Theory of Arachnid Prey Localization

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Sand scorpions and many other arachnids locate their prey through highly sensitive slit sensilla at the tips (tarsi) of their eight legs. This sensor array responds to vibrations with stimulus-locked action potentials encoding the target direction. We present a neuronal model to account for stimulus angle determination using a population of second-order neurons, each receiving excitatory input from one tarsus and inhibition from a triad opposite to it. The input opens a time window whose width determines a neuron's firing probability. Stochastic optimization is realized through tuning the balance between excitation and inhibition. The agreement with experiments on the sand scorpion is excellent.

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Arachnids, a large class of eight-legged arthropods such as scorpions and spiders, have an exceptional ability to localize their prey using vibrational cues from the substrate [1]. Here we analyze the biophysics of extracting the spatial direction of a stimulus from a temporally encoded signal at the sense organs of the sand scorpion *Paruroctonus mesaensis*. We present a theory for a neuronal mechanism that allows the sand scorpion and many other arachnids to localize their prey in a two-dimensional plane. We first formulate the problem, then present the model with numerical simulations, and finish with the underlying theory.

The sand scorpion is a nocturnal animal whose eyes are rudimentary. It lives in the deserts of Southern California and feeds mainly on small insects and other scorpions. During the daytime it stays in a burrow about 30 cm below the surface to escape surface temperatures of over 60 °C. After sunset it appears and, standing on the sand, is waiting for its prey. If, say, a moth is landing and moving in the scorpion's neighborhood (at a distance of at most half a meter), it produces two types of waves that are relevant in this context: longitudinal volume waves (velocity $v_l \approx 150$ m/s) and Rayleigh waves ($v_R \approx 50$ m/s). The latter are surface waves that are nearly transverse and take about 70% of the energy. The vibrational power spectrum of desert sand has a sharp peak at 300 Hz, corresponding to a period of about 3 ms [2,3].

Rayleigh waves are essential to the scorpion's facility of determining the prey's direction through sense organs, the basitarsal compound slit sensilla (BCSS), that are located just above the joint of the tarsus (foot) and basitarsus of each of its eight legs; see Fig. 1 and the literature [4,5]. The tarsus, acting as a lever, compresses the slits of the BCSS as a transverse wave passes along. The two neurons behind each slit react only if it is squeezed. The reaction mechanism [1,6–8] is sensitive to movements of less than 0.1 nm.

The BCSS are on a circle [6] of radius $R \approx 2.5$ cm at angles $\gamma_k = \pm 18°, \pm 54°, \pm 90°$, and $\pm 140°$, where 0° is ahead; see Fig. 1. We label them by $1 \leq k \leq 8$ clockwise, starting with the right front leg. The Rayleigh wave generated by a stimulus at angle φ_S and distance r from the center approximates a plane wave once $r \gtrsim 8$ cm. For a given stimulus angle φ_S, the time difference $\Delta t(\gamma_k, \gamma_l \,|\, \varphi_S)$ between the arrival of a wave at two BCSS of tarsi at angles γ_k and γ_l is then

$$\Delta t(\gamma_k, \gamma_l \,|\, \varphi_S) = \frac{R}{v_R}[\cos(\varphi_S - \gamma_l) - \cos(\varphi_S - \gamma_k)] \tag{1}$$

so that $\Delta t \in [-\Delta t_0, \Delta t_0]$ with $\Delta t_0 = 2R/v_R$ as the maximal time difference of about 1 ms.

The key question is now: given the data from these eight sense organs, how does the sand scorpion—or for that matter any vibration-sensitive arachnid—determine the stimulus direction? To answer this question we must know the "hardware," viz., the anatomy of the relevant part of the animal's brain [9–12]; anatomical and other details will be spelled out elsewhere. Surprisingly, we will face a few-neuron problem.

The two neurons behind each slit may, and quite often will, respond to a Rayleigh wave passing along. Hence all

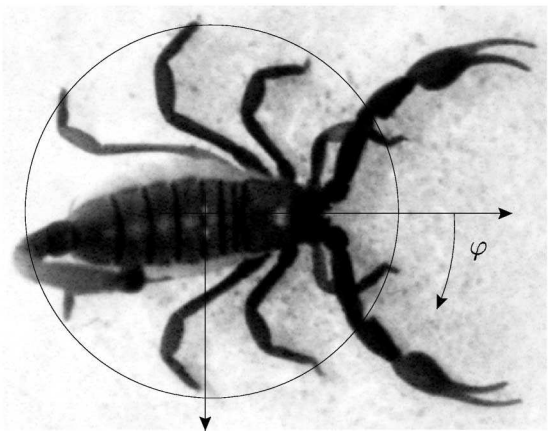

FIG. 1. Desert scorpion *Paruroctonus mesaensis* (real size) as seen from above. It is in a defense position with its eight tarsi on a circle with radius $R = 2.5$ cm and its huge pedipalps in front. Tail and venom gland are ready for attack. The picture is a negative of a scorpion that is fluorescent in the dark under the influence of ultraviolet light. The stimulus angle is $\varphi = \varphi_S$.

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we can predict is a probability density. The response is a set of stimulus-locked action potentials (or spikes) [2,5]. For each Rayleigh wave maximum, there is at most one spike per neuron that is transported to a ring-shaped structure [13] in the suboesophageal ganglion (SOG), where the axons from the eight legs meet.

We consider M active axons per BCSS and assume that each direction γ_k with $1 \le k \le 8$ innervates an excitatory neuron, which we call a *command neuron* since together they evaluate the sensory input and "command" the motor neurons; cf. Fig. 2 where $M = 1$. Moreover, the neighboring directions γ_{k-1}, γ_k, and γ_{k+1} innervate the inhibitory interneuron k. The interneuron blocks the action of the "opposite" neuron coding the direction $\gamma_{\bar{k}}$, where $\bar{k} = [(k + 3) \bmod 8] + 1$. So for each command neuron we have a $3/1$ configuration with one excitatory input from the direction under consideration and one inhibitory input from three opposite directions forming an inhibitory "triad" that determines Δt given by (1). This configuration has been suggested by Brownell and Farley [6]. A verification such as that in Fig. 3 has never been provided. Neither did one analyze the mechanism at a neuronal level. Both are done here.

Because of the inhibitory triad, each command neuron has a time window during which it can respond to the stimulus. If the inhibition arrives before the excitation, there is a spike with low probability. This happens, if the direction φ_S of the stimulus is roughly opposite to the direction γ_k of the command neuron k under consideration. On the other hand, if $\varphi_S \approx \gamma_k$, excitatory input may trigger a spike before inhibition can block it. Because of the interneuron there is an additional delay $\Delta_I = 0.7$ ms of inhibitory input. As the stimulus angle φ_S varies, the time difference between excitatory input and inhibitory input is $-\Delta t + \Delta_I$, where Δt varies in a range as given by Eq. (1);

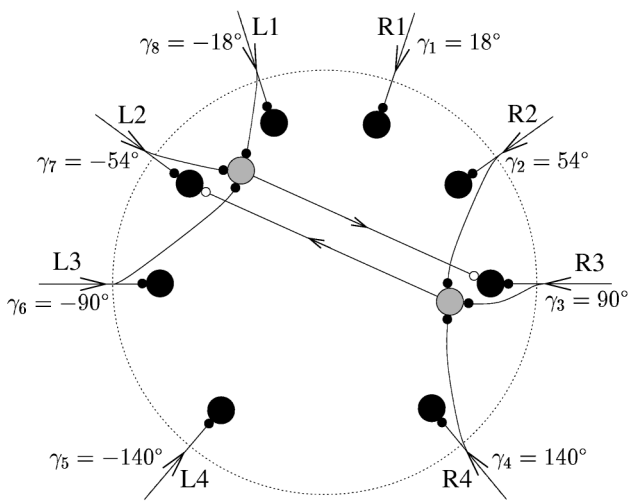

FIG. 2. Diagram of eight command neurons (black). For two of them, $k = 3$ and $k = 7 = \bar{3}$ corresponding to R3 and L2, respectively, the inhibitory partner neurons (grey) are shown as well. The triad of R3 consists of L1, L2, and L3.

$\Delta t < 0$ if k is hit before its triad $\bar{k}$. We neglect conduction delays from the slit sensilla to the SOG, since they are practically identical for all feet and for inhibitory/excitatory input. Because of the sharp peak at 300 Hz of the vibrational power spectrum of sand [2,3], spikes belonging to different amplitude maxima of Rayleigh waves hardly interact with each other.

The direction of a Rayleigh wave is coded by spikes in that each command neuron in the SOG generates spikes according to the width of its time window, a time code. How, then, does the animal decide what to do? The motor system of the legs, whose input is in the direct neighborhood of the direction-coding ring [13], uses a rate code. It is generally accepted that conversion from time to rate code is performed by means of a population vector [14–16], a notion whose reliability has been tested extensively. Here the $N = 8$ command neurons constitute a population. The

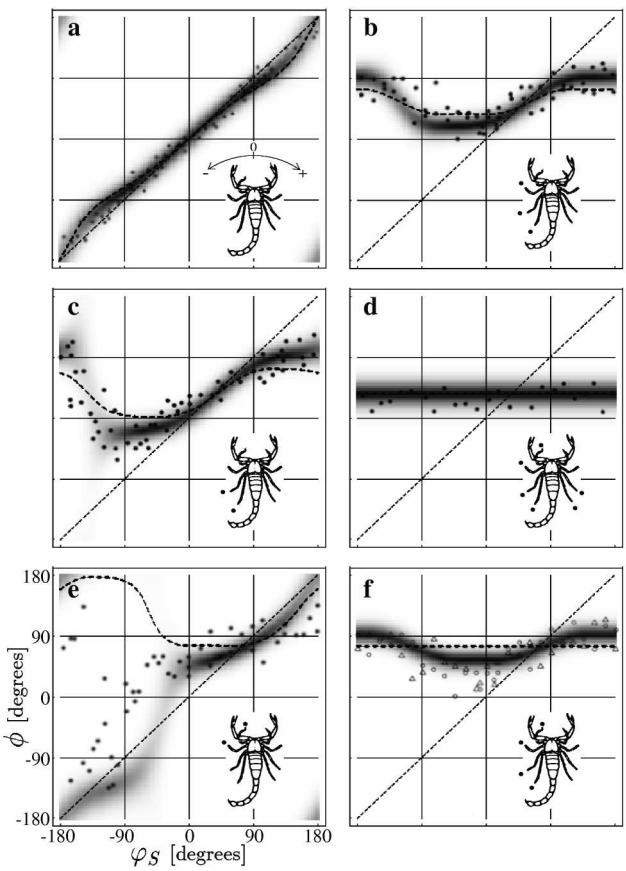

FIG. 3. Response angle ϕ of a scorpion (vertical axis) as a function of the stimulus angle φ_S (horizontal axis). (a) Systematic deviation of the response of an intact animal that hardly ever manages the complete turn φ_S. (b)–(f) Ablated basitarsal compound slit sensilla (BCSS) are indicated by dots at the end of the tarsi. Both the probability density $P(\phi)$ (dark shadings) and experimental points (dots) are indicated. Experimental data have been taken from Brownell [4,6]. Parameters are as in Fig. 4 and as specified in the main text. If the inhibitory triad is replaced by a *single* inhibitory neuron, we find the dashed line as the mean response; the agreement with experiment is in general less good.

stimulus time T_S is in general short, between 100 and 500 ms. During this time, command neuron k fires n_k spikes. Let us imagine directions as complex numbers and define

$$ne^{i\phi} := \sum_{k=1}^{N} n_k e^{i\gamma_k} \Rightarrow \phi = \arg\left(\sum_{k=1}^{N} n_k e^{i\gamma_k}\right). \quad (2)$$

The complex number $n\exp(i\phi)$ is called the population vector and its argument ϕ is the direction the animal will adopt. The procedure is counting spikes, viz., n_k, and the result is a rate code. Now the n_k are stochastic variables and so is the population vector's argument $\phi = \phi(\varphi_S)$. Given the stimulus angle φ_S, its probability density $P(\phi)$ is to be computed.

Since for each command neuron $\Delta t := \Delta t(\gamma_k, \gamma_{\bar{k}} \mid \varphi_S)$ is given, it is convenient to compute the neuron's average number $\langle n_k \rangle$ of spikes as a function of the time difference Δt, the so-called tuning curve. As we will see in Fig. 4, it is a good approximation to take

$$\langle n_k \rangle(\Delta t) = a - b\Delta t\,, \quad (3)$$

where a and b are positive constants. With the spontaneous rate ν_0 containing no directional information, we replace [15] n_k in (2) by $n_k - n_0$ with $n_0 = \nu_0 T_S$.

Taking advantage of (1) and (3) we verify that $\langle \phi(\varphi_S) \rangle = \varphi_S$ if the legs and, thus, the angles γ_k were equidistributed according to $\gamma_k = -22.5° + k\,45°$ for $1 \le k \le 8$, and if each triad were a single neuron $\bar{k}$. Since $\langle \phi(\varphi_S) \rangle := \arg[\sum_k \langle n_k \rangle \exp(i\gamma_k)]$ where $\langle n_k \rangle$ is given by (3), we find

$$\langle \phi(\varphi_S) \rangle = \arg\left\{\sum_k [a + 2b' \cos(\gamma_k - \varphi_S)] e^{i\gamma_k}\right\} = \varphi_S\,, \quad (4)$$

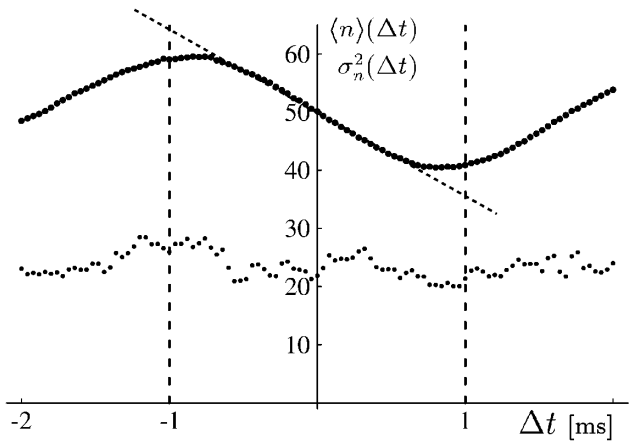

FIG. 4. Tuning curve (top), its linear approximation (dashed), and standard deviation (bottom) for a command neuron with $\tau_{\text{syn}} = \tau_E = \tau_I = 1$ ms, synaptic conductance $g_I = 3$ mS/cm^2, $g_E = 1$ mS/cm^2, and $M = 2$ active neurons per BCSS; cf. Eq. (6). The recording time was 500 ms, as in Brownell's experiments [4,6]. With the interval $[-1, 1]$ ms of the Δt axis being the physically relevant one, the linear approximation leading to (3) is fair.

where $b' = bR/v_R$. For realistic γ_k, an inhibitory triad, and dropping (3), we get a small but systematic deviation from φ_S as shown in Fig. 3a: for positive/negative φ_S the animal is off by about $\mp 10°$.

We have tested the theory on behavioral experiments [4,6] where some of the BCSS were ablated so that the animal reacted differently from normal. Figure 3 presents both theoretical and experimental results for $P(\phi)$ given the input (stimulus) angle φ_S. We now verify (3) and elucidate the role of stochastic optimization.

For the input on a substrate of sand [2,3] we have taken a Gaussian distribution of Rayleigh waves with a mean of 300 Hz and a standard deviation of 50 Hz. Slits in different legs are governed by independent processes so that we focus on a single BCSS. It may, but need not, react when a Rayleigh wave with amplitude $y(t)$ passes along. Since $R = 2.5$ cm we can assume the maximal amplitude to be the same for all legs. Spike generation is governed by an inhomogeneous Poisson process [17] with density

$$p_F(t) = \begin{cases} 0 & \text{for } y(t) < 0\,, \\ A \ln[1 + y(t)/y_0] & \text{for } y(t) \ge 0\,, \end{cases} \quad (5)$$

where $A = 250\ \text{s}^{-1}$ and for sand $y(t)/y_0 = 100 \times [\sum_k D(f_k) \cos(2\pi f_k t + \chi_k)]/[\sum_k D(f_k)]$, $f_k = 300 + (k - 150)$ Hz, $D(.)$ is a Gaussian with mean $\langle f \rangle = 300$ Hz and standard deviation 50 Hz, and the χ_k, $0 \le k \le 300$, are independent equidistributed random variables. The logarithm stems from the experimentally verified sensitivity for small amplitudes and the saturation for large ones.

The spikes generated by a BCSS corresponding to γ_k are fed into its command neuron. Those of the triad surrounding k innervate an interneuron that inhibits the command neuron of $\gamma_{\bar{k}}$ opposite to it. We thus get two independent Poisson processes of spikes labeled by f and arriving at times t_E^f from γ_k and t_I^f from $\gamma_{\bar{k}}$ with densities $p_{F,E}(t) = p_F(t)$ and $p_{F,I}(t) = p_F(t + \Delta t - \Delta_I)$. Here $\Delta t = \Delta t(\gamma_k, \gamma_{\bar{k}} \mid \varphi_S)$ is given by (1) while $\Delta_I = 0.7$ ms is an additional synaptic delay due to the interneuron; cf. Fig. 2. Depending on the given neuronal potential V at time t, the resulting excitatory and inhibitory postsynaptic currents (E/IPSCs) give rise to the total input current

$$I(V,t) = \sum_f [g_E \alpha(t - t_E^f; \tau_E)(V_E - V) + g_I \alpha(t - t_I^f; \tau_I)(V_I - V)], \quad (6)$$

which has to be substituted into the Hodgkin-Huxley equations [18]; here $V_E = 40$ mV, $V_I = -5$ mV, while g_E and g_I are synaptic conductances. The postsynaptic potential $\alpha(t; \tau_{\text{syn}}) := (t/\tau_{\text{syn}}) \exp[1 - t/\tau_{\text{syn}}]$ vanishes for $t < 0$. For the scorpion it is appropriate to take [2] $\tau_{\text{syn}} = \tau_E = \tau_I = 1$ ms, considerably less than an oscillation period of 3 ms. The above setup has been used in all calculations. In particular, Fig. 4 shows that Eq. (3) is a decent approximation.

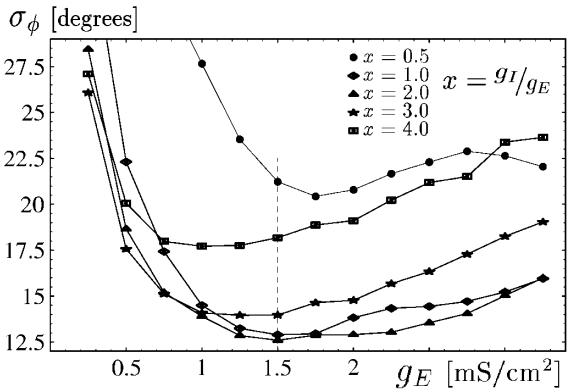

FIG. 5. Standard deviation σ_ϕ of the turning angle ϕ as a function of the conductance g_E appearing in Eq. (6) for fixed ratios $x = g_I/g_E$. For $1 \leq x \leq 3$ the "error" σ_ϕ shows a *broad* minimum near the dashed line. The Hodgkin-Huxley equations being given, stochastic optimization, a reinterpretation [17] of stochastic resonance [19], can be realized through tuning g_I and g_E. The values of σ_ϕ near the minima agree with the scatter of the behavioral data shown in Fig. 3. Of course the precise values are model dependent.

Finally, the influence of the number N of command neurons can be seen from the precision, viz., the standard deviation σ_ϕ, which turns out to be

$$\sigma_\phi^2 \approx \frac{8\,\sigma_k^2}{N(\langle n_k\rangle_{\max} - \langle n_k\rangle_{\min})^2}\,. \tag{7}$$

Here $\langle n_k\rangle_{\max}$ and $\langle n_k\rangle_{\min}$ are the maximum and minimum number of spikes as a function of Δt (see Fig. 4), and $\sigma_k^2 = \mathrm{var}(n_k)$. Figure 5 shows that for $M = 2$ and $N = 8$ a precision of 13°–15° is easily obtained. This is in the natural range, and suffices since the pedipalps compensate for imprecision; cf. Fig. 1.

Since a BCSS neuron may, but need not, fire and the firing times, though phase locked, are not precisely predictable, noise is *inherent* to the scorpion's command neurons evaluating a stimulus direction. A natural question is then [17,19]: can the system's hardware be tuned so as to adapt to the noise as well as possible? To answer this question we have varied g_E in (6) for fixed $x = g_I/g_E$. The broad minima in Fig. 5 for the standard deviation σ_ϕ at intermediate values of x strongly suggest that the system is optimized through evolutionary adaptation [20].

Distance can be determined through tarsal hairs that are sensitive to the longitudinal vibrations preceding the transverse ones. The only remaining task is evaluating the time difference between the two waves.

The present considerations show three things. First, a simple neuronal setup allows an accurate estimate of the stimulus direction. Second, time differences are measured through a $3/1$ balance of excitation and inhibition, the inhibitory triad, that determines the width of the time window during which input spikes can come in. Eight (groups of) command neurons, a population corresponding to eight directions, then "vote" what the animal should do. Figure 3 indicates that the inhibitory triad is a realistic notion in that it accounts for all presently known ablation experiments. Third, the solution is a few-neuron one underlining that time coding through spiking neurons can be very effective.

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