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Rattlesnake Hunting Behavior: Correlations between Plasticity of Predatory Performance and Neuroanatomy

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Abstract

Rattlesnakes may shift between visual (eyes) and infrared (facial pits) stimuli without significant loss of predatory performance during an envenomating strike. The relative equivalency of these proximate stimuli is correlated with the organization of the associated neural pathways in the central nervous system. Visual and infrared information, although gathered by different sensory organs, converges within the optic tectum in an orderly spatiotopical representation where bimodal neurons respond to both stimuli. In turn, the tectum sends efferent pathways directly to premotor areas (brainstem) and indirectly to motor areas (spinal cord) where axial muscles involved in the strike might be activated. On the other hand, rattlesnakes do not maintain a high level of equivalent predatory performance when switching between chemosensory stimuli i.e., olfactory, and vomeronasal information. Deprived of vomeronasal input, strikes drop by about half, and poststrike trailing is lost entirely. Surprisingly, compensation by switching to information delivered via an intact olfactory input does not occur, despite the convergence of chemosensory information within the central nervous system. Finally, the launch of a targeted, envenomating strike involves both these modalities: radiation reception (visual, infrared) and chemoreception (olfactory, vomeronasal). However, in the absence of chemosensory information, the radiation modalities do not completely compensate, nor does the animal maintain a high level of predatory performance. Similarly, in the absence of radiation information, the chemosensory modalities do not completely compensate, nor does the animal maintain a high level of predatory performance. The absence of compensation in this multimodal system is also correlated with an absence of convergence of radiation and chemical information, at least at the level of first and second-order neurons, in the central nervous system.

Introduction

Rattlesnakes scavenge [Fitch, 1949; Gillingham and Baker, 1981; Hennessy and Owings, 1988], but more commonly foraging behavior is characterized by an envenomating strike [Klauber, 1956] to capture directly selected live

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prey. The predatory behavior of rattlesnakes has generally been divided into phases, the number of which suit the research context [e.g., Chiszar et al., 1977; de Cock Buning, 1983]. For discussion, we recognize three phases of unequal duration – prestrike, strike, and poststrike phases. The result of this predatory behavior comes down to one critical phase, the strike itself which may be extremely brief, less than 0.5 s [Kardong, 1986a]. During this brief instant the head moves quickly to the prey, fangs are erected and penetrate the prey, venom is injected, and the head of the snake is withdrawn [Kardong and Bels, 1998]. Missed fang placement [Kardong, 1986a], inaccurate targeting of the prey [Kardong, 1986b], or an insufficient pulse of venom [Hayes, 1991; Hayer et al., 1995] may permit released prey to scamper beyond the recovery range of the snake, resulting in an unsuccessful predatory episode for the snake [Hayes and Galusha, 1984; Kuhn et al., 1991]. Usually, rattlesnake strikes are very precise, with the quantity of venom metered to prey size [Hayes et al., 1995] and fang placement targeted to the location on the prey most vulnerable to envenomation and therefore to rapid death [Kardong, 1986b]. To accomplish this high level of predatory performance, proximate sensory input must be precisely integrated with motor outputs within the brief time of the strike. From behavioral studies, two characteristic features of rattlesnake predatory strikes emerge.

First, rattlesnake strikes are not based equally upon all available sensory stimuli. Visual and infrared reception are more important than chemical cues in eliciting alertness and tongue flick behaviors in crotaline snakes [Chiszar et al., 1981a; Scudder, 1982; de Cock Buning, 1983]. Further, rattlesnakes do not respond to prey odors with an increase in tongue flicking rate unless they are hungry and/or the exposure to prey odor is prolonged [Cowles and Phelan, 1958; Chiszar and Radcliffe, 1977; Gillingham and Baker, 1981]. Chemical and somatosensory cues may also affect behavior [Proske, 1969; Chiszar and Scudder, 1980], although they are subordinate to visual and infrared stimuli [Kardong, 1986a; Haverly and Kardong, 1996].

Second, the success of a rattlesnake strike may depend upon adjustments within the central nervous system to different available stimuli. Sensory systems gather a variety of environmental cues [Cowles and Phelan, 1958; Dullemeijer, 1961; Proske, 1969]. Each sensory component or organ responds to particular proximate stimuli [Hartline, 1971; Gillingham and Clark, 1981a; Dickman et al., 1987]. But predatory conditions may change (e.g. diurnal/nocturnal; prey species; evasive prey behavior), and availability of sensory cues may change accordingly [e.g. Duvall et al., 1985]. Consequently, the success of the strike depends upon how the nervous system adjusts to the availability of these sensory cues. The predatory behavior of rattlesnakes involves the integration of sensory information primarily from the eyes (visual), facial pits (infrared), sensory nasal epithelium (olfactory/chemosensory), and vomeronasal organ (chemosensory), all of which monitor a variety of proximate factors directly affecting the prestrike, strike, and poststrike behavioral patterns [de Cock Buning, 1983; Graves and Duvall, 1985; Chiszar et al., 1986]. Deprivation of sensory cues, as might occur at night or in a burrow, may alter the sequence or the degree to which other senses are utilized [Chiszar et al., 1981b; Kardong, 1992].

The predatory behavioral patterns and the ability (or not) to adjust to availability of sensory cues from the prey might be expected to have a correlation with the underlying neurological organization of the central nervous system and projections within and to the motor areas. To examine this, we recognize two classes of proximate stimuli, radiation (visual and infrared) and chemosensory inputs, and compare these with the associated neuroanatomy within the central nervous system.

Proximate Stimuli

Two classes of proximate stimuli are important during different phases of rattlesnake hunting behavior and thus important in releasing different types of motor activity. One class includes the spectrum of electromagnetic radiation. The wavelengths most used by rattlesnakes within this spectrum are 'visible light' and slightly longer wavelength infrared radiation. After orienting and positioning, radiation stimuli are predominant during the immediate lead up to and perhaps aiming of the rapid strike. The other class of proximate stimuli includes chemical stimuli. Chemosensory stimuli are predominant during poststrike trailing.

Radiation Stimuli and Predatory Plasticity

In rattlesnakes, as in all pit vipers, two separate pairs of receptors receive radiation stimuli: the eyes and the facial pits. The performance of rattlesnakes during the strike phase is almost equivalent whether it is based separately upon visual or upon infrared stimuli [Kardong and Mackessy, 1991; Kardong, 1992]. The only significant compensation a blindfolded rattlesnake makes is to reduce the range and launch its strike when it is closer to the prey. A blindfolded rattlesnake with infrared-sensitive facial pits available will still target the most vulnerable regions of the prey, the thorax, and produce an envenomating strike that kills the prey as rapidly as when the eyes alone are available.

Simultaneous deprivation of both visual (eyes) and infrared (facial pits) information simultaneously produces considerable change in prestrike and strike behavior, including a tendency for longer latency to strike, a shortening in the range, and a drop of about 50% in number of predatory strikes elicited [Haverly and Kardong, 1996]. In fact, most such double deprived rattlesnakes that strike mice do so only after tactile contact with the mouse [Haverly and Kardong, 1996]. However, when rattlesnakes are double deprived, their poststrike behavior and ability to quickly kill struck prey do not diminish significantly [Haverly and Kardong, 1996].

Chemosensory Stimuli and Predatory Plasticity

Release of the envenomated prey reduces the risk a snake faces from retaliation, such as a rodent might inflict with a bite of its incisor teeth. But, released prey may scamper beyond the immediate vicinity of the snake and must be relocated. Relocation presents another set of problems to rattlesnakes. Envenomated fishes or frogs in a water current might be carried away, or birds might fly beyond a recovery range, and these prey are sometimes held rather than released by rattlesnakes [Hayes and Duvall, 1991]. Some tree vipers, which would lose released prey to the forest floor below, also commonly hold struck prey. Even released rodents may travel some distance and disappear from visual or thermal view. Although such prey leave a chemical trail of cues to follow, the scent trails of envenomated rodents can cross the scent trails of other rodents, potentially frustrating the ability of a snake to track the envenomated prey. Rattlesnakes however, can distinguish the scent of an envenomated mouse from that of even a litter-mate, leading to the suggestion that the suite of chemicals in venom includes some principles that increase the perceptibility of the prey during poststrike trailing [Chiszar et al., 1983; Furry et al., 1991]. There is support for this view. If given the choice of poststrike trails between that of an envenomated prey and that of a non-envenomated litter-mate, rattlesnakes preferentially follow the scent trail produced by the envenomated mouse [Chiszar et al., 1990; Robinson and Kardong, 1991]. However, the chemosensory capabilities of rattlesnakes are more acute than this. If the venom ducts of a rattlesnake are surgically ligated, the snake still orients to and strikes prey accurately, but because of the duct ligations, no venom is delivered. These 'venectomized' snakes nevertheless exercise normal poststrike trailing behavior. Even in the absence of injected venom, these snakes are still able to distinguish the scent trail of the mouse they struck (but did not envenomate) from a scent trail laid by the same mouse before it was struck [Lavín-Murcio et al., 1993]. Apparently, fang penetration alone produces a distinctive change in the perceptibility of the struck mouse which permits the snake to distinguish its poststrike from its prestrike odor. Therefore, the chemosensory ability of rattlesnakes is very acute, and can discriminate very subtle differences in mouse scent.

Neuroanatomy

The neuroanatomy underlying the perception and processing of the two classes of proximate stimuli is reviewed below.

Radiation Projections (fig. 1). Infrared and visual information converges in the optic tectum in rattlesnakes. This suggests that the tectum is an integrative center for radiation input [e.g., Kass et al., 1978].

Infrared Receptors. The oral mucosa of rattlesnakes includes a diffuse collection of infrared receptors [Chiszar et al., 1986; Dickman et al., 1987]. However, these oral receptors are innervated independently and are not served by the trigeminal nerves as are the facial pits. Although these oral infrared receptors have been suggested to play a role during strikes, when the mouth is open [Chiszar et al., 1986], there is yet no evidence that rattlesnakes change trajectory of their head during a strike [Kardong and Bels, 1998].

As has been recognized for some time [Bullock and Cowles, 1952], the facial pit of crotaline snakes affects predatory behavior. In crotaline snakes, the infrared receptors reside within a thin membrane suspended across the sunken facial pit. The receptors are innervated by branches of the ophthalmic nerve and by branches of the maxillary nerve (superficial and deep) [Goris et al., 1989]. Each terminal nerve receptor is connected to a single peripheral nerve fiber [Molenaar, 1992].

Snakes have a common sensory trigeminal system, comparable to that in other vertebrates, plus a lateral descending tract of afferent fibers from the facial pits [Meszler et al., 1981; Molenaar, 1992]. (Some afferent infrared fibers reach the lateral tegmental nucleus near the base of the cerebellum [Stanford et al., 1981], but further connections are so far unknown.) From the lateral descending tract, fibers project to the nucleus reticularis caloris, ventromedially positioned within the medulla oblongata, and from here second-order neurons project to the optic tectum [Gruberg et al., 1979; Kishida et al., 1980; Newman et al., 1980; Schroeder, 1981, 1985; Stanford et al., 1981]. The nucleus reticularis caloris is absent or undifferentiated within the lateral descending tract of boids with infrared sensitivity [Molenaar, 1978a, b; Meszler, 1983] and therefore represents a derived feature within crotaline snakes. The tectal

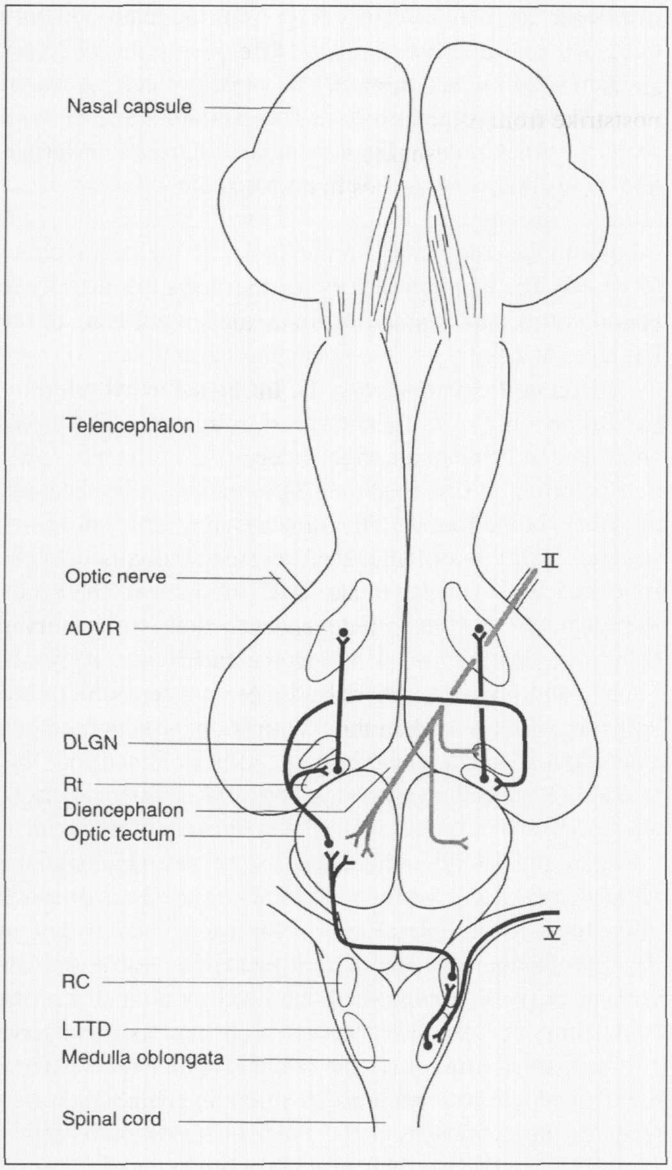

Fig. 1. Diagram of visual (gray) and infrared (black) projections in a rattlesnake brain as seen in dorsal view. ADVR = Anterior dorsal ventricular ridge (telencephalon); DLGN = dorsal lateral geniculate nucleus (thalamus); LTTD = nucleus descendens lateralis trigemini (medulla oblongata); RC = nucleus reticularis caloris (medulla oblongata); Rt = nucleus rotundus (thalamus).

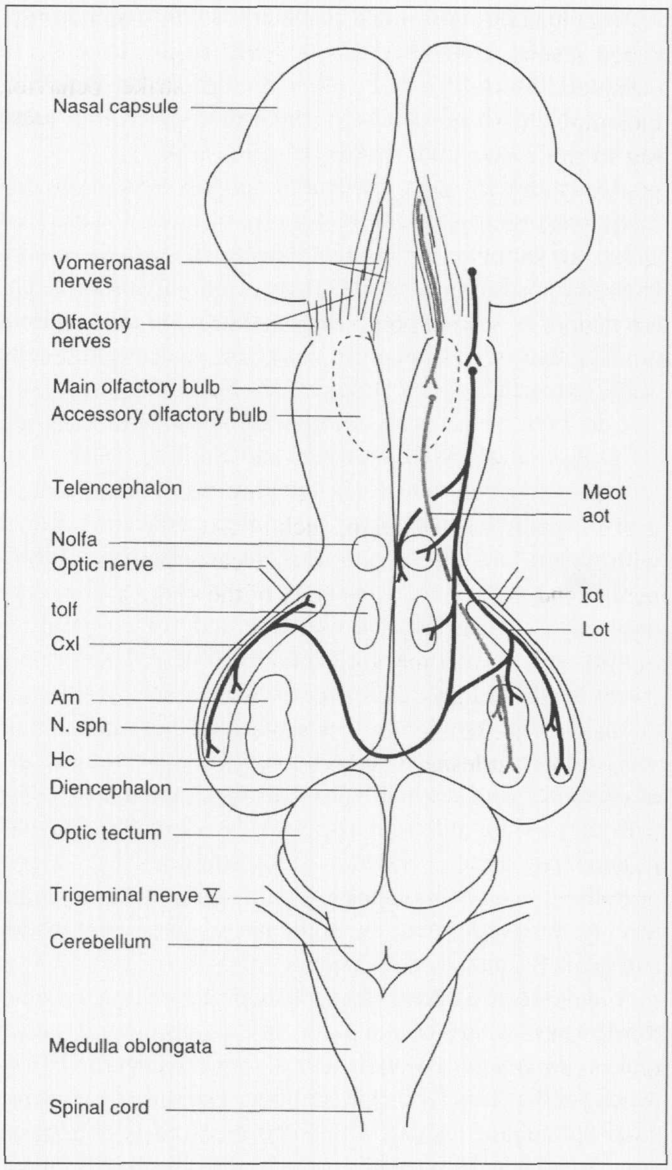

Fig. 2. Diagram of the vomeronasal (gray) and olfactory sensory (black) projections in a rattlesnake brain as seen in dorsal view. After Lohman and Smeets [1993] and Halpern [1976]. Am = Amygdaloid complex; aot = accessory olfactory tract; Cxl = cortex lateralis; Hc = habenular commissure; lot = intermediate olfactory tract; Lot = lateral olfactory tract; Meot = medial olfactory tract; Nolfa = nucleus of the lateral olfactory tract; N. sph. = nucleus sphericus; tolf = tuberculum olfactorium.

area receiving these ordered projections [Terashima and Goris, 1975] from the nucleus reticularis caloris is the central gray layer, deep within the tectum. Subsequent major tectal projections reach the ipsilateral thalamus, and minor ones reach the contralateral thalamus (complex of nuclei rotundus and pararotundus) and ipsilateral relays to the anterior dorsal ventricular ridge (ADVR) within the telencephalon [Berson and Hartline, 1988].

Visual Receptors. Retinal projections in snakes reach the thalamus (dorsal lateral geniculate nucleus) and the optic tectum on contralateral and ipsilateral sides. Second-order relays project from the optic tectum to the thalamus in snakes [Ulinski, 1977]. In other reptiles, tectal-thalamic-telencephalic visual pathways reach the ADVR, but these are less well known in snakes [Ulinski, 1980].

Although they enter the central nervous system via different receptors along different routes of input, the infrared and visual pathways are brought together in the optic tectum. Here, the spatiotopical arrangement is a highly ordered representation of overlapping visual and infrared fields within the tectum, with visual cells superficial and infrared cells deep. Between these tectal layers are bimodal cells responsive to both visual and infrared stimuli [Hartline et al., 1978; Kass et al., 1978; Newman and Hartline, 1981]. Projections from the tectum via tectal-rotundal-telencephalic pathways may further convey integrated visual and infrared information to the forebrain [Berson and Hartline, 1988].

Chemosensory Projections (fig. 2). Within reptiles, chemosensory inputs from the olfactory and vomeronasal receptors appear to be segregated or processed separately [Halpern, 1976, 1992; Lohman and Smeets, 1993], although in snakes this may be more complicated. The chemosensory ability of snakes is based upon these two different sets of receptors with distinct neuropathways, and the two systems may exhibit different responsiveness to different types of chemical stimuli [Halpern, 1992; Mason, 1992]. However, these two chemosensory systems may converge at the level of third-order neurons in the lateral cortex and rostral amygdala [Lanuza and Halpern, 1997].

Vomeronasal System. The best studied vomeronasal neuropathways in snakes are three in two species of garter snakes: *Thamnophis sirtalis* and *T. radix* [Halpern, 1976], which are the basis for this description. The sensory vomeronasal epithelium resides within the recessed vomeronasal organ to which chemicals are delivered by a combination of tongue action and presentation by anterior oral processes [Gillingham and Clark, 1981b; Young, 1990]. Axons from the sensory layer project to the accessory olfactory bulb within the telencephalon. Second-order neurons from the accessory olfactory tract ipsilaterally reach the medial amygdala and nucleus sphericus (fig. 2). In lizards with poorly developed vomeronasal organs, nucleus sphericus is small [Northcutt, 1978]. But in reptiles with a well developed vomeronasal organ, such as snakes, it is the most prominent structure of the telencephalon [Halpern, 1980].

Olfactory System. The olfactory system in snakes [based on Halpern, 1976; Lohman and Smeets, 1993] begins with axons projecting from the sensory epithelium within the nasal capsule to the main olfactory bulb. Second-order neurons from the main olfactory bulb form the main olfactory tract, which sends some fibers to the anterior olfactory nucleus (Nolfa), but most of the tract projects to nuclei through three main divisions. The medial olfactory tract projects ipsilaterally to the dorsomedial retrobulbar formation (= rostral septum). The intermediate olfactory tract projects ipsilaterally to the olfactory tubercle and contributes to the contralateral projection with the lateral olfactory tract. The lateral olfactory tract projects ipsilaterally to lateral cortex and rostral amygdala, joins with fibers of the lot, then decussates via the habenular commissure to reach the lateral cortex and apparently the dorsomedial retrobulbar formation as well [Lanuza and Halpern, 1998] in the contralateral hemisphere (fig. 2).

Processing of Chemosensory Information. After the main olfactory bulb, the lateral cortex is the main olfactory structure in the brain; after the accessory bulb, the nucleus sphericus is the main vomeronasal structure in the brain. Reptilian efferent and afferent connections are complex [Martínez-García et al., 1991; Bruce and Neary, 1995a, b; Lanuza and Halpern, 1998], and now the third-order convergence of these chemosensory inputs in snakes has been examined [Lanuza and Halpern, 1997]. Based on this research, especially upon Lanuza and Halpern [1997], chemosensory information in snakes converges at two locations: in the lateral cortex and in the rostral amygdala. *Lateral cortex:* the nucleus sphericus (vomeronasal) sends projections to the lateral cortex (olfactory). Even though these projections are to different territories within the lateral cortex, it is hypothesized that local pyramidal neurons could integrate this information [Lanuza and Halpern, 1997]. *Rostral amygdala:* the nucleus sphericus (vomeronasal) sends projections to the rostral amygdala which also receives projections from the main olfactory bulb (olfactory). Here in the rostral amygdala, olfactory and vomeronasal information seem to overlap [Lanuza and Halpern, 1997].

Efferent Pathways to Motor Areas

Extensive pools of axial motorneurons reside in the cervical motor column of snakes, similar to the general arrangement in mammals [Fetcho, 1986]. In squamates, the striatum (telencephalon) and the tectum (mesencephalon) have extensive direct and indirect projections to premotor areas in the brainstem and to the spinal cord. The striatum sends projections into nucleus entopeduncularis and the substantia nigra as well as into the reticular formation [Hoogland, 1977; ten Donkelaar and de Boer-van Huizen, 1981]. Nucleus entopeduncularis and the substantia nigra in turn project to the tectum. The striatum itself is under the influence of the anterior dorsal ventricular ridge in the forebrain [Voneida and Sligar, 1979]. The optic tectum has projections to motor neurons in the spinal cord via the brainstem [Ulinski, 1977; Dacey and Ulinski, 1986] along two major pathways: the tectobulbar tract (ventral, intermediate, dorsal) and the predorsal bundle, each of which projects to different parts of the reticular formation [Schroeder, 1981]. These pathways to premotor and motor areas may be important for a snake's prestrike orientation toward the prey, and they may be involved in releasing the strike. The connections from nucleus entopeduncularis and the substantia nigra to the optic tectum may have a role in the modulation of tectally mediated orientation and behavior guided by radiation stimuli. Convergence of visual and infrared information in the tectum therefore brings this information to efferent motor pathways.

Discussion

The correlations between neuroanatomy and predatory performance we find and the hypothesis we put forth are based on current descriptions of rattlesnake behavior and of the structure of their nervous systems. The differences between species and the possible involvement of other sensory modalities, in addition to radiation and chemosensory, must eventually be examined.

Species-Specific Differences. The evolution of snakes may have included a fossorial or semifossorial ancestry that produced substantial changes in their sensory systems, especially their visual systems [Walls, 1942]. Certainly there are correlated features of snake nervous systems that differ substantially from those of other reptiles [Senn, 1969; Senn and Northcutt, 1973; Northcutt and Butler, 1974; Ulinski, 1977]. However, at the gross level, rattlesnakes have main and accessory bulbs receiving olfactory and vomeronasal nerves [Alving and Kardong, 1996], and the described chemosensory pathways in snakes seem to be similar to those in other reptiles [Lohman and Smeets, 1993]. Within snakes, infrared systems based on discrete surface receptors (e.g. facial pits) seem to have evolved independently several times and are associated with distinct neuroanatomical features [e.g. Newman et al., 1980; Molenaar, 1992]. Therefore species-specific differences may include significant differences in neuroanatomy, especially where derived sensory organs are incorporated into the input to the central nervous system. Where parts of the neural circuitry were undescribed in rattlesnakes, we extrapolated from nonvenomous species [e.g., *Thamnophis*, Halpern, 1976]. Fortunately, the parts of neural pathways most likely to represent derived conditions (e.g. facial pits) are in fact based on studies of rattlesnakes. Therefore, even though species-specific differences may eventually be discovered, we feel that the neuroanatomy summarized for rattlesnakes (fig. 1, 2) is a reasonable representation of known pathways.

Multiple Sensory Inputs. Proximate stimuli reach the central nervous system of rattlesnakes from many sources. Therefore, it has been difficult to evaluate the relative importance of different sensory modalities. However, recent studies, reviewed above, now make it possible to identify the primary sensory modalities releasing given behaviors. For example, in rattlesnakes radiation stimuli reach the central nervous system primarily via the eyes and facial pits. Although infrared receptors are located elsewhere – for example in the oral epithelium [Dickman et al., 1987] – it can be assumed that their contribution is not equivalent to that of the facial pits during predatory behavior. These oral infrared receptors would be activated only when the mouth was open, as during the strike, suggesting they may play a role in adjusting the trajectory of the snake's head, although there is no evidence that rattlesnakes adjust the trajectory of their rapid strike once it is initiated [Kardong and Bels, 1998]. Further, deprivation experiments, reviewed above, now indicate that the eyes and facial pits are the primary sources of proximate information releasing the targeted strikes of rattlesnakes.

Other sensory inputs might include air or substrate sound (vibrations) [e.g., Proske, 1969]. However, such stimuli, if present, do not permit a rattlesnake to switch and rely equally on different modalities [Haverly and Kardong, 1996]. Various routes of sensory input certainly exist and no doubt contribute to the representation of the prey within the central nervous system, but none of these alternative sensory inputs have been demonstrated to play a central role in the predatory behavior of rattlesnakes.

Rattlesnake predatory behavior is therefore based predominantly upon sensory information gathered via radiation receptors (eyes and facial pits) and chemoreceptors (olfactory epithelium, vomeronasal organ). It seems reasonable that the associated neural pathways should be correlated with the plasticity of the predatory behavior based on these primary sensory modalities.

Radiation Sensory Ability. When striking, rattlesnakes can switch between visual and infrared stimuli, as they certainly must do when they enter a dark burrow while hunting in daylight or when conditions change from diurnal to nocturnal. With few adjustments in their strike behavior (reduction of range), rattlesnakes maintain a high level of predatory performance and successful prey capture under such conditions. This behavioral switching between radiation senses is correlated with the highly ordered and closely associated visual and infrared pathways in the optic tectum. Maintaining this high level of strike performance, based on either of two modalities, may be further served by the bimodal responsiveness of some cells within the optic tectum which facilitate production of the appropriate motor pattern of the strike and venom delivery.

Multisensory Systems. The absence of predatory compensation for deprived VNO stimuli further suggests that little switching occurs between the radiation and chemosensory systems. This too is correlated with the observation that these two sensory systems have different distributions in the central nervous system. The two systems do not meet in the optic tectum or in the telencephalon, at least not at the level of first-, second-, or third-order neurons. Therefore, strike performance in rattlesnakes, at least in *Crotalus viridis oreganus*, is organized primarily around the processing of radiation stimuli, with very little reliance on chemosensory stimuli, reflecting the independence of the neuronal circuitry underlying radiation and chemosensory input.

Chemosensory Ability. During poststrike trailing, rattlesnakes exhibit a remarkable ability to distinguish subtle odor characteristics of prey. In the absence of input from the vomeronasal organ, the strike frequency drops by almost half [Alving and Kardong, 1996]. Proximate chemical cues arriving via the intact olfactory system are not utilized to significantly compensate for loss of vomeronasal input. This is somewhat surprising, given the apparent convergence of olfactory and vomeronasal information in the lateral cortex and in the rostral amygdala [Lanuza and Halpern, 1997]. Compensation may occur in the other direction, however: i.e. the vomeronasal organ may compensate for olfactory deprivation, although not the other way around. Experiments involving deprivation of olfactory inputs have not been done in rattlesnakes. In garter snakes *(Thamnophis)*, covered nostrils or olfactory nerve lesions do not impair response to prey extracts [Burghardt and Hess, 1968; Burghardt and Pruitt, 1975], trailing of prey [Kubie and Halpern, 1979], or prey attack and feeding [Halpern and Frumin, 1979]. It should be noted, however, that olfactory nerve lesions may compromise tongue sampling (vomeronasal organ) [Halpern et al., 1985] or even result in significantly improved performance following olfactory nerve sections [Halpern and Frumin, 1979; Heller and Halpern, 1982].

Anatomical convergence of chemosensory inputs that do not underlie functional compensation could result from the nature of information processing within the brain. For example vomeronasal information may be processed mostly within an interconnected unit – accessory olfactory bulb, nucleus of the accessory olfactory tract, olfactostriatum, and nucleus sphericus [Lanuza and Halpern, 1997] – before being integrated with information from other sensory modalities in the lateral cortex and rostral amygdala.

Finally, if the olfactory system detects volatile chemicals, and the vomeronasal system detects chemicals of high molecular weight [see Halpern, 1992; Mason, 1992; for reviews], then the two types of chemosensory stimuli may be fundamentally different within the context of predation. If so, the two types of chemical stimuli may provide different types of information, and switching between them would bring no equivalency.

In other behavioral contexts, such as courtship, neural convergence may be used to switch between or enhance the overall chemical stimuli of olfactory and vomeronasal inputs. Within the context of predation, however, rattlesnakes do not significantly compensate for loss of vomeronasal input with available olfactory information.

Conclusions

Multisensory Modalities. When deprived of both radiation receptors (eyes and facial pits), rattlesnakes do not switch to chemosensory modalities to maintain a high level of predatory performance when aiming and launching a strike. This correlates with an absence of convergence of neural pathways carrying radiation and chemosensory inputs within the central nervous system.

Radiation Receptors. When deprived of input from one or the other radiation receptor (eyes or facial pits), rattlesnakes maintain a high level of prestrike and strike performance. The anatomical convergence of visual (eyes) and infrared (facial pits) information in the optic tectum is correlated with this ability to compensate behaviorally during the predatory strike.

Chemosensory Receptors. When deprived of vomeronasal input, rattlesnakes decrease strike by about one half, and poststrike trailing is extinguished. This suggests that the intact chemosensory input, olfaction, does not permit recovery of these behaviors, even though there is anatomical convergence of both chemosensory inputs in the central nervous system. The processing of chemosensory information or differences in the chemical cues themselves may account for the absence of effective behavioral switching based on chemical input.

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