The Biological Function of Pavlovian Conditioning: The Best Defense is a Good Offense

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Signaled presentations of a rival male produce an aggressive conditional response in several species of fish. Although conditioning of such species-specific display behavior has been described previously, the biological function of this learning phenomenon has remained unknown. I present experimental evidence that signaled territorial intrusion enables a male blue gourami to defend his territory more aggressively than when the intruder is unsignaled. In Experiment 1, pairs of territorial males, with different conditioning histories, confronted one another for the first time. One member of the pair previously had received Pavlovian conditioning, whereas the other pair member had received explicitly unpaired presentations of the same signal—conditional stimulus (CS)—and rival male—unconditional stimulus (US). In the subsequent encounter, which was signaled by CS presentation, Pavlovian males delivered significantly more bites and tailbeatings than did their control group opponents. Experiment 2 relied upon a different control procedure, a US-only condition, but, again, Pavlovian males enjoyed a significant aggressive advantage. These results suggest an important ecological role for Pavlovian conditioning.

Signaled presentations of food, rivals, predators, and mates result in anticipatory and, frequently, signal-directed species-typical behavior (e.g., Farris, 1967; Hearst & Jenkins, 1974; Rackham, 1971, cited in Moore, 1973; Thompson & Sturm, 1965). Although the Pavlovian conditioning process has been long the domain of psychologists interested primarily in the underlying mechanism of association, the ethological significance of these classically conditioned action patterns has not gone unnoticed. Researchers of the autoshaping phenomenon have speculated that the conditioning procedure probably mimicks naturally occurring situations in which animals locate food (Jenkins, Barrera, Ireland, & Woodside, 1978; Moore, 1973), secure mates (Graham & Desjardins, 1980), or encounter rivals (Thompson, 1966). But, although the biological function of Pavlovian conditioning has been recognized theoretically, it has been ignored experimentally. How does such an associative mechanism contribute to reproductive success and fitness?

Elsewhere (Hollis, 1982) I have suggested that the biological function of the conditional
response (CR) is to allow the animal better to deal with the forthcoming unconditional stimulus (US); the CR is essentially a preparatory response. But preparatory, as used here, is a descriptive term that refers to the biological function of the CR, not the mechanism whereby the CR is produced. (Thus, preparatory is not at all theoretically synonymous with that term’s use in other learning contexts, for example, in the preparatory-response hypothesis of Perkins, 1968, where the term is used to refer to a non-Pavlovian mechanism of learning.) More specifically, anticipatory conditional responses function to optimize interactions with predators, rivals, mates, and food—a function that I have labeled prefiguring (Hollis, 1982).

For example, the prefiguring hypothesis presupposes that the function of the anticipatory conditional aggressive behavior demonstrated by anabantid fish is to increase the likelihood of successful territory defense. Naturally occurring stimulus events that would reliably accompany a territory intruder would serve, like the conditional stimuli of the laboratory, as learned releasers of the agonistic display. The result of this conditioning process is that an intruder would be met at the territory boundary by an already aggressively disposed owner who is, therefore, better prepared to do battle (Hollis, 1982).

Functional questions, because they involve inferences regarding an animal’s inclusive fitness, are frequently difficult to address because the behavior in question is often far removed from actual reproductive gains. However, anabantid fish, like Betta splendens and the blue gourami (Trichogaster trichopterus), offer a rare opportunity to test a functional interpretation of the learned aggressive response. As the natural history of these fish will reveal, the importance to reproduction of their territory defense cannot be overestimated (Forsellius, 1957; Miller, 1964; Simpson, 1968).¹

In their natural habitat, males migrate to freshwater pools, establish their territories, and build their floating foam bubble nests in advance of the females. Later, when the females arrive in the nesting area, the courting males attempt to lure them into the territory. Spawning takes place under the bubble nest wherein the eggs, tended by the male, remain until they hatch. Because the nest—and, thus, the territory—plays such a major role in reproduction, it is not surprising that females rarely mate with nonterritorial males.

Territory intruders, be they later arriving males in search of a territory themselves or neighbors attempting to expand their own territory, are, therefore, risks to reproduction and are met with a vigorous aggressive defense. The territory owner charges to the site of the intrusion in the head-on frontal display. If the intruder does not immediately assume the submissive posture or flee, the contest escalates and biting soon ensues, followed by tailbeating. In few other situations, except perhaps courtship itself, is the biological function of a conditional response so closely tied to reproductive gains.

Perhaps of even greater relevance to the hypothesized advantage of signaling is the observation that most aggressive contests are decided quickly, unequivocally, and, for the most part, permanently. Confrontations usually last about 15 min and rarely longer than 30 min; thus, an early aggressive advantage could be of utmost importance.

Given the suitability for functional analysis of this well-documented conditional response, the purpose of the experiments reported here was to determine whether Pavlovian conditioning of aggressive behavior would confer some advantage on a territorial male, enabling the male better to defend his territory in a signaled encounter. Pairs of territorial males formed the basis of a comparison between the Pavlovian conditioning and control group treatments. One member of the pair received Pavlovian conditioning, whereas the other pair member received a control group treatment. Following this training, pair members confronted one another for the first time in an encounter preceded by the Pavlovian conditional stimulus (CS). The benefit, if any, to the classically trained male of that signaling was assessed in terms of each fish’s ability to defend its own territory against invasion.

¹ All details of the reproductive and aggressive behavior of these fish, both in the summary to follow as well as in later sections, have been taken from Forsellius, 1957. Similar observations have been made by Miller, 1964, and Simpson, 1968.
Experiment 1

In this experiment, classically conditioned males confronted pairwise mates that received explicitly unpaired presentations of the same signal CS and rival male US. The CS was presented immediately prior to that confrontation, and, although both males were equally familiar with its presentation, the CS was predictive of intrusion only for the Pavlovian males.

Method

Subjects and Apparatus

The subjects were four pairs of adult male blue gouramies (Trichogaster trichopterus). They were selected from large stock colonies so that, within a single pair, the fish were nearly identical in body size and fin depth. Each pair occupied a standard 20-gal (75.7 L) aquarium (77 cm x 30 cm x 36 cm), maintained at 27 °C with a 14-hr light (L)-10-hr dark (D) illumination schedule. Pair members were visually separated from one another by a divider with two doors (19 cm x 30 cm), one of transparent acrylic plastic and another of opaque white acrylic plastic, which could be raised and lowered independently by means of a string and pulley system. Both sides of the tank contained a gravel floor, a clay flower pot (in which to hide), and a few plants. A wooden light box, containing two 60-W bulbs, was positioned immediately behind the tank, perpendicular to the plane of the divider. The front of the box (25 cm x 20 cm) was white acrylic plastic backed with red acetate. When the bulbs were turned on, the white front of the box glowed red, as did both sides of the white divider door, which reflected the red light.

Procedure

Within each pair, 1 fish was chosen at random to receive the Pavlovian (PAV) conditioning treatment; the other member of the pair received the explicitly unpaired (UNP) control treatment. Each fish received its training in the home tank. While 1 fish was being trained, the pairmate was temporarily removed to a small bowl containing water from the home tank. In the place of the removed fish, a glass jar (19 cm x 12 cm x 25 cm) containing another male blue gourami, not one of the experimental subjects, was inserted on the vacant side, flush against the divider door. This fish served as the rival male US. Two such rivals were used, one for each of 4 subjects. A tank pair was exposed to the same rival throughout training. Following a training session, the rival was removed, and the displaced pair member was returned to its half of the home tank. An analogous procedure was followed for the training of the other pair member.

The netting and removal procedure did not appear to affect the behavior of the fish. Nevertheless, a fish's training session neither followed, nor was followed by, its removal from the tank for at least 1 hr, and the order in which the pair members were trained was counterbalanced over days of training.

Pavlovian conditioning consisted of a 10-s presentation of the red light CS followed immediately by a 15-s presentation of the rival male US. US presentation was accomplished by lifting the opaque divider door, revealing the rival in the glass jar on the other side. A PAV training session consisted of 15 pairings per day with an intertrial interval (ITI) of 60 s-180 s (M ITI = 120 s). Fish in the UNP treatment group daily received fifteen 10-s presentations of the red light CS followed, on average, 1 hr later (range = 1 hr-7 hr), by fifteen 15-s presentations of the rival US. During training, four agonistic behaviors were recorded: frontal display, biting, tailbeating, and submissive posturing. These behaviors are described in Table 1. An observer, seated approximately 3 m from the tank and partially hidden by a black screen, merely noted whether or not each of the four behaviors had occurred during the 10 s immediately before CS onset (prewarning behavior) and during both CS and US presentation.

For 6 days prior to training, fish were habituated to the procedures associated with US presentation. On the first 3 days of habituation, the rival was positioned in the tank, as described above, and, following a 5-min delay, the divider door was lifted very slowly. US exposure continued uninterrupted for 20 min. On the remaining 3 days of habituation, fish received 15 separate presentations of the rival US using the US schedule that would be employed in training. Over the course of these 3 days, the divider door was lifted and dropped more and more abruptly. (Although these US preexposures might be expected to retard subsequent conditioning in the PAV group, the fishes' initial startle responses to door movement suggested that this habituation procedure was necessary.) Conditioning treatments began on the following day, Day 1, and continued until Day 24. All sessions were preceded by a 5-min acclimation period.

On Day 25 the territorial defense test was conducted. Just prior to this session the clear door was removed from the divider leaving only the opaque divider door between the two fish. Following the usual 5-min acclimation period, the test was administered. It consisted of presenting the 10-s CS to both fish simultaneously and then, at CS-offset, lifting the opaque divider door, allowing the PAV and UNP pairmates to confront one another for the first time, both defending their home territory. During this confrontation, a complete record of all agonistic behavior (see Table 1) was made with the use of a computer event recorder.

Data Analysis

To analyze test performance data, the four pairs of fish were treated as paired samples; paired t tests (also called t tests for related measures, McGee, 1971) were performed on the frequencies of the agonistic behaviors. The datum here is the difference between the pair members along some response measure and n = 4. Training data were analyzed by means of ANOVAS.

Results and Discussion

Training Data

Conditional responding. The frontal display, the first component of the aggressive
Table 1
Agonistic Behavior of the Blue Gourami

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
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<tbody>
<tr>
<td>Frontal display</td>
<td>Unfolding and spreading of the dorsal, ventral, and caudal fins (fin erection) in the characteristic “face-to-face” posture. During CS presentation, a frontal display was scored whenever the fish assumed a fin erection within 5 cm of, and oriented toward, the light box or the barrier door. During US presentation, a frontal display was scored whenever the fish assumed a fin erection within 5 cm of, and oriented toward, the barrier door (training) or the pairmate (test).</td>
</tr>
<tr>
<td>Biting</td>
<td>Contacting with open mouth, accompanied by an abrupt forward lunge. During CS presentation biting was scored whenever the behavior was directed at the light box or the barrier door; during US presentation biting was scored whenever the behavior was directed at the barrier door (training) or the pairmate (test). Biting is always accompanied by a fin erection.</td>
</tr>
<tr>
<td>Tailbeatting</td>
<td>Side-to-side undulations of the body, including the fins, usually carried out in a normal swimming position but occasionally at a head-upward or head-downward angle of from 30° to 80° to the horizontal plane. These undulations are responsible for directing water currents of great force against the body of the opponent, striking the sensory nerve endings of the lateral line organ. Tailbeating was scored whenever any noticeable side-to-side undulations of the body and fins occurred. Tailbeating is always accompanied by a fin erection.</td>
</tr>
<tr>
<td>Submissive posturing</td>
<td>Assuming a body angle of from 15° to 60° with the horizontal, typically at the air-water interface, with all fins in a folded position. This posture is eventually accompanied by a Blanching of color until the fish looks pale gray to silver. Submissive posturing was scored whenever the fish assumed the definitive angle, either at the surface or not and either with or without coloration changes.</td>
</tr>
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</table>

Note: Descriptions of agonistic behavior are after Simpson (1968) and Forsellius (1957).

display sequence, was the only conditional aggressive behavior elicited by the CS. The acquisition of this response is shown in Figure 1, which presents the mean number of frontal displays elicited by the CS over the 24 days of training. Responses on Day 1, which are included in the data of Block 1, are also plotted separately in Figure 1 and in subsequent training figures. Although the Day 1 data of both PAV and UNP males indicate that the CS was not itself capable of eliciting a frontal display, PAV males exhibited an increase in the number of CRs over days whereas UNP males rarely, if ever, displayed, procedure, \( F(1, 6) > 50.00, p < .001; \) blocks, \( F(5, 30) = 5.11, p < .01; \) Procedure × Blocks interaction, \( F(5, 30) = 5.32, p < .01 \).

The specificity of the frontal display CR is revealed in Figure 2, which presents the mean number of frontal displays exhibited during the presignal period, the 10 s immediately prior to the CS, over the 24 days of training. UNP males, as well as their PAV pairmates, rarely, if ever, responded with a frontal display during this period (all \( Fs < 1.00, p > .50 \)).

Unconditional responding. Aggressive responses elicited by the rival male US consisted of frontal displays and biting behavior, the first two components of the aggressive display sequence. Frontal displays, shown in Figure 3, were performed by UNP and PAV males.

Figure 1. Mean daily number of frontal displays elicited by the conditional stimulus over 24 days of training. (Responses on Day 1, D-1, which are included in Block 1 means, are also plotted separately. PAV = males receiving the Pavlovian conditioning treatment; UNP = control treatment.)
liftings of the door; in any case, the effect is both so small and so transient that it is virtually obscured when Block 1 means, which include Day 1 data, are plotted.

The picture is somewhat different, however, for rival US-evoked bites, shown in Figure 4. PAV and UNP males did not differ from one another initially—on Day 1 of training, $t = 0.47, p > .30$—nor did an ANOVA indicate any effects of procedure, $F(1, 6) = 0.13, p > .50$, or of blocks, $F(5, 30) = 1.96, p > .10$; however, PAV and UNP males did differ from one another in their responses over days of training. Procedure $\times$ Blocks interaction, $F(5, 30) = 4.05, p < .01$. Inspection of the significant interaction using tests on simple main effects revealed that, whereas the frequency of biting did not vary over days in the PAV group, $F(5, 30) = 0.63, p > .50$, there was a significant change in the behavior of UNP males, $F(5, 30) = 163.58, p < .001$, the number of bites increasing steadily over days. Individual comparisons of UNP and PAV males, at each block, revealed no significant differences in biting, all $F$s(1, 6) < .80, $p > .25$. But, regardless of whether any real differences in biting behavior exist between PAV and UNP males, the apparent inferiority in biting is evidenced by the PAV group—a bias which, if anything, would have reduced the
likelihood of their demonstrated superiority in the subsequent test confrontation.

Finally, occurrences of tailbeating behavior were rare during the 15-s US presentation. This result is somewhat surprising in that tailbeating was observed in both PAV and UNP males during all three of the 20-min habituation sessions (and in the test confrontation as well). However, the absence of a tailbeating UR during training might be attributable to the difference in US duration; the 15-s training US may have been of insufficient duration for tailbeating to occur. This explanation is consistent with the usual sequence of aggressive behavior in which an initial frontal display is followed, first, by biting and, somewhat later, by tailbeating.

**Test Confrontation**

All four PAV males, but none of the UNP males, responded with a frontal display to the CS preceding the test confrontation. When the barrier was lifted, the PAV males, with fins erect, swam immediately to the other side and approached UNP males in a frontal display. UNP males then raised their fins. Although these fin erections were maintained mutually for the duration of the encounter, PAV and UNP males differed significantly in the number of bites and tailbeatings they performed.

Figure 5 shows the mean cumulative number of bites, and Figure 6 shows the mean cumulative number of tailbeatings in the first 3 min, 5 min, and 10 min of the confrontation. PAV fish were able to deliver significantly more bites than were their UNP rivals at all of these intervals, \( t = 3.29, p < .025; \ t = 4.86, p < .01; \) and, \( t = 2.94, p < .05, \) respectively. Reported here are statistical analyses based on the absolute number of occurrences of an aggressive behavior, but the results were qualitatively the same when proportions, or arc sine transformations of proportions, were analyzed instead. Nor does it make any difference whether the data were analyzed cumulatively or not. Indeed, all 4 PAV males exhibited the aggressive advantage throughout the confrontation. Even in the closest contest, the PAV male delivered 44% more bites than did the UNP male in the first 3 min, the margin decreasing to 30% by Minute 10. (Percentages were computed using the formula, \( \text{PAV} - \text{UNP}/\text{PAV} + \text{UNP} \times 100. \) A similar picture emerges for tailbeating (see Figure 6); PAV fish delivered significantly more tailbeatings than did their control pair-
mates in the first 3 min, 5 min, and 10 min of the confrontation, $t = 7.36, p < .01; t = 4.12, p < .025$; and, $t = 3.58, p < .025$, respectively. Here, too, the aggressive advantage was exhibited by all 4 PAV males, the closest contest never falling below a 50% margin in the number of tailbeatings exhibited.

The choice of intervals at which to compare PAV and UNP males was based on preliminary observations of encounters between male blue gouramies as well as on the test confrontations themselves. Most of the biting and tailbeating behavior typically occurs between the 2nd and 10th minute of a confrontation. In the present experiment, for example, over 75% of all tailbeating and biting took place during that time period. Because three contests were terminated at various times between the 11th and 15th minute of the encounter (when the UNP male assumed the submissive posture and the PAV male then ceased fighting), the 10-min interval necessarily formed the upper boundary of active aggressive behavior by both PAV and UNP males.

An objection might be raised concerning the choice of time intervals at which to compare PAV and UNP males. The aggressive advantage provided by Pavlovian conditioning might have been manifested very early in the confrontation, perhaps in the first few seconds, and thereafter have been contaminated by other factors arising from the interaction itself. That is, Pavlovian conditioning was responsible for the origin of the advantage but not necessarily for its maintenance. However, the comparison intervals were chosen only as a means through which to demonstrate that aggressive advantage, and not to delineate when and how the advantage was realized. This and related issues will be addressed in the General Discussion.

Summary

Throughout training, brief presentations of the rival male US elicited in all males the first two components of the aggressive display sequence, namely the frontal display and biting. Tailbeating, normally a later component of aggressive defense, did not occur. As a result of CS–US pairings, the CS also elicited an aggressive response in PAV males. The conditional response was limited to frontal display, the initial display component, and was not performed by control males. The training CS was then used to signal the test confrontation, and here, too, it elicited a frontal display in PAV males. In the following encounter, the aggressive display sequence—frontal display → biting → tailbeating—was performed by both PAV and UNP males; however, PAV males performed significantly more biting and tailbeating.

Experiment 2

In the previous experiment I sought to determine whether Pavlovian conditioning of aggressive behavior would confer an advantage on a territorial male in a signaled encounter. However, one might argue that the superiority of the classically conditioned males resulted not because the learned signal allowed those males to “prepare” better than their control group rivals, as I have hypothesized, but because the control males were explicitly “unprepared.” The explicitly unpaired control treatment might have resulted in the conditioned inhibition of aggressive behavior: The red light CS was predictive, for UNP males, of the absence of the rival male US and, as such, may have resulted in the inhibition of aggressive responding. This inhibition in itself could account for observed differences between PAV and UNP males in the test confrontation.

In Experiment 2 a different control procedure was employed. Control males received the same amount of experience with the rival US as did their Pavlovian pairmates; however, they were never presented with the red light CS, neither in training nor in the test confrontation. One might expect, then, that this US-only control group would be more representative of the male territory owner that experiences a sudden intrusion by a rival male.

Method

Subjects and Apparatus

The subjects, 8 naive adult male blue gouramies, were selected, housed, and maintained as described in Experiment 1. The apparatus was modified so that the CS
could be presented to one side of the tank only and without admitting red light to the other side. This was accomplished by inserting an opaque plastic shield flush against the inside back wall of one half of the tank and anchoring it with opaque tape to the divider door, which abutted the shield at a 90° angle. All other features of the apparatus were identical to those described in Experiment 1.

Procedure

Within each pair, one fish was chosen at random to receive the Pavlovian conditioning treatment (PAV); the other member of the pair received the aggression-only control treatment (AGG-only). The fish received their respective training in the home tank separately as described in Experiment 1.

Pavlovian conditioning was conducted as described in Experiment 1: There were 15 daily presentations of a 10-s CS followed immediately by a 15-s US, with an ITI of 60 s–300 s (M ITI = 180 s). Fish in the AGG-only treatment group experienced the same daily rival US presentation schedule as did the PAV fish but did not experience any of the CS presentations.

For both groups the habitation and training regimes were similar to Experiment 1. On the first 3 days of habitation, all fish received a single uninterrupted 20-min exposure to the US; on the remaining 3 habitation days, all fish received fifteen 15-s US presentations; finally, the PAV and AGG-only conditioning treatments began on Day 1 and continued until Day 24. Data were collected as in Experiment 1.

On Day 25 the territorial defense test was conducted. Just prior to this session, the clear door was removed from the divider leaving only the opaque divider door between the two fish. Following the usual 5-min acclimation period, the test was administered and consisted of presenting the CS to only the PAV male (but not to the AGG-only male) and then lifting the opaque divider door, allowing the PAV and AGG-only pairmates to confront one another for the first time. During the confrontation, a complete record of all agonistic behavior was made as in Experiment 1.

Data Analysis

Test performance data were analyzed as in Experiment 1. Where suitable, training data were subject to ANOVAS.

Results and Discussion

Training Data

Conditional responding. As in Experiment 1, the frontal display was the only conditional aggressive behavior elicited by the CS. Figure 7 shows the acquisition of this response in PAV males relative to their presignal responding. The Day 1 data suggest that the CS did not elicit a frontal display prior to training. However, PAV males increasingly exhibited an aggressive response to the CS over days of training.

CS–US pairings, a response that the presignal behavior suggests is specific to the CS, procedure, F(1, 6) = 50.00, p < .001; blocks, F(5, 30) = 31.65, p < .001, Procedure × Blocks interaction, F(5, 30) = 30.46, p < .001.

Unconditional responding. Aggressive responses elicited by the rival male US consisted of the frontal display and biting behaviors. As in Experiment 1, the PAV and AGG-only groups were not significantly different from one another in the number of frontal displays elicited by the US, procedure, F(1, 6) = 0.95, p > .25 (see Figure 8). Moreover, the frontal display was readily elicited, in both groups, by presentation of a rival male from the outset of training, blocks, F(5, 30) = 0.98, p > .25; Procedure × Blocks interaction, F(5, 30) = 0.60, p > .50.

Although Figure 9 might suggest that PAV males displayed more biting behavior than did AGG-only males during US presentation, an ANOVA revealed no differences between the groups, procedure, F(1, 6) = 1.52, p > .25. Both PAV and AGG-only males, however, showed an increase in the incidence of this behavior over days, blocks, F(5, 30) = 5.25, p < .01; Procedure × Blocks interaction, F(5, 30) = 0.25, p > .90.
Test Confrontation

The results of the test confrontation between PAV and AGG-only males were similar to the confrontation of PAV and UNP males in Experiment 1. Once again PAV males delivered significantly more bites and tailbeatings (see Figures 10 and 11) than did their AGG-only rivals at each of the test intervals, \( t(\text{biting}) = 2.58, 4.93, \) and \( 5.61, \) respectively, \( p < .05; t(\text{tailbeating}) = 4.39, 2.97, \) and \( 3.03, \) respectively, \( p < .05. \) And, here too, all PAV males exhibited this aggressive advantage throughout the confrontation, both in terms of the number of bites delivered and the number of tailbeatings. In the closest contest between the pairs, the PAV male nonetheless delivered 18% more bites and 23% more tailbeatings in the first 10 min of the confrontation.

One interesting difference between the test confrontations of Experiments 1 and 2 is that far more biting and tailbeating occurred in the present experiment (cf. Figures 5 and 6 with Figures 9 and 10). Experiment 2 pairs exhibited, overall, at least 2–3 times as much aggressive behavior as did Experiment 1 pairs. An explanation of this difference, invoking the phenomenon of conditioned inhibition, is evaluated in the General Discussion.
Yet Pavlovian conditioning may not be limited to defensive strategies alone. In the same way that signals of territory invasion elicit an adaptive response to deal with that threat, so, too, we might expect that signals predicting the absence of territory invasion also elicit an adaptive response. To the male blue gourami which must defend a territory at the same time that it must watch for females, tend the nest, and forage for food, a CS—, indicating a period of time free from threat, would be as important a signal as a CS+. Some evidence that a CS— can control behavior emerges from a comparison of aggression across the two experiments. AGG-only males in Experiment 2 delivered six to ten times as many tailbeatings and up to three times as many bites as the explicitly unpaired males of Experiment 1 (cf. Figures 5 and 6 with Figures 9 and 10). Of course, the Pavlovian males of the two experiments evidence the same aggressive trend; however, the difference in overall level of aggression between the two experiments more likely is attributable to the differences in the control treatment. The stronger AGG-only rivals required considerably more effort to be vanquished than did the less aggressive UNP males. In Experiment 1, the CS was presented to both pair members just prior to the test confrontation; for the UNP male this CS was predictive of the absence of territorial threat. Thus, UNP males received a CS— just prior to the test confrontation, whereas AGG-only males received neither excitatory nor inhibitory signals. These data are merely suggestive. Current experiments are being conducted in which the ability of the CS— to control behavior is tested directly.

Notably absent from the present experiments is a random control group in which CSs and USs are presented independently of one another during the course of an experimental session (Rescorla, 1967). Although the random control procedure often can be an important tool in distinguishing between associative and nonassociative effects, it sometimes results in conditioning (e.g., Benedict & Ayres, 1972; Kremer & Kamin, 1971), and other control groups must be used instead. Previous research with another anabantid (Hollis & Overmier, 1982) suggests that the random control procedure would
not be adequate in the experiments described here because it results in some excitatory conditioning to background cues. Unpublished observations of several species of anabantids has revealed that, whenever specific CSs predicting the appearance of a rival (the PAV condition) are unavailable, these territorial fish tend to treat session cues (the appearance of the experimenter, e.g.) as "low intensity" CSs: The fish position themselves facing the barrier, at some distance, and hover in this alert posture for much of the session. Such behavior, especially the specificity of its orientation, is not likely to be attributable to nonassociative effects, at least those for which the psychologist attempts to control. I have argued that fish in the US-only control group, which never encounter the CS in training or in the test, are representative of male territory owners that experience a sudden intrusion by a rival; one also might argue, however, that even this control group is not totally unprepared for such an intrusion. But, again, the present experiments do not attempt to delineate the exact nature of the conditioning mechanism; my purpose is to demonstrate that signaling confers an advantage in a (somewhat) naturalistic situation. That US-only fish (possessed of some excitatory conditioning, perhaps) are nonetheless impotent in aggressive encounters with PAV males seems to provide yet stronger evidence for the advantage of an explicit signal.

Essential to the type of analysis suggested here is a consideration of conditioning as it operates in the wild. Of immediate concern, then, is the potential availability of naturally occurring CSs, both excitatory and inhibitory. For example, what might the conditional stimuli be which, in the wild, would reliably accompany an intruder and thus serve as the learned releasers of the territorial male's aggressive display? Certainly, visual signals could play an important role. Moving shadows, approaching color patterns, disturbances of underwater vegetation, are all likely candidates. Additional signal support might be provided by olfactory stimuli, such as "skin slime," which fish are known to discriminate at a distance (Wrede, 1932), as well as stimulation of the lateral line organ, which is produced by relatively small changes in water flow. Finally, spatial cues, alone or in combination with visual, olfactory, and lateral line stimuli, could also provide a basis for predicting threatening encounters, as when an imperialistic neighbor repeatedly invades from a common border. Although the literature on conditioning in fish suggests a surfeit of potentially utilizable cues, these are merely suggestive. Studies that demonstrate the effectiveness of naturally occurring signals to elicit conditional aggressive behavior—or to serve as CSs—are clearly necessary.

In addition to the present, functional analysis, are two questions that involve the underlying mechanism of Pavlovian conditioning. The first involves the topographical difference between the unconditional response (UR) in training and the test confrontation UR, as well as the difference between CR and UR. The second involves the means by which a CR provides an aggressive advantage. These are discussed briefly below.

In both experiments, the CR was limited to the frontal display. The URs, on the other hand, contained additional elements of the display sequence, namely biting behavior during the 15-s US exposure in training and, in the test confrontation, both biting and tailbeating behaviors.

As was proposed earlier, the topographical difference between the training and test URs might be attributable to the difference in US duration. Tailbeating, the last component of the aggressive sequence, might not have had time to emerge during the 15-s training US. Thus, both URs contained the frontal display and biting components, but only the longer (i.e., test confrontation) encounter permitted the occurrence of tailbeating.

Why was the CR limited to only the first component of the aggressive display? Here, too, the brief duration of the CS might, in itself, have prevented the appearance of later components of the sequence; however, experiments by Holland (1977, 1980) and by Timberlake (1983; Timberlake & Grant, 1975) suggest that CR topography is influenced to a large degree by the nature of the CS. Holland has shown, for example, that for a given (food) US, the form of the CR is dependent not only on the CS-US interval (1980) but also on both the type and the localizability of the CS chosen (1977). In
rats, CRs evoked by an auditory CS differed substantially from CRs evoked by a visual CS. And, localizability of the light CS was an important variable in determining whether a particular behavior, rearing, occurred. Localizability of a visual CS for food is also known to be an important determinant of the CR in pigeons (Hearst & Jenkins, 1974).

Similar, though less systematic, observations have been made in Betta splendens, a relative of the blue gourami. A small localized red light CS elicited more of the aggressive sequence than did an undifferentiated red glow (Hollis, 1979; see Hollis & Overmier, 1982). The CS used in the present experiments is, in fact, highly similar to this second, more undifferentiated, stimulus.

In anabantids, charging is the initial response to territorial intrusion, whereas biting and tailbeating occur later in the sequence and demark an escalated contest. Thus, one might predict that biting and tailbeating never would be elicited by undifferentiated CSs of short duration. Such energy-consuming behavior should be invoked only as the last resort of a territory owner to repel a persistent rival.

An obvious question remains concerning the basis, or mechanism, of the Pavlovian aggressive advantage: How does the signaling arrangement enhance a males' defense? One possibility, of course, is that signaling enables males to be more aggressive than they would be were the confrontation not signaled. (For example, CS presentation might heighten aggressive motivation or lower the threshold for aggressive behavior.) Another possibility is that the conditional response is an early show of strength that produces faster capitulation in unprepared rivals. Differences in biting and tailbeating behavior between Pavlovian and control group males would occur in both cases so the present experiments cannot decide between these fight and fright strategies. Although this causal question is beyond the scope of the present experiments, a particularly rich area for research lies in determining how the Pavlovian conditioning mechanism achieves its preparatory goal.

A comparison of Experiments 1 and 2 suggests that whichever strategy the Pavlovian process may program, the aggression that results seems to be tailored carefully to the strength of an opponent. Thus other factors, besides Pavlovian conditioning, are probably operating here. The aggressive interaction itself, as well as the eventual outcome of that interaction, are most certainly multiply determined. Some of these determinants probably arise from the contest itself and a male's assessment of his opponent's strength. Other factors may be related to the stage of the reproductive cycle or to a male's past history of aggressive interactions. In the absence of knowing how the Pavlovian mechanism operates, it is impossible to determine specifically what is the influence of signaling and what is the influence of other, non-Pavlovian, factors. Therefore, the conditional response should probably be viewed, not as a guarantee of victory, but simply as a means by which territory owners are provided an initial, competitive, edge. For the male blue gourami, the best defense is a good offense, a strategy obtained through Pavlovian conditioning.

References


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Roediger Appointed Editor, 1985-1990

The Publications and Communications Board of the American Psychological Association announces the appointment of Henry L. Roediger III, Purdue University, as Editor of the *Journal of Experimental Psychology: Learning, Memory, and Cognition* for a 6-year term beginning in 1985. As of February 1, 1984, manuscripts should be directed to

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