pling between the population dynamics of this anemone and the biological zonation of exposed outer coast areas with established mussel beds.

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20. Supported by an NSF predoctoral dissertation award (K.S) and NSF grant OCE 74 02307 to R. T. Paine. I thank M. Koehl, C. J. Slocum, and T. H. Suchanek for helpful field assistance and R. T. Paine, B. L. Thorne, D. Denninger, and L. Buss for reading and commenting on the manuscript.

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10 November 1980; revised 19 January 1981

## Intracellular Recordings from Thermosensitive Preoptic Neurons

Abstract. *Intracellular recordings were made from locally thermosensitive preoptic neurons in the green sunfish,* Lepomis cyanellus. *Stable resting potentials, action potentials, and spontaneous synaptic activity were observed over approximately 4° to 5°C changes in local brain temperature. A small percentage of the warm-sensitive neurons showed exponential firing-rate responses to temperature. These cells discharged rhythmically, lacked visible synaptic input, and showed slowly depolarizing potentials leading to action potentials. Other linear and nonlinear warm-sensitive and cold-sensitive neurons showed spontaneous excitatory and inhibitory synaptic potentials giving rise to action potentials. Cells that appear to be endogenously active may be true thermodetectors, and other thermosensitive neuronal activity may be synaptically mediated.*

Neurons in the anterior brainstem of various species of endothermic vertebrates undergo changes in their activity in response to localized changes in brain temperature (*1*). Many ectotherms, both aquatic and terrestrial, actively select a preferred temperature in a thermal gradient (*2*) and, by this means, regulate their body temperature (*3*). Thermoregulatory responses, both behavioral and autonomic, are elicited by local alteration of hypothalamic temperature in ectotherms (*4*) and endotherms (*1*). On the basis of these and other findings, centrally located temperature-sensitive neurons are thought to be components of a thermoregulatory system in all vertebrates.

Extracellular single-unit studies of neurons in the anterior hypothalamus–preoptic area of endotherms (*5*) and ectotherms (*6*) have revealed the existence of temperature-sensitive and -insensitive neurons. Cells that increase their firing rate with increases in local brain temperature are classified as warm-sensitive and are thought to stimulate heat loss and inhibit heat gain mechanisms (*7*). The converse is true for cold-sensitive neurons (*7*). Thermosensitive cells exhibit both linear and nonlinear responses to temperature changes (*1*, *7*). Various models describing the central nervous control of thermoregulation are based on the discharge characteristics of warm-sensitive, cold-sensitive, and thermoinsensitive neurons (*1*, *7*, *8*). The presence of central warm and cold thermodetectors, as well as various interneuronal cell types, has been hypothesized (*1*, *4*, *8*). Other investigators suggest that only warm thermodetectors exist, from which all other neuronal responses are derived through synaptic interactions (*7*). However, this dichotomy has yet to be resolved, as has the underlying mechanism making these neurons thermosensitive. On the basis of intracellular recordings, we report that some warm-sensitive cells appear to be endogenously active and may function as thermodetectors and that other thermosensitive activity is synaptically generated.

Intracellular recordings of preoptic thermosensitive neurons were made from 22 green sunfish, *Lepomis cyanellus*, acclimated to 25° ± 1°C and approximately 8 to 10 cm long. Fish were anesthetized with MS-222 during surgery and immobilized with tubo-curare during experimentation. Gills were perfused with aerated water held at 25°C. The brain was exposed through a small hole in the skull. Local brain temperature was altered through the use of a water-perfused thermode positioned on the telencephalic surface. A fine thermocouple inserted to the level of the recording site in the contralateral preoptic region monitored brain temperature. Fine intracellular micropipettes filled with 2*M* potassium citrate were used. The most useful electrodes had d-c resistances of 30 to 50 megohms. Electrical activity was recorded according to standard intracellular techniques. An active bridge circuit in the preamplifier allowed simultaneous recording and current injection. Firing rate was recorded with a rate meter.

Spontaneously active neurons in the medial and lateral preoptic region were impaled, and there was activity monitored for several minutes with the brain temperature held constant at 25°C. Brain temperature was then altered and its effect on activity recorded. Responses were curve-fitted by computer. Several criteria were used for intracellular impalements, including a rapid ≥ 30 mV drop in d-c potential, an increase in action potential amplitude to ≥ 25 mV, often a change in the action potential waveform to monophasic positive, often the appearance of synaptic potentials and a rapid return to original d-c level after withdrawal of the microelectrode. Because of thermal expansion and compression of the brain tissue, activity could be monitored over temperature changes of 3° to 5°C. Larger changes usually resulted in loss of the impalement.

Stable recordings (15 to 50 minutes) were made from 126 preoptic neurons, of which 29 showed local thermosensitivity based on criteria established in other investigations (*7*). Cells responded in lin-


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ear and nonlinear fashion as previously reported in extracellular studies of neurons in this region (*9*). Both warm- and cold-sensitive cells were present, but warm cells constituted the majority of the thermosensitive cells (85 percent). Figure 1 illustrates a typical recording and thermoresponse curve from a linearly responding warm-sensitive neuron. Intracellular activity consisted of spontaneous excitatory synaptic potentials, most of which were subthreshold (Fig. 1), and all-or-none action potentials with little or no positive overshoot. The action potential amplitude was 55 mV and 2.4 msec long; the resting potential was −62 mV at 25°C. This cell discharged at a rate of 18 impulses per second at 24°C, and its rate increased linearly to 38 impulses per second at 27°C (Fig. 1). Increasing the local brain temperature resulted in a greater number of subthreshold and threshold synaptic potentials, thus increasing the firing rate. In many cells (approximately 40 percent), action potentials were followed by depolarizing afterpotentials. This effect of temperature on synaptic input and activity was typical of almost all warm-sensitive neurons. In addition to excitatory synaptic input, inhibitory synaptic potentials were visible in two warm-sensitive cells.

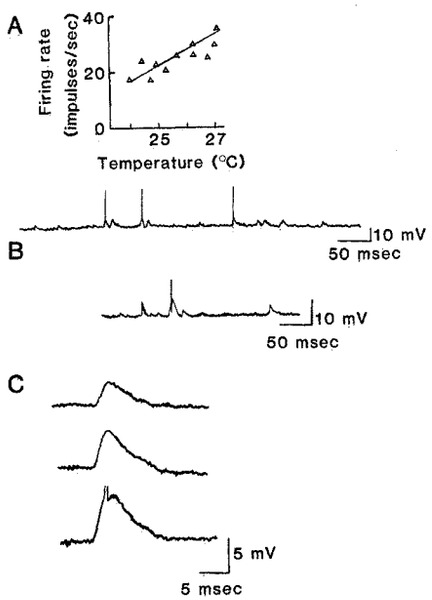


Fig. 1. Intracellular activity of a linearly responding warm-sensitive preoptic neuron. (A) Firing rate response of the neuron to approximately 4°C change in local brain temperature ($r$ = .91). (B) Top: Intracellular recording trace showing spontaneous threshold and subthreshold excitatory synaptic potentials and all-or-nothing action potentials. Brain temperature was 24°C. Bottom: Higher gain trace showing fast rise and slow decay of synaptic potentials and depolarizing afterpotential accompanying one action potential. Action potential has been truncated. (C) Traces of three different amplitude potentials at high gain and sweep speed. The third potential generated an action potential (truncated).

Cold-sensitive cells displayed thermosensitivities of 0.2 ± 0.4 impulses per second per degree Celsius. The intracellular activity patterns observed in cold-sensitive neurons ($N$ = 4) was similar to the warm-sensitive neurons except that inhibitory synaptic potentials were prominent in all cells. For those cells which appeared to be synaptically driven, resting potential averaged 61 ± 3.9 mV, spike amplitude 58 ± 4.5 mV, and spike duration 2.3 ± 0.3 msec at 25°C. Action potentials were followed by small (2 to 3 mV) after-hyperpolarizations in some cells. Excitatory and inhibitory synaptic potentials ranged from 1 to 10 mV in amplitude and decayed in a typical manner with approximately the same time constant. Inhibitory potentials, however, generally had a slower rate of rise than the excitatory potentials and were usually smaller in amplitude (mean ± standard deviation was 4.7 ± 1.2 mV for excitatory potentials, $N$ = 200; 2.3 ± 0.9 mV for inhibitory potentials, $N$ = 200).

A radically different activity pattern was observed in those warm-sensitive cells with low firing rates at 25°C and exponentially responsive to increasing temperature (Fig. 2). Intracellularly recorded activity consisted of slow depolarization, which reached threshold and generated an action potential. These action potentials were generally longer (3.8 ± 0.6 msec) than those observed in synaptically driven neurons, often showed a 5- to 10-mV overshoot, and were followed by a large hyperpolarization (approximately 10 mV) which decayed with time (Fig. 2). Resting potentials averaged 71 ± 2.3 mV at 25°C. These cells discharged in a rhythmic pattern with very constant interspike intervals when maintained at a constant temperature as previously observed extracellularly (*9*). Increasing the temperature increased the decay rate of the post-spike hyperpolarization and increased the firing rate. This activity pattern was observed in all four warm-sensitive cells displaying an exponential response to changing temperature. If this type of cell was caused to discharge during the hyperpolarized period by a short duration injection of depolarizing current, the interval following the elicited action potential and the next spontaneous action potential was constant and equal in duration to the other spontaneous interspike intervals (Fig. 2).

The results of this study seem to indicate that two basic types of thermosensitive cells exist in the preoptic region of sunfish. Warm-sensitive cells displaying high firing rates (> 5 impulses per second) and linear and nonlinear responses to temperature and cold-sensitive cells constitute one class. Their activity is derived from synaptic input. Those warm-sensitive cells which show low firing rates (< 5 per second) and an exponential activity response to temperature constitute the other class; they seem to be endogenously active and to lack visible synaptic input. The pattern of activity and response to injected threshold current pulses is typical of cells with this type of activity (*10*).

It does not seem unreasonable that this latter class of neurons could function as thermodetectors. They are highly sensitive and discharge in a rhythmic, continuous, and stable manner. Although the exact mechanism is unknown, these cells apparently have a pacemaker system responsible for their activity. Pacemaker cell activity in many diverse systems is highly temperature-sensitive (*10*, *11*), and some are known to respond exponentially to temperature changes (*11*).

If these cells are indeed involved in thermoregulation, only one type of true thermodetector cell seems to exist in this region. The thermosensitive activity of

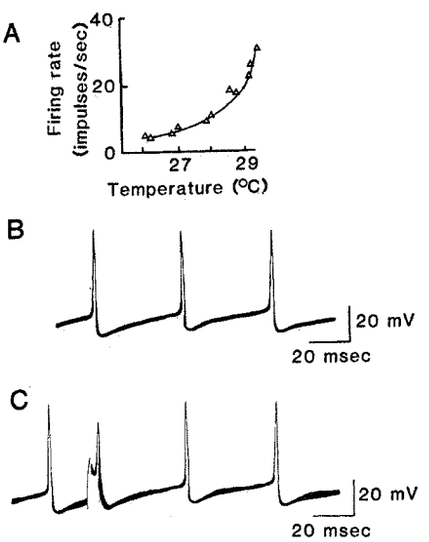


Fig. 2. Typical intracellular activity from an exponentially responding warm-sensitive preoptic neuron. (A) Firing rate response to 4°C change in brain temperature ($r$ = .94). (B) Intracellular trace of spontaneous action potentials. Each action potential is followed by a large hyperpolarization that decays. Interspike intervals in this cell remained constant at a constant brain temperature but were altered by increasing or decreasing local temperature. (C) Excitability of the cell was tested by a 2.5-nA injection of depolarizing current pulse through recording pipette. This pulse elicited a somewhat smaller action potential and reset the firing pattern.

other cells results from synaptic input from other thermosensitive cells and may originate from the endogenously active neuron. Such schemes of neuronal interaction have been previously inferred from extracellular activity patterns. Preoptic thermosensitive cells in mammals responding in a linear fashion to temperature have been reported to be thermodetector cells (*8*, *12*). More recent extracellular work (*13*), however, suggests that those cells with low firing rates and exponential response curves are thermodetectors and that they remain endogenously active and thermosensitive after synaptic blockade.

The research presented here is based on a lower vertebrate, and the inherent mechanisms may be unique to these animals. While our results generally agree with hypothesized mechanisms based on extracellularly recorded data from mammals (*13*), extrapolation between such widely separated species may prove fallacious; further investigation of central thermosensitive neurons in mammals by intracellular techniques is necessary. techniques.

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9 December 1980; revised 10 April 1981

# Integration of Visual and Infrared Information in Bimodal Neurons of the Rattlesnake Optic Tectum

Abstract. *Bimodal neurons in the rattlesnake tectum, which receive sensory input from the retina and from the infrared-sensing pit organ, exhibit novel, highly nonlinear cross-modality interactions. Some units respond only to simultaneous bimodal stimulation. Others respond to only one of the two modalities, but show greatly enhanced or depressed responses when stimulated simultaneously in the second modality. These cross-modality interactions may play an important role in recognizing and orienting toward biologically important objects.*

The optic tectum (*1*) is an important integrative center of sensory information. Besides receiving a projection from the retina, the tecta of many species receive somatosensory and auditory inputs (*2–4*). These are often organized in spatiotopic maps that are, to a degree, in register with the more precise retinotectal map of the visual system (*2*, *3*, *5*). The organization of these inputs, along with evidence obtained from behavioral studies (*6*), suggests that the tectum aids in the control of orientation movements and the spatial shift of attention.

Many tectal neurons receive inputs from two or more sensory modalities. In the mouse, hamster, and rabbit, visual-tactile bimodal cells and visual-tactile-auditory trimodal cells have been reported (*5*, *7*). Other studies have described visual-auditory cells in the cat and monkey (*4*, *8*). In most of these investigations, tectal multimodal responses were tested through the use of unimodal stimuli exclusively (*9*). Interactions between modalities were not studied.

We now report an investigation of cross-modality interactions in tectal neurons of the rattlesnake. The rattlesnake tectum receives a major input from a specialized infrared (IR) sense as well as a normal retinotopically organized visual projection (*10*, *11*). The pit organ of rattlesnakes and other pit vipers is sensitive to IR radiation, and receives a crude IR image of the world with its pinhole-camera optics (*12*). The IR projection onto the tectum is organized spatiotopically and is roughly in register with the visual tectal map (*13*).

Hartline *et al.* (*13*) showed that many tectal cells of the rattlesnake receive input from both the visual and IR systems. They described two types of multimodal neurons: OR units, which are reliably driven by a unimodal stimulus of either modality, and AND units, which do not respond well to unimodal stimuli but which are reliably driven by simultaneous visual-IR stimulation. In addition to these two types, we now describe neurons showing other unusual kinds of cross-modality interactions. These cells display highly nonlinear summation characteristics, including cross-modality enhancement and depression, properties that indicate a complexity of multimodal integration not previously described (to our knowledge) in tectal neurons of any species.

We used NaCl-filled micropipettes to record the electrical activity of single units from the exposed tectum of the southern Pacific rattlesnake (*Crotalus viridis*). During recording, the snakes were lightly anesthetized with Metofane (methoxyflurane). Visual and IR stimuli were rigorously segregated through the use of visible and IR filters and mirrors positioned in front of the contralateral eye and pit organ. Visual stimuli (white spots, 0.1° to 15° in diameter projected onto a rear-projection screen) were flashed on or off or moved at controlled velocities. The IR stimuli (wavelengths > 850 nm, with an unattenuated intensity of 3.3 mW/cm$^2$ at the pit organ) were stationary ON flashes of an incandescent bulb ~ 3° in diameter. Visual and IR stimuli were adjusted to obtain maximal responses for each unit characterized. Stimuli were positioned near receptive field centers in both modalities. The diameter, velocity, and trajectory of visual stimuli were also adjusted for maximal responses; when white spots proved ineffective, bars and black spots and bars were tested.

Of the 196 tectal units we characterized, 103 showed some degree of cross-modality interaction. We categorized these 103 units into six groups according to response properties (Table 1 and Fig. 1). (A few units shared properties of two or more groups.)

The OR units responded well to both visual and IR unimodal stimuli and gave combined responses to simultaneous visual-IR stimulation. Some OR units displayed greater than linear summation [cross-modality facilitation (*14*)]; responses (total number of spikes) to simultaneously presented visual-IR stimuli were larger than the sum of the two unimodal stimulus responses. Other OR units summed less than linearly [cross-modality occlusion (*14*)], in extreme cases giving bimodal responses equal to


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