Putative lateral inhibition in sensory processing for directional turns

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Yafremava LS, Gillette R. Putative lateral inhibition in sensory processing for directional turns. J Neurophysiol 105: 2885–2890, 2011. First published April 13, 2011; doi:10.1152/jn.00124.2011.—Computing targeted responses is a general problem in goal-directed behaviors. We sought the sensory template for directional turning in the predatory sea slug Pleurobranchaea californica, which calculates precise turn angles by averaging multiple stimulus sites on its chemotactile oral veil (Yafremava LS, Anthony CW, Lane L, Campbell JK, Gillette R. J Exp Biol 210: 561–569, 2007). Spiking responses to appetitive chemotactile stimulation were recorded in the two bilateral pairs of oral veil nerves, the large oral veil nerve (LOVN) and the tentacle nerve (TN). The integrative abilities of the peripheral nervous system were significant. Nerve spiking responses to punctate, one-site stimulation of the oral veil followed sigmoid relations as stimuli moved between lateral tentacle and the midline. Receptive fields of LOVN and TN were unilateral, overlapping, and oppositely weighted for responsiveness across the length of oral veil. Simultaneous two-site stimulation caused responses of amplitudes markedly smaller than the sum of corresponding one-site responses. Plots of two-site nerve responses against the summed approximate distances from midline of each site were markedly linear. Thus the sensory paths in the peripheral nervous system show reciprocal occlusion similar to lateral inhibition. This outcome suggests a novel neural function for lateral inhibitory mechanisms, distinct from simple contrast enhancement, in computation of both sensory maps and targeted motor actions.

chemotactile sensation; orienting; Pleurobranchaea; peripheral nervous system

FOR MOTILE FORAGERS the calculation of precise directional turns is fundamental to tracking and avoidance, nutrition, reproduction, and defense. The computations for directional turns have been examined in invertebrates and vertebrates (Eaton and Emberley 1991; Ewert et al. 1999; Levi and Camhi 2000; Murphey 1973; Teyke et al. 1990; Yafremava et al. 2007). However, intervening neural mechanisms of precisely directed orienting and avoidance remain for the most part to be described.

Elements of foraging and tracking were recently addressed in a study of turn behavior in the predatory sea slug, Pleurobranchaea californica, that tested the role of the anterior oral veil of the head (Yafremava et al. 2007). It was found that the angle of the turn response to a punctate chemotactile stimulus on the animal’s oral veil followed a linear relationship as the stimulus site was moved horizontally across, and increased with stimulus strength, similar to relations for turn angle/stimulus site observed for directional behaviors in other invertebrates and vertebrates. Moreover, the sea slugs were found to average two simultaneous stimuli to different oral veil sites to produce turns of precise intermediate angles.

In active mollusks like Pleurobranchaea, computation of stimulus-induced turning may well begin in the extensive peripheral nervous system, which mediates aspects of both sensory and motor integration (reviewed by Bullock and Horridge 1965). In Pleurobranchaea’s oral veil, chemotactile afferents from sensory papillae converge to peripheral ganglia in the lateral tentacle and medial region of the oral veil complex; these ganglia then send information centrally through two distinct pairs of nerves, the large oral veil nerve (LOVN) and the tentacle nerve (TN) (Bicker et al. 1982b; Lee and Liegeois 1974).

We measured the nerves’ spiking responses to chemotactile oral veil stimulation. We asked two experimental questions: 1) Does peripheral processing contribute to the linearity of the relation between turn angle and the stimulus site on the oral veil? 2) Does averaging of the response to simultaneous two-site stimulation begin in the peripheral nervous system? Computations for turn behavior were found to be already well formed in the periphery. Moreover, evidence from physiological measures, simple modeling, and anatomy suggested that site-specific chemotactile information was integrated across the oral veil by integrative mechanisms similar to lateral inhibition and differentially distributed to LOVN and TN for subsequent processing in the central nervous system (CNS). In this simple mollusk the complexity of the peripheral integrative operations is reminiscent of exteroceptor systems characteristic of advanced invertebrates and vertebrates.

METHODS

Whole animal preparations. Specimens of Pleurobranchaea californica were obtained from SeaLife Supply (Sand City, CA) and maintained in artificial seawater at 12°C. A total of 14 animals were successfully used in this study. Animals in the size range of 100–500 ml were prepared for recordings under cold anesthesia (4°C). A 1- to 2-cm dorsal longitudinal cut was made in the head region over the cerebral ganglion. The animal was placed into a chamber filled with ice-cold seawater and suspended by hooks around the incision. The exposed cerebral ganglion was pinned to a micromanipulated wax platform, and nerves of interest, the large and small oral veil nerves and the tentacle nerve (Fig. 1), were stabilized on the platform with insect pins in connective tissue sheaths. Nerves were cut, and suction electrodes were placed on the distal ends for recordings. Nerve activity was digitized at a sampling rate of 10 kHz per channel. Spikes were counted with in-house software (L. S. Yafremava). Data are presented as means and SE. Unlike the LOVN and TN, responses of the small oral veil nerve were not affected by stimulus site on the oral veil, consistent with previous observation of a largely motor function of this nerve (Lee and Liegeois 1974). Thus analysis of the small oral veil nerve was omitted from this study.

The preparation chamber was continuously perfused with fresh seawater at 12°C. Experimental preparation took <15 min, and all experiments were completed within 3–4 h. Within this period of time preparations remained viable and sensory nerves yielded good responses.
Stimuli. Chemotactile stimuli were prepared as gelatin pellets made with artificial seawater solutions of the appetitive stimulant betaine (trimethylglycine, Sigma-Aldrich; Gillette et al. 2000) at concentrations of $0$, $10^{-3}$, $10^{-2}$, and $10^{-1}$ M; $10^{-2}$ M was most often used, which elicits robust orienting turn responses in the intact animal (Yafremava et al. 2007). A few drops of food coloring (Red #40) added to the gelatin improved visualization as in earlier behavioral experiments (Yafremava et al. 2007). Gelatin pellets cut in 5-mm cubes were impaled on a Pasteur pipette for chemotactile stimulation of the oral veil. Pellets were replaced after two or three applications. We aimed to simulate conditions of the behavioral experiments (Yafremava et al. 2007), where pellets were placed immediately in front of the animal, which approached and touched the pellet with its oral veil. Here, animals were suspended immobile. Thus each pellet was applied by submerging it ~1–2 cm away from the desired oral veil locus, then moving it forward to immediately next to the oral veil papillae, then allowing them to extend toward the pellet to make physical contact. An ergonomic platform stabilized the experimenter’s forearm to reduce natural tremor. These application methods reduced variability in mechanical stimulation by the pellet.

Preparation responsiveness declined with both time and repetitive stimulation. Three to five presentations of a stimulus at any single location on the oral veil were attainable within limitations of the length of the experiment in 14 animals. Two-minute intervals separated applications, in which the oral veil was gently washed with fresh seawater from a Pasteur pipette and after which responses were largely restored.

Single-point and two-point stimulus applications. For localized response quantitation, the oral veil was divided into nine roughly equal regions (Fig. 1; Yafremava et al. 2007), with 0 denoting midline, +4 at right tentacle, and −4 at left tentacle.

Stimuli were applied to the oral veil both ipsilaterally and contralaterally to the nerves being recorded. Sensory nerves were insensitive to contralateral stimuli (see RESULTS), so only ipsilateral data are shown here.

In single-point applications, single pellets were applied sequentially either from midline to tentacle or in the opposite direction. Data were collected from the initial 4–7 s of stimulus applications, differing across preparations with variation in stability of application and spontaneous movement. Spike frequency within nerve responses showed adaptation, with exponential decay time constants ranging from 4 to 10 s. In the absence of stimulation, spontaneous activity was typically <1 Hz; the insignificant baseline activity was not subtracted from responses.

For two-site stimulation, two gelatin pellets were presented simultaneously. Only unilateral pairs of stimuli were tested, since the nerves of interest were not bilaterally sensitive (see RESULTS). All 10 possible combinations of loci were tested (Table 1) as many times as possible while an animal remained responsive, usually 4 or 5 tests per combination. In these experiments a full set of two-site permutations was achieved in four animals out of many more attempted.

One-point nerve responses in different animals varied greatly in their intensities, with maxima ranging from 10 to 30 Hz. Because of this variance the raw data on nerve response frequencies from different animals were normalized to that animal’s maximum response to one-site stimulation for each nerve. These data were then combined and averaged across the entire set of animals tested in a particular experiment.

RESULTS

The oral veil complex, including the lateral tentacles and medial oral veil region, is the main chemotactile apparatus for tracking prey and the detection of noxious stimuli (Yafremava and et al. 2007). Recordings from cut distal ends of LOVN and TN monitored neuronal activity coming from the multiple small oral veil ganglia associated with sensory papillae and from the larger tentacle ganglia.

Overlapping chemotactile maps in the sensory nerves. Betaine-infused gelatin pellets were applied singly at oral veil sites to map oral veil sensitivity for the sensory nerves. Receptive fields of the individual nerves were entirely unilateral; contralateral applications of stimuli did not cause responses noticeably different from background. Response amplitudes of LOVN and TN were specific to stimulus application sites and indicated overlapping but distinct unilateral receptive fields (Fig. 2). The stimulus/response site relations approximated oppositely directed sigmoid functions, where the LOVN was most sensitive at the midline (site 0) and least sensitive at the tentacle (site +4 on the right side of the oral veil or −4 on the

<table>
<thead>
<tr>
<th>$s_M$</th>
<th>$s_L$</th>
<th>$s_M + s_L$</th>
</tr>
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<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>0</td>
<td>2</td>
<td>2</td>
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<td>0</td>
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<td>6</td>
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<td>3</td>
<td>4</td>
<td>7</td>
</tr>
</tbody>
</table>

$s_M$, medial locus; $s_L$, lateral locus.
left side). Conversely, sensitivity of the TN was greatest at the tentacle and declined toward the midline. The areas of sensitivity of the two nerves overlapped at sites 1–3, thus forming a partly redundant sensory map of the oral veil.

Graded chemotactile stimuli. Dose-dependent effects of betaine were measured in single-point applications. To test oral veil responses to appetent intensity, gelatin pellets were prepared with betaine concentrations from 0 to $10^{-3}$ M and applied as in the single-point experiments. In these prolonged experiments it was difficult to obtain complete data sets for the extensive stimulus permutations for both LOVN and TN. However, complete sets were obtained for recordings from three animals, of which a set pair from one animal is shown in Fig. 3. Statistical analyses of each set showed significant differences for both increasing responses with betaine concentration and response amplitude site-specific differences (e.g., Fig. 3 legend). These observations indicate that responses were likely mediated by secondary chemotactile afferents like those found previously to innervate the oral veil in Pleurobranchaea (Bicker et al. 1982b) and the nudibranch Tritonia (Audesirk and Audesirk 1980).

Occlusion and response linearity in two-point applications. Observations of responses to simultaneous two-site stimuli indicated significant and unexpected contribution of peripheral neural processing to integration of sensory information prior to passage to the CNS. Notably, when simultaneous stimuli were delivered to two different oral veil sites in the electrophysiological preparation, the nerve responses were markedly smaller than the expected summed responses for the respective one-site stimuli. Moreover, the two-site responses followed strong linear relationships with the sums of the distances of the stimulation sites from the midline, $x_M$ and $x_L$, where $x_M$ and $x_L$ were respective medial and lateral application loci (Fig. 4, Table 2). The results for two-site stimuli contrasted with the simple nonlinear, sigmoidal relations obtained for one-site stimuli.

The occlusion of the summed effects was not due to a simple coincidence of spike occurrences, since the frequency of any two-site response was less than expected for the largest of the

Fig. 2. A and B: averaged responses and SEs of left and right LOVN (A) and TN (B) sensory nerves to single, punctate chemotactile stimuli applied to defined regions on the oral veil. Application site 0 is midline, while +4 and −4 denote respective right and left tentacle (cf. Fig. 1). Nerve responses are presented as the averaged fractions of the maximal responses of 14 animals. Because different animals had maximal responses at different loci, the averaged values do not attain 1.0. Left (●) and right (×) sides of the oral veil were tested in separate animals. C: an example of simultaneous responses of right LOVN (RLOVN) and TN (RTN).

Fig. 3. Sensory nerve response amplitudes were augmented with increasing appetent stimuli. Shown are averaged data for TN (A) and LOVN (B) from 1 of 3 animals. Gelatin pellet stimuli were applied in ascending order of betaine content: 0 [artificial seawater (ASW)], $10^{-3}$ M, and $10^{-1}$ M. Both TN and LOVN responses were significantly augmented by betaine ($P < 0.01$, ANOVA; response to zero $< 10^{-1}$ M: $P < 0.01$, Tukey-Kramer multiple comparisons test for TN and LOVN independently). Nerve responses also varied significantly with stimulation site ($P < 0.001$ and 0.0001 for TN and LOVN, respectively, ANOVA).
component one-site responses. Moreover, at the relatively low spike frequencies in question such coincidence would be of negligible rate.

**Peripheral integration of distributed stimuli.** The above results suggested that the two-site data were a biased average, or central tendency, of the corresponding one-site nerve responses. We tested this hypothesis in a correlation analysis. The data followed markedly linear relationships that were well described by

\[ NR_2 = k \cdot (NR_M + NR_L) + b \]  

where the two-site nerve response, \( NR_2 \), was a linear function of the sum of the medial site response, \( NR_M \), and the more lateral site response, \( NR_L \) (Fig. 5). The slope \( k \) was significantly less than 1 for both nerves (Table 3), consistent with an occlusive mechanism (e.g., lateral inhibition) contributing to signal processing at the level of the peripheral nervous system in the oral veil.

Probing the neural occlusion profile in the oral veil. *Equation 1* made the assumption of a flat occlusion profile in which both sites inhibited each other to the same extent, decreasing firing output from both active loci by the factor \( k \). We questioned this assumption, since in systems previously studied the strength of lateral inhibition usually fell with distance between loci (Ratliff and Hartline 1959), suggesting that \( k \) ought to depend on locus separation. In addition, LOVN and TN were not equally sensitive to all loci; thus it was possible that occlusion profile maxima were not the same across the entire oral veil. We tested for a bias of \( k \) between the medial and lateral oral veil.

Correlation analysis of the two-site data using the formula

\[ NR_2 = k_M \cdot NR_M + k_L \cdot NR_L + b \]

yielded goodness of fit comparable to *Eq. 1* for both nerves (Table 3). In LOVN the medial coefficient (\( k_M \)) was significantly greater than the lateral coefficient (\( k_L \)), displaying a bias toward the midline, where the nerve is most sensitive. In TN these coefficients were not statistically different and were equal to 0.5, a simple arithmetical averaging of afferent responses. Thus there was no reason to prefer either model, and so analysis did not reject the hypothesis that the efficacy of lateral inhibition is site specific.

**DISCUSSION**

These results build on earlier studies in *Pleurobranchaea* that demonstrated the anatomic potential for extensive peripheral sensory processing. Bicker et al. (1982a,b) and Matera and Davis (1982) showed that primary sensory cells project from the sensory epithelium into the peripheral sensory ganglia and there synapse on the sensory interneurons that send axons into sensory nerves. The small oral veil ganglia and the larger tentacle ganglia are peripheral integrating stations where the primary afferents converge from receptors to interneurons with a ratio of >1,000:1. This study enlarges the potential for integration of sensory information in the periphery to occlusive interactions of site-specific sensory information. The results also provide candidate neuronal mechanisms for results obtained in studies of turn behavior (Jing and Gillette 2003; Yafremava 2006; Yafremava et al. 2007) and suggest the nature of further integrative computations for orienting and avoidance turns that must occur in the CNS.

The major findings were four: 1) Sensory responses from different sites of oral veil and tentacle stimulation, including integration of simultaneous two-site stimuli, were integrated unilaterally in the peripheral nervous system prior to passage to the CNS; 2) receptive fields of LOVN and TN overlapped and were oppositely weighted for responsiveness as stimulus moved between tentacle tip and midline, with LOVN response greatest at midline and TN sensitivity greatest at the tentacle; 3) responses to two-site stimuli in the nerves were intermediate to the sums of the separate one-site stimuli, following a linear relationship with the approximate summed distances from midline across the oral veil; and 4) the preliminary processing of sensory information in the peripheral nervous system of the oral veil was consistent with computations of a lateral inhibitory network where outputs were differentially distributed to LOVN and TN on a site-specific basis.

A nonlinear and redundant chemotactile sensory map. Responses to single-point stimulus applications to oral veil

### Table 2. Linear regression of 2-site nerve responses to application sites for data combined from 6 animals

<table>
<thead>
<tr>
<th></th>
<th>( y )</th>
<th>( NR_2 )</th>
<th>( NR_M + NR_L )</th>
</tr>
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<tbody>
<tr>
<td>LOVN</td>
<td>( a )</td>
<td>-0.13 ± 0.01</td>
<td>-0.17 ± 0.01*</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>1.11 ± 0.04</td>
<td>1.51 ± 0.04‡</td>
</tr>
<tr>
<td></td>
<td>( R )</td>
<td>-0.99</td>
<td>-0.99</td>
</tr>
<tr>
<td></td>
<td>( \rho )</td>
<td>3.2e-5</td>
<td>5.86e-6</td>
</tr>
<tr>
<td>TN</td>
<td>( a )</td>
<td>0.08 ± 0.01</td>
<td>0.15 ± 0.01†</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>0.23 ± 0.05</td>
<td>0.27 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>( R )</td>
<td>0.96</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>( \rho )</td>
<td>8.03e-4</td>
<td>3.02e-6</td>
</tr>
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</table>

All data were fitted to a line \( y = a(x_M + x_L) + b \). \( R \), Pearson’s correlation coefficient; \( \rho \), Significance value; \( NR_2 \), 2-site nerve response; \( NR_M \), medial site nerve response; \( NR_L \), lateral site nerve response. Student-Newman-Keuls tests of corresponding quantities within the same nerve: *\( P < 0.05 \); †\( P < 0.01 \); ‡\( P < 0.001 \).
showed that sensory information was shared between the two sensory nerves, LOVN and TN. Response amplitudes in LOVN increased as the stimulus locus moved from tentacle to midline. Conversely, TN was more responsive as stimuli approached the tentacle. The observations confirmed and extended those of Bicker et al. (1982a) in demonstrating the restricted unilateral receptive fields of the nerves, in showing that receptive fields of the sensory nerves overlap significantly, and in showing that nerve firing frequencies are nonlinear functions of stimulus position.

The overlapping innervation of the oral veil/tentacle by TN and LOVN reflected a differential distribution in the periphery of the information collected from sensory afferents between the two nerves based on locus. Thus the reciprocal sigmoidal functions of the one-site stimuli responses may arise from a shared and differential distribution of outputs from the oral veil sites into TN and LOVN based on site of axon excitation. That is, the closer a peripheral ganglion to the tentacle or midline, the more excitation it supplies to the axons of the TN or LOVN, respectively. At present, it is unknown whether the axons being recorded in the nerves originate from somata in the peripheral ganglia or the CNS, or whether single axons may collect outputs of more than a single ganglion. These questions are critical to understanding of the integrative mechanisms.

Putative lateral inhibition in the peripheral neuronal network. Occluded responses to two-site stimuli indicated inhibitory interactions between sensory paths in the oral veil. Responses were appreciably lower than expected for simple summation of the separate, unitary responses, suggesting that lateral inhibition-like mechanisms performed the computations observed in the oral veil.

Neural interactions in the peripheral nervous system of the oral veil. Further investigation is needed to answer the question of where and how occluding interactions take place in the oral veil. We presume that branchlets of LOVN and TN coinnervate some of the ganglia. Inhibitory interactions among sensory afferents or interneurons could take place in the small glomerular, ganglion-like structures associated with the sensory afferents or in the nearby subepithelial meshworks associated with sensory epithelium (Moroz et al. 1997). More exact details of synaptic interconnections in the oral veil demand a greatly more detailed study of anatomy and physiology. However, the data are consistent with a mechanism of peripheral lateral inhibition.

Lateral inhibition in Pleurobranchaea’s oral veil may serve a quite different function than elsewhere documented. It is a widely distributed mechanism of stimulus feature extraction and sharpening in visual (Blakemore and Tobin 1972; Hartline et al. 1959), auditory (Ma and Suga 2004; Nobilli et al. 1998), and olfactory (Mori et al. 1999; Schoppa and Urban 2003; Vucinic et al. 2006) systems of vertebrates and invertebrates. Lateral inhibition networks also have particular power for modeling biological patterning in growth and development, as in the intricate structure and pigmentation of molluscan shells (Boettiger et al. 2009). However, here it may provide an averaged, intermediate value for responses to multisite stimulation. Of particular relevance in our study is that the linear functions computed for two-site stimuli in LOVN and TN anticipate the similar linearity of the turn angle vs. two-site averaging function measured in the intact, behaving animal (Yafremava et al. 2007). Thus in this system lateral inhibition may not only serve to average sensory inputs but thereby provides clear templates for the calculation of turn amplitude in the turn motor network. The resulting computation essentially encodes a central position between both stimulated sites. The resulting turn to the averaged position would thus center on an

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Table 3. Linear regression of 2-site nerve responses to the summated 1-site responses at corresponding loci for data combined from 6 animals

<table>
<thead>
<tr>
<th>Formula Used for Fitting</th>
<th>LOVN</th>
<th>TN</th>
</tr>
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<tbody>
<tr>
<td>( \text{NR}_2 = k \cdot (\text{NR}_M + \text{NR}_L) + b )</td>
<td>( b = 0.75 \pm 0.03 )</td>
<td>( b = 0.51 \pm 0.06 )</td>
</tr>
<tr>
<td>( b = -0.02 \pm 0.03 )</td>
<td>( b = 0.09 \pm 0.05 )</td>
<td></td>
</tr>
<tr>
<td>Pearson’s ( R )</td>
<td>0.99</td>
<td>0.97</td>
</tr>
<tr>
<td>( p )</td>
<td>1.6e-6</td>
<td>3.1e-4</td>
</tr>
<tr>
<td>( k = 1 )</td>
<td>( \dagger )</td>
<td>( \dagger )</td>
</tr>
<tr>
<td>( k = 0.5 )</td>
<td>Not significant</td>
<td>Not significant</td>
</tr>
<tr>
<td>( b = 0 )</td>
<td>Not significant</td>
<td>Not significant</td>
</tr>
<tr>
<td>( k_M = 0.97 \pm 0.11 )</td>
<td>( k_M = 0.42 \pm 0.11 )</td>
<td></td>
</tr>
<tr>
<td>( k_L = 0.61 \pm 0.11 )</td>
<td>( k_L = 0.62 \pm 0.13 )</td>
<td></td>
</tr>
<tr>
<td>( b = -0.05 \pm 0.06 )</td>
<td>( b = 0.04 \pm 0.05 )</td>
<td></td>
</tr>
<tr>
<td>Multiple ( R^2 )</td>
<td>0.96</td>
<td>0.91</td>
</tr>
<tr>
<td>( p )</td>
<td>1.21e-5</td>
<td>2.3e-4</td>
</tr>
<tr>
<td>( k_M = k_L )</td>
<td>( \ast )</td>
<td>Not significant</td>
</tr>
<tr>
<td>( b = 0 )</td>
<td>Not significant</td>
<td>Not significant</td>
</tr>
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</table>

\( p \), Significance value. Notations as in Table 2. Student-Newman-Keuls tests: \( *P < 0.05; \dagger P < 0.01 \).
odor trail or potential prey, enabling accurate trail-following or a strike. These observations document novel computational function in the molluscan peripheral nervous system. It remains to be tested whether other higher nervous functions, such as odor discrimination and learning (Davis et al. 1980; Mpitsos and Cohan 1986), might also occur in the “simple” peripheral neuropils of Pleurobranchaea.

Peripheral and central information processing for turning behavior. Sensory information undergoes considerable transformation between oral veil and turn motor output. As shown here, the averaging of unilateral stimulus sites is separately and redundantly encoded and carried to the CNS via LOVN and TN. In the intact animal, one-site stimuli result in a linear turn angle/stimulus site relationship across the entire oral veil (Yafremava et al. 2007). Two-site stimuli are arithmetically averaged to also yield a linear function of the turn (Yafremava et al. 2007). Thus central neuronal circuitry must integrate the information arriving from the two sensory nerves of both sides into a precise representation of stimulus localization, in order to compute the response averaging and direction of the turn seen during bilateral stimulus applications. Such bilateral integration is essential to sensory processing for directional responses (McMahon et al. 2005; Toda and Taoka 2004). In Pleurobranchaea the central circuitry must integrate the biased averages for multisite stimuli in LOVN and TN so as to negate the biases, and to result in the simple arithmetical averaging observed in the behavioral turn response. The synaptic mechanisms through which these further computations are done await future recordings from the identified neurons of the turn motor network (Jing and Gillette 2003).

The present findings complement the known neural mechanisms of precisely directed orienting and avoidance. The computational sophistication found in precise spatial averaging of sensory stimuli through apparent lateral inhibitory mechanisms was wholly unsuspected. Future integration of these findings with central activity in the turning motor network may provide a nearly complete description of directed action in foraging behavior.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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