EVIDENCE FOR A CENTRAL CHOLINOCEPTIVE COMPONENT IN DESPOTIC BEHAVIOR IN THE MALE COLLARED LIZARD, *CROTAPHYTUS COLLARIS*[1]

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The effects of stereotaxically implanted drugs upon the intraspecific agonistic behavior of *Crotaphytus c. collaris* was tested using atropine methyl nitrate as a cholinergic blocking agent. Pair interactions were scored as: warning, assertion, attack, chase, escape, submission, and threat. Atropine suppressed dominant motor patterns and increased subdominant behavior in despotic pairs and increased aggression in a co-dominant pair. A possible neural mechanism is discussed.

The differential sensitivity of neural elements in the peripheral nervous system (PNS) to various neurotransmitter substances has been well established. Furthermore, the role of these transmitters in mediating specific visceral and somatic functions via the automatic and somatic PNS has been highly investigated. A large body of evidence accumulated primarily during the past decade suggests that the existence of an analogous neurochemical coding in the central nervous system for behavioral as well as visceral and endocrine control. For example, placement of minute amounts of adrenergic substances into the lateral hypothalamus of rats has been shown to induce changes in motivational threshold leading to hyperphagia, while comparable quantities of cholinergic substances in the identical area produced polydipsia (1). Mouse-killing by rats has been induced by implantation of cholinomimetic substances into the lateral hypothalamus and suppressed by cholinergic blocking agents (2).

Certain species of lizards, including the collared lizard, *Crotaphytus collaris*, will form male-oriented social despotisms when maintained in enclosures (3). The "choice" areas within the enclosure, such as the top of a rock pile, are occupied by a single despot. Subdominants generally remain under cover or in the vicinity of a hole to which a rapid retreat is possible. Alternatively, a subdominant confronted by a despot may assume a submissive position which renders him immune to aggressive attack, i.e., the dominant "pins" him down and then continues normal foraging and thermoregulatory activities. Subdominant general activity is, therefore, largely attenuated.

Dominance between a pair may be established almost immediately. This is especially true if there is a size differential between the lizards. When a pair is matched for size, a series of mutual displays, consisting of warnings, assertions, attacks, and/or chases usually ensues. In consequence, one individual may emerge as a dominant while the other assumes a subdominant position. Subdominance is evidenced by specific action patterns such as submission, threat, or escape. In some cases a codominance may evolve between the two lizards. Each member may warn, but rarely assert, to the others. Neither member of the pair, however, exhibits subdominant behavioral patterns, and choice areas tend to be shared equally by the pair.

In view of the hypothalamic cholinoceptive mechanism described for mouse-killing, it was of interest to investigate the possibility of a similar mechanism operating in intraspecific agonistic behavior in *Crotaphytus*.

MATERIALS AND METHODS

Four pairs of adult male *Crotaphytus c. collaris*, collected in the vicinity of Bowie, Montague Co., Texas, were utilized in this study. Snout-vent lengths averaged 8 mm with body weights at about 25 gm. Pairs were maintained in 15 x 15 ft metal-sided observation enclosures containing two cement block piles for cover. Water was available *ad lib.* and the contents of a sweep net (mainly Orthoptera) were scattered in the cage about every five days. Each pair was observed for at least two

[1] Contribution from the University of Oklahoma Biological Station, Willis, Oklahoma.

days after introduction into the enclosure in order to discern and mark the despot and subdominant. Both were then stereotaxically implanted (modified Kopf small-animal stereotaxic instrument) with a chronically indwelling 21-gauge stainless steel tube. A hole was drilled through the skull 0.5 mm left of the midline to a depth sufficient to expose the dura. A cannula was then inserted into the brain and secured in position with dental cement. Histological examination of implanted brains revealed cannula placement to be in the left telencephalic hemisphere. The shaft passed through the hippocampal cortex and medial portions of neostriatum. The tube orifice, representing the point of entry of drugs into the brain, was in the region of the lateral ventricle and paleostriatum (4). A drug cannula, equal in length to the indwelling tube, was constructed from a 26-gauge stainless needle. Drugs tamped into the smaller tube could, therefore, be introduced directly into the brain by inserting it into the larger cannula. Doses of drugs used were about 20 mg per treatment. During periods when no drugs were used, the cannula was replaced with a stainless steel rod held in place with a covering of bone wax.

Pair interaction was generally observed during the morning hours between 0800 and 1200 hr. Dominant agonistic behavior was scored in terms of the following categories.

Warning. Approaching partner in a more or less direct line at any speed (walk to run); always precedes assertion, attack, and chase.

Assertion. Arching of back, dewlap extension, body inflation, anterior and sometimes posterior leg extension; may involve circling the partner.

Attack. Physical contact with partner, usually touching of pelvic region with snout.

Chase. Locomotory attempt to maintain or reduce the distance to partner while latter is moving.

Subdominant agonistic behavior was measured in terms of the following categories.

Escape. Locomotion of a partner, usually at a run, that tends to increase the distance between the pair; occurs only in response to warning, assertion, attack, chase, or neutral passing (= movement of one partner across the visual field of the other while foraging or exploring).

Submission. Body, and usually head, pressed flat against the ground, body deflated, eyes open, no locomotion.

Threat. Submission, but with mouth open and directed toward partner in response to a warning, assertion, or neutral pass.

Subdominant behavior is characterized by a more or less protracted period of hiding, during which time agonistic interactions do not occur. In a number of instances it was necessary to remove the subdominant from cover and place him in the vicinity of the despot in order for agonistic communication to be observed. Interactions are therefore reported in terms of: per hour of time during which interaction was potentially possible, *viz.*, when both could observe each other and neither was in a hole except for short periods of time associated with thermoregulation.

A cholinergic blocking agent, atropine methyl nitrate (Sigma Chemical Co., St. Louis, Mo.) was used in an effort to modify despotic behavior. In order to control for possible osmotic and anionic effects independent of drug action, comparable amounts of sodium nitrate were used. Modification of subdominant behavior was attempted by administration of the cholinomimetic drug, carbachol, and the adrenergic, norepinephrine. At least 24 hr elapsed between any two consecutive administrations to a given individual. Since cannula implantation and sodium nitrate did not elicit any detectable changes in despotic behavior, the data for these treatments were combined. Similarly for the subdominants, pre- and post-implantation, norepinephrine, and carbachol data were combined since these treatments did not appear to modify the characteristic subdominant responses associated with display by a despot.

RESULTS AND DISCUSSION

Results of this investigation are presented in Table I. It is evident that three pairs established well defined despotisms while the remaining pair (D-E) interacted as a codominant unit.

Administration of atropine to the despot suppressed dominant motor patterns, and in all but one case (I-h) increased the frequency of observed subdominant behavior in the despot. Subdespotic response, presumably resulting secondarily from decreased despotic confrontation, consisted of a decrease in the frequency of subdominant displays and in one pair (G-f) resulted in the initiation of a dominant pattern (warning).

Atropine given to either member of the codominant pair increased aggressive be-

TABLE 1. *Effect of atropine on agonistic behavior in four pairs of* Crotaphytus *(interactions/hr).*

	Specimens	Warn	Assert	Attack	Chase	Escape	Submit	Threat	Total time observed (hr)
Without drug	A	3.0	1.1	0.4	0.1	0	0	0	21.8
	b	0	0	0	0	1.0	1.6	0.5	
With drug	A[b]	0	0	0	0	0.7	0.1	0	8.7
	b	0	0	0	0	0.1	0	0	
Without drug	G	1.1	0.6	0	0	0	0.3	0	5.0
	f	0	0	0	0	1.7	5.5	0	
With drug	G[b]	0.3	0	0	0	0	1.5	0	2.7
	f	0.6	0	0	0	1.4	0.8	0	
Without drug	I	1.5	1.0	0	0	0	0	0	3.0
	h	0	0	0	0	0	1.2	0.3	
With drug	I[b]	0.7	0	0	0	0	0	0	3.6
	h	0	0	0	0	0.4	0.7	0	
Without drug	D[c]	0.2	0	0	0	0	0	0	3.3
	E	0.2	0	0	0	0	0	0	
With drug	D[b]	1.9	0	0	0	0.4	0.4	0	4.0
	E	1.1	0.4	0	0	1.1	0	0.4	
With drug	D	1.0	0	0	0	2.3	1.3	0	2.8
	E[b]	2.3	0	0	0	0	0	0	

[a] Upper case letters represent dominant
[b] Mean values for two implants of atropine
[c] D and E interact codominantly

havior in both but most notably in the atropinized individual. The drug also increased the frequency of submissive patterns in one member (D). Subdominant patterns were also induced in the untreated member.

The induction of increased aggressive interaction by atropine between the two members of the codominant unit is in direct opposition to the responses observed in the despotic pairs. The reasons for this remain problematic. It is possible for example, that the neurochemical components of a codominance differ from those of a dominant-subdominant relationship such that in the former case cholinergic systems are inhibitory with respect to aggression, while in the latter they are stimulatory and hence blocked by atropine.

It is tempting to attribute reduced aggression to drug-treated specimens to a blocking action of specific neuronal pools associated with these action patterns. The possibility of generalized diffusion of the drug in the brain renders the hypothesis, at best, speculative. For example, if drug effect was mesencephalic and the reticular formation subserves various stages of sleep and wakefulness as in mammalian forms, a block of cholinergic component involved in general activation might occur. It is not possible to distinguish behaviorally between these alternatives in *Crotaphytus*, however, because drug-induced abolition of dominance is characterized by a decrease in all motor activities. Two observations argue for neural specificity. First, atropine-suppressed despots alert to the movements of neutral-passing subdominants and display escape or submissive behavior if the latter moves "too close." Second, locomotion in these animals when forced to move, *i.e.*, prodded, is characteristically normal with respect to coordination and speed. Until the role of the reticular-activating system and other structures, such as those associated with the telencephalon, is elucidated in lizards, and adjunct techniques, such as lesioning and stimulation of specific areas, are utilized, the solution to the problem of specificity remains conjectural.

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