Temporal Coding by Populations of Auditory Receptor Neurons

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Sabourin P, Pollack GS. Temporal coding by populations of auditory receptor neurons. J Neurophysiol 103: 1614–1621, 2010. First published January 13, 2010; doi:10.1152/jn.00621.2009. Auditory receptor neurons of crickets are most sensitive to either low or high sound frequencies. Earlier work showed that the temporal coding properties of first-order auditory interneurons are matched to the temporal characteristics of natural low- and high-frequency stimuli (cricket songs and bat echolocation calls, respectively). We studied the temporal coding properties of receptor neurons and used modeling to investigate how activity within populations of low- and high-frequency receptors might contribute to the coding properties of interneurons. We confirm earlier findings that individual low-frequency-tuned receptors code stimulus temporal pattern poorly, but show that coding performance of a receptor population increases markedly with population size, due in part to low redundancy among the spike trains of different receptors. By contrast, individual high-frequency-tuned receptors code a stimulus temporal pattern fairly well and, because their spike trains are redundant, there is only a slight increase in coding performance with population size. The coding properties of low- and high-frequency receptor populations resemble those of interneurons in response to low- and high-frequency stimuli, suggesting that coding at the interneuron level is partly determined by the nature and organization of afferent input. Consistent with this, the sound-frequency-specific coding properties of an interneuron, previously demonstrated by analyzing its spike train, are also apparent in the subthreshold fluctuations in membrane potential that are generated by synaptic input from receptor neurons.

INTRODUCTION

The temporal structures of sensory signals often carry behaviorally important information and this is particularly evident in communication systems. For example, in many acoustically communicating animals, including birds, frogs, insects, and humans, information such as the species and individual identity of the signaler, or the signal’s “message” (e.g., speech; Shannon et al. 1995), is carried by features such as the durations of sounds and of the intervals between them (Bradbury and Vehrencamp 1998). Sensory neurons are often tuned to these behaviorally relevant temporal features; they may respond most strongly to these features (rate code) or the structure of their spike trains may capture most accurately the timing of these stimulus components (time code; Pollack and Krahe 2009).

Two classes of sound stimuli are particularly important for the behavior of crickets: conspecific songs and echolocation calls of insectivorous bats. Both types of stimulus consist of series of discrete sounds (sound pulses), but they differ in tempo. Pulse rates in echolocation calls span a wide range, increasing from 5 to 10 Hz when the bat is searching for a target to >100 Hz during the final approach to the prey (Jones and Rydell 2003). By contrast, pulse rates in conspecific signals of the cricket _Teleogryllus oceanicus_ are restricted to a range of about 8–32 Hz (Balakrishnan and Pollack 1996). The two types of signal also differ in dominant sound frequency, which is about 4.5 kHz for _T. oceanicus_ songs and >20 kHz for most bats. Previous work found that the response properties of identified, first-order auditory interneurons are matched to both the spectral and temporal characteristics of these signals. Marsat and Pollack (2005) showed that the spike train of the ascending auditory 1 (AN1) interneuron, which is most sensitive to low, cricketlike sound frequencies, captures information selectively about the low range of amplitude-modulation (AM) rates that occur in the species’ songs, whereas AN2, which is most sensitive to ultrasound, encodes a broader, batlike range of AM rates. A third interneuron, omega neuron 1 (ON1), responds robustly to both cricketlike and batlike sound frequencies. It encodes, in the timing of action potentials, only cricketlike AM rates for low-carrier-frequency stimuli, but it encodes a broader, batlike range of AM rates for ultrasonic stimuli (Marsat and Pollack 2004; Sabourin et al. 2008).

The interneurons just referred to receive excitatory input from primary sensory neurons, of which there are about 65 in each ear. About three quarters of these are tuned to cricketlike sound frequencies, but these comprise two distinct anatomical groups, only one of which (denoted “MT”) has terminal processes in the same region as the dendrites of ON1 (Imaizumi and Pollack 2005). The other anatomical type (“BC” of Imaizumi and Pollack 2005) is not considered in this study. Based on the frequency with which MT and BC receptors have been recorded, they are approximately equally numerous (Imaizumi and Pollack 2001). Thus about 25 receptor neurons that are tuned to cricketlike frequencies potentially provide direct synaptic input to ON1. The remaining receptor neurons in the ear (_N_ = 15) are tuned to higher frequencies, including ultrasound (Imaizumi and Pollack 1999). Based on anatomy, all of these are candidates for providing direct input to ON1 (Imaizumi and Pollack 2005).

It can be expected that the coding properties of the interneurons will be affected by several factors, including their intrinsic properties and the characteristics of synaptic transmission from afferents, as well as by the coding characteristics of receptor neurons and the dynamic relationships within the populations of afferents impinging on common targets. Herein we investigate the relationship between the temporal coding properties of receptor neurons and those of ON1. We extend an earlier preliminary characterization of the temporal coding properties of receptor neurons (Marsat and Pollack 2004) and use these results to examine, through modeling, how spiking activity within receptor populations might contribute to the sound-frequency-specific coding properties of ON1.

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METHODS

Electrophysiology

To assess the coding ability of the population of receptor neurons, we recorded intracellularly in the cricket's foreleg, slightly lateral to its junction with the prothoracic ganglion. The animals were anesthetized by chilling and were mounted on a support ventral side uppermost. The prothoracic ganglion was exposed by ventral dissection, supported on a metal platform, and bathed in physiological saline (Strausfeld et al. 1983). The cricket’s front legs, which bear the ears, were held fixed between the pronotum in a position similar to that assumed during flight.

Receptors were recorded intracellularly in the leg nerve, slightly lateral to its junction with the prothoracic ganglion, using glass microelectrodes filled with 1.5 M potassium acetate (KAc) (resistance, >30 MΩ). Previous work (Imaizumi and Pollack 2005) identified four types of receptor neuron: two anatomically distinct types of low-frequency-tuned receptors, denoted MT (medially terminating) and BC (bifurcating), a mid-frequency-tuned group, and a group tuned to ultrasound. Both of the latter groups respond robustly to ultrasound stimuli and we combine these here with the designation HF (for high-frequency). These were identified in the present study by their greater sensitivity to 30- than to 4.5-kHz stimuli. HF receptors terminate in the same region of neuropil as the dendrites of ON1. Only one of the two low-frequency-tuned receptor types, the MT type, has terminal boutons in this region (Imaizumi and Pollack 2005). These were differentiated from BC types by their lower threshold at 4.5 kHz (<50 dB for MT-type and >60 dB for BC-type; Imaizumi and Pollack 2001). In our data set, thresholds were: MT-type, 43.3 ± 1.9 dB SPL; BC-type, 64.5 ± 2.0 dB SPL (mean ± SE). In a few cases we also confirmed the receptor type through visual identification after fluorescent staining (ALEXA red); three MT-type receptors were successfully stained and visual inspection of their morphology confirmed the identification based on auditory threshold. Typically, only one receptor per animal was recorded.

Omega neuron 1 (ON1) was recorded intracellularly in its somatopileal dendrites.

Stimuli

Stimuli were generated via a National Instruments (Austin, TX) A/D/D/A board with 12 bits of resolution, at a sampling rate of 100 kHz. Sound was broadcast from loudspeakers situated to the cricket’s left or right, perpendicular to the longitudinal axis. Sound level was adjusted with a custom-built programmable attenuator and calibrated using Bruel & Kjaer (Nærum, Denmark) instruments (4135 microphone; 2610 sound-level meter).

Stimuli were 5-s tones, the amplitude of which was modulated through time (random amplitude modulation [RAM]) by multiplication with a low-pass-filtered Gaussian signal (fifth-order Butterworth, cutoff frequency 200 Hz) that defined the stimulus envelope (see Fig. 1A for an example of a RAM stimulus). The modulation depth (in dB) of the RAM was defined as the SD of this envelope (3, 5, or 7 dB). Before multiplication with the carrier sine (4.5 or 30 kHz), the envelope was converted from dB to linear scale using the formula:

$$\text{STIM}_{\text{envelope}} = 10^{\text{ENVOLPE}_{\text{dB/20}}}$$

The method for stimulus construction and spectral characteristics of the stimuli are illustrated in Supplemental Fig. S1.1 The amplitude of the stimulus was defined as the root-mean-square intensity and, except where otherwise noted, took values of +5, +15, or +25 dB, where the “+” sign means that intensity is relative to the receptor’s threshold, defined as the lowest intensity (resolution, 2 dB) for which one to two spikes occurred consistently (N ≥ 5) within 30 ms of the onset of a 30-ms stimulus. Threshold was determined by decreasing the amplitude of an initially effective stimulus until reliable responses no longer occurred.

The shape of the RAM signals was “frozen,” meaning that the same Gaussian signal was used to produce the stimulus envelope throughout the experiment and only the intensity and the modulation depth were varied. Except where otherwise noted, each unique combination of stimulus amplitude and modulation depth was presented only once per receptor neuron. Stimuli were preceded by silent periods of ≥15 s.

Analysis

Responses of auditory receptors adapt substantially. To ensure that analyses were performed when response statistics were stationary, the first 2 s of the responses, where most of the adaptation occurs, were discarded. Phonotaxis toward cricket song persists for minutes (see, e.g., Weber et al. 1981) and bat–insect interactions may persist for several seconds (Simmons 2005). Thus the adapted portion of neuronal responses has ethological relevance.

Information analysis

Firing rate was obtained by first converting the spike train recordings to vectors containing values of 1 at the times of occurrence of spikes, or 0 otherwise, a procedure that we refer to as binarization. Firing rate was calculated by multiplying the binarized spike train by the sampling rate (10 kHz), so that the firing rate at each time point was either 10,000 or 0 spikes/s. When information was calculated from subthreshold membrane potential values (ON1), the signal (i.e., membrane potential) was used as is without conversion. Next, the firing rate r(t) (we use the same notation to describe the subthreshold membrane-potential signal) and stimulus s(t) had their means subtracted to yield r′(t) and s′(t), respectively. The coherence was then calculated from the following formula

$$\text{COH}_{rs} = \frac{\langle S\ast R \rangle \langle R \ast S \rangle}{\langle S \rangle \langle R \rangle}$$

where R and S are the Fourier transforms of r′(t) and s′(t), respectively; the centered asterisk symbol (“*”) indicates complex conjugation; and indicates that the Fourier transform was averaged across 300-ms Hanning-windowed segments overlapping by 50% (i.e., 150 ms) (Borst and Theunissen 1999). Frequency-dependent lower-bound information was then obtained through the following equation

$$\text{Information}_{LB}(f) = -\log_2 (1 - \text{COH})$$

and the total information rate transmitted between frequencies f1 and f2 was obtained by integrating Eq. 2

$$\text{Information}_{LB} = -\int_{f_1}^{f_2} \log_2 (1 - \text{COH})df$$

Information content per spike was obtained by dividing the information rate of a neuron by its mean firing rate. Herein we compute only lower-bound information, which reflects only linearly coded information. However, previous work (Marsat and Pollack 2004) showed that for ON1, the carrier-frequency-specific shapes of information curves—our main focus here—were similar for upper-bound curves, which reflect both linearly and nonlinearly coded information (Borst and Theunissen 1999).

To approximate the lower-bound information that might be available to a postsynaptic neuron receiving input from all receptors, information for superimposed spike trains was obtained as follows. In a set of N receptor responses, a group of n spike trains were picked at random, binarized, and superimposed so that a new composite spike train was created for which each point is the sum of the corresponding time points in the n spike trains. The composite spike train was converted to firing rate and lower-bound information was then com-

1 The online version of this article contains supplemental data.

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We sought to determine, for model afferent populations, the incremental increase in information content as additional spike trains were added, to assess the extent of redundancy between the additional spike train and the population to which it is added. Although several methods for calculating spike-train redundancy have been described (e.g., Latham and Nirenberg 2005; Reich et al. 2001), these do not capture redundancy in an incremental fashion. To estimate the portion of information that is redundant when adding an \( r \)th neuron to a composite spike train of \( i - 1 \) neurons, a redundancy index \( R_r \) was defined as follows:

\[
R_r = \frac{I(N_1, N_2, \ldots, N_{i-1}) + I(N) - I(N_1, N_2, \ldots, N_{i-1}, N_r)}{I(N)}
\]

where \( I(N_1, N_2, \ldots, N_{i-1}, N_r) \) is the lower-bound information of a composite spike train made up of neuron 1 to neuron \( i \). \( I(N) \) is simply the information content of the spike train of neuron \( r \). An \( R_r \) of 0 means that all the information contained in the \( r \)th neuron is contributing to the information content of the composite spike train \([i.e., I(N_1, N_2, \ldots, N_{i-1}, N_r) = I(N_1, N_2, \ldots, N_{i-1}, N_r)]\), whereas an \( R_r \) of 0 means that all the information content of the \( r \)th neuron is contributing to the information content of the composite spike train \([i.e., I(N) = I(N_1, N_2, \ldots, N_{i-1}, N_r) = I(N_1, N_2, \ldots, N_{i-1}, N_r)]\). This index quantifies the marginal information coding benefit from the addition of another neuron to a group.

To measure the amount of correlation between receptor responses, mutual information was calculated for every possible pair of responses for each type of receptor. Mutual information was obtained using Eq. 2 with two neuron responses as parameters (instead of stimulus and response) and mutual information rates were calculated as in Eq. 3.
Information analysis is biased in that it cannot yield negative values; thus even random spike trains will result in nonzero values of information. We removed the effect of this bias as follows. For a given spike train, 1,000 new spike trains were generated by randomly shuffling the interspike intervals of the original spike train. Information was then computed for each randomized spike train and averaged. Finally, the mean of information values for the shuffled spike trains was subtracted from the information calculated from the nonshuffled data.

Data analysis, including statistical tests, was performed using Matlab (Release 2008a, The MathWorks).

RESULTS

Temporal tuning of ON1 is apparent at the level of subthreshold membrane potential

The coding properties of ON1 were examined previously by analyzing its output, that is, the sequences of action potentials that it produces. To examine the subthreshold variations in membrane potential that might contribute to these coding properties we suppressed action potentials by injecting hyperpolarizing current (Fig. 1, A and B). Figure 1C shows information transfer curves for ON1 calculated both from spike trains and, after hyperpolarization, from subthreshold variations in membrane potential. As reported previously (Marsat and Pollack 2004), the coding properties of ON1 differ for stimuli with low and high carrier frequencies. For low-carrier stimuli, only a restricted, relatively low range of AM frequencies is well coded, whereas for high-carrier stimuli coding extends over a broader range of AM frequencies. The shapes of the curves for spiking responses and the underlying variations in membrane potential are similar; thus neither currents associated with action potentials nor recurrent circuitry activated by action potentials is required for the neuron’s frequency-specific coding properties. This result also suggests that subthreshold voltage-sensitive currents, which will have been diminished if not blocked completely by hyperpolarization, are also likely to be relatively unimportant in determining the frequency-specific differences in coding properties of ON1. Rather, it would appear that these properties are determined mainly by the pattern of synaptic inputs, which in turn should reflect the structures of the afferent spike trains. Not surprisingly, subthreshold variation in membrane potential, which provides a continuous report about afferent input, encodes more information than the spike train, which does so only occasionally (i.e., when spikes occur).

We examined coding properties of receptors using stimuli with a carrier frequency of either 4.5 kHz (for MT receptors) or 30 kHz (HF receptors), with various intensities and modulation depths (Fig. 1, D–F). Coding by HF afferents spans a similar range of AM rates and reaches a similar level of information, as coding by ON1 of ultrasound stimuli (compare gray curves in Fig. 1, C and D). However, individual MT afferents encode stimulus temporal structure only poorly and, unlike ON1, show little evidence of tuning to low AM rates. Overall information content of receptors, integrated from 0 to 150 Hz, is greater for HF receptors than that for MT receptors (Fig. 1E; three-way ANOVA, receptor-type effect, P < 0.001). The firing rate is generally higher in HF receptors (Imaizumi and Pollack 2001; Sabourin and Pollack 2009) and information in neural spike trains increases linearly with firing rate (Borst and Haag 2001); however, this does not account for the greater information content of HF receptor responses, which remains higher than that of MT receptors on a per-spike basis (Fig. 1F). Information rates were generally higher at higher intensities and deeper modulation depths (three-way ANOVA, intensity and modulation-depth effects, P < 0.001), except for HF receptors, which showed a decrease at 25 dB above threshold (see Supplemental Fig. S2 for complete data set). The difference in information rates between HF and MT receptors was most marked at 15 dB above threshold, where the former (111.4 ± 6.3 bits/s) was approximately double the latter (55.5 ± 5.3 bits/s).

Anatomical data (Imaizumi and Pollack 2005) suggest that groups of MT and HF receptors, of which there are about 25 and 15, respectively (see INTRODUCTION), converge onto ON1. This might permit pooling of information across receptors and could account for the superior low-frequency coding properties of ON1 relative to that of individual receptors. However, this could be the case only if the information carried by different receptors were nonredundant. Indeed, Fig. 2A shows that the spike trains of different MT receptors differ substantially from one another. By contrast, spike trains of HF receptors are more similar to one another. Moreover, as expected, spike trains of individual receptors for repeated presentations of the same stimulus are more similar than those of different receptors. We quantitatively examined the similarity of receptor spike trains by calculating the mutual information between pairs of responses. Mutual information among spike trains of MT receptors (Fig. 2B) is low compared with that among spike trains of HF receptors (Fig. 2C). Most data from this study consist of recordings of single receptors from different individuals. However, this is unlikely to account entirely for the lack of similarity in the MT spike trains because: 1) similarity is apparent for HF receptors, which were also recorded in separate individuals; 2) similarity of spike trains of several receptors recorded sequentially in the same individual is only slightly greater than that among responses recorded in different individuals (Fig. 2B, thin and thick solid curves); and 3) mutual information among spike trains from the same receptor in response to repeated stimuli is again only slightly greater than that among receptors from different animals (Fig. 2, B and C; see also Supplemental Fig. S3 for complete data set). As another measure of the similarity, we computed the cross-correlation between responses of pairs of neurons (Fig. 2D). By this measure as well, the similarity of spike trains is much higher for HF receptors than that for MT receptors. We previously showed that HF receptors tend to fire in bursts (Sabourin and Pollack 2009). Both the high correlation between spike trains in Fig. 2D and the dips surrounding the peak are due mainly to burst-associated spikes (data not shown).

To model the input that ON1 would receive from receptor populations, we superimposed spike trains of individual receptors to produce composite trains. For example, if receptor 1 produced spikes at times t1 and t2 and receptor 2 at times t3, t4, and t5, then the composite train had spikes at times t1, t2, t3, t4, and t5. Figure 3, A and B shows the information content of composite spike trains with different numbers of contributing HF and MT receptors, respectively. In both cases, composite spike trains carry more information about the stimulus as more neurons are included. However, two major differences can be observed. First, HF receptors show a gain in information...
over a broad range of AM frequencies extending to >100 Hz, whereas for MT receptors information increases mostly for the lower AM rates (≤50 Hz). As a result, the shape of the population information curve for MT receptors begins to approach that of the curve for ON1 for low-carrier stimulation (see Fig. 1C). Second, information saturates faster in HF receptors. This is evident in Fig. 3, C and D, which shows the successive increases in information rate as additional receptors are added to the model population. For HF receptors, the increments of information become small once the model population size reaches three or four neurons, especially for lower AM rates. For MT receptors, saturation is less pronounced, which is consistent with the lower mutual information of their spike trains. The difference in rate of information accrual is reflected in the slopes of the linear portions of the curves in Fig. 3, C and D, i.e., for receptor population sizes of 5–11 ($R^2$ values for the four curves are all >0.97). For the low range of AM rates, the slope for MT receptors is steeper than that for HF receptors by a factor of 3 (slopes: MT, 3.09 ± 0.36; HF, 2.30 ± 0.39; $P < 0.01$).

We also calculated a redundancy index, which reflects the redundancy between an individual spike train and the compos-
ite to which it is added (see METHODS); a redundancy index of 1 means that the new spike train adds no additional information to the composite to which it is added, whereas an index of 0 means that all of the information of the new spike train is incorporated into that of the new composite. Figure 3, E and F shows the redundancy index of HF and MT receptors in the lower (0–50 Hz) and upper (50–150 Hz) ranges of AM rates. The redundancy index of HF receptors increases rapidly at low AM rates and approaches 1 (complete redundancy). MT receptors, by contrast, show relatively low redundancy that does not substantially increase as the number of neurons increases (Fig. 3E). In the upper range of AM rates, redundancy is similar, and high, in both HF and MT receptors (Fig. 3F). In part, this reflects the relatively poor coding of high AM rates by both types of receptor: little additional information is added to a composite because there is little information available to add.

DISCUSSION

Our results show that a behaviorally relevant, complex feature of an interneuron’s spike train, selective information tuning, can be accounted for in part by the temporal characteristics of the spike trains of primary receptor neurons. This differs from previously described systems, where the mechanisms for selective temporal coding have been ascribed to the biophysical properties of, and synaptic interactions among, central neurons. Pyramidal cells in the electrosensory lateral-line lobe of weakly electric fish show selective temporal tuning for low-frequency modulations in amplitude of their self-generated electric field when stimuli are applied locally, matching the local, low-frequency amplitude modulations induced by prey. For spatially distributed stimuli, such as are produced when the electric fields of neighboring fish are superimposed, tuning shifts to the higher-frequency range that characterizes interactions between conspecifics (Chacron et al. 2003). Thus as for ON1, temporal tuning of these pyramidal cells shifts adaptively according to stimulus context, in this case as a result of interactions between the electrotonic filtering properties of pyramidal-cell dendrites and stimulus-specific activation of feedback pathways (Chacron et al. 2005). In the torus semicircularis of electric fish, characteristics such as synaptic plasticity, subthreshold voltage-sensitive currents, and possibly membrane biophysics contribute to low-pass or high-pass temporal filtering properties (Rose and Fortune 2003). In the torus of frogs, selectivity for the repetition rate and number of sound pulses arises from the interplay between inhibitory and rate-dependent excitatory synaptic inputs (Edwards et al. 2007). The interaction between excitatory and inhibitory syn-
aptic inputs also underlies pulse-rate selectivity in the medial superior olive nucleus of bats (Grothe 1994). Unlike these examples, the temporal selectivity of ON1 appears to arise, in part, at the level of primary receptor neurons. However, this does not exclude the possibility that other factors, such as intrinsic biophysical properties or the dynamics of synaptic transmission, also come into play.

Information cannot be generated de novo in a processing chain (Cover and Thomas 1991); thus the information capacity expressed by ON1 must already be present in its inputs. We showed, using a simple summing of spike trains, that information coding of a population of MT receptors approaches that of ON1, in terms of both magnitude and frequency selectivity. In a study on another insect auditory system, Machens et al. (2001) showed that information capacity increased for afferent populations of increasing size. In that system, however, the information coding properties of interneurons have not been described using the same analytical methods, so it is not yet possible to know to what extent their properties are accounted for by those of receptors.

The estimated numbers of MT and HF receptors are about 25 and 15, respectively (see Introduction). Our model afferent populations were limited, by our data set, to 11 receptors. This is a reasonable approximation of the entire HF population, particularly because there is little additional increase in information once population size reaches three or four. Our model MT populations, however, fall far short of the actual population size. The lack of any sign of saturation of information for population sizes ≤11 suggests that information would continue to accrue for at least the next few increments in the afferent population.

Information carried by converging inputs can be combined only if it is nonredundant and, indeed, that largely the case for MT receptors. Reduction of redundancy of neuronal responses has most often been discussed in the context of maximizing the efficiency of information transmission along a channel (Barlow 2001). In the present case, the reduction in redundancy is evident across parallel channels. What might account for the low redundancy among MT receptors? A possibly related feature of MT receptors is their relatively high level of spontaneous firing (median, ~ 9 Hz), compared with HF receptors, which are silent or nearly so in the absence of stimulation (Imaizumi and Pollack 2001). This suggests that the resting membrane potentials of MT receptors might be close to spiking threshold, perhaps accounting for their high sensitivity (mean threshold in our data set, 43.3 ± 1.9 dB SPL). Individual MT receptors might thus be poised to respond to small increases in stimulus amplitude, but differences in their firing history and intrinsic noise might result in different receptors firing for different amplitude increases, thus reducing redundancy in their spike trains.

In contrast to MT receptors, redundancy among HF receptors is high. Indeed, there is a clear tendency for different HF receptors to fire in near synchrony, particularly when they produce bursts. This can be expected to result in strong depolarization of their target neurons, helping to ensure that they, too, respond with bursts (Sabourin and Pollack 2009). In this respect, HF receptors are well suited to participate in coincidence-detector-type processing, in contrast to MT receptors, which are better suited to an integrator-type circuit.

The information-coding properties of populations of neurons have been investigated previously in a number of systems. In the wind-sensitive cercal system of crickets, coding of variations in wind velocity increases dramatically when spike trains of neurons responding to opposite wind directions are combined (Theunissen et al. 1996). Similarly, pairs of pyramidal cells in electric fish encode variations in stimulus amplitude more accurately than single cells, particularly when the two cells of a pair respond to different directions of amplitude change (i.e., “on” and “off” cells; Krahe et al. 2002). The same situation holds in the retina of salamanders, where coding by cell pairs exceeds that of single cells substantially only when the response types (“on” or “off”) of the two cells are dissimilar (Warland et al. 1997). In these cases, the differing response types of the neurons ensure that their spike trains are nonredundant. As already noted, redundancy is low among MT responses, despite the fact that all of the neurons are “on” types.

In conclusion, our results show that an important feature of the spike trains of central sensory neurons—information tuning—may be explained in part by the properties of neurons at the earliest level of sensory processing: i.e., the primary sensory neurons.

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