Sociality, stress, and the corpus striatum of the green anolis lizard

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Abstract

The green anolis lizard, *Anolis carolinensis*, is a uniquely convenient species with great potential for providing insights about the causes and consequences of social behavior from an evolutionary perspective. In this species, social interactions are mediated by visual displays in which specific units of behavior are combined in various ways to communicate several more-or-less specific messages. Two related research programs that utilize this species converge in provocative ways to provide insight into this phenomenon. The first program is centered on the basal ganglia, now known to be crucial to the expression of aggressive territoriality in this species, and the second research program examines the way the physiological stress response is involved in aggression and its subsequent adaptive outcomes. Both the neural and the neuroendocrine systems affect the progress of social interactions as well as the subsequent social dominance relationships when combatants subsequently live together. Further, because body color depends almost exclusively on the stress response, skin color provides a unique in situ bioassay of otherwise inaccessible information about the animal's internal state. The fullest understanding of the physiological ethology of this model species will depend on an interdisciplinary approach that considers both proximate (physiological) and ultimate (evolutionary) causes of displays. Questions thus arising include how the nervous system controls and assembles the specific units of behavior—motor patterns and autonomic reflexes—into displays that are adaptive in specific contexts.
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1. Introduction

Between stimulus and action, the intervening neurobiology of display behavior is poorly understood. Displays of more-or-less complexity are manifest in all taxa and are often presumed to represent or have evolved from chains of reflexes or fixed action patterns (FAPs). The adaptive value of modulating and coordinating such behavioral patterns to help organisms deal with vagaries, exigencies, and emerging challenges of their environments is a major force in the evolution of the brain. Among the best studied of these behavioral patterns are social displays, and among the most interesting of these displays are those of lizards. Among lizards, the green anole, *Anolis carolinensis*, may be the most studied.

Two ideas converge in this brief account of the neuroethology of display behavior in the green anole: the role of the basal ganglia in the coordination and expression of social displays and the influence of the physiological stress

response on displays during and subsequent to aggressive encounters. First, I will review the social behavior of the green anolis lizard with an emphasis on units of behavior. Then I will review and discuss brain research on the social displays of the green anole inspired by and first done in collaboration with Paul D. MacLean [41], and more recently extended by Cliff Summers (e.g. Refs. [81,82]) and Lewis Baxter (e.g. Ref. [4]). Next, research on the interplay of stress endocrinology, brain, and behavior will be outlined. This work followed the brain research but was inspired by Daniel Lehrman and David Crews, and often researched in collaboration with Crews (e.g. Ref. [38]). Finally, I'll comment on implications of these projects for understanding the evolution of brain and behavior.

2. The green anole—a model reptile

The small, diurnal, arboreal lizard, the green anole (*Anolis carolinensis*) is one of the most scrutinized lizards in science, and a valuable model for several biomedical research programs [35]. Specific elements of social behavior

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Table 1
Inventory of social behavior in *A. carolinensis*

Dewlap	extension of gular flap produced by the erection of the retrobasal process of the hyoid apparatus upon the fulcrum of the basi-hyal component (TCM) [fan]
Push-up	a raising and lowering of the forebody by rhythmic flexion and extension of the forelimbs (TCM) [bobbing]
Four-leg push-up	push-up performed with all four limbs (T)
Head nod	vertical movements of the head, (submission, subordination), often coordinated with pushups [bobbing, assertion, signature] (TCM)
Rapid nod	an oscillating vertical movement of the head, often following an arrhythmic nod+pushups, occasionally appearing without preceding display (C) [jiggling]
Sagittal expansion	enlargement of the sagittal profile of the animal by lateral compression of the body (T) [lateral flattening, lateral compression; with "arrhythmic" nod=challenge]
Extended throat	enlarged profile of throat produced by erection of the basi-hyal component of the hyoid apparatus (T) [engorged throat]
Nuchal crest	elevated ridge of tissue along the back of the neck (T)
Dorsal crest	elevated ridge of tissue, slightly narrower than the nuchal crest, extending along the spine from the posterior margin of the nuchal crest to the base of the tail. Occurs shortly after nuchal crest in prolonged interactions (T)
Gape	wide sustained opening of jaws, often accompanied by tongue-gorge (TD)
Tongue-gorge	tongue apparently enlarged and pushed forward along the floor of the mouth creating a ridge near the front of the mouth (TDM)
Tongue-out	tip of tongue appears between loosely closed jaws (TM)
Tongue-touch	apparent touching of substrate or specific target with tongue [30] (TM)
Air-lick	tongue extruded but never contacts surface (TM)
Tail-writhe	slow sinuous lashing movements of the distal tail (T) [tail waggling]
Tail-lash	wide side-to-side sweeping movements of the tail from the base (TCDM)
Head-up-high	head tipped upward from the neck at a right angle to the body axis; suggestive of arousal and active surveillance (T)
Head-down	[chin-down] head pressed to the substrate; effected even if the movement is against gravity (T)
Brown	body color, sometimes combined or blending into symmetrical areas of green (TCMD)
Green	body color, sometimes combined or blending into symmetrical areas of brown (TCMD)
Dark brown	body color (TD)
Blotchy	green and brown coloration simultaneously but in asymmetrical patches; generally includes eyespot (TD)
Eyespot	darkening of postorbital patch of temporal scales (TD)
Defecate	extrusion of fecal material (TDM)
Cloacal discharge	contents of cloaca discharged; may be fluid or feces (TD)
Lateral orientation	sagittal plane of lizard is made to face ("aimed" at) stimulus point, generally an adversary, by postural adjustment (T)
Face-off	two lizards in mutual lateral orientation, generally facing opposite directions with their heads at right angles to their body axes (T) [often with mutual circling=parallel advance and retreat]
Stalk	slow cautious approach to stimulus (TM)
Limp–stalk	slow cautious approach to stimulus, rear legs appear limp or stiff and are often dragged (T)
Lunge	rapid short range movement of body towards stimulus; typically combined with bite (TDM)
Bite	sustained gripping with teeth, frequently follows lunge (TCDM)
Circling	mutual stalking during a face-off (T)
Jaw spar	mutual attempts to orient gaping jaws in order to bite the jaw of the antagonist (T)
Jaw-lock	mutual sustained bite of two antagonists' jaws; accompanied by twisting (T) [interlocking bite]
Strut	forward movement with stiff front legs creating a unique gait (C)
Neck-bend	raising neck while nose tipped down; only seen in females (CM)
Neck-grip	gripping the skin around the neck or shoulders of another lizard (C)
Straddle	while maintaining neck-grip, one lizard (usually male) rests parallel next to and partly upon another lizard (usually female) (C)
Tail-tuck	the base of the tail of a straddling lizard is tucked under the base of the tail of an adjacent lizard bringing cloacae into apposition (C)
Insertion	insertion of hemipenis into the vent of tail-tucked lizard during apposition of cloacae
Negative perpendicular orientation	body axis perpendicular to stimulus point, head facing away
Positive perpendicular orientation	body axis perpendicular to stimulus point, head facing point (CM)
Rear legs-back	rear legs extended back alongside tail (TDM) (contributes to crypsis)
Squirrel	abrupt lateral movement to side of perch away from stimulus (TDM)
Posture change	adjustments in body posture not associated with locomotion, predominantly head movement [visual surveillance, scanning] (TCDM)
Site change	displacement of the body's center of gravity; slow, deliberate movements of entire animal in habitat; may be positive, negative, or indifferent [exploration, foraging] (TCDM)
Charge	rapid approach towards stimulus (TD)
Escape	rapid movement away from stimulus (TCD)
Allogroom	bite and pull at loose slough on another lizard; slough usually ingested (M)
Autogroom	bite and pull at loose slough which is usually ingested (M)
Food-steal	lunge and bite at object held in the jaws of another lizard; object or part of object pulled or broken off ingested if possible (M)

Adapted and updated from Ref. [26]. Behavioral units delineated from observations of lizard interactions. Letters in parentheses indicate the context(s) in which a behavioral unit has been observed: T=territorial defense and fighting; C=courtship and mating; D=nonspecific defensive behavior; M=maintenance behavior. [Terms in brackets are synonyms in the literature].

An updated annotated version of this table is maintained at http://notes.utk.edu/bio/greenberg.nsf.

have been studied and reported since the 1930s [21,25,68]. More recent detailed ethological accounts were prepared in support of neuroethological studies of social behavior [27]. These and subsequent reports detailing the display behavior of the species [51] and its behavioral ecology [47,49] as well as behavioral endocrinology of reproductive patterns [17,18] have contributed to a detailed inventory of behavioral patterns characteristic of the species (Table 1).

2.1. Units of behavior

Many social displays are found to consist of multiple units of behavior, the forms and coordination of which are valuable sources of clues about the evolutionary background to the behavioral pattern. An inventory of 50 units of behavior ("ethogram") associated with sociality has been developed for the green anole (Table 1). It is important to note that units of behavior in such lists must be identified with as little reference as possible to function because it is a common observation in comparative behavior studies that similar behavioral patterns can serve very different functions in different individuals or species (or in the same individual at different times). The units in Table 1 are also identified with respect to the life-history contexts in which they appear—*maintenance behavior* (such as foraging, feeding, defecating, grooming), *aggression* (territorial defense and conspecific fighting), *reproductive behavior* (courtship, mating, egg-laying), and *nonspecific defensive behavior*. The occurrence of specific units of behavior in either multiple categories or in very restricted contexts suggests more-or-less conservatism in their stimulus control as well as hypotheses about their proximate (physiological) causes and consequences. For example, some units of display behavior are commonly seen expressed in the absence of any specific stimulus (dewlap) and suggest nothing more than elevated arousal, while others (such as rapid nodding) are restricted to very specific contexts that may require endocrine priming and a specific stimulus (receptive female).

Most units of behavior fit the criterion of reflexes or fixed action pattern (FAP). A *reflex* is often regarded as the simplest of behavioral units. They are highly stereotyped and can be chained together in cascades of highly complex motor patterns. An FAP, on the other hand, refers to a more complex ensemble of motor acts orchestrated into a performance involving an unlearned stereotyped temporal and spatial pattern. The term "fixed action pattern" is a misleading translation of the original German, *Erbkoordination*, which is more correctly rendered as "inherited movement coordination" [45]. When found to be species-typical, FAPs are regarded much like a morphological trait as a distinctive attribute of a particular species.

2.2. The social behavior of the green anole

What follows is an account of social behavior seen in naturalistic laboratory vivaria. In many specific details, particularly those involving FAPs and social displays, they are much like those seen in the field. Still, there are important differences (see Ref. [49]), apparently attributable to the larger diversity of alternative actions available in the field, but also as a result of the opportunities for closer scrutiny in the laboratory. Ideally, findings in both kinds of studies would inform each other in reciprocal fashion [32,71].

In nature, male green anoles emerge from seasonal inactivity and establish territories by aggressively competing with other males of the same species (see Ref. [17] but also Ref. [50] for key differences between laboratory and field). Species recognition and subsequent competition usually involves exchanges of distinctive displays. When aggressive, animals will *face-off* and begin *circling* each other, displaying occasionally, possibly *jaw-sparring* (see Table 1) and manifesting signs of acute stress indicated by their body color changes (see below); only rarely is physically dangerous combat observed—the contest *appears* to be one of stamina. Losers typically flee, but there is some evidence that in nature they may remain in a winners territory as a social subordinate. A typical first display has been termed "assertion," and includes a distinctive pattern of vertical movements of the head performed with more-or-less amplitude (*head-nods*) that provides the definitive species-typical "signature" display for many lizards [47], the green anole included. The assertion display consists of such *head-nods* emphasized with coordinated *push-ups* and accompanied by a brief *dewlap* extension (Tables 1 and 2).

In the lab as in the field, males often "spontaneously" manifest assertion displays often as they move about "patroling" their territories. At least there is no external stimulus the human observer can detect that might evoke such displays. Such displays suggest elevated nonspecific arousal rather than a response to any specific evocative stimulus. The display also serves as an "advertisement". If a male's assertion display is observed by another male not previously observed, that second male may call attention to himself by reacting with his own sequence of *head-nods* coordinated with *push-ups* and extension of the *dewlap*. The resident, observing this, may then rapidly escalate its display into "threat" (with *extended throat* only) or "challenge." In this display, the elements of *assertion* are complemented by *extended throat* and *sagittal expansion* (of the body profile) and (in interactions of sufficient duration) erection of *nuchal* and *dorsal crests* along the back, all effectively enlarging the animal's apparent size. If a male's display is observed by a female, on the other hand, her *head-nod* response will cause the aggressive male to switch to "courtship": he will approach the female with a unique "strutting" gait punctuated by one or more series of rapid nods. Interestingly, this *head-nod* display (no *push-ups* or *dewlap*) is also occasionally performed by males defeated in combat and are taken by some observers to express "subordination" (Table 2).

Table 2
Shared elements of social displays in the green anole

Display context	Display components					
	Head-nod	Push-up	Dewlap	Extended throat	Sagittal expansion	Rapid nodding
"Subordination"	T					
"Assertion"	T	T	T			
"Threat"	T	T	T	T		
"Challenge"	T	T	T	T	T	
"Courtship"	T	T	T			T

The "core" species-typical element of *head-nod* may be deleted from a sequence of displays after an initial performance; the display component *dewlap* is frequently deleted from displays of combative males in close proximity to each other.

Displays exchanged between two lizards are easily studied in the laboratory by carefully removing an opaque divider between two vivaria in which the animals appear acclimated. When two males, each the exclusive occupant of adjacent vivarium, have their divider removed, they each act as though the other is an intruder in their territory (details in Ref. [31]). This procedure minimizes the stress of handling or an observer effect. Reproductively competent males that see each other in this way almost always respond to each other with an assertion or challenge display. When territorial males escalate their competition, a full "challenge" display is seen. This is an *assertion display* (the species-typical component) complemented by postural changes ("modifiers"). An early response might also be "extended throat" but an experienced aggressor might rapidly effect the challenge display, in which an enlarged sagittal profile of his body complements the assertion display to the intruder. As aggressive encounters proceed, the male's behavior is accompanied by autonomic responses: Body color may at first darken rapidly and then revert back to green—but with a critical difference, a dark *eyespot* will appear just rostral to the eye. In some cases, the initial darkening does not occur and the animal's color changes quickly to green. In as little as 30 s, a crest of erectile tissue will appear along its neck and back. The antagonist typically responds in kind and they stalk each other with slow, deliberate, apparently tense movements; the tips of their tails may twitch. Prolonged encounters by evenly matched males may result in *jaw-sparring* or (more rarely) *jaw-locking* and *biting* (Table 1). Most commonly however, fights conclude with no trauma to either combatant.

In the course of such extended interactions, the animals appear to assess their position relative to each other. This may be reflected in multiple changes between green and brown body color, although once present, the eyespot will remain. There is evidence that the eyespot can serve as a signal that evokes sympathetic activation and inhibits aggression in conspecifics [57]. Body color "reversals" of aggressively engaged lizards is attributable to highly elevated epinephrine (EPI) and sometimes they go directly from green to green with an eyespot and apparently skip the

intervening brown phase. Colors may then darken considerably, and in (rare) extreme situations, colors may become blotchy (Table 1). As aggressive posturing and displaying subsides, the animal that is brown is probably the one subdued, typically lowering their chins to the substrate (*head down*). Even if clinging to the underside of a limb, the "loser" will press his chin to the perch surface. The winner climbs to the top of his perch and may perform a few assertion displays with his head raised (*head-up-high*). The head-lowering of losers and raising of winners (seen in many reptile taxa) may be a potential evolutionary origin of the bobbing display, corresponding to Desmond Morris's category of "alternating ambivalent movements" in his analysis of ritualization [67].

After territorial confrontations, winners, apparently little affected, return to their routine, while losers, if forced by the vivarium or environmental circumstances to remain in sight of the winner, change in obvious ways: They behave as social subordinates, selecting lower perches, and do not court females; they also manifest a brown body color most of the time [38]. There may be brief aggressive skirmishes for another day or two, but by Day 3, the relationship seems stabilized and such pairs can, in the laboratory, cohabit for extended periods. The preference for lower perches and the disinterest in females appear to be more an altered motivational state rather than a response learned in the presence of the winning male—even when the dominant is removed, subordinates may take up to 2 days to recover their former habits.

The several types of social displays identified in the green anole represent a more-or-less specificity in form and of stimulus control. There is an apparently highly conservative central species-typical element (the head nod), the meaning of which is modified by the coordinated expression of hormone-dependent or context-dependent display components (Table 2). The display modifiers have been characterized as "static" (such as crests or eyespot) or "dynamic" (such as a pulse of dewlap erection) by Jenssen [47].

2.3. Assembling the units of behavior

Taken together, the information in Tables 1 and 2 indicate that the species-typical bobbing pattern, while stereotyped, is evoked by a broad spectrum of situations but specific units of behavior are added or deleted in more limited contexts, presumably to modify the meaning of the display [47,48]. *Head nods* are commonly emphasized with forelimb movements and a brief dewlap extension, which as an ensemble constitute the *assertion* ("signature") display. Complementing the bobbing pattern and observed in more specific contexts are slight variations such as *rapid nods* ("*courtship*"), a hindlimb contribution to the *head-nodding* movement (*four-leg push-up*), erection of a fleshy *nuchal crest* ("challenge"), or erection of parts of the hyoid apparatus ("assertion" or "threat"). The hyoid can be erected in two stages: extension of the long retrobasal

process will extend the dramatic red dewlap (an element of the "assertion" display) and extension of the basihyal element (the fulcrum upon which the retrobasal element rests) will simply enlarge the apparent size of the throat (*extended throat*, "threat"). The expression of these and related units of behavior is presumed to have become progressively more precise and stereotyped because of an advantage that precision confers, such as the correct identification of the species or gender doing the display or the motivational state of the performer (but see Ref. [43]). Autonomic responses include color changes (of which only the eyespot appears to have signal value—see below).

3. Basal ganglia influences social displays of anolis

Social displays are of great intrinsic interest, but their relative stereotypy and well-understood stimulus control provides powerful models for structuring investigations of neural mechanisms. The basal ganglia is of particular interest because of their long historical association with control of motor sequences. "Basal ganglia" is an alternate term for an array of related structures called the striatal complex, nicknamed the R-complex by Paul D. MacLean ("R" for "reptilian") because of its remarkable prominence in reptiles, seemingly corresponding to evolutionary innovations in behavior first seen in reptiles (see Ref. [62]). The basal ganglia includes the *corpus striatum* (*caudate* and *putamen*) and is sometimes termed "non-limbic" or dorsal" striatum. The putamen is so intermeshed with an afferent projection (the *globus pallidus*, *pallidum*) that the two structures are occasionally regarded together as the *lenticular nucleus*. The *nucleus accumbens* is, along with the *olfactory tubercle*, sometimes called the "ventral" or "limbic" striatum. The caudate, putamen, and globus pallidus are sometimes referred to collectively as the "neostriatum" while the nucleus accumbens, olfactory tubercle, and ventral pallidum are called the "paleostriatum" (PS) [33]. Closely associated structures are the substantia nigra (possessing reciprocal connections with the dorsal striatum) and the ventral tegmental area (possessing reciprocal connections with the ventral striatum) [69].

The reptilian PS was the focus of an investigation of forebrain control of display behavior in the green anole. Paul D. MacLean's finding that lesions of the globus pallidus in squirrel monkeys disrupts species-typical displays [61] and studies that indicated that species-typical displays could be reliably evoked in a reptile [26,28] converged at MacLean's Laboratory of Brain Evolution and Behavior at the National Institute of Mental Health on an investigation of the function of the PS in green anolis display behavior. Preceding investigations of forebrain influences on reptilian behavior [20,77,83] used stimulation techniques and provided clues about our candidate sites for the neural control of displays but were not conclusive. With the help of a forebrain atlas developed for *A. carolinensis*

[29], the paleostriatal complex was probed with microlesions [27].

The lesion studies took advantage of the absence of a corpus callosum in this taxon, providing us with a natural split-brain preparation. By making only unilateral lesions and directing visual input to the lesioned or the intact hemisphere, each individual served as its own progressive matched control ([41]; animal care and experimental protocols in Ref. [31]). There was little concern about lateralized brain function, but hemispheres to be lesioned were selected at random. Recent findings of right versus left dominance in control of lizard aggression [44] were not observed in these cases.

Lesioned lizards recovered very rapidly and appeared amazingly unaffected. Most animals remained alert, foraged and fed as normal, often expressing the *assertion display*. Only when an intruding conspecific was provided was a profound deficit observed [27]. When vision was restricted to the lesioned hemisphere, the subject remained responsive to the presence of an intruder but was *unresponsive* to the releasers of territorial aggression it provided [41], a behavioral deficit that might be characterized as "social agnosia."

More recent investigations of basal ganglia in social displays of green anoles have been conducted by Lewis Baxter [5], who initiated a series of experiments based on his insight that the control of the stereotyped displays of anoles shared some features with the control of obsessive–compulsive disorder (OCD). Using the *Anolis* lizard model, he showed that beyond a sharp increase in forebrain serotonin during dominant displays and a decrease during subordinate displays, there was an activation of dorsolateral basal ganglia and deactivation of the ventromedial area. Related experiments went further to analyze the subtypes of serotonin receptors and their distribution in *A. carolinensis*, confirming important commonalities with other taxa [12]. In a series of analyses on dopamine receptors, the occurrence, distribution, and pharmacological specificity of dopamine D_1 and D_2 receptor subtypes were also seen to be similar to those of mammals. One interesting difference, however, is that neural tissue in the parts of basal ganglia outside the ventral striatum characterized by D_1 and D_2 receptor subtypes is largely separated, rather than co-mingled as in mammalian basal ganglia [13].

4. Neurotransmitters in the behavior of anoles

The relatively stable changes in body color that accompany reduced social status in green anoles indicate important changes in endocrine tone. Might the differences in the display behavior of social dominants and subordinates be attributable to comparable changes in the brain? Cliff Summers led a series of investigations that analyzed specific neural structures isolated by micropunches through slabs of brain tissue. The use of Coulochem electrode array

high-pressure liquid chromatography allowed analysis of specific sites in the brains of dominant and subordinate males for indolamines, catecholamines, and their metabolites (summarized in Refs. [78,79]). We learned that central serotonin production and turnover is more rapidly activated in losers of fights (destined to behave in a subordinate way) than in winners. A closer analysis revealed that serotonergic activity in dominants and subordinates had a distinctive time course as well as a regional distribution in the brain [82].

There is abundant evidence that changes in serotonergic activity in the brain is associated with stress and subordinate social behavior in many taxa including *Anolis* (see Refs. [4,58]). In green anoles, the greatest serotonergic changes were detected in the telencephalon of subordinate males. One hour after a fight, the hippocampal cortex and nucleus accumbens showed increased ratios of 5-hydroxyindoleacetic acid/serotonin. Just as in earlier studies of the brainstems of these animals [81], the ratio gradually decreased as the animal's social status became consolidated, and within one month, ratios had returned to normal. Measured in the brains of lizards sacrificed at an hour, day, week, and month following a fight, changes were seen to be more rapid in dominant males. The patterns of serotonergic activation are so similar in the hippocampus, nucleus accumbens, and brainstem that a coordinated response may be involved in mediating short-term social stress and aggression. Similarly, medial and lateral amygdala exhibit corresponding but delayed patterns in subordinate males, suggesting a coordinated response in these regions mediating a longer-term stress response ([82]; summarized in Refs. [78,79]). Work on free-ranging spiny lizards (*Sceloporus jarrovi*) provided consilient findings: brain serotonin activity and turnover was greater in nonterritorial males than in those holding territories [65]. Comparable findings in fish [85] and mammals ([86], in primates) suggest a phylogenetically conserved mechanism of monoamine behavioral modulation of social dominance.

5. Stress in anoles

5.1. Body color in anolis is uniquely sensitive to stress hormones

The body color changes seen in green anoles occasionally during their maintenance and often when subjected to any of a wide array of disturbances has given rise to their popular nickname, "American chameleon." The appearance of a potential predator in the field or a careless observation protocol in the lab will evoke a brown body color. During aggressive interactions (as mentioned above), color shifts also occur as interactions proceed. Both males will likely develop eyespots early in their interaction, but near their conclusion, probable losers are usually brown, and winners green.

Unlike chameleons and other lizards investigated, body color changes are attributable only to circulating hormones (Fig. 1). A role for direct neural control was excluded in a series of studies by Kleinholz [55,56]. This allows body color in green anoles to serve as a partial in situ assay of the endocrine tone of the chromoactive hormones: EPI, norepinephrine (NE), and melanotropin (melanocyte-stimulating hormone [MSH]). Several patterns of body color can be distinguished (Table 1) that suggest the underlying acute flux of circulating hormones. Body color can also be affected by nonsocial activities such as predator avoidance, but generally in contexts reasonably construed as stressful. A shift from green to brown, or darkening involving speckling, and the appearance of a small "eyespot" just behind the eye indicate specific patterns of activation of α_2- and β_2-adrenoceptors
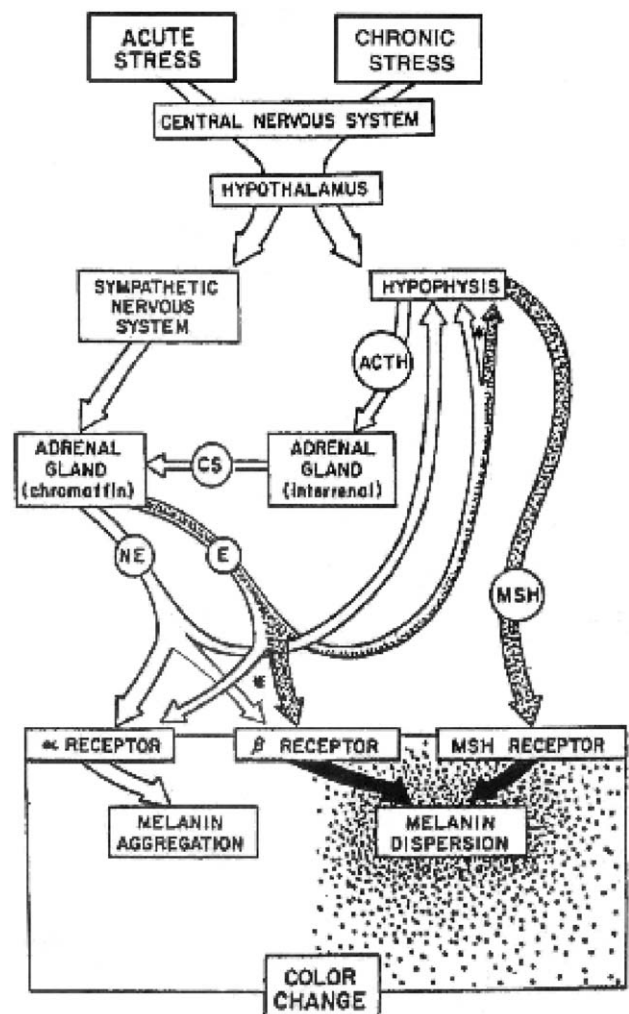

Fig. 1. The effects of stress on a dermal chromatophore of *A. carolinensis*. Acute and chronic stressors are integrated to cause the release of hormones that interact with each other and converge in affecting the darkness of a chromatophore. ACTH, adrenocorticotropic hormone; CS, corticosterone; E, epinephrine; MSH, melanocyte stimulating hormone; NE, norepinephrine. CS can elevate the ratio of E to NE by facilitating a key enzyme within the adrenal gland. E stimulates receptors preferentially and then receptors resulting in opposing effects (adapted from Ref. [34]).

(sympathetic elements of the acute stress response in Fig. 1), and MSH.

5.2. Stress responses are both causes and consequences of social dominance relationships

Stress is inevitably evoked in agonistic or competitive behavior. Our research has shown that in the dominant–subordinate relationships that are established by green anoles in laboratory vivaria, the typically brown subordinates have elevated circulating corticosterone levels [38] and lowered androgen [39]. Subordinates also manifest changes in activity of central neurotransmitters consistent with elevated stress and lowered aggression (see Refs. [79,82] and references therein). It is significant that elevated circulating corticosterone levels can potentially result in a shift in the ratio of EPI to NE released from the adrenal chromaffin tissue because of its facilitation of a key enzyme in the conversion of NE to EPI. An increase in EPI relative to NE is associated with behavioral patterns characteristic of fearful or subordinate animals. Further, relative autonomic tone of the two combatants may be important: the male that first manifests the eyespot invariably wins the contest [80].

6. Prospects for insights about the evolution of brain and behavior

My approach to understanding the evolution of brain and behavior was to look at the influences of the basal ganglia and the physiological stress response on the expression of stereotyped social displays in the green anole. The display repertoire of the green anole is much like other species that involve a conservative "base" display evoked in many contexts that serves as the core element in other displays that are more precisely controlled and convey more specific information. Such adaptive variations on a theme, to the extent that their substrate is understood, can suggest specific hypotheses about the mutual influences of brain and behavior in evolution.

For example, how do the psychoactive properties of the hormones involved in the physiological stress response affect the pathway to the basal ganglia or one of its parallel loops with the thalamus or cortex? Most displays are "motor programs" and often involve both highly stereotyped as well as more flexible elements, depending on the context and stimulus. Motor programs range in complexity from strings of reflexes through automatized learned behavior. An additional influence, that of reproductive status and the presence of relevant hormones, has been relatively neglected but is almost certainly deeply involved. For example, sex steroid hormones, like those of stress, can affect virtually every major component of the path from input to action. How does control of a specific unit of behavior "shift" from internal control of a fragment of a motor

pattern or an autonomic phenomenon to external control by a specific stimulus and or a specific environmental context. More specifically, how do behavioral responses to indistinct but arousing stimuli become progressively more specific in their control? Here is where an understanding of the stress response may be of value, since responses to potentially challenging perturbations are often hierarchically arranged. In such a scheme, a minor disturbance evokes a modest response, and progressively more challenging disturbances evoke responses at progressively higher levels of organization.

6.1. Fixity and flexibility: how are the functions of units of behavior transformed?

A perspective that can illuminate some of the most compelling questions—those related to how units of behavior come to have their communicative function—was engaged by the ethologist Desmond Morris [67] almost 50 years ago. In his review of "ritualization," the evolutionary changes that result in communicative displays, Morris identifies and describes somatic and autonomic units of behavior. Somatic units such as fragments of motor programs and autonomic responses such as the green anole's body color changes, either individually or as a coordinated ensemble, were initially associated with relatively nonspecific phenomena. Among the autonomic responses, Morris identified alimentary (changes in salivation, sphincter control, urination, defecation), circulatory (pallor, flushing, vasodilation of organs, fainting), respiratory (changes in rate or amplitude, sighing, panting, vocalizing), and thermoregulatory (panting, sweating, pilomotor) responses.

Morris also iterated the most common kinds of changes that could occur to isolate or emphasize a unit of behavior, including changes in thresholds, rhythmic repetition, exaggeration of certain components of the movement, omission of components, "freezing" of movements, changes in sequence or in coordination of components, and change in speed or vigor of performance. The known specific and nonspecific effects of stress-related hormones on the nervous system can contribute substantially to hypotheses about how such changes are effected. For a recently discussed example, an acute stress episode can impair the ability of "higher" neural centers to inhibit "conservative" patterns of behavior controlled by lower centers (see Ref. [2]). Basic information about how specific aspects of the stress response affect specific neural areas may provide the key to understanding the control and evolution of core theme, variation, and how modifiers act in display repertoires. Although it is reasonable that adaptive variations in the regional distribution of neurotransmitter and hormone receptors play a large role in evolutionary change, there is as yet little comparative data. Although of great intrinsic interest for understanding the neuromodulatory influence of experience on brain function, the basic information being provided for the brain of the green anole by researchers such

as Cliff Summers (see Ref. [78,79]) may prove to be of comparably great value for comparative studies and insight into evolutionary processes.

6.2. The stress response

Broadly construed, stressors are any of a large array of real or perceived challenges to an organism's ability to meet its real or perceived needs. These challenges activate an ensemble of coordinated physiological coping mechanisms collectively called the stress response. Traditional definitions of stress have historically been rooted in a medical model and typically focus on coping with challenges to homeostasis (for example, Ref. [52]). While arguably the most compelling of needs, homeostasis is, in terms of an animal's Darwinian fitness, only the most urgent of several needs. The broader definition used here avoids the limitations of traditional models and more fully accommodates Hans Selye's original vision [75], as well recent views such as that of McEwen's [66], who sees stress as "a threat, real or implied, to the psychological or physiological integrity of an individual." Similarly, Mac Hadley [42], in his popular textbook, wrote, "Discrepancies between perceptions of internal or external circumstances and innate or acquired expectations lead to patterned stress responses…." Such definitions (see also Goldstein [23] and Levine [60]) allow the extension of insights from medically oriented research to the growing interest in subclinical expression of stress and its subtle if relentless influence on the evolution of life histories (see Refs. [34,36]).

The stress response involves fairly well-understood phases that provide both rapid response and long-term accommodation. The rapid system involves an ensemble of responses centered on the sympatho-adrenomedullary system (SAMS), involving release of EPI and NE from specialized extensions of the sympathetic nervous system, adrenal chromaffin tissue (adrenal medulla in mammals). Continued (or frequently repeated) stressors then activate the hypothalamic–pituitary–adrenal (HPA) axis (Fig. 1). Although the stress response is prominently associated with coping with significant threats to survival, it is important to note that many coping responses are "subclinical" and are manifest mainly in modest, sometimes difficult to detect, adjustments of tone in an endocrine or neurophysiological system. Further, most hormones are "pleiotropic" in that they have multiple effects some of which may be unrelated to the phenomenon that evoked them (below).

6.3. Hormonal pleiotropy

It is significant that most hormones are pleiotropic—they manifest multiple effects. Hormone release may have been evoked in a specific adaptive context, but their other ("collateral") effects may or may not complement or support the primary effect. In any event, they are available to be transformed or incorporated into other adaptive traits, including life-history habits or social displays (see Ref. [36], and references therein). This diversity of hormone effects, in concert with variations in the distribution of receptors on neurons in different parts of the brains of closely related species (see, for example, Ref. [76]) suggests an important emerging perspective on the evolution of species-specific differences.

Relevant examples of the multiple—pleiotropic—effects of hormones are provided by adrenal corticosterone and the pituitary hormone that causes its release, corticotropin (adrenocorticotrophic hormone, ACTH); they each have independent psychoactive effects that include amelioration of aggressive responses, at least in rodents [59]. In our lizard, the stress of social subordination may be responsible for reduced androgen [39] and reduced motivation to court. When a dominant male is removed from a laboratory vivarium that he has cohabited with a subordinate, the recovery of interest in courtship may take many hours or even days [40]. Interestingly, if testosterone in subordinates is artificially increased by means of an implant placed before the dominant–subordinate relationship is established, the subordinate will court as soon as the dominant is removed (unpublished observations)—a situation that may be much more like that in nature, and consistent with observations of the effects of testosterone on arousal and attention (see Ref. [1]).

Stress results in elevated circulating corticosterone. One potential consequence of the release of pituitary corticotropin (ACTH) needed to stimulate release of this adrenal steroid is a collateral release of melanotropin (MSH) [70] and this is, in fact, detectable in the blood of subordinate animals [37]. Melanotropin has positive effects that aid in growth and recovery from trauma and psychoactive properties that reduce aggression. In addition, subordinate animals select different perch sites than dominates where the effect of the darkening effect of melanotropin on dermal chromatophores may provide a significant survival advantage (Ref. [34] and references therein).

In summary, stressors that challenge homeostasis, the most urgent of needs, are the best known but by no means the only experiences that can activate the stress response. Further, the direct effects of coping mechanisms frequently have collateral effects that may or may not reinforce each other. Indeed, a collateral effect of a specific hormone might well serve other needs. The evolutionary process is intellectually fascinating in part because of its capacity for making the most of available resources to serve adaptive needs, a process sometimes nicknamed "bricolage," after the French term (*bricoloeur*) for a handyman able to make a virtue of necessity.

6.4. Stereotyped behavior, stereotypies, stress, and the basal ganglia

Species-typical displays and clinical stereotypies are related not only by the fixity of expression but by their responsiveness to stress. All contexts in which green

anoles display reasonably involve elevated arousal and at least a mild stress response. In other words, this "core" display ("assertion") can be performed even in the absence of specific stimuli, but always in situations of elevated alertness.

Dysfunctional behavior such as stereotypies, addictions, neuroses, and psychoses are all known to be affected by the stress response. This is reasonable given the well-known psychoactive effects of stress-sensitive hormones on alertness and arousal as the organism under stress adjusts to enhance its assessment of potential environmental stressors. The physiological stress response, in its fullest expression, can also affect integrative and efferent components of behavior. Altogether, we can expect enhanced arousal and vigilance, lowered sensory thresholds, increased attention width and capacity for sustained attention, and conservatism in the perceived salience of stimuli. These are all stress-sensitive aspects of behavior ([36], Table 1), so it is unsurprising that energized or aroused lizards may repeat specific patterns frequently. But there is as yet no clarity as to *where* in the circuit from input to output the stress hormones are most active. Some clues are likely to emerge from examinations of regional neurotransmitter changes correlated with behavior [78,79] and regional changes in metabolism detected by various imaging technologies ([4], this issue).

Clues will also emerge from fuller understanding of the causes of clinical stereotypies in which repetition is clearly inappropriate or dysfunctional. Most dysfunctional stereotypies are manifest in abnormal contexts such as zoos or laboratories or as a result of stress where they are often viewed as evoked by stress or an errant attempt at stress reduction ([7,14,15] but see Ref. [64] for a critical review).

Such dysfunctional stereotypies may be unlike only in degree from the adaptive expressions of stereotyped behavior observed to be spontaneously expressed in natural habitats. The form of such ethological stereotypies, often correspond to the "fixed action patterns" of early ethologists [84], which were presumed to be genetically determined responses to specific stimuli (a "sign stimulus" or "releaser"). FAPs also resemble clinical stereotypies in that although they may be shaped by external influences (and to that extent "modified by experience" and therefore "learned"), they complete themselves with relative independence of external feedback—They will continue until their pattern is concluded even though their functional ends have been accomplished.

Why should we suspect that the performance of a stereotyped display or even a dysfunctional stereotypy is stress reducing? Real or perceived familiarity and a sense of control are additional variables in the stress response that must color an interpretation of anxiety. Recalling Seligman's views of the modulation of the stress response by perceived helplessness (e.g., Refs. [73,74]), the apparent "controllability" of a stress-evoking situation is at the heart of Geralt Huether's [46] concept of a "central adaptation syndrome."

In Huether's view, different coping strategies are effected depending on the animal's perception of the controllability of the stressor. Controllable situations refine existing strategies while uncontrollable situations can cause changes in behavioral responsiveness and a reorganization of neural circuits affecting learning—an "adaptive reorganization of the associative brain."

Perceived controllability of a stressor was specifically identified as an influence on the basal ganglia system's mesoaccumbens dopaminergic system [9], a phenomenon that might be linked with emerging understanding of the basal ganglia's role in expectations [54,72].

The strategies of the "central adaptation syndrome" are likely related to those of passive versus active coping strategies evoked to cope with unescapable versus escapable stressors discussed by Bandler et al. [3]. In their work, alternative autonomic strategies (sympathoexcitatory or sympathoinhibitory) were correlated with activity in discrete columns of the midbrain periaqueductal gray [3].

6.5. Basal ganglia connection: clues from dysfunction

Stereotyped displays have been compared to obsessive–compulsive behavior [5], possibly associated with the impairment of one of the several parallel thalamocortical loops in which the basal ganglia participates. The architecture of the motor loop, involves a direct pathway (ultimately facilitatory) and an indirect (inhibitory) pathway (see Ref. [53] for a brief review). In that respect, it is interesting that OCD, like many other neuropsychiatric disorders, is exacerbated by the stress response. Alternatively, at least in some cases, trauma to the striatum rather than reconfiguration may be implicated in the pathophysiology of OCD. For example, striatal neurons might be destroyed by prolonged immunologic stress triggering a cross-reaction between antistreptococcal antibodies and striatal neurons [19].

The several social displays of green anoles are stereotyped and more or less context-dependent. In their form the recall *motor plans*, in which specific simple acts are performed in set sequences [63]. Sequential triggering can be visual or proprioceptive feedback, but failing that, internal cues can be generated by the motor system [6]. Interestingly, in Parkinson's disease, the most prominent of the degenerative disorders involving basal ganglia and responsible for profound problems in motor control, the deficits in sequencing attributable to faulty basal ganglia can sometimes be overridden by external stimuli that demand heightened arousal. This phenomenon, known as paradoxical kinesia led Brown and Marsden [8] to hypothesize that the basal ganglia is integral to nonconscious attention.

Anne Graybiel's [24] work, extending our understanding of basal ganglia and its adaptive possibilities, has led her to hypothesize that the sequences of units organized by central pattern generators of the motor system are complemented by "cognitive pattern generators". She suggested that "by analogy with the central pattern generators of the motor

system . . . these pattern generators operate to organize neural activity underlying aspects of action-oriented cognition. Disorders of the basal ganglia may thereby contribute to neural circuit dysfunctions that are expressed as positive and negative symptoms of schizophrenia.'' A specific mode of basal ganglia influence is indicated by the observation that an apparent imbalance of activation between the neurochemical zones of the striatum—the striosomes and the matrix in which they are embedded—can result in stereotypies. When psychomotor stimulants were applied in concert with dopamine receptor agonists, the degree of motor stereotypy manifest by rats could be predicted by the imbalance created between activity of striosomes and their matrix [10].

6.6. Proximate and ultimate causation of behavior

It is an ethological truism that questions about ''how'' behavior is caused and regulated involve proximate factors such as physiological mechanisms. ''Why'' questions, on the other hand, emphasize the adaptive and therefore evolutionary significance of behavior, the so-called ultimate factors. Between these extremes, developmental and ecological factors abound and must also be considered if behavior is to be most fully understood. Ethology is a profoundly interdisciplinary enterprise.

The proximate expression of behavior is frequently viewed as the outcome of a hierarchical organization. The most proximate causes of overt behavior are the activities at a neuromuscular junction. Working backwards, then, from a manifest action, we are often led to more central neural structures and pathways. For example, beginning with the ceratohyoid muscle that controls the anolis dewlap. A path could be traced by a retrograde neuronal tracer back to the motoneurons in the nucleus ambiguus, an element in the brainstem motor system associated with pharyngeal and laryngeal muscles [22] and with vocalization and swallowing in higher vertebrates.

The specific paths that information takes from the afferent stimulus to the efferent action are all more or less responsive to modulating agents such as the powerfully psychoactive hormones associated with the stress response. Motor systems are often viewed as hierarchical, such that activation at a relatively centrally located level of limited activation diverges to affect progressively more peripheral levels until they get to final expression. Unlike a simple ''military'' hierarchy, however, there is also converging information from other sources of information as well as information flow in the opposite direction to effect a feedback consolidation or reconfiguring of the activity along the path.

Although the behavioral system in which causes and consequences are envisioned is immensely rich and there are numerous sites at which alternative actions and interactions can be brought into play, their *ultimate* causation is constrained by history and thereby limits the possible evolutionary mechanisms we can propose. The ultimate consequences of this richness, on the other hand, can only

be imagined. The manifest adaptive functions of displays, with their expressions of fixity and flexibility tightly correlated with specific environmental contexts, are among the most likely of social phenomena to yield significant insights into the past processes and future possibilities of the coevolution of brain and behavior.

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