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Laterality of Aggressive Responses in *Anolis*

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ABSTRACT This experiment examined whether or not aggression in the lizard *Anolis* (suborder Lacertilia, family Iguanidae) is lateralized. Five pair of adult *Anolis* were subjected to several 20 min behavioral trials, during which one animal was placed in the cage of the other. Behaviors were captured on video and coded according to eye preference, motor activity, posture, and color. Analysis of the data found that the most aggressive behaviors, including biting, threatened biting, and aggressive movements, were done under the guidance of the left eye. Both left and right eyes were used with equal frequency during non-aggressive movements. Most of these aggressive episodes were done while the animals were "lightly" colored. Because of an almost complete crossing-over of the optic tract in *Anolis*, along with the absence of a corpus callosum, it is likely that most, if not all, of the information in the left eye was processed by the right hemisphere. These results suggest that the lizard *Anolis*, like humans, rats, and chicks, may mediate aggressive responses predominantly through right-hemispheric brain mechanisms.

The lizard *Anolis* (Reptilia, Lacertilia, Iguanidae) is a common species that is indigenous to the southern United States. *Anolis carolinesis* (*A. carolinesis*), in particular, has been studied neuroanatomically (Armstrong et al., '53; Butler and Northcutt, '71; Bennis et al., '91 Greenberg, '77, '82; Greenberg et al., '79; Hennig et al., '79; Northcutt, '78; Willard, '19) and behaviorally (Carpenter, '78; Conant, '75; Evans, '36; Greenberg, '77; Greenberg and Noble, '44; Greenberg et al., '79, '84; Kleinholz, '38; Jenssen, '77, '78), and much is now known about its central nervous system. Unlike mammals, the visual system of *Anolis* can, in some ways, be considered as a "split brain" preparation, i.e., a condition where the left hemisphere of the brain is relatively "unaware" of information perceived and processed by the right hemisphere of the brain. In *Anolis*, the vast majority of its retinal fibers cross to the contralateral hemisphere of the optic tectum via the lateral geniculate nucleus, with only a vestigial number of these fibers projecting to the ipsilateral thalamus (Butler and Northcutt, '71). Aside from a small anterior commissure, and a small interhemispheric hippocampal (dorsal-pallial) commissure that interconnects regions of the dorsal cortex (Armstrong et al., '53; Butler, '78), there appear to be no other interhemisphere connections in *Anolis*, and the large corpus callosum present in mammals, which connects one hemisphere to the next with "point-to-point" connections, is missing. Work done by Greenberg et al. ('79) suggests that these small interhemisphere projection systems do not functionally "integrate" the separate cerebral hemispheres of *Anolis*. These authors found that animals with amygdala lesions fail to respond to certain forms of social stimulation when the contralateral, but not ipsilateral, eye is patched. Conversely, they reported that, in intact animals, patches of the ipsilateral, eye did not affect responses to visual, social cues. This work suggests that the cortex ipsilateral to the patched eye does not have access to the visual input available to the contralateral cortex.

In the natural state, the eyes of the two most common and indigenous forms of *Anolis* in the United States (Conant, '75), *A. carolinesis* and *A. sagrei*, are set posterior-laterally on the snout. Their physical placement prevents the eyes from converging on the same visual targets, as the eyes are physically obstructed by the snout from viewing the same half of space. Behavioral observations of *Anolis* show that they tend to "scan" their environment separately, first using one eye then the next. They will, for example, often close one eye when examining a new cage they have been placed in. Similarly, when placed in close opposition to an

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intruding male, they will often alternate the orientation of their head and body, physically changing from a right or left sided view to the other side in order to view the intruder. This behavior may serve to integrate visual information in the brain. In any case, the placement of the eyes, which does not allow convergence of visual fields, along with the lack of cerebral commissures other than the relatively small commissures discussed above, suggests that *Anolis* functions as a "split brain" animal during its interactions. This peculiarity of *Anolis* makes it a useful subject for studying asymmetries in the brain's regulation of different behaviors, such as aggression.

Anolis have a number of clearly identifiable aggressive responses that frequently occur both in the wild and in captivity (Carpenter, '78; Greenberg, '77; Jenssen, '77,'78). These behaviors include headbobbing, dewlapping (i.e., forced extension of the colored throat fan in the male), changes in body posture, "threatened" bites, and "actual" bites. Combinations of these behaviors occur frequently among male *Anolis* placed in proximity to one another. In other species, including birds, rodents, and humans (see Hellige, '93, for recent review), aggression is believed to be mediated predominantly by mechanisms under the control of the right hemisphere. Although Greenberg et al. ('79, '84) have reported that lesions to the paleostriatum, but not amygdala, can modify or ablate "challenge" responses in *A. carolinesis*, we are unaware of any research in lizards that examines whether or not aggression is lateralized to the right hemisphere.

This experiment tests the hypothesis that aggression in *Anolis*, as in other animal species, is mediated by the right hemisphere, and that right hemisphere mediation of aggression is "conserved" across this species. It hypothesized that the majority of aggressive episodes in *Anolis* would occur with left eye use, as opposed to right, since 1) there is an almost exclusive projection of the left eye to the right cerebral hemisphere, 2) work in other animals has implicated the right hemisphere as mediating aggression, and 3) *Anolis* is an animal with no large cerebral commissures. Specifically, it was postulated that the majority of aggressive episodes during *Anolis* interactions would occur with the aggressing animal preferring the use of its left eye, while non-aggressing animals would show equal preference of the left and right eyes during these interactions.

MATERIALS AND METHODS

Ten adult lizards of the family Iguanidae and genus *Anolis* (Conant, '75), including seven *Anolis carolinesis* (i.e., green anole), and three *Anolis sagrei* (i.e., brown anole) were obtained from commercial sources and used for this experiment. Eight males and two females were used in this experiment.[1] Animals were maintained on a 16 hr light/dark cycle, kept warm with continuous exposure to a 75 W lamp, and kept at room temperature individually in their home cages, which measured 5" × 5" × 8". The bottom of the cage was covered with gravel, and "perches" were provided for animals to climb on. All subjects were watered twice daily and maintained on an ad lib diet of meal worms and/or crickets. While in their home cages, all animals were "socially restricted" such that they were not able to see any other animal.

After at least 3 days of "social isolation," animals were removed from their cages and placed for a 20 min period in the cage of a second anole.[2] Pairings were kept constant over the course of the experiment—*A. carolinesis* were paired only with *A. carolinesis*, while *A. sagrei* were paired only with *A. sagrei*. Animals underwent from three to ten trials of these pairings, as in some cases occasional pairs took several days to begin to respond to each other. Each pairing was separated by at least 24 hr. Each pairing was captured on video tape for play back and scoring at a later time. Following the completion of each trial, animals were placed back in their cage to await the next trial. For each interaction between pairings, four variables were recorded, including 1) eye used (i.e., left vs. right), 2) motor response, 3) posture of the animal, and 4) color.

Eye use

The placement of the eyes of *Anolis* on the posterior and lateral head regions, together with the fact that the shape of its head prevents "convergence" of its eyes on a target, force the animal to "eye" its environment with either the left or right

[1]Eight males and two females served as the subjects of this experiment. Female anole do not have a "throat fan," and do not show the aggressive behaviors males exhibit. However, pairing of each of these female anole with their male partner produced aggressive responses of the male at a rate and frequency similar to male-male pairings. Furthermore, the females' responses to the male aggression were not different from those of the "subordinate" males in the male-male pairings, either in eye usage or in behavioral responses.

[2]Typically, the male in the "home" cage defends its territory against the intruder.

eye. Because of this, it is possible to record eye usage, either left or right, for every interaction the animal has. Eye use was scored simply by assessing on the video which side of the body or head (i.e., right side or left) was oriented towards the other lizard. Eye use for each socially relevant behavior, including aggressive response, escape response, and/or "assertion" response was recorded for each animal over the course of the 20 min behavioral trials.

Aggressive responses

Based on the work of a number of authors (Carpenter, '78; Greenberg, '77; Greenberg et al., '79; Jenssen, '77, '78) aggressive actions were defined as including the following behaviors, in order of ascending aggressivity: 1) head bobbing (i.e., a series of rapid head bobs unaccompanied by any other behaviors), 2) dewlapping (i.e., extension of the dewlap fully, unaccompanied by any other behavior), 3) whole body bobbing (i.e., a series of rapid body bobs, often with accompanying tail-lifting movements but unaccompanied by other behaviors), 4) head bobbing plus dewlapping, 5) aggressive locomotion towards the other animal, 6) "threatened" bite, as evidenced by an open mouth on the part of the aggressing animal, and 7) "actual" bite.

Nonaggressive behaviors

For each episode of aggression, the non-aggressing animal generally adopted one of five possible behaviors, each of which was recorded along with the aggressive animals behavior. These behaviors included 1) holding still, 2) walking away from the aggressing animal, 3) running/jumping away, 4) climbing up the walls of the cage away from the aggressor, and 5) "submission" signatures, i.e., a series of rapid, low amplitude bobbings. For each response of the non-aggressive pair, the eye facing the aggressive animal was recorded. Stop-motion playback was used where necessary to discriminate these parameters.

Postures

Five postures were recorded, including 1) "normal," 2) "neck cresting" (i.e., raising of the nunchal crest), 3) "sagittal flattening" (i.e., a posture that included lateral compression of the sides which gives the animal an enlarged appearance from the lateral view), and 4) "sagittal flattening with neck crest." These behaviors have been described in detail by others (Carpenter, '78; Greenberg, '77; Jenssen, '77, '78). The later postures are seen only in aggressing animals. Previous authors have distinguished between behaviors such as "assertion" vs. "challenge" based on the posture adopted by the animal as well as on the social context in which the behavior was seen (Carpenter, '62, '67; Greenberg et al., '79; Jenssen, '78).

Color

In addition to posturing and action, the color of each animal was recorded during each interaction and was graded on the five point scale used by Hennig et al. ('79). This included 1) "maximally light" (green for *A. carolinesis*, light brown for *A. sagrei*), 2) "light, with speckling," 3) "midway" between light/dark, 4) "mostly dark" with some light speckling, and 5) "maximum dark" (brown, for both *A. carolinesis* and *A. sagrei*).

STATISTICAL ANALYSIS

For each trial, the number of aggressive episodes, the type of aggression, the eye being used, the posture, and the color was recorded, both for the aggressing and non-aggressing animal. SPSS/PC+ chi-square analysis was used to analyze the resulting data.

RESULTS

Both *A. carolinesis* and *A. sagrei* showed similar patterns of responding in terms of left-eye/right-eye utilization, and as a result the data for both groups was combined for analysis. A total of 945 interactions were monitored and scored over a total of 25 monitoring periods. Of the 945 interactions, 514 were "aggressive," and 431 "non-aggressive," responses. Of the 514 aggressive responses, a predominance of left-eyed (n = 334) use over right (n = 180) was found. As shown in Table 1, significant differences in left vs. right-eye use was found on the most aggressive responses, including aggressive movements (P = .001), head bobbing while dewlapping (P = .003), threatened bites (P < .001), and actual bites (P < .001). Movements of a less obvious aggressive nature, including head bobbing, dewlapping, and whole body bobbing showed no statistically significant differences. Ratio's of left-to-right eye use was approximately 7.5/1 for "bites," 3/1 for threatened bites, and 2/1 for aggressive movements, head bobbing with dewlap, and whole body bobbing.

Conversely, non-aggressive (i.e., threatened) animals did not preferentially use their left eye for any behaviors. Indeed, when "holding still" while watching the aggressing animal, there was a near significant trend (P = 0.57) for the non-aggressing

TABLE 1. Eye preference by the aggressive anolis during behavioral trials: left/right eye utilization in aggressing animal

Behaviors	Left eye	Right eye	Chi-square (df)	*P*
1. Head bobbing only	77	63	1.4 (1)	ns
2. Dewlapping only	8	7	.07 (1)	ns
3. Whole body bobbing only	10	4	2.6 (1)	.11
4. Head bobbing with dewlap	104	65	9.0 (1)	.003
5. Move towards other animal in aggressive posture	56	24	12.8 (1)	<.001
6. Threatened bite (mouth opened)	34	11	11.8 (1)	.001
7. Actual bite	45	6	29.8 (1)	<.001
Total	334	180	47.1 (1)	<.001

animal to use the right eye. On all other measures, including walking away, running/jumping away, and climbing away from the aggressor, non-aggressive animals used left/right eyes with approximately equal frequency. These results are shown in Table 2.

Aggressive episodes were far more commonly seen when the animals were "light," as shown in Table 3, while darkly colored animals were far more likely to be non-aggressive in nature. These differences reached statistical significance, with a greater number of aggressive episodes found for maximally light ($P < .001$), mostly light ($P < .001$), and midway light/dark ($P < .001$). Conversely, a greater number of non-aggressive, in comparison to aggressive, episodes were seen for mostly dark ($P < .001$) and maximally dark ($P < .001$) animals.

Aggressing animals not only used their left eye significantly more often than their right, but also were of a lighter color when using the left eye. As Table 4 shows, aggressing animals used their left eye approximately twice as often as their right when they were also lightly colored. These differences reached significance for the three "lightest" conditions, including "maximally light," "light with some dark speckling," and "midway between." On the other hand, darkly colored animals showed no difference in eye preference, either in the "maximally dark," or in the "mostly dark," condition.

To discriminate eye usAGE in "assertion" (i.e., head bobbing and dewlap extension with normal posture) vs. "challenge" displays (i.e., head bobbing and dewlap extension in the presence of sagittal/nunchal expansion), chi-square analysis comparing left- vs. right-eye use in aggressive animals in these different postures were run. Animals with assertion displays showed no difference in left- vs. right-eye use (P = ns), while challenge displays were accompanied by significantly more left- (n = 86) than right- (n = 58) eye use (chi-square = 9.5; $P = .002$)

DISCUSSION

This experiment found that aggressive behaviors in *Anolis*, including "aggressive movements," "challenge displays," "threatened biting," and "actual biting," were exhibited in animals showing a clear and statistically significant preference for left eye use. No differences in eye preference were seen for "assertion" displays (head bobbing and dewlapping with normal posture), head bobbing only, dewlapping only, or whole body bobbing. These later behaviors are less clearly aggressive in nature, and likely convey other "social signals," including social assertion, territorial marking, etc. These results are not likely due simply to an overall left-eye preference, as the non-aggressive animals watched their opponent, ambulated, and fled the aggressive partner using the left and/or right eye with equal frequency. Indeed, a trend towards right-eye preference in non-aggressing animals was seen for one of these behaviors, i.e., motionless observation of the aggressive *Anolis*. These results clearly implicate a left-eye preference for the "most aggressive" of responses in two species of *Anolis*, including *A. carolinesis* and *A. sagrei*.

TABLE 2. Eye utilization by the non-aggressing animal during those periods of time when aggression was directed against it by its paired cage-mate: left/right eye utilization in non-aggressing animal

Behaviors	Left eye	Right eye	Chi-square (df)	*P*
1. Holding still	117	148	3.63 (1)	.057
2. Walking away	42	39	.11 (1)	ns
3. Jumping away	35	44	1.02 (1)	ns
4. Climbing away	4	2	.66 (1)	ns

TABLE 3. Frequency of aggressive episodes under different skin color conditions (a clear preference for aggression during "light" conditions, and non-aggression during "dark" skin coloration, was found): relationship of aggression and color

Color of anole during interactions	Number of aggressive episodes	Number of non-aggressive episodes	Chi-square	*P*
1. Maximally light	125	10	97.9 (1)	<.001
2. Light, but some speckling	132	17	53.4 (1)	<.001
3. Midway between light and dark	119	51	27.2 (1)	<.001
4. Mostly dark, but lightly speckled	35	121	47.4 (1)	<.001
5. Maximally dark	100	239	56.9 (1)	<.001
Total	334	180	47.1 (1)	<.001

Left-eye use and aggression seemed also to be linked to color of the animals. The vast majority of aggressive episodes occurred in "light colored" animals, and light coloration appeared linked to left eye use. Aggressive, light-colored anole, used their left eye statistically more often than their right, while aggressive, dark-colored animals showed no eye preferences. Conversely, non-aggressive behaviors occurred when animals were darkened, but unlike aggressive episodes, showed no linkage to eye preference.

In *A. carolinesis*, it is known that the optic decussation from the retina to the opticus tegmenti is virtually total with no projection the ipsilateral nucleus (Butler and Northcutt, '71), although there is a sparse projection to the ipsilateral nucleus geniculatus lateralis, pars dorsalis (i.e., lateral geniculate). These anatomical findings imply that information perceived by the left eye projects, in a near total fashion, to the right hemisphere, while information from the right eye likely projects to the left hemisphere. While *A. carolinesis* possess a hippocampal commissure and an anterior commissure (Armstrong et al., '53; Greenberg, '82), and does likely have some transfer of information between the hemispheres, it appears to be relatively devoid of the "point-by-point" homologous hemisphere connections possessed by many other species. Thus *Anolis* appears to be similar to a "split brain" mammal, in that only primitive, subcortical projection systems appear to link hemispheric structures. Work by Greenberg et al. ('79) would support this reasoning. These authors found that unilateral lesions of the subpallial telencephalon in *A. carolinesis* obliterated aggressive responses when only the contralateral eye was able to see its target, but was unaffected when the "same sided" eye only was uncovered, suggesting that information gathered by each eye was available only to the contralateral hemisphere.

Results from the current experiment suggest that aggression in *Anolis* is in some way mediated by the right hemisphere, as aggressive episodes were seen predominantly with left-eye/right-hemisphere use. These results are consistent with information in the literature suggesting that, in higher animals such as rodents, aggressive episodes are predominantly mediated by right-hemisphere functioning. For example, rats with left hemisphere lesions/intact right hemispheres kill mice more often than rats with right hemisphere lesions/intact left hemispheres, or rats with both hemispheres intact (Denenberg and Yutzey, '85). In work done in chicks, Rogers ('86) has found that the right hemisphere activates the aggressive "attack" response, while the left hemisphere suppresses it. In humans, also, an asymmetry in emotional expression has been re-

TABLE 4. Relationship between eye preference and skin color in aggressive anolis: relationship of color and eye use in aggressing animals

	Left eye	Right eye	Chi-square (df)	*P*
1. Maximally light	88	37	20.8 (1)	<.001
2. Light, but some speckling of dark	85	47	10.9 (1)	.001
3. Midway between light and dark	84	35	20.2 (1)	<.001
4. Mostly dark, but lightly speckled	18	17	.03 (1)	ns
5. Maximally dark	57	43	1.9 (1)	ns

ported. EEG responses in adults have been found to be "activated" over nondominant hemisphere, frontal regions, in subjects rating "negative" emotions as they watched a TV show (Davidson et al., '79). Fox ('91) has reported that infants show greater right hemisphere activation of the EEG pattern when they make facial expressions rated as "disgust" by independent observers. In 10-month-old children, Davidson and Fox ('89) reported that "criers" had greater activation of resting EEG patterns in their right frontal regions. Based on these and other findings, Hellige ('93) has suggested that activation of the right hemisphere, relative to the left, may be predictive of temperament, with right-hemisphere activation somehow related to negative emotions, and left-hemisphere activity related to more positive ones. When the results of the current experiment are interpreted in light of the above findings, they suggest that the right hemisphere may be predominantly involved in the regulation of aggressive and/or "negative" emotional behavior in this lizard species, and in this way show a similarity to the mammalian literature.

Although we found that aggression and left-eye usage were associated with light skin color, this experiment did not examine the mechanisms that might explain this phenomena. However, a growing body of literature has implicated serotonin in the regulation of aggressive behavior in humans as well as in other species (Lewis, '91). While we did not directly assess the effect of serotonin on aggression in this experiment, coloration of *Anolis* has been reported to be under the control of both melatonin and serotonin. Others (Hennig et al., '79; Kleinholz, '38) have reported that serotonin and its precursor, 5-hydroxytryptophan, darken the *Anolis* skin via CNS mechanisms, while both the metabolite of serotonin (5-HIAA) and melatonin lighten skin color. These findings suggest that light-colored aggressive *Anolis*, like aggressive mammals, may have lower levels of serotonin in the CNS.

In summary, this experiment found that aggression, but not other motoric responses, in the lizard species *Anolis* is more commonly found with left eye use, and occurs predominantly when the animals are lightly colored. When these results are considered in light of anatomical and neurochemical work done on *Anolis* in other laboratories, these results imply that aggression in *Anolis* is mediated primarily by right-hemisphere mechanisms. Results from this experiment imply that the neural "wiring" of aggression may be conserved across widely divergent species and may be mediated by similar systems in animals as diverse as lizards, birds, and mammals.

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