cell. At each of these stimulus locations, a single P cell has a maximal spike count, and all other cells have spike counts near 0 on average. The resulting population vector is dominated by the preferred location of this maximally active P cell, and this preferred location is close to the actual stimulus location in these cases, resulting in a small error. Decoding with T-cell spike trains results in a smaller error (1.2% or 4°) that does not depend on stimulus location. The smaller overall error is due mostly to less variability in the neuronal responses of T cells (compare panels A and B in Fig. 4). Also contributing to the smaller error is the increased number of cells and the greater
tension measurement site (45 mN, the T_D-cell spike count does not change significantly. factor (i.e., the total number of spikes; see Fig. 7 Å SE; 5 animals) are plotted vs. stimulus intensity. Re-
sponses of the T and P cells were measured by the normalized spike count, and the behavioral response was measured by normalized peak body wall tension.

extent to which their tuning curves overlap. In another study, we characterized the local bend response as a function of stimulus location (Lewis and Kristan 1998a). The RMS difference between stimulus location and the direction of the evoked bend (i.e., behavioral error) was 8% and is shown in Fig. 5B for comparison. With the stimulus encoding by the sensory neurons more than twice as accurate as the behavior, it is clear that a neural code for stimulus location involving only the spike count contains more than enough information to account for the behavior.

Relative importance of T and P cells

Because both T and P cells independently encode stimulus location with an accuracy greater than the behavioral accuracy, we tested whether the encoded information from each cell type is actually used by the local bend networks.

The thresholds and specific modalities differ for each of these cell types; T cells have a low threshold and are most sensitive to the velocity of indentation of the body wall by mechanical stimulation (Carlton and McVean 1995), whereas P cells have a higher threshold and respond best to changes in the magnitude of body wall indentation. To test the relative contributions of T and P cells to local bending, we quantified the behavioral output and response of the sensory cells to mechanical stimuli of different intensities. We limited our studies to one stimulation site and one body wall tension measurement site (45° for both). At this stimulus location, one P cell (right P_D) and two T cells (the right T_D and T_L) are activated to >70% of their maximum level, and a third T cell (the left T_D) is activated to ~25% of its maximum (see Fig. 5A). The remaining cells are not activated.

Figure 6 shows the normalized spike count of the P_D and T_D (mean ± SE, 5 animals). For stimulus intensities >1 mN, the T_D-cell spike count does not change significantly. The P_D-cell spike count increases substantially over the range of 1–37 mN (Fig. 6). [A third type of mechanosensory neuron, the high-threshold N (nociceptive) cell, never produced more than one spike for the largest stimulus intensity shown here. We did not investigate stimulus intensities greater than these because the N cells would be activated to a greater extent and produce other behavioral responses.] By using the same set of stimuli in a different group of five animals, we found that the mean tension response increases with stimulus intensity in a manner similar to P-cell activation but quite different from that of T-cell activation. The T-cell spike count saturated at stimulus intensities >1 mN; at this intensity, the behavioral response was only 25% of the response produced by the 37-mN stimulus. In agreement with a previous study with a different approach (Kristan 1982), this result suggests that P cells provide the major input for controlling the magnitude of the local bend response.

However, it is still possible that the T cells provide spatial information, but their influence is gated by the P cells (i.e., the information is not manifest in the behavior unless the P cells are sufficiently active). To test this possibility, we attempted to bias the tension response (measured at 45°) evoked by a mechanical stimulus (S = 45°; 22 mN) with simultaneous intracellular stimulation of the T_D cell (>20 Hz, 1-s trains). If the T cells provide spatial information, the evoked tension should be diminished by T_D stimulation caused by an effective shift in the bend direction to a more ventral location (toward the preferred location of the T_D cell). If the T cells provide nonspecific amplification to the local bend response, the tension response should increase. We found that T_D stimulation had no effect on the tension response measured at 45° (P > 0.05, 2 animals, 8 trials), indicating that the T cells play no detectable role in this response. In similar experiments, intracellular P-cell stimulation produced a significant and predictable effect on the behavior (Lewis and Kristan 1998b). From these and previous results, we conclude that the P cells are the major carriers of spatial information to the local bend network.

Varying encoding time

In Fig. 5 we showed that the decoding error with P-cell spike trains was ~5%. These estimates were made for spikes occurring for an entire 700-ms interval after stimulus onset. The latency for a behavioral response (muscle tension) is typically ~200 ms. How much information is available at this short latency? To address this question, we calculated the mean decoding error for different encoding times (i.e., time since stimulus onset). An encoding time of 700 ms corresponds with the control condition (Fig. 5). We measured the tuning curves and spike count variability again but only considered spikes that occurred in the time window corresponding to a particular encoding time. For all encoding times tested, the tuning curves, normalized to maximum response, were not significantly different from the control (P > 0.05). In addition, the variability in the normalized spike count for the different integration times was not significantly different from control (P > 0.05). This means that the tuning curves in all cases differ only by a scaling factor (i.e., the total number of spikes; see Fig. 7A); for longer encoding times, more spikes are available to contribute information.

Again, with the tuning curves and the variability of the responses, we estimated the decoding error for different encoding times (Fig. 7B). At 100 ms, the error decreases below that found in the behavior, and interestingly counting spikes...
given at one of the preferred locations produces only 2.1 spikes (Fig. 7A). Averaging over all stimulus locations, the total number of spikes elicited in all four P cells by any single stimulus is \(\sim 2.7\) (i.e., assuming cosine tuning as in Fig. 5A), translating to about 1.1 bits per spike. Other studies estimated similar values for the information content of a single spike (e.g., Theunissen et al. 1996). This may be purely coincidental, or perhaps more interestingly it may point to some fundamental property of spike encoding.

**DISCUSSION**

We characterized the mechanosensory system responsible for eliciting the local bend reflex. The focus of this characterization was to determine the accuracy with which this sensory system encodes the location of a touch stimulus on the leech body wall. The behavior consists of a bend directed away from the stimulus, and the only information about stimulus location available to the networks that produce the behavior is encoded by the mechanosensory neurons. Thus the accuracy of stimulus encoding by these neurons limits the behavioral accuracy. Conversely, any model of sensory encoding must be able to account for the behavioral accuracy. The ability to measure sensory encoding in a completely characterized behavioral system is a unique and important aspect of this study, allowing us to test ideas about neural coding directly.

Our studies have several implications regarding the functional mechanisms of the local bend network. We confirm the previous hypothesis that, of the two classes of mechanosensory cells activated by a mechanical stimulus, the P cells are the major source of information about stimulus location for the local bend network. Although the T cells apparently encode information more accurately than the P cells, this information does not seem to be used by the local bend network. Stimulating T cells electrically did not bias the behavior in any way; whereas similar stimuli given to P cells produced a dramatic effect on the behavior (Lewis and Kristan 1998b). This illustrates the importance of considering behavioral significance when evaluating encoding properties of individual neurons.

The P cells apparently represent stimulus location by a population code. Because their tuning curves are well described by a set of cosine functions with peaks evenly distributed around the body perimeter, the P cells are well suited to accurately encode stimulus location (Salinas and Abbott 1994). For an optimal decoding process, the accuracy of stimulus decoding is limited only by the variability in the neuronal responses. Because of the cosine tuning curves and uniform distribution of preferred locations, the population vector method is optimal for decoding the P-cell spike trains. In this special case, the variability of P-cell spike trains allows decoding that is more than twice as accurate as the behavior. This is true when the sensory information is contained only in the P-cell spike count, and no details of spike timing are required. In addition, the sensory information in the first 100 ms of the P-cell spike train is still sufficient to account for the behavior. In this interval, only a few P-cell spikes are produced at most, and the movement related to the behavior has not begun. It will be interesting to see whether different stimulus durations have a similar effect on...
behavioral accuracy. (The additional spikes would, of course, influence other features of the response, such as its amplitude.)

The lower accuracy at the behavioral stage, compared with the accuracy of P-cell decoding, could be due to noise at the levels of the interneurons, motorneurons, and muscle, or it could be due to the algorithm implemented by the local bend network to process P-cell input. Salinas and Abbott (1995) proposed a strategy for developing the set of connections between sensory and motor networks that enables the accurate transfer of information. The known synaptic connections among neurons in the local bend network (Lockery and Kristan 1990b) are consistent with this hypothesis (Lewis 1997). It would appear then that neuronal variability is the limiting factor in behavioral accuracy (Lewis and Kristan 1998b). Characterizing the variability of the rest of the network will enable us to test this hypothesis.

Neuronal population coding has been studied in a number of diverse systems (e.g., Georgopoulos et al. 1986; Lee et al. 1988). In particular, our study is complementary to two similar studies in other mechanosensory systems, one in crickets and the other in humans. The accuracy of representation of the direction of a wind stimulus in the cricket cercal system was characterized in detail (Miller et al. 1991; Theunissen et al. 1996). Specifically, these studies characterized the encoding performance of a set of four interneurons that appear to be the major carriers of information on wind direction for low-amplitude stimuli (Theunissen et al. 1996). The tuning of these interneurons to wind direction was similar to the P-cell tuning shown in this study. The neuronal variability was less and the mean spike counts were greater, and subsequently the accuracy of stimulus representation was slightly higher in these interneurons than we have found for the P cells (RMS error of 1–2% compared with 3% error). It will be interesting to see how the performance of these interneurons in the cricket relates to the behavioral response that consists of a body turn away from the wind source. Some behavioral studies addressed this issue (e.g., Tauber and Camhi 1995), but the higher wind velocities used in these studies make comparisons with the studies of Miller and coworkers difficult. More recently, studies focused on the encoding of dynamic stimuli by the cricket interneurons (e.g., Theunissen et al. 1996). This may be an interesting approach to apply to the T cells, whose transient response properties suggest that they encode the dynamics of mechanical stimulation accurately (Carlton and McVean 1995).

In another study, Wheat et al. (1995) characterized the response properties of the RA and SA afferents underlying touch perception in humans and monkeys. These afferents are similar to the T and P mechanosensory neurons in the leech in a number of ways. The qualitative firing patterns are similar for both sets, rapid adaptation in the case of RA and T neurons and slow adaptation in the case of SA and P neurons. In addition, the activation thresholds appear to be similar, although different definitions of threshold complicate this comparison. When threshold is defined as the stimulus intensity that results in a response in 50% of trials, the RA and SA afferents have thresholds of ≈0.5 mN (RA), 1 mN (SAI), and 7.5 mN (SAII) (Johansson et al. 1980). Although we have not quantified threshold in this way, inspection of Fig. 6 suggests that such thresholds for the T and P cells would be of the same order of magnitude (and perhaps slightly lower) as those measured for the RA and SA afferents. To assess the accuracy of representation of touch location, Wheat et al. (1995) quantified the tuning curves and response variability of the RA and SA afferents. Although they did not use quantitative methods, they concluded on qualitative grounds that the psychophysical performance could be accounted for by the neuronal responses. By showing that the response variability of the neurons did not proportionately decrease by counting spikes for >200 ms, they suggested that touch stimuli of longer duration should not enhance psychophysical performance. This conclusion is remarkably similar to our observations in this study.

The study of information processing in neuronal networks addresses three important questions. What stimulus features are being encoded? How is this information represented in neuronal spike trains? How is this representation translated or extracted by downstream networks? Quantitative approaches are being developed and effectively applied to each of these questions (e.g., Rieke et al. 1997). When interpreting the results of such studies, it is important to consider that, although a set of neurons encodes a certain amount of information, downstream networks may not extract all of this information. Our results suggest that information is lost through the local bend networks. The accuracy of sensory encoding is apparently much higher than that reflected by the behavior. We may have overestimated the accuracy of P-cell encoding by not considering the proper mechanism of representation (e.g., spike count during a certain time interval). However, because encoding time did not greatly affect our results, this is probably not the case. In the least, our results emphasize the importance of quantifying encoding accuracy (i.e., information) at different stages of a neural pathway.

We present a quantitative description of the complete set of mechanosensory inputs to the local bend network of the leech. The level of detail to which we can characterize the accuracy of sensory representation and behavior has not yet been possible in other systems. The evidence for sensory population coding in this relatively small network of identifiable neurons presents a unique opportunity to investigate the detailed mechanisms of information transfer through different layers of a population coding network.

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REFERENCES


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