Information Transfer Rate of Nonspiking Afferent Neurons in the Crab

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DiCaprio, Ralph A. Information transfer rate of nonspiking afferent neurons in the crab. J Neurophysiol 92: 302–310, 2004. First published February 18, 2004; 10.1152/jn.01176.2003. The thoracic-coxal muscle receptor organ (TCMRO) is the only proprioceptor at the thoracic-coxal joint in the crab leg. The S and T afferent neurons of the TCMRO convey signals to the CNS solely by means of graded changes in membrane potential. The rate of information transfer of these afferents was determined by measuring the signal-to-noise ratio (SNR) of these cells after repeated stimulation of the receptor with identical sequences of random movement and applying the Shannon formula for the information capacity of a Gaussian channel. Intracellular recordings were made from the S and T afferents adjacent to the transduction site at the origin of the receptor and along the axon 5–7 mm distal to this site. These nonspiking afferents transduce receptor movement and transmit this information with extremely high fidelity. The SNR of both neurons near the transduction site was >1000 over most of the 200 Hz stimulation bandwidth, and the mean information transfer rate was ~2,500 bits/s. When calculated over a wider bandwidth of 500 Hz, the information rate was >4,600 bits/s. The effect of axonal cable properties on the information rate was evaluated by determining the SNR from membrane potential recordings made 5–7 mm distal to the transduction region. The major effect of graded transmission along the axon was attenuation and low-pass filtering of the sensory signal. The consequent reduction in signal power and bandwidth decreased the information transfer by ~10–15% over 200 Hz and ~30% over a 500 Hz bandwidth.

INTRODUCTION

There has been considerable recent interest in applying information theoretic techniques to describe information encoding and transmission in the nervous system (Borst and Theunissen 1999; Rieke et al. 1997). Most neurons use action potentials to encode and transmit information as the relatively small length constants of most axons do not permit the transmission of passive changes in membrane potential over long (electrotonic) distances. However, there are numerous examples of neurons with sufficiently large length constants to transmit information in a purely graded, or nonspiking, manner (Pearson 1976; Roberts and Bush 1981).

Nonspiking neurons were first found to play a central role in motor systems when Mendelson (1971) described a single nonspiking interneuron essential for generating the rhythmic motor pattern for gill ventilation in crustacea. Subsequent work demonstrated that this system contains numerous nonspiking neurons that are primary elements in ventilatory pattern generation and control in the crab (DiCaprio 1989, 1990, 1999; DiCaprio and Fourtner 1988; Simmers and Bush 1980). Nonspiking neurons also play critical roles in other invertebrate central pattern generator and sensorimotor systems (Angstadt and Calabrese 1991; Burrows et al. 1988; Burrows and Siegler 1976, 1978; Büschges 1990, 1995; Büschges et al. 1994; Büschges and Schmitz 1991; Graubard 1978; Laurent and Burrows 1988, 1989; Nagayama and Hisada 1987, 1988; Paul and Mulloney 1985; Pearson and Fourtner 1975; Raper 1979).

In insect locomotor systems, spiking and nonspiking neurons operate in parallel pathways to process sensory information. For example, spiking and nonspiking local interneurons in the locust receive sensory inputs from other interneurons and leg mechanoreceptors and project to leg motor neuron pools. These nonspiking neurons play a significant role in the recruitment of motor neurons and in the fine graded control of motor neuron firing (Burrows 1980).

The sensorimotor system controlling the basal joints of crustacean walking legs is an excellent model system for investigating graded and spike-mediated information transmission as both nonspiking and spiking proprioceptors monitor the movement of the first two joints of the crab leg (Bush 1981; DiCaprio 2003a; Gamble and DiCaprio 2003). In the crab, the only proprioceptor signaling position and movement of the thoracic-coxal (TC) joint is the nonspiking thoracic-coxal muscle receptor organ (TCMRO). Movement of the coxo-basal (CB) joint is signaled by the spiking afferents of the coxo-basal chordotonal organ (CBCTO) and also by nonspiking afferents arising from two elastic strand receptors. Sensory feedback from leg proprioceptors and other sensory structures plays an important role in postural and locomotor control systems (Pearson 1995). These inputs can modify motor neuron activity directly via monosynaptic reflex pathways and indirectly by providing input to local interneurons in leg control circuits or to the central pattern generating networks that underlie locomotor rhythms (Marder and Bucher 2001; Pearson 1995, 2000).

The TCMRO lies in parallel with the coxal promotor muscle of the TC joint and consists of an elastic connective tissue sheath enclosing an intrinsic muscle (Alexandrowicz 1967; Alexandrowicz and Whitear 1957). This most basal leg joint produces forward movement (promotion) and backward movement (remotion) of the entire leg. Remotion therefore stretches, and promotion relaxes, the TCMRO. In addition to afferent neurons, the TCMRO is innervated by two motor neurons controlling the receptor muscle (Alexandrowicz and Whitear 1957).

Only three sensory neurons (T, S, and P fibers) originate from the TCMRO, all of which have centrally located cell bodies in the thoracic ganglion. The S and T fibers are nonspiking neurons with large (50–60 μm) diameter axons and transmit information to the CNS solely by graded changes in membrane potential (Bush and Roberts 1971; Ripley et al. 2000). The SNR of both neurons near the transduction site was >1000 over most of the 200 Hz stimulation bandwidth, and the mean information transfer rate was ~2,500 bits/s. When calculated over a wider bandwidth of 500 Hz, the information rate was >4,600 bits/s. The effect of axonal cable properties on the information rate was evaluated by determining the SNR from membrane potential recordings made 5–7 mm distal to the transduction region. The major effect of graded transmission along the axon was attenuation and low-pass filtering of the sensory signal. The consequent reduction in signal power and bandwidth decreased the information transfer by ~10–15% over 200 Hz and ~30% over a 500 Hz bandwidth.

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Given the continuous changes in membrane potential in nonspiking neurons (as opposed to the binary nature of neuronal spike trains), graded neuronal transmission would be expected to have a higher information transfer rate than spike-mediated transmission. Some studies have demonstrated that graded encoding of a stimulus does result in high information rates (de Ruyter van Steveninck and Laughlin 1996; Juusola et al. 1997). In the T fiber, these voltage-dependent channels produce a small (1–3 mV) spike-like component seen at the peak of the depolarizing phase of the graded generator potential elicited by receptor stretch (Ripley et al. 1968). This active component is not present in the S fiber response as these channels are apparently inactivated at the normal resting potential (Bush 1981; Bush et al. 1980).

In this study, we assessed the rate of information transmission of proprioceptive afferent neurons that convey signals over a relatively long distance via graded changes in membrane potential. This transmission occurred with very high fidelity, with a signal-to-noise ratio (SNR) >1,000 over most of the stimulation bandwidth of 200 Hz. At this bandwidth, the mean information rate was 2,500 bits/s at the transduction site, with only a modest (~10–15%) decrease in the information transfer rate as the signal propagated along the axon.

**Methods**

An isolated ganglion-receptor preparation from male or female green shore crabs, *C. maenas*, was used in all experiments. The walking legs and chela were automotized and the dorsal carapace, viscera, and brain removed. The sternal artery to the thoracic ganglion and leg nerves and transferred to a small-volume (5 ml) bath. The preparation was chilled (16–17°C) oxygenated saline at a rate of 2–3 ml/min for 15–20 min before proceeding with further dissection. The saline composition (in mM) was (in mM) 500 Na\(^{+}\), 12 K\(^{+}\), 20 Mg\(^{2+}\), 12 Ca\(^{2+}\), 576 Cl\(^{-}\). Buffered to pH 7.2 with 10 mM Tris maleate (Ripley et al. 1968).

The remotor, levator, and depressor muscles were removed to expose the promotor muscle in the fifth leg segment. The promotor muscle tendon was then cut at the coxopodite and the main leg nerve cut. The skeletal plate containing the origin of the promotor muscle, and the TCMRO was dissected free of surrounding structures along with the thoracic ganglion and leg nerves and transferred to a small-volume (5 ml) bath. The chamber was continuously superfused with chilled oxygenated saline during the experiment. The preparation was pinned to a silicone elastomer (Sylgard) base, and the promotor muscle was removed to expose the TCMRO. A small piece of the promotor tendon was left attached to the distal insertion of the TCMRO and attached to the puller with a stainless steel pin. The nerve to the TCMRO was dissected free from the main leg nerve and supported with a small Sylgard block near the origin of the TCMRO (Fig. 1, A and B). The in situ length of the TCMRO was measured with a caliper when the TC joint was held in the middle of the physiological range and the resting length of the isolated TCMRO was set to this value by mechanically adjusting the position of the puller. The motor nerve innervating the intrinsic TCMRO muscle was cut to eliminate any feedback to the receptor from the CNS (Fig. 1B).

The electromechanical puller was constructed from a 5-in low-midrange loudspeaker. The position of the speaker cone was monitored by an optical position sensor consisting of a light source, photodiode, and optical wedge (Hofmann and Koch 1985). The puller was controlled by a proportional-integro-differential (PID) controller operating in length feedback mode. The frequency response of the puller was flat to a cut-off frequency of ~220 Hz over a displacement range of ±1 mm. For the size of animals used in these experiments (4–5-cm carapace width), a length change of 0.35 mm corresponds to a joint angle change of ~15° where the total joint angle range is ~90° (Clarac 1977). The TC joint is held in a relatively constant angle during lateral walking in the crab (Clarac 1977) but covers a 20–30° range during forward and backward walking in the lobster (Ayers and Davis 1977) and during swimming in the crab (Hartnoll 1971). The maximum peak-to-peak receptor length change applied in these experiments was ±0.35 mm, equivalent to a maximum joint movement of approximately ±15°.

Intracellular recordings from TCMRO afferents were made with microelectrodes filled with 2 M KAc and amplified with a bridge electrometer (NPI SEC 05L). Recordings were made close to the site of mecano-transduction, ~0.5 mm from the receptor origin. Intracellular recordings were also made 5–7 mm along the axon at the point where the sensory nerve enters the thoracic ganglion. These recordings were usually made first at one site before the electrode was moved to the second recording site. The order of the recordings was varied and checked by re-impalement at the initial site, and no changes in the response or information transfer rate were observed with repeated measurements. In two experiments, two microelectrodes were used to make simultaneous recordings at both locations.

White noise was generated by a 31-bit pseudo-random number generator clocked at 10kHz resulting in a pseudorandom sequence length of >200,000s. The digital output of the generator was filtered to the desired bandwidth using a variable eighth-order low-pass filter (Wavetek 852), and DC offset and amplified as required. Trapezoidal stimuli were generated by a custom-built waveform generator with variable rise/fall time, amplitude, and duration. All signals were digitized on-line using a CED Power1401 laboratory interface (16-bit A/D converter, ±5-V range, 0.4 μs conversion time) controlled by CED Spike2 software (v4.13) with a sampling rate of 12.5 kHz.

Repeated sequences of white noise were produced by sampling a segment of the signal used to drive the puller and storing this waveform in the memory of the CED Power1401. The start and end of a repeating sequence were marked at zero-crossings of the waveform at points of similar slope to minimize transients during circular stimulus replay. The output from the D/A converter (16-bit converter, ±5 V range) was passed through a low-pass filter (4-pole, corner frequency = 800 Hz) to remove the high-frequency steps in the D/A output waveform. A reference mark for the start of each repeating sequence cycle was provided by a 2 V pulse that was output via a second D/A channel. Stimulus waveform playback was initiated manually after the start of (simultaneous) data acquisition and allowed to replay continuously for 60–80 cycles.

All calculations were made using programs written in the CED Spike2 script language (v4.13), and data were exported to Grapher (v4.0, Golden Software) for plotting. Figures were prepared using Canvas (v8.0.6, Deneba Systems).

**Information rate**

A method for determining the upper-bound for the information transfer rate of a continuous neural signal has been described in detail (Borst and Theunissen 1999; de Ruyter van Steveninck and Laughlin 1996; Juusola and French 1997; Rieke et al. 1997). In brief, the
afferent membrane potential recorded during repeated presentation of the same random input to the system is averaged to determine the average response of the neuron. This noise-free average is subtracted from each individual cycle response to determine the noise during each individual cycle. The power spectrum of the average response (signal) and the noise is computed by taking the Fast Fourier Transform (FFT) of the response and the noise, and the signal-to-noise ratio calculated for each frequency bin. The information transfer rate of the nonspiking neurons is then calculated using the Shannon (1948) formula for the information capacity of a Gaussian channel where the information rate $R$ (in bits/s) is defined as, $R = \frac{1}{2} \log_2 \left( 1 + \frac{S(f)}{N(f)} \right)$, where $S(f)$ and $N(f)$ are the power spectral densities of the signal and noise, respectively.

The integration limit for this calculation is usually at a frequency where the signal to noise ratio is zero, as at this and higher frequencies the total (cumulative) information is maximum. In this study, the rate of information transfer was calculated using two limits for the integration, 200 and 500 Hz. The 200 Hz limit was selected because this frequency is equal to the maximum (flat) bandwidth of the white noise used to drive the electro-mechanical puller. Above 200 Hz, the decrease in membrane potential signal power is dominated by the steep attenuation of the low-pass filter (48 dB/octave) used to set the bandwidth of the driving signal and does not therefore reflect the true performance of the receptor system, as the signal power for the S and T fibers decreases at 6 dB/octave above ~80 Hz (DiCaprio 2003a). In addition, we wished to compare the information transfer rate of the nonspiking neurons with the information rates of spiking CBCTO afferents at this bandwidth. Lower-bound estimates of the information rate of the CBCTO afferents (DiCaprio 2003b) derived from stimulus reconstruction (Bialek et al. 1991; Rieke et al. 1997) were calculated. 

FIG. 1. A: schematic diagram of the experimental preparation. The thoracic ganglion, the thoracic-coxal muscle receptor organ (TCMRO), and its sensory innervation are isolated and continuously superfused with oxygenated saline in a small volume chamber. The skeletal fragment containing the proximal attachment of the TCMRO is pinned to the Sylgard substrate with stainless steel pins, whereas the distal end of the receptor is attached to the output shaft of an electromechanical puller by a pin inserted through the receptor tendon. Intracellular recordings from TCMRO afferents were made close to the point where the S and T fibers insert in the receptor or 5–7 mm along the axon at the point where the nerve enters the thoracic ganglion (gray electrode). B: the TCMRO and sensory innervation (modified from Roberts and Bush 1971). A dorsal view of the thoracic cavity (left) shows the position of the TCMRO in series with the promotor muscle of the 5th leg TC joint. The sensory axons arise from the flanking connective tissue sheath (S fiber) of the TCMRO or at the insertion of the receptor (T fiber) and are therefore mechanically in parallel (S fiber) or in series (T fiber) with the receptor (left). In all experiments, the receptor efferent nerve (rm) to the TCMRO was cut (parallel slashes). Also shown is the elastic depressor receptor (dep.) and its nonspiking sensory neuron (D fiber), which runs in the same nerve as the TCMRO afferents. C: response of T and S fibers to trapezoidal stretch of the TCMRO. The resting membrane potential of these neuron ranges from ~65 to ~70 mV when the receptor is slack and is approximately ~55 mV when the receptor is held at a length equivalent to the mid-position of the TC joint. The initial stretch of the TCMRO (len) produces a rapid depolarization of T and S fibers followed by a relatively steady depolarization with increased receptor length. The length change imposed here is equivalent to ~20° of TC-joint movement. D: intracellular recording from T and S fibers during stimulation of the TCMRO with 200 Hz bandwidth white noise. The response of the S and T fibers are rather similar except for the slightly more linear response of the S fiber to receptor length changes and the approximately twofold difference in the amplitude of the membrane potential response.
using a 200 Hz integration limit for similar technical reasons, and because the SNR of these spiking afferents approached zero at 200 Hz.

As the SNR was still >1,000 at 200 Hz, an integration limit of 500 Hz was also used to calculate the information transfer rate. At this frequency, the SNR for both afferents was ≤10 for recordings made near the transduction zone and was close to 1 for the recordings made along the axon. This bandwidth also corresponds to the frequency range used to calculate the information transfer rate at graded synapses (de Ruyter van Steveninck and Laughlin 1996), in spider mechanoreceptors (Juusola and French 1997), and for the graded response of fly photoreceptors (Juusola and de Polavieja 2003) and thus allows a more appropriate comparison with the information transfer rates in these systems. In both cases, the information transfer rate will be an underestimate of the actual rate. At 200 Hz, a portion of the available signal (and noise) power is ignored, while at 500 Hz, the signal power is reduced above 200 Hz due to the steep decrease in the amplitude of the driving signal.

RESULTS

Recordings were made from 24 TCMRO preparations that yielded 18 T fiber and 17 S fiber recordings. Typical T and S afferent responses to trapezoidal receptor length changes are shown in Fig. 1C. The TCMRO afferents respond to trapezoidal stretch of the receptor with graded changes in membrane potential consisting of phasic and tonic components, that is, to both the rate of change of length (velocity) and to the absolute length of the receptor (Bush and Roberts 1971). At the beginning of a constant velocity TCMRO stretch, the T and S fibers respond with a rapid depolarization. When the receptor is then held at a constant length, the T and S afferents maintain a relatively constant level of depolarization that is roughly proportional to the receptor length (Bush and Roberts 1971).

The membrane potential recorded from T and S fibers in response to random TCMRO movement is shown in Fig. 1D. These 200-ms records were extracted from the middle of a 80-s period of stimulation. The peak-to-peak amplitude of the membrane potential fluctuation of the T fiber is approximately twice as large as the S fiber response, and the amplitude of the response of both afferents was essentially constant throughout the entire stimulation period, with no significant change (<1%) in the peak-to-peak amplitude of the membrane potential.

The TCMRO was stimulated with repeating cycles of identical white-noise movement for 60–80 trials. The average membrane potential of the S and T neurons was calculated for 40 stimulus cycles starting ≥20 s after the start of stimulation. The average response to the repeated random-movement sequence was subtracted from each individual cycle response to determine the noise in each cycle. Figure 2 shows the average response of the S and T neurons and the calculated noise in a single cycle for a 150 ms interval. In both afferents, the amplitude of the noise is <2% of the average response of the afferent (peak-to-peak amplitude of signal and noise: S fiber, 25.1 vs. 0.47 mV; T fiber, 63.6 vs. 0.59 mV). The probability density functions for the signal and noise amplitudes are shown at the right of each record. The amplitude distribution of the noise was well fit by a Gaussian distribution in all experiments, whereas the probability density function for the membrane potential (signal) is slightly skewed (see DISCUSSION).

The power spectra of the membrane potential and noise the SNR for S and T fibers are shown in Fig. 3. The SNR in both neurons is >1,000 at all frequencies within the 200 Hz bandwidth of the applied stimulus. For the neurons shown here, the information rate calculated over the 200 Hz stimulus bandwidth was 2,602 bits/s for the T fiber and 2,455 bits/s for the S fiber. The average information transfer rate over this bandwidth for each afferent in all experiments was 2,522 ± 319 bits/s (n = 18) and 2,543 ± 163 bits/s (n = 17) for the T and S fibers, respectively. With a 500 Hz integration limit, the average information transfer rates were 5,495 ± 510 bits/s (n = 18) and 4,690 ± 675 bits/s (n = 17) for the T and S fibers, respectively. In individual experiments, essentially identical estimates of the information transfer rate were obtained for S and T fibers when TTX (5 × 10^{-7}M) was added to the saline to block the voltage-dependent sodium channels present near the transduction region of the axons (Mirolli 1979, 1981).

Cable properties

The results described in the preceding text were obtained from recordings close (~0.5 mm) to the site of sensory trans-
duction. However, the axonal cable attenuates and low-pass filters this signal as it propagates along the axon. The (best-fitting) linear estimates of the frequency response of the receptor system indicate that the cutoff frequency is reduced by $\frac{\pi}{110}$ Hz from the value of 70–80 Hz measured from recordings near the transduction site (DiCaprio 2003a). This bandwidth reduction, in addition to the signal attenuation and any additional noise introduced by sources along the cable, should reduce the information transfer rate of the T and S fibers. To assess the effect of the axonal cable properties on the rate of information transfer rate, intracellular recordings from T and S fibers were made 5–7 mm distal to the transduction region, and the SNR and information rate calculated as before.

The signal and noise power and the calculated SNR for the S and T fibers determined from recordings made near the receptor origin (black) and along the axon (gray) are shown in Fig. 4. The length constants of the axons were measured under steady-state conditions and were 19 mm for the S fiber and 21 mm for the T fiber. Because of the attenuation of the membrane potential fluctuation along the axon, both signal and noise power decreased when recorded at a distance from the transduction site. The SNR was consequently similar at both recording sites for frequencies $\approx 60–70$ Hz. Due to the low-pass filtering by the axonal cable (DiCaprio 2003a), the signal power of the axon recording starts to attenuate at a lower frequency than the signal power measured at the transduction site. Therefore above 70 Hz, the SNR at the distant recording site decreased for the remainder of the stimulation bandwidth, primarily due to the decrease in signal power. For a 200 Hz bandwidth, the average reduction in information transfer rate as the signal propagates along the axonal cable was 9.9% ($n = 5$) for the T fiber and 11.1% ($n = 5$) for the S fiber. When using a 500 Hz integration limit for the information rate calculation, the average reduction in information transfer rate was 31% ($n = 5$) for the T fiber and 33% ($n = 5$) for the S fiber. Again, blockage of the small voltage-dependent response of the T fiber with TTX did not change the estimates of information transfer rate.

**Signal amplitude and information rate**

The TCMRO was driven with three amplitudes of movement ($\pm 0.4$, $\pm 0.08$, and $\pm 0.02$ mm) to determine the effect of the reduction in signal power, and the associated noise power, on the information transfer rate of the afferents. Figure 5 shows the power and noise power spectra and resultant SNRs for an S fiber response. The signal power decreased with the decrease in movement amplitude as did the noise power, although to a lesser extent. The noise powers for the two smallest amplitudes of movement were essentially identical and were the same magnitude as the power for the afferent membrane potential when the receptor was held at a constant length (gray line). The membrane potential noise power at a constant receptor length is the lower limit of the system’s noise and thus at low stimulation amplitudes, the S fiber noise power approaches and eventually reaches this limit. The SNR decreased as the signal amplitude decreased as did the
corresponding information transfer rate. Similar results were obtained for the T fiber (not shown), although signal power only decreased significantly when the TCMRO movement amplitude was less than \( \Delta x = 0.2 \) mm.

**DISCUSSION**

The information transfer rates of the two nonspiking afferent neurons of the crab thoracic coxal muscle receptor organ were analyzed using white-noise stimulation of the receptor. TCMRO movement elicits graded changes in the membrane potential of both neurons. These graded signals propagate passively along the sensory axons and reach the CNS with only modest decreases in amplitude due to the large (~20 mm) length constant of the axons. With recordings made close to the site of mechano-transduction that therefore reflect the information transfer rate just after the transduction from receptor length to membrane potential, the SNR was between 1,000 and 10,000 over the 200 Hz bandwidth, resulting in average information transfer rates for both neurons of ~2,500 bits/s. When a 500 Hz integration limit was used for the information rate calculation, the average information transfer rates at the transduction site were 5,990 and 5,145 bits/s and at the distal recording site, 4,035 and 3,405 bits/s for the T and S fibers, respectively.

**FIG. 4.** Signal power, noise power, and SNR for T and S afferents recorded close to the transduction region of the receptor (black) and at a distance \( \Delta x \) along the axon from the first recording site (S fiber, \( \Delta x = 6.5 \) mm; T fiber, \( \Delta x = 6.8 \) mm). The intracellular recordings were made with sequential penetrations of each neuron with the same electrode. The peaks in the noise power spectra are due to 60-Hz noise (and the harmonics at 120 and 180 Hz) in the intracellular recordings. The information rate for each recording site is shown next to each SNR plot for a 200 Hz bandwidth. Over a 500 Hz bandwidth, the information transfer rates at the transduction site were 5,990 and 5,145 bits/s and at the distal recording site, 4,035 and 3,405 bits/s for the T and S fibers, respectively.

**FIG. 5.** Signal and noise power, SNR, and information transfer rate with different movement amplitudes. The TCMRO was driven with white noise at \( \pm 0.4-, \pm 0.08-, \) and \( \pm 0.02 \) mm peak-to-peak amplitude movement. The average signal and noise power for each amplitude are shown along with the power of the membrane potential when the receptor was maintained at a constant length (gray line). The rate of information transfer at each signal power level is given next to the individual SNR plots for a 200 Hz bandwidth. The information rates calculated for a 500 Hz bandwidth were 6,130, 4,375 and 3,360 bits/s, in order of decreasing signal power. The peaks in the noise power spectra are due to 60 Hz noise (and the harmonics at 120 and 180 Hz) in the intracellular recordings.
fer rate at the transduction site was 5,495 bits/s for the T fiber and 4,690 bits/s for the S fiber. In recordings made distal to the transduction site, the signal was attenuated and low-pass filtered by the axonal cable, resulting in a decrease in signal power and hence SNR at frequencies $>60$–$70$ Hz. The SNR decreased by a factor of $\sim 10$ at the cutoff frequency of the applied noise (200 Hz), which resulted in an average decrease of $\sim 10\%$ in the information transfer rate over a 200 Hz bandwidth. Over a 500 Hz frequency range, the information transfer rate decreased by $\sim 30\%$ for recordings made in the axons 5–7 mm away from the transduction site. The S and T fibers contain fast TTX-sensitive sodium channels. When the information rate was determined when these channels were blocked with TTX (and the small-amplitude active component of the T fiber response eliminated), there was no change in the rate of information transmission.

The information transfer rate of a communication channel is limited by the signal power it can accommodate and by the minimum noise power present in the system (Shannon and Weaver 1949). When the S fiber response amplitude was reduced by reducing the amplitude of the applied movement, signal power decreased but noise power remained essentially constant for low-amplitude signals (Fig. 5) as it was equal to the magnitude of the noise power of the afferent membrane potential recorded when the length of the receptor was kept constant. Although the noise power was larger than this level when the receptor was stimulated with high-amplitude movement, this was only true for frequencies less than $\sim 70$ Hz where the noise power was two- to fivefold greater than this minimum level. For TCMRO movement amplitudes below $\pm 0.4\, \text{mm}$, equivalent to a joint angle range of approximately $\pm 15^\circ$ the information transmission rate of the S fiber is therefore determined primarily by signal amplitude. The information transfer rate is therefore limited by the intrinsic noise from the mechano-transduction channels and any ion channels in the axon as well as any noise caused by the receptor mechanics or unconstrained movement of the receptor.

**Effect of non-Gaussian signal distribution**

The Shannon formula for information capacity of a communication channel is only strictly applicable to a Gaussian channel, where the channel output consists of the sum of the signal and the noise, both of which have Gaussian distributions. For a signal with a given variance, a Gaussian distribution has the highest entropy. As the estimates of the information transfer rate of S and T neurons were made with the assumption that this condition was satisfied, the calculated information rates will be overestimates of the true information rate for this system if these conditions are not met.

The S and T neuron responses to stimulation of the TCMRO with band-limited white noise were skewed toward positive values (Fig. 2) and therefore only approximately Gaussian, although the noise distribution was Gaussian. This was expected as the transfer function of the receptor system is nonlinear (DiCaprio 2003a). In a study where the same methodology was used to assess the rate of information transfer across a graded synapse in fly visual interneurons (de Ruyter van Steveninck and Laughlin 1996), similar deviations from a Gaussian distribution were also present and judged to be tolerable. A recent study of the information rate of graded photoreceptors in the blowfly provides some insight into the expected error resulting from the assumption of a Gaussian signal distribution (Juusola and de Polavieja 2003). The information transfer rate of photoreceptors was calculated from the Shannon formula as well as estimated using a variation of the method of Strong et al. (1998) for determining the information rate of spiking neurons. The photoreceptor membrane potential amplitude distribution was skewed to an extent similar to the S and T fiber responses, and applying the Shannon formula resulted in an apparent 10–20% overestimate of the information rate. Assuming that a similar error applies to our estimates, the information rate of the TCMRO afferents (at 200 Hz) is likely to be on the order of 2,000–2,250 bits/s versus the mean value of 2,500 bits/s stated in RESULTS.

**Comparison with other nonspiking neurons**

The information rate of the nonspiking TCMRO afferent neurons is greater than the information transfer rate measured in other nonspiking neural systems. In the fly visual system, the information transfer rate of individual photoreceptors was estimated to be 1,000–1,200 bits/s (de Ruyter van Steveninck and Laughlin 1996; Juusola and de Polavieja 2003). The overall information rate of this system was also assessed at the interneuronal level for the LMC interneurons, which receive inputs via graded synapses from multiple photoreceptors. The information transfer rate for the graded synaptic transmission was $\sim 1,650$ bits/s (de Ruyter van Steveninck and Laughlin 1996). Juusola and French (1997) determined the information rate of spider mechanoreceptor (slit sensilla) afferents with respect to the transduction of receptor deformation to a graded receptor current and receptor potential, and also after the generation of action potentials. The information rate for the graded receptor potential in these neurons was 2,240 bits/s. However, when the afferents were allowed to generate action potentials, the information transfer rate of the spiking output of this system decreased markedly to 200 bits/s.

All of these studies used 500 Hz bandwidth noise to drive the systems, and the information rate was calculated over this frequency band. Although 200 Hz noise was used to drive the TCMRO, the SNR for the S and T fibers was still between 1 and 10 at 500 Hz. At this bandwidth, the mean information rates for the S and T fibers were 5,495 and 4,690 bits/s, respectively. The information transfer rates for the nonspiking TCMRO afferents are therefore two to five times larger than the comparable rates for other systems. Even after graded propagation along the axon, the mean information transfer rates for the T and S fibers were 3,800 and 2,990 bits/s, respectively, which is still comparatively large. A major factor accounting for this difference is likely the high signal (membrane potential) amplitude of the T and S afferents, which is $>25\text{mV}$ (peak to peak). In contrast, the amplitude range of the fly photoreceptor membrane potential is $\sim 10\text{mV}$ (Juusola and de Polavieja 2003) while the amplitude range of the spider slit sensilla receptor potential is $\sim 15\text{mV}$ (Juusola and French 1997).

**Comparison with spiking neurons**

There have been numerous studies assessing the information rate of spiking neurons in several systems (for a summary, see
Borst and Theunissen 1999). In general, these studies have demonstrated that spike timing in response to a given input can be extremely precise, and hence the noise in the response is low. In studies of primary afferent neurons, the stimulus-reconstruction technique (Bialek et al. 1991; Rieke et al. 1997) has been used to determine a lower bound for the information rate of these cells. For example, the lower bound for the information rate of cricket cercal filiform hair afferents was in the range of 75–220 bits/s (Roddey and Jacobs 1996) and the information rate of electroreceptor afferents (P-type) in electric fish was in the range of 0–200 bit/s (Wessel et al. 1996). The information rate of the spiking output of spider slit sensilla mechanoreceptors (Juusola and French 1997) was also determined to be ~200 bits/s.

The performance of spiking (H1) and graded potential (HS) motion-sensitive interneurons in the fly visual system has been compared with respect to the representation of visual motion information (stimulus velocity). Based on the calculation of the coherence function for the input-output relationship for each cell, the nonspiking HS cells were found to encode motion information with a higher fidelity than the spiking H1 cells (Haag and Borst 1997). In large part this was due to the low spontaneous firing rate of the H1 cells, resulting in a restricted dynamic range of the H1 response to (null-direction) motion that inhibits the neuron. The graded potential HS neurons also contain voltage-dependent conductances that give rise to small-amplitude spike-like depolarizations. These transient depolarizations are superimposed on the graded response to visual input when the neuron is at its normal resting membrane potential. Manipulation of the membrane potential of this neuron can alter the amplitude of these spike-like components (Haag and Borst 1998). Hyperpolarization increases the amplitude of these “spikes” while depolarization reduces their amplitude or completely abolishes them. The active component of the response serves to enhance the signal level of the neuron as the overall amplitude of the change in membrane potential is increased. Reducing the amplitude of the spike-like component with depolarization of the neuron lead to a decrease in mean response amplitude and a concurrent decrease in the signal to noise ratio. When HS was hyperpolarized and the (enhanced) spike-like component transformed into a spike train (via thresholding), the artificial spike train carried less information about the visual stimulus than the graded membrane potential signal (Haag and Borst 1998).

A modeling study of graded and spiking neurons based on the HS and H1 neurons (Kretzberg et al. 2001) found that spikes can be superior (with respect to stimulus discrimination) to graded responses if the spikes sharpen the neuronal response by amplifying fast transients in the graded membrane potential. However, graded signals were able to transfer more information over short time intervals (<100 ms) than could the spiking model neurons.

In the crab leg motor-control system, both nonspiking and spiking proprioreceptors are present at the CB joint while TC-joint movement is signaled by the nonspiking TCMRO afferents. The lower bound for the information transfer rate of spiking CBCTO afferents has been determined using the stimulus reconstruction technique, and ranged from 80 to 200 bits/s (DiCaprio 2003b). The information rate of the nonspiking TCMRO afferents is thus ~10 times greater than the information rate of the spiking CBCTO afferents and other invertebrate sensory receptors.

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