

Left vs. Right-Hemisphere Regulation of Aggressive Behaviors in *Anolis carolinensis*: Effects of Eye-Patching and Fluoxetine Administration

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ABSTRACT Two experiments examined aggressive responding in *Anolis carolinensis*. In experiment one, ten adult male anoles had either their left (LEP) or right (REP) eye patched and were then subjected to ten behavioral trials during which a second male was introduced into the cage. Greater numbers of headbobs, or bites, were observed during the LEP condition, while greater numbers of dewlaps and head bobs were observed during the REP condition. In addition, while baseline skin color showed no difference between groups, by the completion of the trials LEP greened, while REP browned. Changes in skin color were correlated with aggressive responding, with a "greening effect" showing high correlation with increased aggression, while browning was associated with decreased responding. In experiment two, 15 unpatched *A. carolinensis* males served as subjects and were subjected to 19 5 min trials during which an antagonistic male was placed into the cage. In these subjects, a preference for left-eye aggression was found to develop over the course of the first 6 days of training, while a decrease in use of the right eye simultaneously occurred. Following injection with fluoxetine, a decrease in aggressive responding in both the right and left eyes was found in comparison to the control group. Collectively, these results suggest that the lateralized control of aggression in *A. carolinensis* is more complicated than suggested by observation of unpatched subjects, although in both conditions the social assertion response (i.e., dewlaps plus headbobbing) is predominantly under the control of the left eye/right hemisphere. *J. Exp. Zool.* 278:9–21, 1997. © 1997 Wiley-Liss, Inc.

Laterality of brain functioning is known to exist in many different species and includes many different types of behavior (see Rogers, '89; Hellige, '93 for reviews). For example, dominance for left-footed manipulation of food objects exists in many species of birds, such as *Cacatua roseicapilla*, *Cacatua galerita*, *Cacatua sanguinea*, *Cacatua leadbeateri*, *Callocephalon fimbriatum*, and *Platycercus flaveolus* (Rogers, '89), while the chicken preferentially uses its right foot for scratching (Rogers, '89). Singing in some songbirds, including chaffinches (Nottebohm, '71), crowned sparrows (Nottebohm, '76), and canaries (Nottebohm, '77), is controlled to a greater extent by the left tracheosyringeal nerve. In other songbirds, such as the zebra finch (Williams et al., '92), the right tracheosyringeal nerve plays the more important role. The right hemisphere (left eye) of the chicken is preferentially involved in attack and copulatory behaviors (Howard et al., '80; Rogers et al., '85). In Japanese macaques, processing of conspecific vocalizations occurs more readily when sound are heard through the right ear compared to those heard through the left ear (Peterson et

al., '79). In rats, the right hemisphere preferentially controls attack behaviors and emotional responding (Denenberg, '84; Denenberg and Yutzey, '85a). Small but statistically significant biases in movements also have been demonstrated in rats (Glick, '83). Territorial aggression in the American chameleon, *Anolis carolinensis*, occurs more frequently when the left-eye is used to view an antagonistic intruder (Deckel, '95) and appears to be tightly linked to hormonally induced changes in skin color (Summers and Greenberg, '94) and to be under inhibitory control by the serotonin reuptake inhibitor fluoxetine (Deckel, '96).

A. carolinensis is a particularly interesting and useful species in which to study lateralized aggression. The left eye of *Anolis* projects preferentially to the right hemisphere, while the right eye projects preferentially to the left (Butler, '78; But-

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ler and Northcutt, '71). Because of several neuroanatomical characteristics, many reptile species, including *A. carolinensis*, essentially have a "split brain." Aside from a small anterior commissure and a small interhemispheric hippocampal commissure (Armstrong et al., '53; Butler, '78), there is no mammalian homologue to the corpus callosum either in *A. carolinensis* or in many other reptilian species, such as the lizard *Tupinambis* (Voneida and Ebbesson, '69; Lohman and Mentink, '72), turtles (Ware, '74), or snakes (Halpern, '76). Thus, visual input to the left hemisphere of *Anolis* is acted upon predominantly by the right hemisphere and vice versa (Greenberg, '77; Greenberg et al., '79). Past studies by Greenberg et al. ('79), which combined brain lesions with behavioral studies, support this reasoning. These authors found that lesions of the paleostriatum or lateral forebrain bundle reduced challenge responses when antagonistic males were observed through the contralateral, but not ipsilateral, eye. In addition, *A. carolinensis* has a small number of stereotypical, easily quantifiable aggressive behaviors (Carpenter, '78; Deckel, '95, '96; Greenberg, '77; Jenssen, '77; Greenberg et al., '79). Past work (Deckel, '95) suggested that while both eyes are equally used in behaviors that include feeding, escape, and general locomotion, the left eye is preferentially used, in males, during aggressive encounters. Finally, this species' ability to change color has been linked to hormonal release of centrally active monoamines, including melatonin and serotonin (Hennig et al., '79; Kleinholz, '38a,b; Thornton and Geschwind, '75), and to peripherally acting catecholamines (see Cooper and Greenberg, '92, for extensive review). Thus, in *A. carolinensis*, observation of skin color changes allows for indirect estimation of the release of important centrally and peripherally active monoamines (Cooper and Greenberg, '92; Hennig et al., '79). Taken collectively, the above research on *A. carolinensis* suggests that aggression in this species may be mediated, in particular, by the right hemisphere.

The current experiments were intended to further explore the phenomenon of lateralized eye use during aggression in *A. carolinensis*. In the first experiment, it was hypothesized that patches on the left eye of male anoles would decrease the frequency of territorial aggression in the comparison to right-eye patches. In the second experiment, it was hypothesized that eye preference for aggression in socially isolated male *A. carolinensis* would be evident immediately upon testing (i.e.,

would not take a period of time to develop). It was further hypothesized the fluoxetine, because of its ability to increase central levels of serotonin and because past work has shown that it inhibits territorial aggression in *A. carolinensis* (Deckel, '96), would inhibit aggression mediated both by the left and the right eyes.

EXPERIMENT ONE

Methods

Ten adult, sexually mature male *A. carolinensis* lizards purchased from local suppliers, weighing 4–5 g at the start of the experiment, were used as subjects for this experiment. Animals were kept individually in clear plastic cages measuring 5" × 5" × 8" on a 14 hr light/10 hr dark photoperiod. The bottoms of the cages were covered with pine shavings, allowing animals to burrow underground during evening hours. All subjects were given ad lib diets of mealworms and crickets and watered at least on a daily basis. Subjects were socially isolated for at least 3 days prior to initiation of the behavioral training and then were not allowed visual contact with other subjects except during the behavioral trials.

Prior to training, animals were randomly assigned either to a left-eye patch (LEP; $n = 5$) or a right-eye patch (REP; $n = 5$) condition. To apply the patches, subjects were briefly placed on ice and chilled to the point where partial anesthesia was induced. Small, commercially available Band-Aids were cut into narrow strips and attached with quick-setting adhesives so that they covered either the left or the right eye. Care was taken not to get the adhesive into the cornea or the eye socket. Animals generally fully recovered from this procedure within 45 min of its completion. Scratching to remove the eye patch generally began shortly after the animals awoke and intermittently persisted until the patches were removed at the end of the experiment. In several cases, patches were scratched off and required reapplication. Otherwise, subjects quickly learned to eat and drink with the patches on and, overall, tolerated them well.

Behavioral training began at least 24 hr after patching was completed. Individual trials lasted for 10 min each and consisted of pairing two subjects in the same cage. During each trial, one subject was removed from its home cage and placed into the home cage of a second subject. For each trial, the skin color of the subject was rated, as described below, at the beginning and the end of

the trial. Trials were videotaped for later categorization and review of the behaviors. Counterbalancing was done, such that each subject spent approximately half of the trials in its cage and half in an opponent's. Pairings of the subjects were varied, such that each animal was paired with multiple different partners. Over the course of the 5 weeks that it took to complete the experiment, each subject underwent an average of ten trials (LEP average number of trials = 9.8; REP average number of trials = 10.2). There were a total of 100 trials during the course of the experiment.

After review of the video of each trial, aggressive actions were classified into one of five possible stereotyped behaviors. These behaviors have been previously described by others as constituting various different types of aggressive action in this species (Carpenter, '78; Deckel, '95, '96; Greenberg et al., '79; Greenberg and Noble, '44; Greenberg, '77; Jenssen, '77, '78). These included (1) headbobbing (i.e., a series of rapid headbobs accompanied by pushups); (2) headbobbing plus dewlaps (i.e., rapid headbobs accompanied by expansion of the colorful throat fan); (3) aggressive locomotion, including circling, walking, or stalking the other animal; (4) threatened bites (i.e., opening of the mouth of the aggressing animal in a posture implying a threatened bite); and (5) actual bites. Two other behaviors we have examined in the past, including dewlaps only and whole-body bobbing only (i.e., a series of rapid body bobs unaccompanied by other behaviors), occurred with such low frequency that they were not tallied in the final analysis.

Skin color of each subject was rated at the beginning and end of each behavioral trial using a five point rating system initially developed by Hennig et al. ('79). More recently, this rating system has been shown to be sensitive for assessing behaviorally induced skin color changes (Deckel, '95, '96). Briefly, skin coloration was graded as (1) maximally light (i.e., green); (2) light, with speckling; (3) midway between light and dark; (4) mostly dark, with some light speckling; and (5) maximally dark (i.e., brown). Change in skin color, obtained by subtracting the scoring for the final coloration from the initial scoring, was then obtained for each subject during each trial.

Statistical analysis

T tests were used to make between-group comparisons. Paired *t* tests were used to make comparisons on skin-color changes that occurred between the start and completion of each behav-

ioral trial. Pearson correlations were used to examine the relationship between changes in skin color and aggressive movements.

RESULTS

LEP animals (i.e., right eye unpatched) had more behavioral responses to the intruder than REP animals (i.e., left eye unpatched) on several different measures. These included headbobbing only ($t = 2.21$, $P = 0.032$), biting ($t = 2.11$, $P = 0.041$), and a trend toward significance on aggressive movements ($P = 0.08$).

Conversely, REP had significantly more combined headbobbing and dewlap responding than did LEP ($t = -2.13$, $P = 0.039$). These results are shown in Figure 1.

No between-group differences were seen on aggressive movements or on threatened bites.

While the skin color of the subjects did not differ between groups at the start of the testing, by the completion of the trials the LEP animals "greened," while the REP animals "browened." The final skin color ratings obtained at the end of the trials were significantly different between groups ($t = -2.4$, $P = 0.02$). These results are illustrated in Figure 2. Despite this trend, neither group showed evidence of persistent browning, nor did either group show indications of acute stress (i.e., postorbital eyespot darkening) except during highly antagonistic encounters.

A final analysis was done to examine if there was a relationship between skin color change and

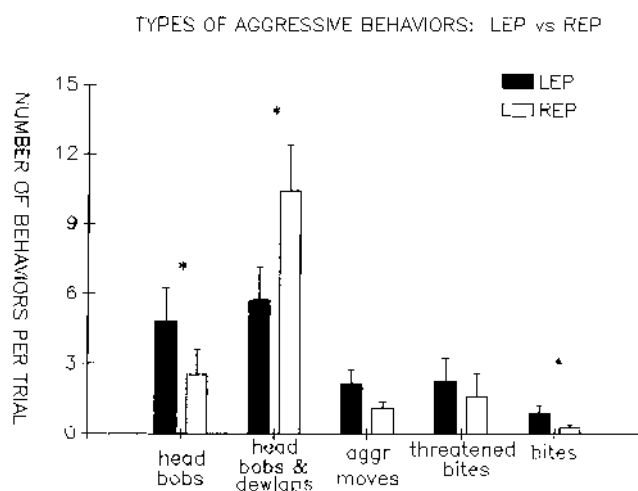


Fig. 1. Aggression in the left-eye patched (LEP) vs. right-eye patched (REP) subjects. REP showed greater headbobs and dewlaps ($*P < 0.05$) than LEP, while an opposite relation was found for headbobs and bites. Bars represent standard deviations.

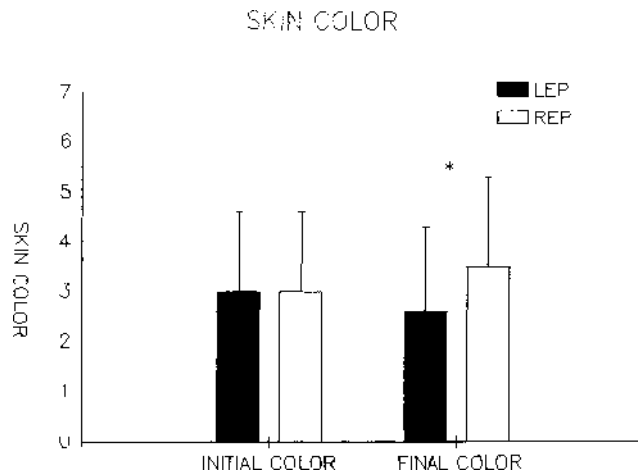


Fig. 2. Skin color changes before the start of the trial (initial) and at the completion of the trial (final). Bars represent standard deviations.

aggressive behaviors. Correlations done on all subjects collectively (i.e., LEP and REP) examined the relationship between aggressive responding and skin color at the beginning ("initial") of the trials, at the end of the trials ("final"), and during the trials (i.e., initial – final: "change" in skin color). As shown in Table 1, initial skin color correlated significantly with several behaviors, including headbobbing only ($R = 0.495$, $P < 0.01$) and threatened bites ($R = 0.417$, $P < 0.05$). Both correlations were positive, indicating that brown skin coloration at the start of the experiment was associated with a greater number of emitted headbobs and threatened bites during the course of the trial, while green skin color at the start of the trial was associated with a reduction in these behaviors. Although final skin color change did not significantly correlate with any of the behaviors, the change in skin color was significantly correlated with all five of the aggressive behaviors. As shown in Table 1, all of the correlations between change and aggressive responding were positive in nature. These results indicate that animals which became greener during the course of the trials had a greater number of aggressive responses, while the

opposite relation was true for animals that darkened in skin color during the course of the trial.

DISCUSSION

The results from the current experiment indicate that control of various different aggressive behavioral repertoires in *A. carolinensis* varies as a function of eye use. LEP (i.e., subjects with the right eye unpatched) had more headbobs and bites than REP, while REP (i.e., left eye unpatched) had more headbobs and dewlaps than LEP.

A. carolinensis, like other reptiles, is a "split brain" animal, with the left eye projecting to the right hemisphere and the right eye projecting to the left hemisphere. Results from the current experiment suggest that the behavioral repertoires emitted during the LEP vs. REP conditions are presumably regulated as a function of control of the contralateral side of the brain. This suggests that the neural mechanism of control for different forms of aggressive behavior may be differentially mediated in the brain of *A. carolinensis*. Specifically, it suggests that neural control of bites and headbobs (increased in the LEP subjects) differs from that of headbobs plus dewlaps (increased in the REP subjects).

The most frequent behaviors observed during the challenge trials were headbobbing and dewlapping, with animals showing more of these behaviors than all others combined. These behaviors appeared predominantly under the guidance of the left eye (and right hemisphere) as REP animals demonstrated approximately twice as many of these responses than LEP. These results are similar to two earlier studies (Deckel, '95, '96), where it was reported that free ranging, unpatched *A. carolinensis* showed a preferential use of the left eye in aggressive behaviors, including dewlaps and headbobbing. Conversely, LEP (i.e., animals with their right eye unpatched) emitted more headbobbing only and bites and showed a trend toward more aggressive movements than animals with the left eye unpatched. As distinct from the current findings, earlier work has reported that

TABLE 1. Correlations between skin color change and aggressive responding

Color	Headbobbing	Headbobbing + dewlaps	Aggressive movements	Threatened bites	Actual bites
Initial	0.495**	0.125	0.324	0.417*	0.175
Final	-0.19	-0.22	-0.24	-0.175	-0.276
Change	0.666**	0.352*	0.564**	0.583**	0.447**

Correlations between changes in skin color over the course of the behavioral trials (Initial-Final) and types of aggressive behavior. * $P < 0.05$, ** $P < 0.01$.

headbobbing only and threatened bites in unpatched, freely behaving *A. carolinensis* are emitted when the antagonist is viewed with the left eye (Deckel, '95, '96). Conversely, the right eye in this earlier work was associated with nonaggressive behaviors.

We hypothesize that the apparent discrepancy between past findings and the current experiment may be related to hormonal changes mediated by the right eye/left hemisphere. LEP subjects showed greater change in skin color than REP subjects during challenge. LEP subjects became greener as the trials progressed, while REP animals browned. These findings are in good agreement with several earlier studies, which also have reported that greener anoles are more aggressive than brown anoles (Deckel, '95, '96; Greenberg et al., '90; Summers and Greenberg, '94), that brown coloration is associated with losing fights (acutely) or subordination or submissiveness (chronically; Summers and Greenberg, '94), and that green coloration and postorbital eye-spot darkening is associated with the winning antagonistic encounters between male anoles (Summers and Greenberg, '94). The "greening" of the LEP animals and the "browning" of the REP animals during the trials may reflect hormonal changes induced during the trials. These changes appeared to be expressed behaviorally only during challenge as skin color was identical in both groups at the start of the trials (i.e., prior to the agonistic encounter). A number of past studies have implicated serotonin, melatonin, and their metabolites in the regulation of skin color in *A. carolinensis*. In earlier studies done on this subject, Kleinholz ('38a,b) reported that the light (i.e., green) phase of coloration in *A. carolinensis* was not under control of the nervous system. Skin grafts, transection of the spinal cord, and pithing of the spinal cord did not impair the ability of *A. carolinensis* to turn brown on an illuminated black background and green on an illuminated white one. Stimulation/stressing of these denervated subjects also could produce acute changes in skin color, again suggesting that direct nervous control of color change was not the mechanism which accounted for the color changes. Kleinholz ('38a,b) further reported that subjects with transected spinal cords and cut sympathetic chains which also were subjected to adrenalectomy were in no way different from untreated subjects and maintained the ability to change their skin color under different conditions of illumination. Blinded *A. carolinensis* as well were able to darken. On the other hand, Kleinholz ('38a,b)

reported that hypophysectomized *Anolis* were unable to darken and remained green under conditions usually sufficient to darken the skin. However, when pituitary extracts were added to isolated pieces of skin, the skin darkened. Kleinholz ('38a,b) concluded that the regulation of skin color in *A. carolinensis* was exclusively under the control of endocrine factors manufactured and/or released by the pituitary.

More recent work has found that a number of centrally active agents affect skin color in *A. carolinensis*. Work done by Stratton and Kastin ('76) found that injections of melanocyte-stimulating hormone (MSH) produced darkening of the anole's skin color. Injections of serotonin have been found to darken the skin color in *A. carolinensis* (Hennig et al., '79; Thornton and Geschwind, '75), as does its precursor 5-hydroxytryptophan (Hennig et al., '79). Conversely, melatonin (Hennig et al., '79; Thornton and Geschwind, '75), 5-hydroxyindole acetic acid (Hennig et al., '79), and n-acetylserotonin (Hennig et al., '79) have been found to lighten skin color, while the serotonin reuptake inhibitor fluoxetine has been found to have no effect on overall skin color but to darken the postorbital eye spot only (Deckel, '96). Whether or not decreased levels of 5-HT lighten skin color or decreased levels of melatonin darken skin color has not, to our knowledge, been experimentally investigated.

Peripheral agents, as well, are active in changing the skin color of *A. carolinensis*. Catecholamines, including epinephrine and norepinephrine, induce aggregation of melanosomes in *Anolis* (Cooper and Greenberg, '92; Kleinholtz, '38a). Alpha-adrenergic receptors in *A. carolinensis* dermatomes appear to predominantly control this response (Goldman and Hadley, '69), causing dark melanochromes to lighten and light ones to darken, eventually resulting in a light-green and mottled appearance after chronic stress (Cooper and Greenberg, '92). These circulating chromoactive agents appear to interact. MSH receptors are linked with alpha- and beta-adrenergic receptors (Carter and Shuster, '82; Cooper and Greenberg, '92; Vaughn and Greenberg, '87). MSH and beta endorphin also interact, with the latter potentiating the effect of MSH on melanophores in *A. carolinensis* (Carter and Schuster, '82; Cooper and Greenberg, '92).

These results, when taken in conjunction with the changes in skin color in LEP vs. REP animals in the current experiment, suggest that one effect of patching the eyes in this experiment was

to change serotonin and/or melatonin levels in patched animals. Patching the eyes differentially changed skin color responses under conditions of challenge, and these changes in skin color were correlated with aggression. These findings suggest that the central release of melatonin and/or serotonin under conditions of challenge was different in the REP vs. LEP and had a subsequent effect on aggressive behaviors.

In *A. carolinensis*, melatonin has been reported to show asymmetrical binding in the diencephalon (Wiechmann and Wirsig-Wiechmann, '92). Specifically, higher melatonin binding is seen in the left habenula nucleus, while no binding of melatonin is observed in the habenular of the right hemisphere. In contrast to the right habenular, the left habenular nucleus both has a high density of melatonin receptors and receives input from the parietal eye. Wiechmann and Wirsig-Wiechmann ('92) reported that it is likely that the left habenular is under dual control, both neural and hormonal, of the parietal eye and pineal organ. Results from the current experiment, when taken in conjunction with this work, suggest that the right eye in *Anolis* may be involved in the regulation of melatonin release in this species, at least under conditions of challenge. If true, these results would further suggest that this control over melatonin and/or serotonin release could be related to the left vs. right eyes in one or more of the following ways: (1) the right eye may facilitate stimulation of melatonin release during challenge (accounting for a lightening of skin color in LEP animals relative to REP during challenge), (2) the right eye may be linked to inhibition of serotonin release during periods of challenge (this also would account for a lightening of skin color), (3) the left eye/right hemisphere may be inhibitory to the release of melatonin or facilitate the release of serotonin during periods of challenge (accounting for skin darkening), and (4) some combination of the above effects may occur. The current experiment does not allow for a clear distinction between these possibilities.

Because the correlation between skin color change and aggressive responding was high across all aggressive behaviors, it is likely that the skin color changes reflect hormonal/chemical changes in the brain that affect behavior (i.e., central nervous system [CNS] structures) as well as peripheral systemic responses (i.e., skin color). Although the relationship of melatonin to aggressive behaviors is not well documented, past work in many species has found that low levels of CNS seroto-

nin are associated with high levels of aggression, while high levels of serotonin are associated with low levels of aggression. These other species include rats (Olivier and Mos, '92; Sijbesma et al., '91; White et al., '91), mice (Sanchez et al., '93; Sanchez and Hyttel, '94), monkeys (Higley et al., '92; Mehlman et al., '94), foxes (Popova et al., '91), fish (Munroe, '86), chicks (Buchanan et al., '94), and *A. carolinensis* (Deckel, '96). We hypothesize that, in the current experiment, LEP subjects may have shown increased headbobs and bites for one of two reasons: (1) the left hemisphere may control these behaviors or (2) the left hemisphere may control systemic release of melatonin that directly or indirectly (via its effect on serotonin) affects brain structures in the contralateral hemisphere, leading to subsequent behavioral changes. If the latter explanation is true, then the increase in aggressive responding in LEP subjects could be due to "hormonal activation" of aggressive "programs" in either the right, left, or combined hemispheres as hypophyseal release of this compound could spread systemically. Conversely, the simultaneous expression of headbobbing and dewlap extension, which was the most frequently emitted behavioral response in this experiment, appears to be predominantly under the control of the left eye/right hemisphere, although it, too, was correlated with skin color changes and was likely mediated by CNS changes of serotonin and/or melatonin.

EXPERIMENT TWO

Methods

Twenty-eight adult, sexually mature, male *A. carolinensis*, weighing 4–5 g at the start of the experiment, served as subjects in this experiment. Subjects were kept on a 14 hr light/10 hr dark cycle and were maintained at an average room temperature of 72°F. The temperature inside the cages of the subjects was higher due to the presence of heating lamps, which were approximately 12 inches from the cages. Subjects were socially isolated and kept in small, clear plastic cages 5" × 5" × 8". The cage bottoms were covered with pine shavings, and animals were watered daily and fed mealworms/crickets on an ad lib basis. Fourteen animals were assigned to a control (CON) and 14 to a fluoxetine (FLU) condition. Thirteen animals were removed from the experiment because of their failure to exhibit aggressive behaviors when confronted with another male, leaving a total of nine subjects in the CON condition and six subjects in the FLU condition.

One male anole served as the antagonist for all subjects. All behavioral trials were 5 min in length. A trial began when the antagonist was placed in the cage of the subject and concluded when the antagonist was removed 5 min later. Animals were run on a total of 19 trials, five trials per week. Each trial was separated from the next by at least 24 hr.

Each aggressive behavior was rated by an experimenter. In addition, eye usage was recorded at the time that each aggressive behavior was observed, including left eye only, right eye only, or both eyes. As in the first experiment, aggressive actions were examined and classified into one of five possible stereotyped behaviors using the method described for experiment one. In addition, the time to the first aggressive response was measured for each subject during each trial throughout the course of the experiment. The first six trials were prior to the first injection (preinjection). Injections were made on days 7 and 14; six trials were done between these two times (i.e., 8–13, between-injection). Finally, 5 days of observations were made following injection (postinjection).

At the seventh and fourteenth trials, animals were injected either with lactated Ringer's solution (CON) or fluoxetine (FLU; gift of Eli Lilly, Indianapolis, IN), s.c. in the right hindflank. FLU subjects were injected with 0.1 mg fluoxetine in 0.1 ml sterile lactated Ringer's solution per gram body weight, for a total of approximately 60 mg/kg. CON subjects received the equivalent volume of lactated Ringer's only. The antagonist male was placed in the cage 20 min following injection.

Statistical analyses

Several statistical analyses were used to examine the data. First, "day by day," within-group comparisons of the number of aggressive movements were done using non-parametric Wilcoxon analyses. Between-group comparisons, comparing fluoxetine-injected vs. control-injected groups, were done using Mann-Whitney analyses. Non-parametric analyses were utilized due to the skewed distribution of the data. Finally, comparisons of the relationship between aggressive movements and skin color changes were done using Pearson correlations.

RESULTS

Laterality of responses seen during the first 6 days of testing (i.e., preinjection)

Over the first 6 days of testing, the number of behaviors emitted while the antagonist male was

observed with the left eye (LE) vs. right eye (RE) was recorded. Dewlap and headbobbing (DHB) responses showed changes in the opposite direction. The number of RE-mediated DHBs showed a decrease in their frequency on days 3–6 in comparison to days 1 and 2. The decline reached statistical significance on nonparametric analysis of variance (Wilcoxon) by days 3 and 4 in comparison to day 1 (Fig. 3). Conversely, LE-mediated DHBs showed an increase in frequency during days 2–6 in comparison to day 1, reaching statistical significance on day 5 (Fig. 3). Thus, a double dissociation was seen in DHB responses, with a decrease in the number of DHB responses mediated by the right eye and an increase in the number of responses mediated by the left eye.

Similar patterns were seen on other measures of aggression. For example, an increase in the number of aggressive movements mediated by the left eye was observed over the first 6 days of training, while a decrease in the number of right eye-mediated aggressive movements was seen (Fig. 4). Similar patterns in responding were seen with threatened bites as well. However, the frequency of actual bites over the first 6 days was very low, and none was observed over days 4–6.

The level of "aggressivity" of the various movements differs from simple "displays" (i.e., headbobs, dewlaps and headbobs) to aggressive and

DEWLAPS AND HEADBOBS DURING THE 1ST SIX DAYS OF TRAINING

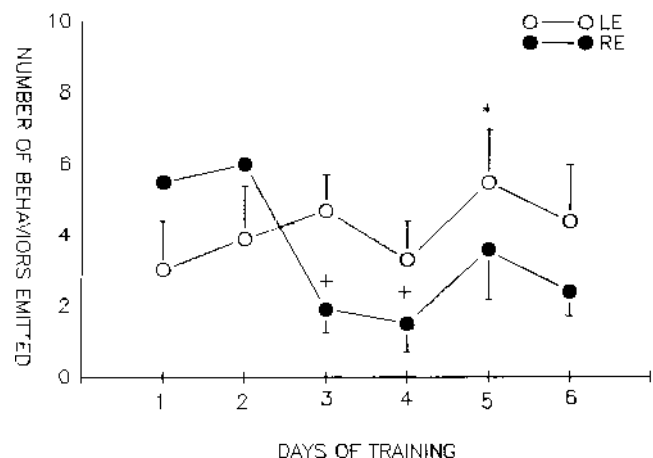


Fig. 3. Daily number of dewlaps and headbobs (i.e., social assertion) emitted during the first 6 days of training and prior to the first injection with fluoxetine on day 7. LE, behavior emitted while antagonist was viewed with the left eye. RE, behavior under the control of the right eye. * $P < 0.05$, greater than day 1. + $P < 0.05$, less than day 1. Bars represent standard deviations.

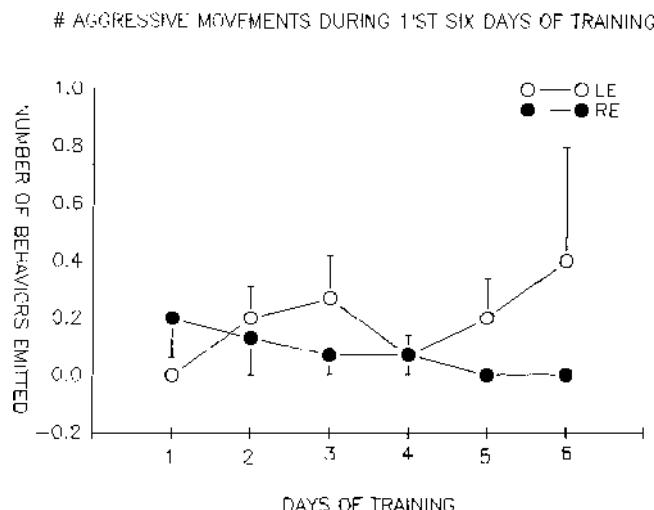


Fig. 4. Total number of aggressive movements other than the social assertion response (threatened bites, actual bites, aggressive movements) emitted during each day of training. LE, left eye; RE, right eye. Bars represent standard deviations.

offensive actions (i.e., aggressive movements, threatened bites, actual bites). When DHBs, aggressive movements, threatened bites, and actual bites (i.e., offensive actions) were added up on a daily basis and compared over time, the LE group showed a statistically significant increase ($P = 0.05$, Wilcoxon) in the total number of aggressive actions on day 5 in comparison to day 1. Conversely, the RE subjects showed a statistically significant decrease ($P = 0.029$) in the total number of aggressions on day 4 in comparison to day 1, and a trend toward significant decreases on days 3 ($P = 0.062$) and 6 ($P = 0.075$). Thus, a double dissociation in control over aggressive movements was observed during the first 6 days of testing, with LE showing increases and RE showing decreases.

Changes in aggressive behaviors following fluoxetine administration

Subjects received fluoxetine (FLU) or vehicle (CON) injections on days 7 and 14. FLU subjects, on the average, aggressed more quickly at the intruding male during the 6 days of preinjection training than did the CON group, although this difference did not reach statistical significance. During injection on days 7 and 14, both FLU-injected and CON-injected subjects showed longer latencies to their first aggressive response. There were no between-group differences from the effect of injection after the first injection on day 7. However, FLU-injected subjects took longer to re-

spond, on the average, on both days in comparison to CON-injected subjects (Fig. 5), with this difference reaching statistical significance by day 14 ($P < 0.05$) on Mann-Whitney nonparametric analysis. After the second injection on day 14, on days 15–19 the FLU group showed an overall slowing of initial aggressive response in comparison to the CON group, although this difference did not reach statistical significance.

Both left and right eye-mediated aggressions were reduced following fluoxetine administration. No evidence of any laterality effect following FLU administration was found.

Changes in skin color

Weak, but statistically significant, correlations were seen between skin color changes and several aggressive behaviors. The relationship between these factors appeared to become stronger as the number of trials progressed. As shown in Table 2, no significant correlations between skin color and aggression were found during the first six trials. However, by trials 15–19, the time it took before the subject emitted the first aggressive response was positively correlated with both initial and final skin color, indicating that brown animals took longer to demonstrate an aggressive movement, while green animals took less time. In addition, the number of dewlaps and headbobs was inversely correlated with final skin change, indicating that brown subjects had fewer, while greener subjects had more, of these behaviors.

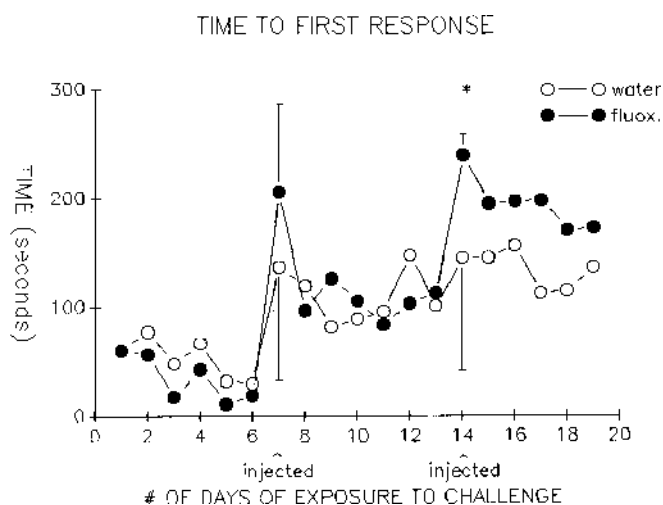


Fig. 5. Length of time during each trial until the first aggressive response was initiated by the subject. Standard deviation error bars are shown for the 2 days of fluoxetine administration (i.e., days 7 and 14). * $P < 0.05$.

TABLE 2. Correlations between skin color and aggressive behaviors

	Time to first response	Dewlaps and headbobbing	Bites
Days 1–6			
Initial	0.172	–0.206	–0.103
Final	0.139	–0.209	–0.162
Change	0.026	0.001	0.060
Days 8–13			
Initial	0.019	–0.002	–0.140
Final	0.203	–0.179	0.024
Change	–0.204	0.205	–0.272*
Days 15–19			
Initial	0.2554*	–0.159	–0.194
Final	0.2945*	–0.251*	–0.157
Change	0.0279	0.060	–0.098
All days combined			
Initial	0.184**	–0.145*	–0.146*
Final	0.232**	–0.219**	–0.121
Change	–0.011	0.050	0.061

Correlations between aggressive movements and skin color, including skin color at the start of the trial (initial), end of the trial (final), and the change in skin color computed by subtracting final from initial. * $P < 0.05$, ** $P < 0.01$. No statistically significant correlations were seen between skin color and dewlaps, aggressive movements, or threatened bites.

When the analysis was done for all trials combined, correlations found weak but statistically significant relationships between skin color and time to the first aggressive response, the number of bites, and the number of dewlaps and headbobs.

DISCUSSION

Results from experiment two indicate that the previously demonstrated (Deckel, '95, '96) left-eye preference that *A. carolinensis* has during aggressive movements takes several days to emerge. Over the first 6 days of training, the frequency of left eye-mediated responses became greater, while the frequency of right eye-mediated responses lessened. Similarly, the relationship between skin color changes and aggressive responding also appeared to increase as the experiment progressed, with statistically significant correlations emerging during days 15–19, while none was present during days 1–6 of training.

Past work done in our laboratory has consistently found that it typically takes several days before socially isolated male *A. carolinensis* begin to persistently aggress when an intruder is introduced into the cage. Because of this, earlier experiments that examined the relationship between eye use and aggressive movements (Deckel, '95, '96) routinely gave the animals several days of "pretraining" (i.e., pairing with an antagonist before responding was recorded), and thus, the phenomena of a

double dissociation of eye preference for aggression, if present in these experiments, may have been missed. The current findings suggest that the aggressive response in *A. carolinensis* may take a short period of time to turn on. These results suggest that one of three changes may be occurring in the brain of *A. carolinensis* exposed to intruding males: (1) the left hemisphere (because its input comes exclusively from the right eye) over time may become less reactive to the threat posed by the intruding male, (2) the right hemisphere may become more reactive to the threat posed by the intruder as time progresses (because input to the right hemisphere comes exclusively from the left eye), or (3) some combination of the above may be occurring. The current experiment does not allow for a determination as to which of these three possibilities may be occurring.

The relationship between skin color changes and aggression also appears to take some time to develop. No relationship between skin color changes and aggressive responding was seen over the first 6 days of the experiment. By days 15–19, the final skin color was weakly correlated with the time it took for the subject to demonstrate the first aggressive response ($r = 0.29$) and for the number of dewlaps and headbobs ($r = -0.025$). Greener coloration was associated with higher aggressivity. Like eye preference, skin color appears to require a period of time to become linked to aggression, suggesting that this phenomenon may be under endocrinological, behavioral, or genetic control that takes a short period of time to develop. Further experimentation will be required to adequately explore this hypothesis.

Experiment two replicated earlier work (Deckel, '96) reporting that the serotonin reuptake inhibitor fluoxetine inhibits aggression. Aggression was significantly reduced in the FLU subjects after the second injection, and there is evidence from the current findings that aggression remained low for several days following this injection. While earlier work suggested that there may be an aggressive "rebound effect" once the effects of FLU pass (Deckel, '96), no evidence of such an effect was seen in this experiment.

FLU-injected animals showed no left-eye vs. right-eye change in their aggression following injection. Aggressive movements in both eyes were reduced following injection, suggesting that serotonin is equally efficacious in reducing aggression mediated by both hemispheres in the anole brain.

GENERAL DISCUSSION OF EXPERIMENTS ONE AND TWO

The findings from the current experiments replicate and extend earlier work on the laterality of aggression in *A. carolinensis*. Experiment one demonstrates that eye preference for aggression remains lateralized even when the eyes are patched. However, in comparison to studies of laterality of aggression in unpatched *A. carolinensis* (Deckel, '95, '96), patching the eyes revealed several levels of complexity not otherwise apparent. First, skin color appears to be differentially affected during periods of aggression but not during resting baseline, depending on the eye patched. Regulation of skin color changes is known to be affected by circulating levels of melatonin, serotonin (and their metabolites), catecholamines, and corticosteroids, and skin color in experiment one correlated highly with aggressive responding. Previous work demonstrating that the left hemisphere in *A. carolinensis* has receptors that bind melatonin, while the right hemisphere has no demonstrable receptors (Wiechmann and Wirsig-Wiechmann, '92), strongly implicates the right eye/left hemisphere in regulating the level of the release of peripheral monoamines (as skin color changes do not appear to be under the control of direct nervous innervation) and central monoamines (as behavior changes in a manner correlated with skin color change).

Experiment one also demonstrates that at least one aggressive behavior, the combined dewlaps and headbob response, or the "social assertion" response (Carpenter, '78; Greenberg, '77; Jenssen, '77; Greenberg and Noble, '44; Greenberg et al., '79, '84), is firmly under the control of the left eye/right hemisphere, replicating findings from unpatched *Anolis* (Deckel, '95). Although experiment one suggests that headbobbing only and biting were under the control of the right eye/left hemisphere, this finding is at odds with experiments using unpatched *Anolis* (Deckel, '95, '96). These experiments have reported that the left eye is preferred for social challenge, social assertion, dewlaps only, biting, and other aggressive responses. One resolution of the discrepancy between the current experiment and past work may be that both hormonal/endocrinological as well as lateralized hemispheric control may be involved in regulating these movements. If, for example, the right eye/left hemisphere tightly controls the release of serotonin and/or melatonin and their metabolites, release of these substances may act on "behav-

ioral programs" controlled either by the right, left, or combined hemispheres, whether or not that hemisphere has direct visual input regarding the presence of an antagonistic male. This reasoning is speculative and in need of further experimental exploration. Nonetheless, experiment one suggests that the laterality of aggression in *A. carolinensis* is more complex than suggested by experiments using unpatched subjects and may involve mechanisms that regulate both hormonal/endocrinological control as well as more direct hemispheric activation.

Some support for this reasoning comes from experiment two. Injections of fluoxetine, which increases the bioavailability of central serotonin, lead to decreases in aggressive responding in both the left and right eyes in unpatched subjects. Thus, increases of serotonin appear to dampen all aggressive responding in *A. carolinensis*, suggesting that serotonin functions in an inhibitory fashion in the regulation of aggression across both hemispheres.

Past ethological work has found sagittal expansion to be a definitive marker of aggression in anoles (Carpenter, '78; Greenberg, '77; Jenssen, '77, '78). However, in the current experiments, it was common to have males threatening to bite, or actually biting, one another without showing either sagittal expansion or eye spot darkening. This was particularly true in the later aspects of both experiments. We believe that the lack of sagittal expansion may be due to the fact that the males were generally isolated, given only a short exposure to the intruding males (10 min in experiment one, 5 min in experiment two), and subjected to repeated parings and partial habituation to the experimental procedure. Whatever the cause, the current experimental design may have resulted in a blurring between the commonly described "social assertion" (i.e., dewlap and headbob unaccompanied by sagittal expansion) and "social challenge" (i.e., dewlaps and headbobs accompanied by sagittal flattening and commonly by darkening of the eyespot and subsequent physical aggression) responses.

It also was common in the current experiment to have a male anole dewlap only as an initial response to the introduction of the intruding male and then proceed to dewlaps and headbobs, aggressive actions (i.e., circling, stalking, etc.), and finally bites. It was less common, but occasionally observed, to see the same sequence start with a headbob. This was not the shallow, rapid, submissive response that is frequently seen in colo-

nies of anoles nor a courtship headbob (no females were present) but, rather, headbobs accompanied with pushups. Thus, dewlap only, and dewlap and headbobs frequently appeared as a prelude to more aggressive action and may represent a lower "gradient" of aggressive responding in the current experiment. To what extent this hierarchy was a consequence of the current experimental paradigm is unclear, but the current results may differ from naturalistic observations of aggression in anoles and ethograms developed from such observations.

Work in other species, as well, has found asymmetries in the relationship between visual input, eye preference, and hemispheric lateralization of behaviors. Rogers and colleagues (Rogers, '82, '89, '90; Rogers et al., '85, '93; Schwarz and Rogers, '92) showed that visual input through the right eye to the left hemisphere is of critical importance in the developing chick neural organization of behaviors. Specifically, the left hemisphere in the developing chick embryo plays a decisive role in determining the direction of brain lateralization for two behaviors, including copulation and a visual discrimination task (Rogers, '90), and apparently is critically involved in neural organization of these behaviors as patching the right eye, or rearing the chicks in darkness, can inhibit this effect (Rogers, '82). Beyond this, in the chick the right eye is dominant for learning and recall of visual discrimination tasks (Gaston and Gaston, '84; Mench and Andrew, '86), while the left eye controls attack and copulating behaviors (Rogers, '90; Rogers et al., '85). Finally, asymmetries in the development of thalamofugal visual projections in chicks appear to be regulated by sex steroid hormones and to be more pronounced in the male chick (Rogers and Rajendra, '93; Rogers et al., '93; Schwarz and Rogers, '92). To what extent, if any, these findings apply to the current results is unclear. Further work to see if the lateralization of aggressive behavior in *A. carolinensis* is developmentally under the control of right-eye visual input, as it is in the chick, is planned in our laboratory. In addition to the chick, other species show a lateralization of aggression to the right hemisphere. Denenberg and Yutzey ('85b), for example, have demonstrated that rats with left hemisphere lesions but intact right hemispheres kill mice more often than rats with right hemisphere lesions and intact left hemispheres. Hellige ('93) has suggested that, in humans, activation of the right hemisphere, relative to the left, may be predictive of temperament. Specifically, Hellige ('93) has suggested that right-hemisphere activation may be

related to negative emotions, while left-hemisphere activity may relate to positive ones. Deckel and colleagues ('96) have reported evidence that humans who retrospectively report higher levels of conduct disorder or who are diagnosed as being positive for antisocial personality disorder have greater activation of the resting electroencephalogram in the right hemisphere relative to the left. Thus, there is evidence that lateralization of aggression is a widespread phenomenon that is seen across diverse species.

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