The Infrared “Vision” of Snakes

Snakes of two families can detect and localize sources of infrared radiation. Infrared and visible-light information are integrated in the brain to yield a unique wide-spectrum picture of the world

by Eric A. Newman and Peter H. Hartline

Rattlesnakes can strike accurately even at night when darkness hides their prey. The strike is guided by heat: infrared radiation emitted by the warm-blooded target. The radiation is sensed by an extraordinary system that enables rattlesnakes to “see” in a region of the electromagnetic spectrum where animals generate their own radiant energy.

The infrared “eyes” of the rattlesnake are the pit organs, a pair of deep cavities in the head that open on the side of the head below and in front of the eyes. The pit organs are richly supplied with heat-sensitive nerve fibers connected to the brain. All snakes of the subfamily Crotalinae, the pit vipers, have pit organs and are sensitive to infrared radiation. In North America these snakes include the cottonmouth (water moccasin) and the copperhead as well as the rattle-snake. Pythons and many other members of the family Boidae (boi-dae snakes), distant relatives of the pit vipers, also have heat-sensitive pits. In contrast to the pit vipers, they have many pits on the scales bordering their mouth, as many as 13 pairs.

Infrared sensitivity in pit vipers and boi-dae snakes has apparently evolved from the somatic sensory system. In man and other mammals this sensory system is concerned with the sensations of, among other things, touch, pressure, temperature and pain. In mammals sensory messages are conducted from the facial area to the brain by the trigeminal nerve. In infrared-sensitive snakes a substantial part of the trigeminal nerve is devoted to the pit organs and infrared sensitivity. In the course of evolution the somatic sensory system of pit vipers and boi-dae has developed into a sense much like vision. Pit vipers and boi-dae snakes have also evolved specialized nuclei, or clusters of nerve-cell bodies, in the brain to receive and process the sensory information coming from the pit organs. The nuclei relay information to the optic tectum of the midbrain, a structure known for its role in vision and in the spatial representation of sensory information.

Like other animals, human beings learn to associate several sensory modalities with rea objects of many kinds. For example, both the sight of a bird and the sound of its song help to localize and identify it. In an analogous way the optic tectum of infrared-sensitive snakes combines infrared signals from the pit organs with visual signals from the eyes. The integration of visual and infrared information in the tectum gives pit vipers and boi-dae snakes a unique view of the world, a view that compares and contrasts visual and infrared images.

Although the infrared pit organs were described long ago by anatomists, their function remained obscure until the 1930’s, when G. Kingsley Noble and A. Schmidt of the American Museum of Natural History in New York showed that the pits detect heat. They found that rattlesnakes could differentiate between a warm light bulb (covered with an opaque cloth) and a cold one. Snakes oriented and struck toward warm bulbs as long as their pits remained uncovered. They ignored all bulbs, warm as well as cold, if the pits were blocked.

In the 1950’s Theodore H. Bullock and his colleagues at the University of California at Los Angeles demonstrated that the pit organ functions by sensing the infrared radiation given off by warm objects. These investigators monitored the nerve impulses in the axons (long nerve-cell fibers) of the trigeminal nerve that are connected to the pit. They found that impulses are triggered equally well by a warm object whether it is presented to a rattlesnake in the light or in a totally dark room. The axons do not respond, even in a lighted room, if the pit is exposed to the same object once it has cooled. Furthermore, the axon’s activity in response to a warm object vanishes if a heat-absorbing glass filter is inserted between the pit and the object, even though the glass lets through nearly all the visible light. In the complementary experiment, where a filter was inserted that let through visible radiation but passed most of the infrared, the response was only slightly reduced. Thus it was conclusively demonstrated that the pit organ is sensitive to radiation at infrared wavelengths.

Just how good is the rattlesnake’s infrared sense? How accurately can a rattlesnake localize a warm object? How sensitive are the infrared detectors? Answers to these questions have come from a combination of behavioral and neurophysiological experiments. In order to determine how accurately a rattlesnake can localize a warm object Laurence R. Stanford and Michael S. Loop, working with one of us (Hartline) at the University of Illinois at Urbana-Champaign, measured the striking accuracy of blindfolded snakes. A rattle-snake whose eyes (but not its pits) had been occluded with blinders was put on a raised pedestal in the middle of a circular enclosure. An infrared source (the heated tip of a soldering iron) was then presented to the snake just beyond its striking range. An experimenter introduced the soldering iron at various angles from zero to 60 degrees to the left or right of where the snake was facing. A video camera was ready to record the expected strike; the accuracy of the strike would be measured from the videotape.

The snakes refused to cooperate; they almost never struck toward the soldering iron. Apparently the stimulus was not sufficiently meaningful to them. The somewhat diabolical solution was to give the snake a mild electric shock just before each presentation of the soldering iron. The snakes now struck often enough so that we could measure the accuracy of their response. Even with both eyes securely covered the strikes were accurate to within about five degrees of dead center, regardless of whether the target originally lay straight ahead or off to the side. That is very impressive, and for a mouse it is deadly.

How can an investigator measure the sensitivity of the infrared sense? Bullock’s method was to record the frequency of action potentials, or nerve impulses, in the trigeminal-nerve axons leading away from the pit organ. This neurophysiological approach can give an indication of the ultimate sensitivity
SOUTHERN PACIFIC RATTLESNAKE, a native of the western U.S., can locate weak sources of infrared radiation by means of its pit organs, a pair of cavities in front of and under its eyes. In rattlesnakes and other members of the pit-viper family, the radiation is detected by an extremely thin heat-sensitive membrane that stretches across the back of each pit. The field of view of each pit extends from about 25 degrees beyond the animal’s midline to 105 degrees at the side and from 45 degrees below the horizontal to 60 degrees above it.

RETICULATED PYTHON, a native of southern Asia, has 13 pairs of pits in the scales above and below its mouth. This photograph shows five pits on the left side of the snout and one on the right. Six other pits border the lower lip, below and behind the eye. Other boid snakes (snakes of the family Boidae), including the tree boas, have similar arrays of pits. The back surface of each pit is highly sensitive to heat energy. Each pit has a slightly different field of view. Still other boid snakes, including the boa constrictors, do not have discrete pits but have infrared-sensitive scales on their face. Both of the photographs on this page were made by one of the authors (Newman).
STRUCTURES IN THE BRAIN and the nerve pathways associated with the infrared sensory system of pit vipers have only recently been worked out. A principal puzzle, now solved, was how the information gathered by the pit organ and carried by impulses in the trigeminal nerve finds its way to the optic tectum, a midbrain structure that plays a prominent role in the processing of visual information.

Rattlesnake Pit Organ is formed out of a cavity in the soft tissues and bone of the face (left). A heat-sensitive membrane, 30 square millimeters in area but only 15 micrometers thick, is stretched across the cavity. The membrane intercepts infrared radiation that passes through the aperture of the pit. Inside the pit membrane (right) the bushy nerve endings of the trigeminal-nerve fibers terminate within a few micrometers of the membrane’s outer surface. A change in the membrane temperature of only .003 degree Celsius is sufficient to raise the firing rate of the trigeminal-nerve fibers. The biophysical mechanism that accounts for the response to heat is not known.
of the pit receptor. Bullock found that in the absence of a stimulus individual axons carry an irregular low-frequency barrage of action potentials. When the pit is suddenly illuminated with moderately strong infrared radiation, the frequency of the firing of the action potentials increases dramatically. The firing rate rises within 100 milliseconds of the onset of the stimulus, remains high for a brief time and then slowly decays back to nearly the background level. When the illumination is turned off, the firing rate temporarily drops below the background level, then slowly recovers to its prestimulus rate.

Bullock and his colleagues found that individual axons are remarkably sensitive to infrared stimuli. A small warm object such as a human hand or a live rat, introduced as far as half a meter from the pit, triggers a noticeable increase in the firing rate of some of the trigeminal-nerve fibers. Such a stimulus corresponds to an increase of the energy incident on the pit organ of approximately .1 milliwatt per square centimeter. For the purpose of comparison, on a clear winter day in the northern U.S. the sun's rays deliver about 50 milliwatts of infrared per square centimeter.

Bullock and F. P. J. Diecke also made direct measurements of the temperature sensitivity of the trigeminal fiber endings in the rattlesnake pit organ. They controlled the internal temperature of the pit by directing a stream of warm water into the pit cavity. A change in the temperature of the flowing water as small as .003 degree Celsius produced a noticeable change in the firing rate of the more sensitive nerve fibers!

The pit organ's remarkable sensitivity to radiant heat can be traced to its remarkable structure. Each pit organ of a rattlesnake or boid snake consists of a cavity from one millimeter to five millimeters in diameter in the soft tissue and bone of the head. In rattlesnakes a thin membrane about 30 square millimeters in area is suspended across the air-filled space of the cavity. Only 15 micrometers thick, or about a fourth the thickness of this page, the membrane is the key component of the sense organ. Distributed across the membrane surface are some 7,000 thermosensitive endings of trigeminal sensory axons. Each of the endings can excite its nerve fiber if it is warmed. Similar heat-sensitive nerve endings cover the bottom of each pit in boid snakes. In boids the sensitive epithelium is not suspended in air as it is in rattlesnakes. The axon endings, however, come to within 30 micrometers of the surface.

The extreme heat sensitivity of the pit organs is a direct result of the proximity of the thermoreceptors to the outward-facing surface of the sensory epithelium. Infrared radiation falling on the surface immediately raises the temperature of the local membrane and the membrane receptors, causing an increase in the firing rate of the trigeminal-nerve fibers attached to the thermal receptors. If the membrane temperature is raised above its normal level, the firing rate will continue at a high level until the membrane temperature falls back to its normal level. If the membrane temperature is raised above its maximum normal level, the firing rate will momentarily rise to an even higher level and then return to its normal level.

The spatial accuracy of the rattlesnake's infrared system can be measured by presenting a warm object at various angles to the left or the right of a snake whose eyes are covered with blinders. Each filled circle represents a single strike of the snake and shows the angular error between the strike and the target. The stimuli were presented at up to 60 degrees to the left or the right of the animal. The average error of the strikes is less than five angular degrees.

TRIGEMINAL-NERVE FIBERS signal changes in the temperature of the rattlesnake's pit membrane. The colored bar indicates a 10-second test period during which a snake's pit organ was exposed to infrared radiation. The traces on the line above the bar show the impulses recorded from a single trigeminal-nerve fiber. The firing rate is highest when the radiation is turned on but drops to nearly the background level. When the radiation is turned off, there is a short silent period. The properties of infrared trigeminal-nerve fibers were originally discovered by Theodore H. Bullock and his colleagues at the University of California at Los Angeles.
ANATOMICAL PATHWAY OF THE INFRARED SYSTEM was traced with the aid of an enzyme extracted from horseradish, horseradish peroxidase (HRP), which is taken up by the terminals of neurons and transported back to their cell bodies. HRP molecules are colored dots.

HORSERADISH PEROXIDASE INJECTED INTO BRAIN of a rattlesnake was traced by staining thin slices of tissue to reveal the presence of the enzyme. HRP injected into the optic tectum (A) was transported to a previously unknown nucleus, or collection of cell bodies, called the nucleus reticularis caloris (RC). When HRP was injected into the RC nucleus (B), stained cell bodies were found in the LTDD nucleus, which was known to receive a direct input from the pit organ. LTDD stands for a Latin expression that translates as "nucleus of the lateral descending trigeminal tract." The HRP experiments solved the puzzle of how the infrared information originating in the rattlesnake's pit organ ultimately reaches the optic tectum.

MICROGRAPHS OF BRAIN SLICES show how cell bodies labeled with HRP stand out as dark, irregular profiles after staining. The micrograph at the left is a section of the RC nucleus after horseradish peroxidase was injected into the optic tectum. The micrograph at the right is a section of the LTDD nucleus after the enzyme was injected into the RC nucleus. The experiments were done by the authors and Edward R. Gruberg of the Massachusetts Institute of Technology. Earl Kilcher of the University of Puerto Rico collaborated on first experiment.

ture of the sensors. The same amount of radiation falling on the bare skin of a mammal would raise the temperature of the first few micrometers of the skin by about the same amount. The thermoreceptors of mammals, however, lie much deeper. The entire thickness of the tissue between the surface and the receptors, about 300 micrometers, must be heated in order to warm them, and it takes 20 times as much heat energy to warm a layer of tissue 300 micrometers thick as it does to warm a layer only 15 micrometers thick. The sensitivity of mammalian thermoreceptors is further reduced by conductive heat loss to even deeper layers. Rattlesnakes avoid this problem with yet another specialization: since the heat-sensing membrane is surrounded by air on both sides, it does not lose heat to deeper tissues. Energy absorbed from infrared radiation almost exclusively heats the receptors.

Although the temperature sensitivity of rattlesnake trigeminal-nerve axons is impressive, it is not extraordinary when it is compared with the thermosensitive nerve cells of other animals. The skin of the human forehead, for example, has about the same threshold sensitivity to temperature. The great difference between rattlesnakes and other animals in sensitivity to incident radiation is primarily due to the anatomical specializations of the sensory organ and not to physiological differences in the sensory receptors.

The directional capabilities of the infrared sense can also be attributed to anatomical specializations of the pit. The pit organs of rattlesnakes have openings that are less than half the diameter of the sensory surface. Thus a small warm object half a meter or so in front of the pit will illuminate no more than a fourth of the entire thermosensitive membrane. The location of the illuminated patch on the membrane surface should therefore give an adequate clue to the location of a warm object. In short, the pit organ functions much like a crude pinhole camera.

The accuracy with which the snake can localize a warm object must depend on how accurately it can determine the position of the illuminated patch on the membrane. Simple trigonometric calculations show that in order to localize a small source to within five degrees of angle the snake must be able to measure the position of the warm spot on its receptive membrane to within about 175 micrometers. With a mosaic of receptors, each one about 60 micrometers across, such accuracy is quite reasonable. Diffraction of the infrared radiation (whose dominant wavelengths are in the band between six and 12 micrometers) may blur the edges of the warm spot somewhat, but not enough to reduce the pit's accuracy significantly.

Specializations evolved by the infra-
red-sensitive snakes are not limited to the pit organ. Pit vipers and boid snakes have also developed unique brain structures to process the novel information gathered by the pits. Early neurophysiological experiments on the rattlesnake brain demonstrated that the activity of many neurons (nerve cells) in the optic tectum of the midbrain (which was then thought to be primarily concerned with vision) was controlled by infrared stimuli. Evidently the infrared system, in parallel with its evolution from a facial-skin sense to a vision-like remote sense, has achieved a prominent representation in the tectum. This discovery, made independently by one of us (Hartline), who was then working at the University of California at San Diego, and by S. I. Terashima and R. C. Goria of the Tokyo Medical and Dental University, presented an interesting anatomical problem. In other reptiles and in mammals the trigeminal nerve terminates in the trigeminal region of the hindbrain. How does infrared information originating in the trigeminal nerve find its way to the optic tectum of the midbrain in the rattlesnake?

Two groups of investigators began to work on the problem. Dolores M. Schroeder and Loop, working at the University of Virginia Medical School, employed cobalt ions to trace the connections of the rattlesnake trigeminal nerve. They placed the cut end of a branch of the nerve serving the pit in a cobalt chloride solution and passed an electric current between the solution and the brain. The current drove cobalt ions up the axons of the nerve to the axon terminals. When Schroeder and Loop treated sections of brain with a cobalt stain, they found that the trigeminal-nerve fibers, instead of ending in the normal trigeminal hindbrain area, ended in a new nucleus, now known as the LTDD (an abbreviation for the new structure, originally named in Latin “nucleus of the lateral descending trigeminal tract”).

G. J. Molenaar of the University of Leiden independently identified what is almost certainly the same nucleus in the python, a bold snake. The LTDD nucleus appears to be peculiar to snakes that have a specialized infrared capability; it has been found in no other animal. It seems to be exclusively devoted to the infrared sensory system.

Our curiosity was piqued. If the nerve impulses carried by the trigeminal axons are delivered to the LTDD nucleus, what is the pathway that relays the infrared sensory information to the optic tectum? One approach to tracing connections within the brain is to use the peroxidase enzyme extracted from horseradish. The large horseradish-peroxidase molecule is taken up specifically by the axon terminals of individual neurons and is transported to other parts

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**CONNECTIVITY IN THE PYTHON INFRARED SYSTEM** is more complex than it is in the rattlesnake. The python pit organs look out on different but overlapping areas of infrared space. (Only three pits of the multipit array are shown.) The field of view of each pit is displayed over the pit's projection region on the tectal surface. Anterior pits (A) are represented in the front of the tectum, the more posterior pits (C) toward the rear of the tectum. The front area of each pit's infrared-sensitive epithelium is connected to the back of its projection region. The complex pattern of connections yields a more or less continuous representation of infrared space on the python's tectal surface that corresponds fairly well with the visual representation.
of the same cells. A staining procedure makes the horseradish peroxidase clearly visible in slices of brain and reveals the locations of the cell bodies of the neurons that took up the peroxidase.

Working with Edward R. Gruberg of the Massachusetts Institute of Technology and Earl Kicliter of the University of Puerto Rico, we injected horseradish peroxidase deep into the rattlesnake optic tectum where infrared sensory input is found. If cells in the LTLD projected directly to the optic tectum, we reasoned, their axon terminals in the tectum would pick up the peroxidase and transport it back to the LTLD. Somewhat to our surprise we found no stained neurons in the LTLD. Instead we found a group of prominently stained cells in a different region of the hindbrain. We postulated that this group of cells, which we named the nucleus reticularis caloris (RC), served as a relay station between the LTLD and the tectum.

Now we had to determine whether or not our new nucleus was connected directly to the LTLD. We investigated this question with Gruberg by injecting horseradish peroxidase into the RC nucleus. This time we did find stained cells in the LTLD. Stanford and Schroeder looked into the same question with a technique based on the degeneration of nerve cells. They selectively destroyed the cells of the rattlesnake LTLD nucleus and used a staining procedure that revealed the degenerated axons of these cells. They were able to trace the axons from the LTLD to the RC. Therefore both experimental approaches yielded the same answer: cells of the LTLD nucleus project directly to the RC. Although neither of these experiments could clarify the functional roles the LTLD nucleus and the RC nucleus play in the infrared sensory system, they at least explained how infrared information reaches the optic tectum. In the rattlesnake the LTLD and RC nuclei have evolved to process infrared sensory information and relay it to the tectum.

It is clear from the effectiveness of the infrared system in guiding the snake's strike that the system is able to localize objects in space with high accuracy. In this role it functions remarkably like the visual system of other animals. Our neurophysiological studies and those of our colleagues have revealed many similarities between the mechanisms that enable the visual and infrared systems to localize objects.

Bullock, and later J. A. DeSalvo, working with one of us (Hartline), described how individual trigeminal-nerve axons respond to warm stimuli anywhere within a field of view described by a cone originating at the pit. Such cones of view are usually between 45 and 60 degrees across and are called, by analogy with their visual counterparts in the retina, excitatory receptive fields. Most trigeminal fibers therefore behave as if their receptive fields were limited simply by the shadows cast by the lip of the pit. The response of any one trigeminal neuron would not convey the location of a stimulus accurately, but a population of many neurons, whose activity could be analyzed by the brain, might do so. In such analysis an important role is probably played by the optic tectum.

The optic tectum, also known in mammals as the superior colliculus, is one of the major visual centers of the brain. It is perhaps the main center for the processing of information about the location of objects in space. In monkeys the tectum helps to initiate and control "looking," or direction of gaze. In frogs and toads it probably initiates and controls the capture of flies and other prey.

In the optic tectum visual information is organized in an orderly way. Connections between the retina and the tectum (which are linked by the optic nerve) are made in such a way that a map of visual space is formed on the tectal surface. Just as a road map represents the spatial organization of roads on the earth's surface, so the visual map on the tectal surface represents space as it is viewed by the eye. For example, the front part of the tectum represents the part of visual space in front of the animal; the back part of the tectum represents the space toward the side and the rear. The orderly representation of visual space on the tectal surface is a constant feature of vertebrates, from fishes through primates.

Vision is not the only sense that can tell the brain where objects are. Sound also yields valuable location cues. So does touch. Both of these senses are also represented in the optic tectum of mammals. Furthermore, both the auditory system and the somatic sensory system are represented in the tectum in an orderly spatial way that coincides roughly with the visual system's tectal map. The front part of the tectum represents the front region of auditory space; sounds coming from in front of an animal preferentially excite this tectal region. Similarly, the front part of the tectum responds preferentially to touch stimulation of the front part of an animal such as the snout.

Is the infrared system organized in a similar spatial manner in the rattlesnake optic tectum? Leonard J. Kass, Loop and one of us (Hartline) investigated this question at the University of Illinois with the aid of neurophysiological techniques. We recorded the electrical responses of tectal cells from a grid.
of positions on the tectal surface and determined where in space an infrared stimulus elicited a maximal neuronal response.

After analyzing the data from several snakes we were gratified to discover not only that the infrared sense is organized spatially in the tectum but also that the infrared tectal map follows the same rules as the visual map. The front part of the tectum responds to infrared stimuli coming from in front of the snake; the back part, to stimuli coming from the side. In short, the visual and the infrared maps are, at least to a first approximation, in register. As we shall see, the similar spatial organizations of the visual and the infrared systems offer advantages in the processing of signals from the two sensory modalities.

The orientation of the map of infrared space to the tectum represents a major departure from the general vertebrate pattern of connections in the somatic sensory system, even though the infrared system presumably evolved from a somatic sense. In most other animals the front part of the tectum represents the front of the body surface. In the rattlesnake, however, the front part of the tectum represents the part of the pit membrane farthest from the animal's snout rather than the part nearest it. This inverted connectivity preserves in the tectum the normal representation of space but not of the body surface.

Roids snakes present an even more complex example of connectivity between the skin and the tectum. The reticulated python, for example, has 13 pits on each side of its head. Each pit is in essence an inverting optical system, which calls for an inverted tectal map, like the map in the rattlesnake. The pits toward the front of the python's head look farther forward, however, than the pits farther back along its lip. One would expect the front pits to be connected to the front part of the tectum, conforming to the usual noninverting vertebrate scheme. How, then, can the array of pits be connected to the tectum to form a reasonable representation of infrared space there? E. C. Haseltine of Indiana University tackled this intriguing problem in collaboration with one of us (Hartline).

What we found is the most complex somatic connectivity scheme observed in any animal to date. First we located the region of the tectum that receives connections from the entire sensory surface of a single pit, that is, the pit’s projection region. When we mapped the pit’s connections within that region, we found that the back part of each pit’s sensory surface mapped to the front of its projection region in the tectum. The map of each pit is therefore inverted compared with the somatic maps of typical vertebrates. When we compared the projection regions of the different pits,
however, we found that the usual vertebrate mapping scheme holds true: the front pits project to the front of the tectum and the back pits project to the back. There is a final bit of complexity: adjacent pits, whose fields of infrared view overlap substantially, have substantially overlapping projection regions in the tectum.

The end result is a single, coherent representation of infrared space on the python tectal surface. Most important, the visual and the infrared maps in the python tectum correspond fairly well to each other. Evidently an intricate rearrangement of the connections between the somatic sensory system and the tectum has evolved to preserve the spatial registration between the two sensory modalities.

An intriguing possibility is suggested by the correspondence between the visual and the infrared representations of the world in the rattlesnake and python optic tectum. Perhaps the tectum compares or combines signals from the two senses. We knew that some tectal neurons in mammals are responsive to both visual and auditory stimuli or to both visual and tactile stimuli. We conjectured that similar “multimodal” neurons may exist in the tectum of the python.

We were not disappointed. The first bimodal neurons in the tectum of a python snake were identified by one of us (Hartline), Kass and Loop. The infrared stimuli were supplied by a hand or a warm soldering iron, the visual stimuli by a cardboard bar (which was thermally neutral). We found that some tectal neurons respond to warm objects whether the room is lighted or totally dark. The same neurons respond to a cardboard bar, but only if the room lights are on. We called these cells “or” neurons, since they can be excited by stimulation of either of the two modalities.

We also found a small number of tectal neurons that respond to warm objects, but only if the room is lighted. These neurons do not respond to a thermally neutral cardboard bar even when the room is brightly lighted. Nor do they respond to a warm object in a darkened room. They were designated “and” neurons, since both visual and infrared stimuli seem to be essential for their response. Neurons such as these had never been described for any combination of sensory modalities in other animals.

The two of us (Newman and Hartline) realized that we might find other kinds of interactions of the visual and the infrared modalities if we tested specifically for them. We built a computer-controlled stimulator that could present infrared and visual stimuli whose intensity, location and time courses were independent of one another. Like some illusions of magic, this one was achieved with a few well-placed mirrors [see illustration on page 122].

In a typical experiment we lowered a recording microelectrode into the optic tectum of a rattlesnake and advanced it until we could record the electrical responses of a single neuron. Our computer then generated a sequence of infrared, visual and combined infrared-visual stimuli and recorded the responses from the cell. We then advanced the microelectrode until another cell was encountered. In this way we sampled and tested several scores of neurons.

Our hunch about possible exotic modality interactions turned out to be well-founded. We discovered a number of novel infrared–visual interactions. The responses of the tectal cells, and therefore the cells themselves, fall naturally into six classes, two of which are represented by the “or” and “and” neurons. We confirmed that “or” cells respond to both infrared and visual stimuli presented alone as well as to combined infrared-visual stimuli. “And” cells respond only to simultaneous infrared-visual stimulation.

Tectal neurons of two other classes exhibit “enhancing” interactions of visual and infrared modalities. We describe such cells as “infrared-enhanced” or as “infrared-enhanced visual” cells, depending on the stimulus that does the enhancing. For example, a “visual-enhanced infrared” cell will show an enhanced response (up to tenfold) to an infrared stimulus presented alone and will show no response to a visual stimulus. When infrared and visual stimuli are presented together, however, a larger response (eight times the normal response) is evoked. The excitatory influence of the visual stimulus, although the stimulus is not strong enough to generate a response by itself, can significantly enhance the cell’s response to the infrared stimulus. Similarly, an “infrared-enhanced visual” cell will show no response to an infrared stimulus but will show an enhanced response to a visual stimulus when it is accompanied by an infrared stimulus.

Tectal neurons of the remaining two classes display inhibitory interactions of the infrared and the visual modalities. The neurons of one class, which we call “infrared-depressed visual” cells, respond vigorously to a visual stimulus presented alone but fail to respond or respond weakly to the combined infrared-visual stimulus. The inhibitory influence of the infrared stimulus reduces or completely suppresses the response to the visual one. On the other hand, when infrared is removed, the cell’s response reappears. The infrared stimulus, in which an infrared response is inhibited by a visual stimulus, we call “infrared-depressed visual” cells.

What functional role might be played by the infrared-visual neurons we have identified? Let us try to answer the question by considering how the tectum might function when a rattlesnake is searching out its prey. A simplified description of such behavior might divide it into several processes: the detection and localization of a stimulus, the identification of the stimulus and the triggering of the appropriate orientation movement. An “attentional” process may also be involved in which the animal’s attention is focused preferentially on one region of space; a stimulus in that

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**Six Classes of Tectal Cells**

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region would trigger a movement of the head or the eyes but an equivalent stimulus in another region would not.

"Or" cells and "enhanced" cells would be useful in the detection process. "Or" cells would signal events in a particular region of space regardless of whether the events are perceived by way of the visual or infrared modalities or by way of both modalities at once. "And" and enhanced cells respond more strongly to combined stimulation than to stimulation evoked by either visible or infrared radiation alone. Detection and localization would be improved by such excitatory interactions, particularly when neither modality is strongly excited. This might be the case if in the dim light of dusk a mouse was near the maximum detectable distance for the pit organ. Modality summation would occur at the correct tectal location because of the similar spatial organizations of the infrared and the visual modalities.

"Or" neurons and "enhanced" neurons might also be involved in an attentional process, one in which a warm, visible object to one side of a snake might catch the "attention" of the orientation machinery of the brain. The infrared component of the stimulus would generate an elevated excitatory state among "or" and enhanced units in a large tectal region because infrared receptive fields are fairly large. Such a heightened excitation could prime that region of the tectum for visual stimulation by the same object or a nearby one. The infrared stimulation would thereby serve to draw attention to the corresponding part of visual space.

Infrared-visual tectal interactions might also contribute to the identification process by stimulating "feature-detecting" neurons that respond only to specific combinations of infrared and visual stimuli. "And" cells, for example, are activated only by objects that can be detected by the pit organ and simultaneously by the eye. Such simultaneous stimulation causes "and" neurons to give a brief but high-frequency burst of impulses. We have found that the most effective stimulus for these cells is a small, warm, moving object. These neurons might be described whimsically as mouse detectors.

Infrared-depressed visual cells, on the other hand, respond best to thermally neutral or cool visual objects: leaves fluttering in a breeze or perhaps a frog jumping at a pond's edge. The visual activity of these cells would be depressed by the infrared radiation of warm-blooded animals. In such examples cross-modality interactions are essential for correct identification of the stimulus.

The cross-modality interactions we have described show that in the rattlesnake tectum the infrared and visual sense modalities are integrated to a significant degree. Could similar modality-combining interactions be operating in the optic tectums of other species? Are tactile and auditory signals in mammals combined in complex ways with visual input? We simply do not know. The experiments necessary to identify such interactions have not been done. We would be willing to bet, however, that the kinds of modality interactions we have observed in snakes are present and functionally important in the tectums of most other vertebrates.

It is ironic that so little is known about how the infrared sense is exploited by snakes in their natural habitat. No one knows whether rattlesnakes and pythons make use of their infrared detectors to hunt prey during the day, when their visual system is also operational. Nor is it known whether snakes rely on their infrared system to identify predators and to locate a comfortable resting place. These are interesting questions for the future. For the present it is impressive enough to know that in the pit vipers and the boid snakes the trigeminal skin sense has evolved into a sensitive distance sense that is much like vision itself.

HYPOTHETICAL WORLD VIEWS perceived by a rattlesnake are represented schematically. The picture at the left depicts a scene as it might be recorded by the snake's visual system. The picture in the middle is the same scene as it might be perceived through the snake's infrared system. Only objects that are warm (color) or cool (gray) and moving would be detected. Stationary objects such as the bush and the pond would not be represented because they do not stimulate the infrared system well. Even the sun-warmed rock would be absent from the infrared image because it is also stationary. The images would be blurred because of the poor imaging properties of the pit organ. The picture at the right suggests how the optic tectum might analyze the combined input of the two sensory systems. Responses of three of the six classes of bimodal tectal cells are represented by squares, triangles and circles. "Or" cells would be strongly activated (solid color) by the warm, clearly visible mouse and activated less intensely (light color) by the infrared component of the rabbit, which is hard to see against the bush, and by the visual component of the cool frog. "And" cells would be activated only by the mouse, which is both warm and clearly visible. The frog's cool skin would serve to disinhibit the "infrared-depressed visual" cells and cause them to respond strongly.