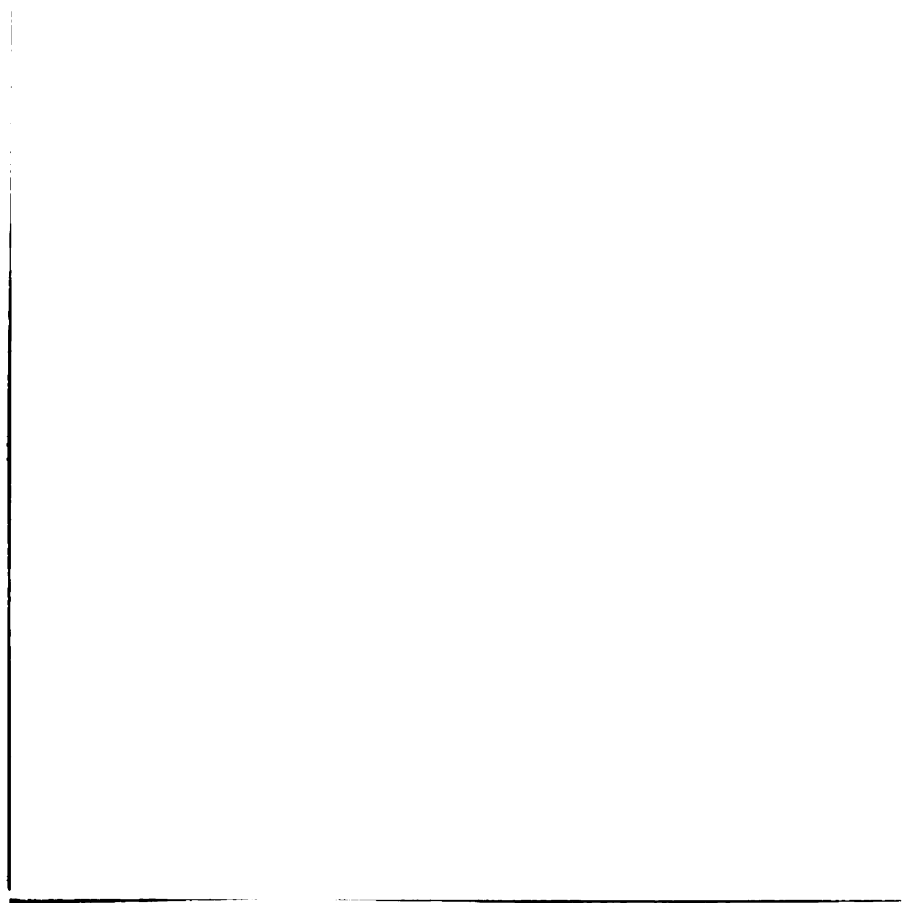








ABSTRACT

THE INTENSITY, HABITUATION, AND RETENTION
OF HABITUATION OF THE THREAT DISPLAY IN
MALE BETTA SPLENDENS (REGAN) AS A
FUNCTION OF ELICITING STIMULI

By

Michael H. Figler

The threat display of the male Siamese fighting fish (Betta splendens) is a highly integrated phenomenon, involving approach, extension of the gill covers (operculae) and brachioistegal membranes, erection of the medial fins, intense deepening of body color, orientation movements, and undulatory movements.

Many qualitatively different stimuli are capable of eliciting the complete threat display (e.g. live male Betta, mirror image, two dimensional cut-out). However, the relations between the initial eliciting strength of the threat stimulus and the degree of habituation, retention, and recovery of habituation have not been systematically investigated. These relations are important in an eliciting stimulus and competing response theory of habituation like that of Ratner (1970).

To investigate the above relations, each S in four independent groups was exposed to one of four different



Michael H. Figler

eliciting stimuli for two 40 minute sessions separated by a 24 hour rest period. The four threat elicitors were: a live unhabituated, highly responsive male Betta (Unhab. male); a mirror image (Mirror); a live habituated, relatively unresponsive male Betta (Hab. male); and a two dimensional cut-out of a male Betta in lateral display (Cut-out). During the observation periods, five different reliable components of the display were simultaneously recorded: air gulping frequency (AG), gill cover erection frequency (GF), gill cover erection duration (GD), fin erection frequency (FF), and fin erection duration (FD).

For all five dependent measures, the Unhab. male stimulus was the strongest elicitor followed by the Mirror, Hab. male and Cut-out stimuli, respectively. Only two of the dependent measures (GD, FD) showed a systematic decrement for all stimulus groups. With respect to both of these measures, initial eliciting stimulus strength was positively related to absolute response decrement, and proportion of recovery of habituation. Initial eliciting stimulus strength was inversely related to the proportion of decrement across sessions, and the proportion of retention of habituation over a 24 hour period. Four of the threat components (GF, GD, FF, FD) were highly positively related. AG was shown not to be an integral component of the display, itself. The data provided support for portions of an eliciting stimulus and competing response theory of habituation.

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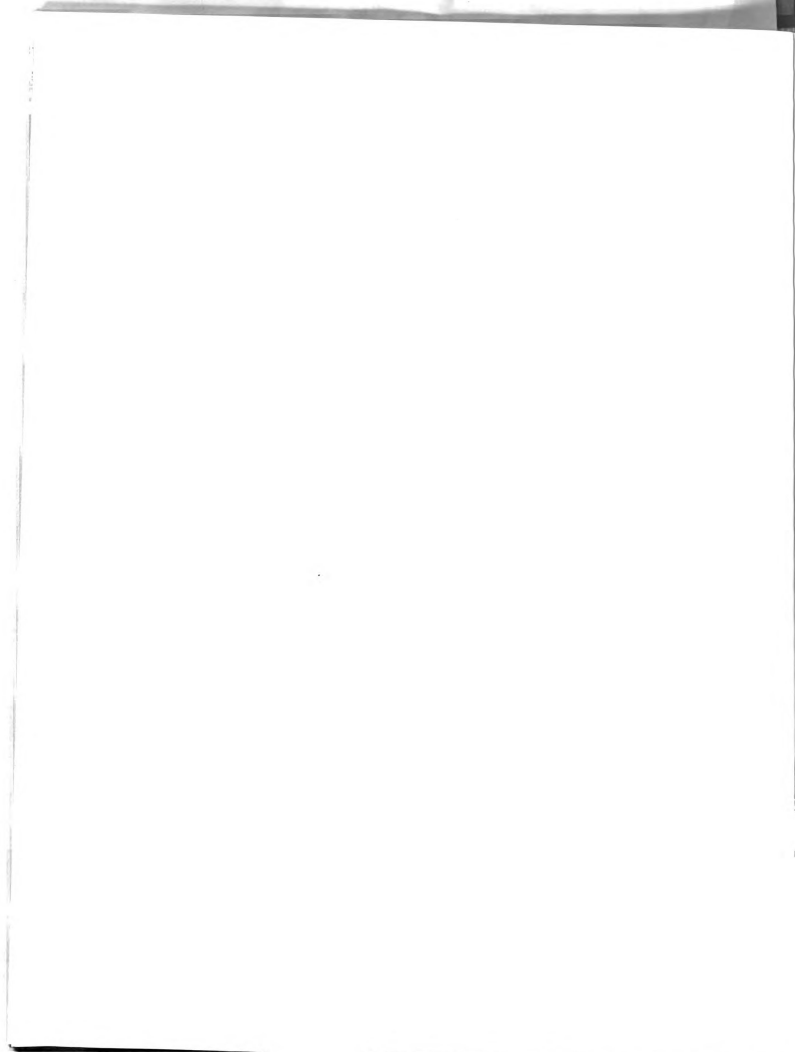
A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology

1970







To
Sonia,
my loving wife





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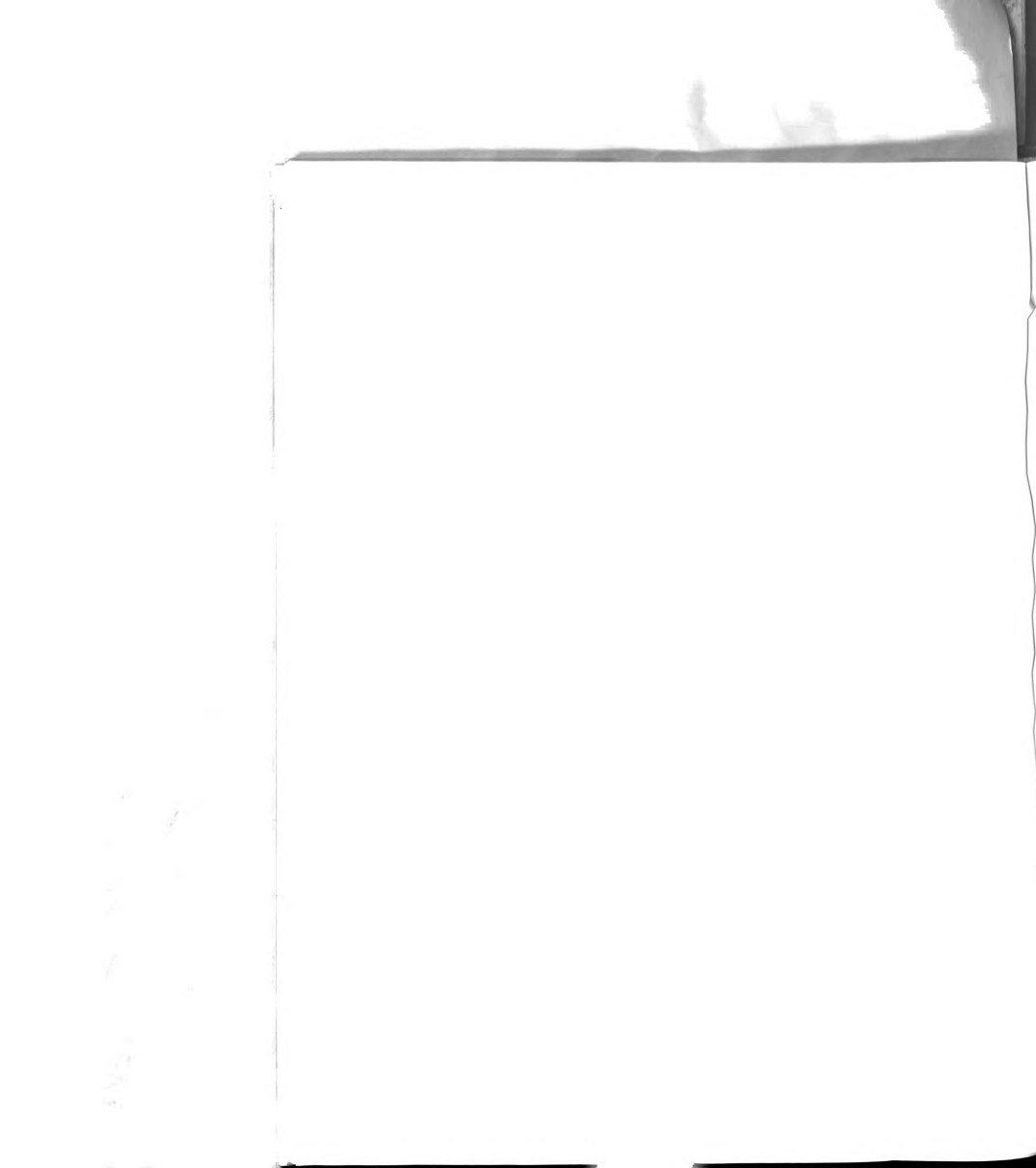
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INTRODUCTION

When a stimulus is repeatedly presented to an organism in a well-controlled situation, a decrement in the response to the stimulus usually occurs. This decrement is termed habituation. The process of habituation does not depend upon effector fatigue since a response which has been completely habituated to a particular stimulus may be immediately and fully elicited by a novel stimulus of equal intensity (Harris, 1943; Thompson and Spencer, 1966). It is also clear that habituation may be separated from sensory adaptation or fatigue since it persists even when long periods of rest intervene between presentations of the stimulus. In other words, there is retention of the response decrement which exceeds that which can be attributed solely to peripheral fatigue (Thompson and Spencer, 1966). It is generally accepted that the process of habituation is a form of learning and, therefore, must involve some sort of changes in the central nervous system and/or some type of long lasting changes (Harris, 1943; Thorpe, 1963; Thompson and Spencer, 1966; Denny and Ratner, 1970).

Habituation occurs for species in all phyla (Harris, 1943; Denny and Ratner, 1970), and is considered to have very important ecological significance for the individual



organism. If an organism ceases responding to a stimulus of little significance to the organism, considerable energy is conserved (Thorpe, 1963). Many different stimulus-response systems are subject to habituation, a characteristic which, combined with wide phylogenetic occurrence, provides the opportunity for a comparative analysis across both stimulus-response systems within a single animal, and cross-species comparisons. A further advantage of habituation as a comparative tool is that it is not restricted to any particular apparatus as are many other forms of behavioral change. A final advantage in investigating the process of habituation is that the behavioral characteristics of this process are parallel to the underlying neural correlates, as postulated by Thompson and Spencer (1966).

Although there are many parametric characteristics involved in habituation (Thompson and Spencer, 1966) and ways of measuring the event (Askew, 1969), the present study focuses on the influence of the initial eliciting stimulus strength on the consequent habituation and retention of habituation of the response. The organism which is to be used is the Siamese fighting fish, Betta splendens (Regan) and the behavior looked at is its species specific threat display. In the succeeding sections of the introduction, a review of the literature on stimulus intensity and its role in habituation will be presented, followed by a description of Betta splendens and some of the previous



work done with that species. Finally, some of the past research on habituation of stimulus-response systems in fish is presented, ending with the statement of the problem for the present study.

Stimulus Intensity

This section summarizes some of the past research done on the effect of stimulus intensity on response dimensions such as initial response level, absolute amount of habituation, degree of habituation, and retention of habituation. Relevant data using fish as subjects is reserved for a later section.

Miller and Murray (1966) reported on the stimulus conditions necessary to elicit an "immobility" response (pause in ongoing drinking behavior) in guinea pigs. Independent groups of animals were exposed to either a 47 or 77 db. tone. It was found that the 77 db. group had a significantly higher initial response level and a greater absolute amount of decrement (initial minus terminal response level) when compared to the 47 db. group. However, the rate of habituation to a zero response level was not significantly different for the two groups.

In a study by Martin and Melvin (1964), the habituation of the freezing response in bobwhite quail was investigated using either a live red-tailed hawk or a life-sized silhouette as the eliciting stimulus. One stimulus



passed over S twice a day for five days. Then the other stimulus was used in a similar manner for six more days. Half of the Ss saw the silhouette first and the other half saw the live stimulus first. The results revealed a much higher duration of the freezing response when Ss were exposed to the live stimulus. There was a larger absolute decrement in response for the "live" group as compared to the "silhouette" group. This particular measure of habituation, however, is complicated by the differences in the initial elicitation values of the two stimuli (i.e. the "live" group had a much greater potential decrement). Some measure taking into consideration the initial differences in response levels would have been more meaningful (proportion or percentage of decrement).

Bobwhite quail were used in another study of habituation of the freezing response, this time a response suppression technique was used (Melvin and Cloar, 1969). The Ss were first trained to key peck on a variable interval reinforcement schedule. When a stable response rate had been reached, the Ss were exposed to either a live Swainson's hawk or a live silver king pigeon, with the stimulus being held behind a glass partition. Each S was exposed to one stimulus twice daily for four days, and then shifted to twice daily exposures of the other stimulus for three more days. Using the duration of freezing and duration of suppression of key pecking as the dependent



variables, it was found that the live hawk stimulus elicited an initial freezing response of much longer duration and thus suppressed key pecking longer. In terms of the habituation of the freezing response a greater absolute amount of decrement was associated with the hawk stimulus. An interesting auxiliary finding was the lack of response recovery (retention of habituation) to the presentation of the hawk, 18 days after the last experimental exposure.

Kuenzer (1958) investigated the habituation of the withdrawal response in earthworms to different intensities of electric shock. He found that a greater initial response was associated with the stronger stimuli. Also, the stronger the stimulus intensity, the greater the absolute amount of habituation, and the slower the rate of decrement to a zero asymptotic response level. In addition, this study seems to be the only one that attempted to look at the retention of habituation. He found that after a 24 hour rest period, recovery was complete for the weaker stimuli but recovery for the strong stimulation was only about 75 percent.

Askew (1969) in a systematic study of the "head-shake" response of male rats (rapid rotation of the head about the front-to-rear axis) to various intensities of air that was blasted into the ear, provided some clear data on the influence of stimulus intensity on the habituation process. He found that the higher the intensity of



the stimulus (air pressure), the greater the initial headshake response level, the greater the absolute amount of habituation, the higher the asymptotic terminal response level, and the slower the rate of decrement. Stimulus intensity did not have a measurable effect upon retention of habituation after a 30 minute rest interval between sessions.

Dunlop, Webster, and Rodger (1966), in a neurological study of habituation, examined amplitude changes in evoked potentials to auditory stimuli at the cochlear nucleus, inferior colliculus, and medial geniculate body of unanesthetized cats. At all three locations initial and terminal response levels were a direct function of stimulus intensity. A significant decrement in response resulted for all stimulus intensities. In the cochlear nucleus and inferior colliculus no significant relation was found between stimulus intensity and amount and rate of habituation. At the medial geniculate, however, the stronger auditory stimuli produced a greater absolute amount of habituation although there did not appear to be any difference in the time taken for the response to reach asymptote.

In a study measuring some components of the orienting reflex, Uno and Grings (1965) used five intensities of an auditory stimulus to investigate the effects of stimulus intensity on habituation of skin conductance, skin potential, heart rate, digital blood volume and digital pulse



amplitude in human subjects. A within-subjects design was used, with each intensity value being given five times during the session. All of the dependent variables showed a different initial response level as a function of the different intensities: the stronger the stimulus the greater the response. There was an indication of a ceiling effect at the higher intensities, however. Although response magnitude generally increased with stimulus intensity and decreased with repetition, the relation between stimulus intensity and response habituation was different for the various dependent measures. Some measures showed no intensity by habituation interactions, while for those that did, the relations varied. One general finding was that the higher intensity stimuli were associated with higher terminal response levels. However, there were exceptions to this relationship, too.

From the above survey of studies on the effects of stimulus intensity (i.e. "adequacy" of the stimulus on habituation, it appears that the simple rules of Thompson and Spencer (1966) meet with many exceptions. It is quite clear that the initial response level is almost always greater for the higher stimulus intensities. Also, for lower asymptotic response levels above zero, higher intensity stimuli are usually associated with higher terminal asymptotes. As far as the absolute amount of habituation is concerned, one usually finds a positive relation with

stimulus intensity, although instances of negative or no relation can be found in the current literature. Few, if any, systematic studies of the relations between stimulus intensity and the degree of retention and/or recovery of habituation have been attempted. Overall, it seems that different stimulus-response systems may have characteristic stimulus intensity-decrement relationships. More research with different species and stimulus-response systems is obviously needed.

Experimental Animal

The Siamese fighting fish, Betta splendens (Regan), is a member of the order Labyrinthici, family anabantidae. Each individual of this family possesses a labyrinth which consists of a pair of vascularized cavities located in the sides of the head above the gills. The fish supplements breathing through its gills, by gulping air from the water surface into these cavities (Smith, 1937; Forselius, 1957). Since Bettas normally inhabit shallow, stagnant ponds and canals with low oxygen content, the labyrinth serves as an auxiliary organ for obtaining sufficient oxygen. The fish makes frequent excursions to the water surface, expels a bubble of vitiated air, takes in a new supply, and rapidly retreats toward the bottom. The bubble blowing behavior is particularly well evolved in the fish, since the species are bubble nest builders. Normally, this facet of



reproductive behavior is performed by the male, although it has been reported that the female will also perform these functions (Forselius, 1957). After an elaborate courting sequence, the male and female squeeze each other under the bubble nest which has been constructed by the male. As the female drops her eggs and the male fertilizes them, he picks them up and blows them into the nest. At this point, the female is usually driven away from the nest area, since the male almost always cares for the young (see Forselius, 1957, for a complete elucidation of the reproductive cycle). In the limited space of the aquarium, the female may even be killed, if allowed to remain for too long a time (Gordon and Axelrod, 1968).

During the incubation period (30 to 40 hours), the male continually repairs the nest by replacing burst bubbles. This replacement has two major functions: to increase the solidity of the mass of bubbles and to raise the eggs in the nest slightly closer to the surface where oxygen is more plentiful (Forselius, 1957). After hatching, the male can be seen incessantly retrieving and replacing any young that may have fallen out of the nest. After the free swimming stage is reached (three or four days), the nest is abandoned.

Threat and Attack Behavior

The characteristic that makes this species so well known, and an ideal preparation for the present investigation,

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is its threat display and attack behavior (which combined will be termed fighting behavior). A conspecific male (Lissman, 1932; Smith, 1937; Adler and Hogan, 1963), a mirror-image (Baenninger, 1966; Simpson, 1968), a model of a male in display (Lissman, 1932; Thompson and Sturm, 1963), a two-dimensional cut-out of a male (Hess, 1952), or a live female Betta (Simpson, 1968) will all elicit the fighting sequence in a male Betta. Stimulus configuration is an important factor in the organization, frequency, and intensity of these behaviors. The behavioral components of the threat display, itself, include approach, extension of the gill covers (operculae) and brachistegal membranes, erection of the medial fins, intense deepening of body and fin color, orientation movements, and undulatory movements. Attack behavior includes biting and nipping, jaw locking, pectoral fin beating, pelvic fin flickering, tail beating, and tail flashing (Simpson, 1968). Although most research has concerned itself with the fighting behavior of males, Braddock and Braddock (1955) have reported that aggressive behavior between females is common and very similar to that of males.

Although fights between males have been reported to last for as long as 24 hours, they usually last less than an hour (Smith, 1937). Contrary to popular belief, Bettas rarely if ever fight to the death under natural circumstances. Sooner or later one contestant discontinues

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the fight and swims away. The loser's color becomes pale as the retreat takes place, and the victor usually manages a final few nips at him (Forselius, 1957). In the process of fighting, the drape-like fins of both victor and vanquished may be seriously shredded and scales lost. However, under proper conditions the damaged fins and lost scales will regenerate in about 48 hours (Gordon and Axelrod, 1968).

As one can see, the richness of the fighting repertoire of Betta splendens provides an excellent preparation for the investigation of aggressive behavior. Many researchers have already capitalized upon the opportunity. Thompson (1963) reported that male Bettas will learn an operant swimming response if reinforced by the visual image of another male of the species. He found that the three types of visual stimuli he used (mirror-image, moving male model, stationary model) were of differential reinforcing value. The mirror image was the strongest reinforcer, in terms of acquisition rate, number of responses, and resistance to extinction. Compared on the same measures, the moving model was superior to the stationary model. In a similar study of fighting cocks, mirror-image reinforcement maintained a lower key-pecking response output, than another live rooster presented behind a window (Thompson, 1964). Another variable important in the operant behavior of the male Betta is the color of the reinforcing stimulus.

Operant response rate varies as a function of the color of the model with respect to the color of the subject, the response rate becoming higher as their colors become more dissimilar (Thompson and Sturm, 1965b; Thompson, 1966). Using additional controls in an attempt to replicate an earlier study of Thompson (1963), Goldstein (1967) taught male Bettas to swim through a ring in order to have an opportunity to display to their mirror-images. Hogan (1967) obtained similar results for the operant swimming response, and also demonstrated that males learn to swim through a runway when a presentation of the mirror was made contingent upon the correct response. A comparison in the runway of performance for mirror display and for food revealed that food reinforcement produced significantly better performance.

In an experiment by Thompson and Sturm (1965a), unconditioned threat display behavior elicited by the mirror image of a male Betta was brought under control of a previously, ineffective stimulus by classical conditioning. Relative rates of acquisition of four components of the display were compared. Fin erection and undulating movements were acquired most rapidly, while gill cover erection and frontal approach were acquired most slowly. A discriminative conditioning procedure, using two different colors of light as the CS, revealed that the responses were not artifacts of sensitization. Using electric shock as

the CS and a mirror image as the UCS, Adler and Hogan (1963) were successful in conditioning the gill cover (operculae) erection. In further experimentation, the same investigators found that gill cover erection in the presence of a mirror image or another live male in an outside compartment could be suppressed by an electric shock contingent upon the elicitation of the response. Mild punishment of an operant swimming response reinforced by a mirror presentation has been shown to temporarily increase the rate of responding and the vigor of the consequent threat display in male Bettas (Melvin and Anson, 1969). This effect may be explained within the pain-elicited aggression paradigm described by Ulrich (1966) for a wide variety of species.

Many other methods have been utilized for increasing or decreasing the organization, frequency, and intensity of the components of the fighting sequence in Betta splendens. Various drugs alter the aggressive patterns in this species. Evans et al. (1956) reported changes in the vegetative, motor, and behavioral characteristics of Bettas following the administration of LSD-25, eight other ergot derivatives, mescaline, and demerol. Although LSD-25 had the most numerous effects, the other drugs had distinct effects on Betta's behavior. In a later study focusing on the change of fighting behavior following LSD-25 administration, Evans et al. (1958) reported a marked increase in the

aggressiveness of the subjects. Whether the drug was given to all the individuals in an established social hierarchy or only to one of the lower ranking members of the group, the results indicated that narcotized female Bettas were more aggressive than controls. After LSD-25 treatment, low ranking individuals rose in the social hierarchy because of their increased aggressiveness. These reversals in social dominance seemed to be relatively long lasting. McDonald and Heimstra (1964) were not able to replicate this data since they could not even get the Bettas to form clearly defined dominance hierarchies. In nearly all instances, the fish that were placed in groups fought to the death before any stable hierarchies developed. The same investigators did succeed with another species (green sunfish). However, it was found that in four subject hierarchies and pairs of fish, LSD-25 increased the frequency of attack behavior by the submissive fish which were given the treatment. In both hierarchical formations and pairs, the drug effects were temporary and no changes in the dominance hierarchies were noticed. Rather, the overall aggressiveness of the four member groups and the pairs increased.

Marrone (1966) found spontaneous performance of gill cover erection, fin erection, and increased coloration in isolated male Bettas when they were placed in solutions containing norepinephrine bitartrate. Subjects placed in an epinephrine bitartrate solution resembled controls



(plain water) except for color change; the epinephrine group bleached during observation periods. In another study concerned with the effect of externally administered amines on threat behavior in the male Betta, Baenninger (1968) studied mirror elicited threat behavior instead of in vacuo responding. Epinephrine and norepinephrine suppressed display behavior, compared with controls in sodium chloride solution or plain water. Since these two investigators were interested in different conditions of display elicitation, it is difficult to interpret their contradictory data. In addition to the above mentioned means of manipulating fighting behavior in the Betta, response changes occur with repeated presentation of the eliciting stimulus. In other words, the components of display are subject to habituation, as will be discussed in the following section.

Habituation in Fish

Until quite recently, little systematic experimentation had been done on habituation in fish (Thorpe, 1963). Within the last few years, however, many workers have demonstrated habituation involving various stimulus-response systems in fish.

Rodgers et al. (1963) found that the "tail-flip" response in goldfish, Carassius auratus, habituated to pressure waves induced by repeated tapping on the side of

the aquarium. A decrement in response also occurred with the repeated passing of a shadow over the top of the test aquarium. Both stimuli presented together produced a higher rate of response and slower habituation than either one alone. Habituation of fear responses (freezing; "jerk response") in guppies, Lebistes reticulatus, has been shown also utilizing an overhead moving shadow as the eliciting stimulus (Russell, 1967). Fear responses decreased in number and intensity during a series of 40 stimulus presentations. Forty-eight hours after testing, however, recovery was practically complete for both dependent variables.

In an investigation of the habituation of aggressive behavior in male three-spined sticklebacks Gasterosteus aculeatus L., Van Den Assem and Van Der Molen (1969) used a novel method for measuring the effects of habituation. Stickleback males which were visually isolated gave more or less constant aggressive responses toward a test stimulus (a live male stickleback in a plastic tube) when it was presented once or twice daily during a four day period. The response to the test stimulus waned for a group of subjects that had a continuous view of a male in a neighboring territory behind a glass partition. Waning also occurred for a group having only an intermittent view of a rival neighbor. Even if the glass partition were removed and the two neighbors allowed to interact freely,

habituation to the test stimulus still occurred. Response decrements were also apparent when a rival male was used as the test stimulus. Having a goldfish in the adjacent compartment, however, did not lead to waning aggressive behavior toward the standard test stimulus. In a final phase of the study, no recovery of the response decrement was evident within a period of five days.

Peeke (1969), also using male sticklebacks as subjects, studied fighting behaviors (frequency of orientation, charges, and bites) directed toward two eliciting stimuli of differing "adequacy." The two stimuli were a moving wooden replica of a male stickleback and a live, nuptially colored male in a clear plastic tube. Each group of subjects was given 15 minute daily trials over a period of ten days. It was found that the initial level of aggressive responding was higher for the "live male" group than for the group exposed to the wooden model. Although the responses habituated in the presence of either eliciting stimulus, the absolute amount of habituation was greater for the live male stimulus group. At the terminal response level, the differences between the two groups disappeared. It should be noted, however, that the absolute amount of recovery of responsiveness between stimulus presentations was greater for the live male group (the stronger elicitor).

In another investigation of the same species, Peeke et al. (1969) focused their attention on the differential

eliciting value of five moving wooden models of a male stickleback. The models were similar to each other except for different amounts of red color on the ventral anterior surface. Red in that anatomical locus is an important component of the eliciting stimulus for aggressive behavior in the stickleback. Each of the models was presented to each S for two minutes each day for 12 successive days. Using the frequency of biting as the measure of aggressive behavior, they found that the initial level of response did not differ for the different models. Pooling the data across models, revealed clear evidence for habituation over the 12 day period.

With respect to work done specifically on habituation in Betta splendens, only a few studies have appeared in available literature. Baenninger (1966) reported a waning tendency to approach a mirror or another live male Betta which had habituated to its own mirror image. Each S spent 32 consecutive hours in the test tank in two conditions. In the control condition, neither the mirror nor the stimulus fish was present at the ends of the aquarium. Over the 32 hour session, the fish in the experimental Condition showed a definite trend toward spending more time in the middle of the tank, out of sight of both stimuli. The changing preference could not be considered avoidance of the ends of the apparatus, since time in the center of the tank in the experimental condition was never significantly

greater than in the control condition. Although the two stimuli, at opposite ends of the test tank, elicited threat displays, all subjects spent more time viewing their own reflections than viewing the live, relatively unresponsive stimulus fish. The dependent variable in this study, however, was the time spent in particular portions of the tank, and not changes in the various components of the display itself. Clayton and Hinde (1968) exposed male Bettas to a mirror for ten days. The mirror was then removed for recovery periods of 15 minutes, 6 hours, 24 hours, 48 hours, and 4 days. Each S was given all recovery period lengths, which were counterbalanced across subjects. At the end of each recovery period, the mirror was replaced for 48 hours and the display observed for the first 26 minutes. Various components of the display habituated over the course of time, although the process was an extremely slow one. Gill cover erection frequency (GCEF) had not disappeared completely, even after the first 10 days with the mirror. Recovery of this particular response after original waning was slow, with some long term effects being evident. There was a positive relation between the length of the recovery period and the amount of recovery for the response (GCEF). A major difficulty with the study was that the data for three of the eight Ss were thrown out and the data that were presented were usually for one S used as "representative" of the five other Ss.

Both of these habituation studies had methodological problems. Baenninger used a very small sample size ($N = 5$), but more serious is the fact that water temperature was kept at 22.2°C . Hess (1952) and Lissmann (1932) have found that aggressive behavior in the Betta is positively related to water temperature, 22.2°C . being a low temperature for this species. Baenninger's results may have been confounded by the fact that the waning of the approach was partially due to the low temperature. Clayton and Hinde also had problems with sample size as discussed above, and also kept water temperature quite low, with a rather wide range ($24-27^{\circ}\text{C}$.) of variation.

Statement of the Problem

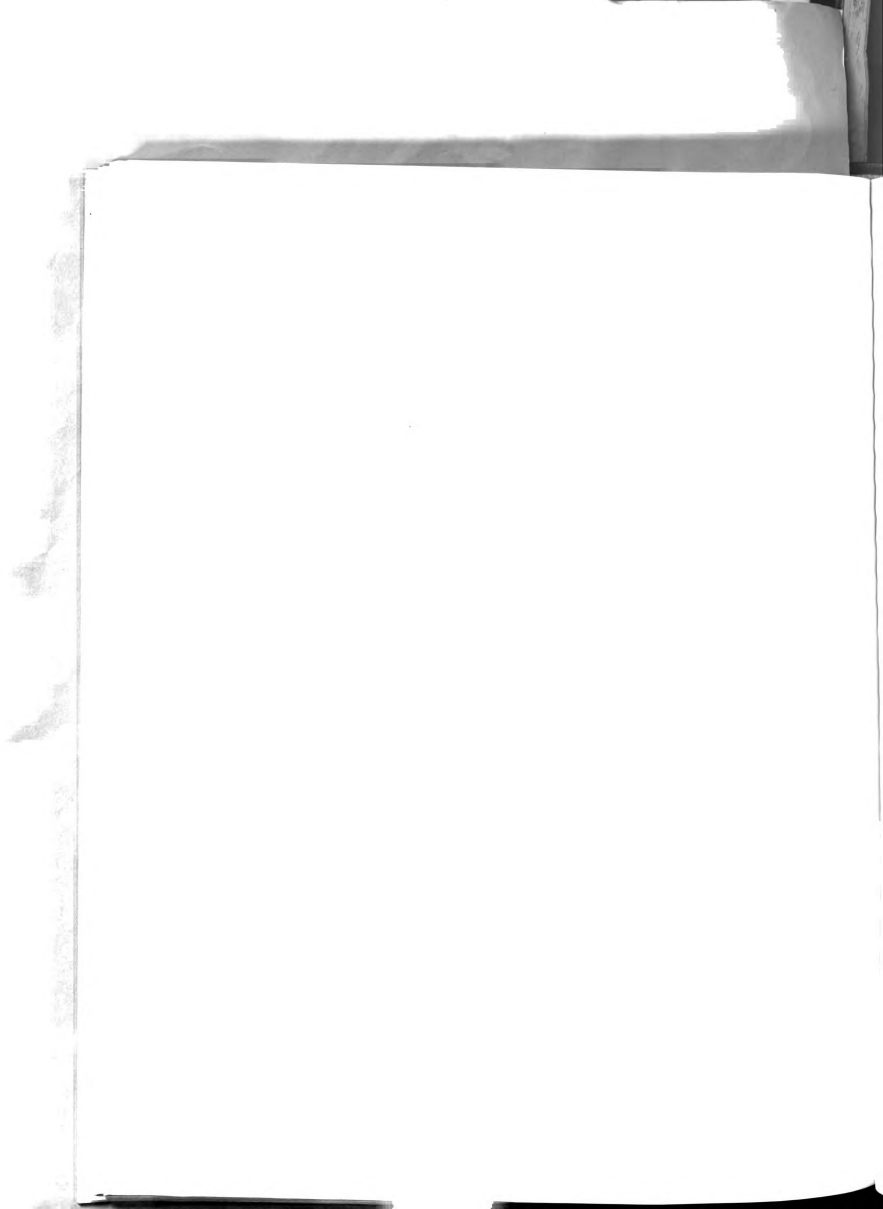
It seems apparent that qualitatively different stimuli (e.g. a live male stimulus, mirror-image, model, or two dimensional cut-out) elicit the complete threat display in male Betta splendens, but to varying degrees. No previous investigation has looked at the comparative eliciting values of a number of different stimuli in terms of the intensity of various components of the threat display. Also, it is evident that the display itself is subject to habituation, although a zero level is rarely reached. What interests the present investigator is trying to ascertain whether a relation exists between the strength of different eliciting stimuli and the intensity of various

components of the threat display and their consequent amount and proportion of habituation. Also of interest is whether the retention and recovery of habituation are affected by eliciting stimulus strength.

Since there is no satisfactory way of ranking qualitatively different stimuli as to their "adequacy", other than looking at the initial response level, the initial response level is used as the measure of stimulus adequacy in the present study. However, there is strong evidence for expecting live stimuli to elicit higher initial response levels than models (Tinbergen, 1951; Martin and Melvin, 1964; Peeke, 1969).

This study also seems to provide an opportunity to evaluate portions of the elicitation and interference theory of habituation presented by Ratner (1970). According to this position, the degree of habituation and degree of retention of habituation is inversely related to the strength of the association between the original eliciting stimulus and its response (e.g. eliciting value of the stimulus). A direct extension of this theory is that the degree of recovery of habituation after a rest period is directly related to the eliciting value of the stimulus. In other words, stronger elicitors are assumed to be associated with a lesser degree of habituation and retention of habituation, and therefore a greater degree of recovery of habituation.

A final purpose of the present study is to investigate the relations between the various measures of threat behavior (e.g. medial fin erection, gill cover erection) in male Betta splendens.



METHOD

Subjects

Fifty adult male Betta splendens were purchased from a commercial breeder and were brought to the laboratory in separate unmarked, sealed containers. The fish were unpacked in random order and placed into individual jars which were numbered from one to fifty. The first forty fish served as experimental Ss, while the remaining ten fish served as extra subjects in case of deaths of any of the forty subjects. Since all fish were unpacked blindly, no bias was present in choosing the first forty subjects.

There was some variability among the Ss with regard to color, but this is common even within the same brood. The sizes of the animals used in the experiment were very similar, ranging between 3.5 and 4.0 cm. from the tip of the snout to the base of the caudal fin. All fish were maintained in the laboratory for one month prior to testing.

The fish were maintained and tested in a special research laboratory located on the third floor of the Natural Science building at Michigan State University. This room contained steam heating apparatus plus an automatic air conditioner which kept the room temperature relatively uniform (27-29°C). A fan kept the air in continuous

circulation. The three windows, facing north, were covered with venetian blinds in order to reduce the amount of natural light entering the laboratory which was lighted with sixteen 40-watt fluorescent bulbs. During the period of the present experiment an automatically controlled timer provided 12 hours of light (8:00 a.m.-8:00 p.m.), and 12 hours of darkness. The continuous operation of the filtering equipment in the laboratory provided a natural "white noise" effect which tended to mask most extraneous auditory stimuli.

The experimental subjects and stimulus fish were housed on the top shelf along the south wall of the room. The shelf, itself, measured 302.26 cm. (length) by 81.28 cm. (depth). The fish were individually maintained in 4.23 liter grayish plastic salad dressing jars which were pre-sterilized with potassium permanganate crystals. Each transparent jar was sanded on the outside with a fine sand paper, making it translucent. The jars were placed about 2.54 cm. apart in rows of four jars per row. The subjects were in complete visual isolation, since one could neither see out of his home jar nor view his own reflections. Each jar was filled to about two-thirds capacity with conditioned tap water, having been passed through a commercial charcoal filtering apparatus. Upon arrival in the laboratory, each fish was placed into one of these jars which was treated with an auromycin solution to prevent bacterial invasion.

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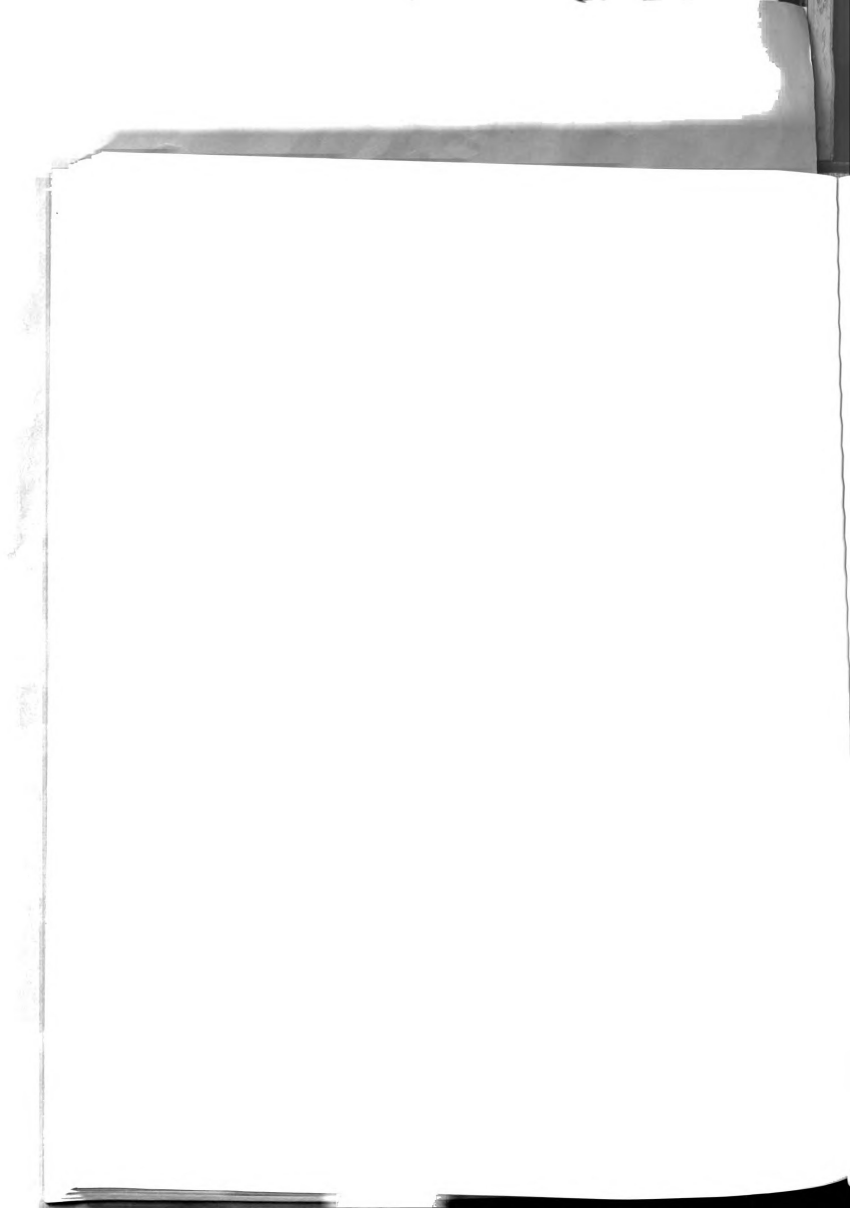
A 12.5 cm. square piece of heavy gauge galvanized steel was placed on the top of each jar to retard evaporation and protect the environment from dust. All waste products and uneaten food were siphoned out weekly, and the jars filled to two-thirds capacity again.

The fish were fed daily with fresh brine shrimp which were cultured in an adjacent room in the laboratory. The brine shrimp were fed to the fish via a medicine dropper, each getting about 0.5 c.c. of highly concentrated food.

Apparatus

The study was conducted in a 106.68 cm. long by 76.2 cm. deep cubicle located on the right side of the bottom shelf immediately below the shelf upon which the jars were placed. The height of the experimental cubicle was 54.61 cm. A 1.27 cm. thick sheet of flat gray enameled plywood provided the base of the cubicle.

The fish were tested in a plexiglas aquarium surrounded by a rectangular wooden amphitheatre which was also painted flat gray. The test aquarium had outside measurements of 24.13 cm. (length) by 12.7 cm. (width) by 20.96 cm. (height) (See Figure 1). This clear .64 cm. thick plexiglas test aquarium was partitioned off into two compartments whose inside measurements were 19.69 cm. long and 2.54 cm. long. The larger area served as the subject compartment while the smaller area enclosed the various



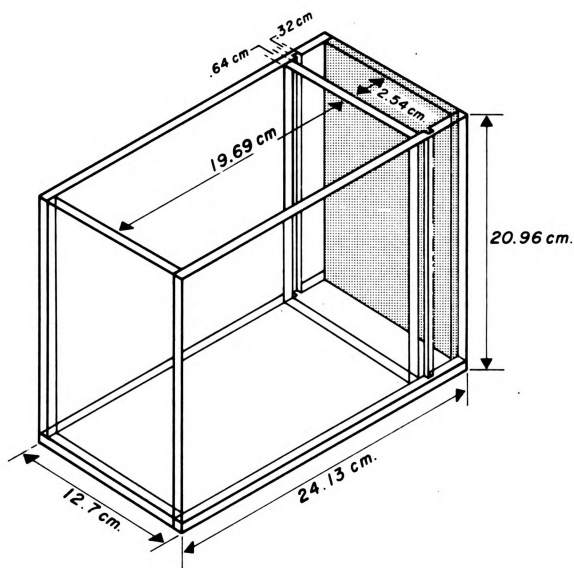
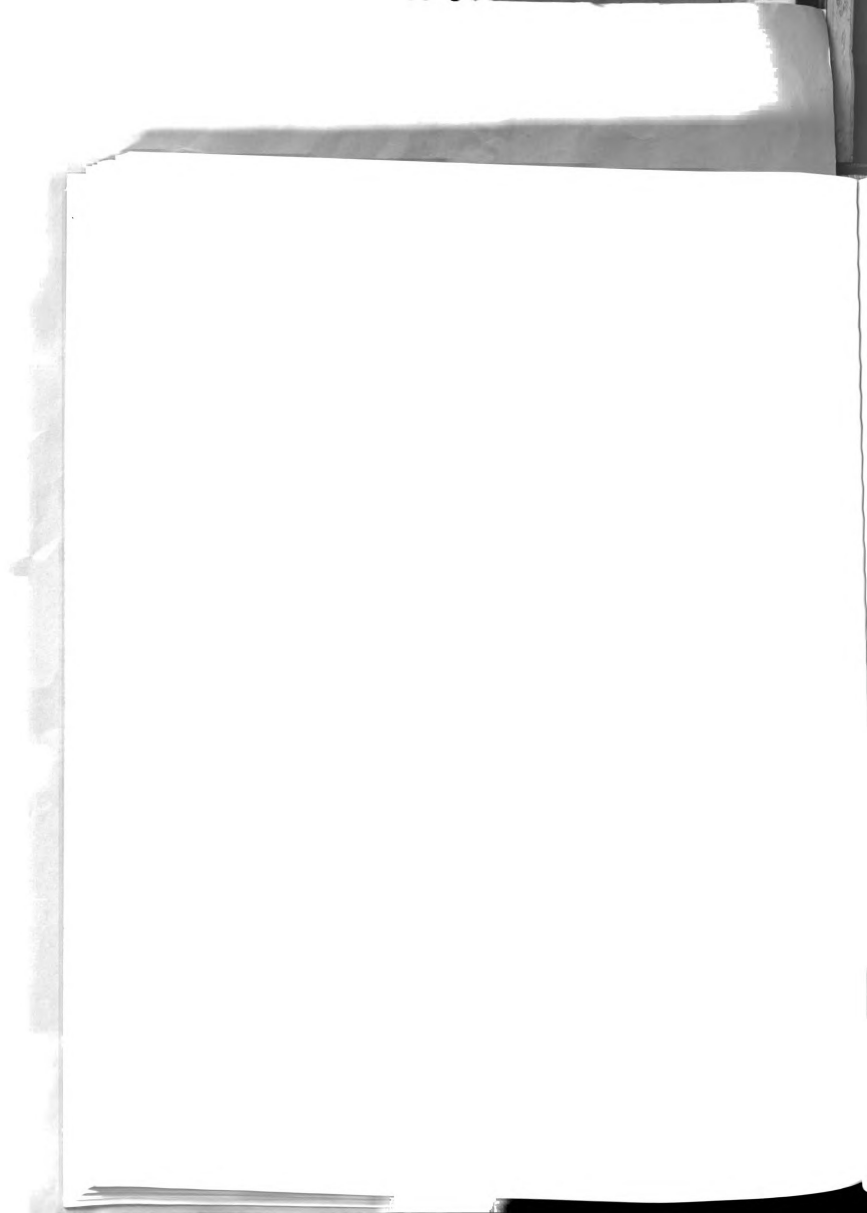


Figure 1. Test aquarium.

stimuli used in the experiment. The partition also was constructed of .64 cm. thick, clear plexiglas. All seams were first joined together with a plastic cement and then made water tight with Dow "silastic" cement. In other words, only visual cues were passed between the two compartments. A vertical notch .32 cm. wide ran down each side of the stimulus compartment. These notches were machined .32 cm. behind the plexiglas partition and accommodated two of the stimulus conditions in the experiment. A 17.78 cm. long by 12.07 cm. wide by .32 cm. thick one way mirror could be slipped into the notches thereby making the far wall into a reflecting mirror. The other stimulus condition which utilized these notches was a piece of translucent plexiglas which had a cut-out of a male Betta secured to it. The dimensions of this plexiglas sheet were identical to that of the mirror. The bottom and three sides of the aquarium were sanded on the inside to reduce reflections and ambient stimuli.

The test aquarium was placed within the four sided viewing amphitheatre, with the long transparent side of the aquarium facing the experimenter. The outside length of the enclosure was 36.83 cm., the width was 30.48 cm., and the height was 23.5 cm. There was no top or bottom and the entire enclosure was painted in a flat gray enamel to minimize reflections. The test aquarium was viewed through a 7.62 cm. long by 5.08 cm. high slot cut into the long



side of the enclosure nearest the experimenter. A piece of blue transparent plastic sheeting was secured over the viewing slot, thereby lessening the opportunity of the fish seeing the experimenter. Illumination was provided by a gooseneck lamp with a white 25-watt soft glow bulb. During testing, the illumination at the top of the test aquarium (within the viewing amphitheatre) was approximately 160 ftc. Outside the amphitheatre at the viewing slot, the illumination was only about 6 ftc. The combination of the lighting differential between the inside and outside of the amphitheatre, and the blue plastic over the viewing slot precluded the chance of a subject seeing the experimenter, while the subject could still be easily observed.

Water for the test aquarium was changed for each test session. It was supplied from a tank immediately to the left of the experimental cubicle. This supply source had a capacity of 42.3 liters and was filled with conditioned tap water and was equipped with a thermometer. Throughout the entire experiment, water temperature was maintained at 25.6-27.2°C.

The recording apparatus consisted of a model 92 Rustrak four channel event recorder which pulled 300 inches of recorder paper across the pens every hour. Each pen was exclusively activated by an individual standard doorbell button embedded in a wooden holder. Each of the buttons was also wired to the 24 VDC power source which

activated the recording pens. Both the event recorder and the power source were connected to a model 171 Universal timer which automatically controlled the duration and termination of the experimental sessions.

Procedure

The forty experimental fish were randomly assigned to one of the four independent stimulus groups. There were ten subjects assigned to each of the following groups:

A. Each S in group A was exposed to a standard reflecting one way mirror which was described in the previous section.

B. Each S in group B was exposed to a live, 3.7 cm. long red male Betta which was in visual isolation for one month prior to testing.

C. Each S in group C was exposed to a live male Betta which was as similar as possible to stimulus B except that it was continuously exposed to other live males for approximately six weeks prior to testing. In all other visible aspects, it was almost identical to stimulus B.

D. For each S in group D the elicitor was a two dimensional cut-out of a 3.7 cm. red male Betta which was secured to a piece of gray translucent plexiglas having the exact dimensions as the mirror (stimulus A). The cut-out was about the same size as the other stimuli and subjects.

The figure, itself, was a lateral view of a male in full display (medial fins and gill covers erected). The entire stimulus configuration slid into the notches in the test aquarium in exactly the same way as did the mirror.

The unhabituated stimulus males (three different ones were used) were kept in translucent jars as were the subjects. Whenever this stimulus group was used, one of the three group B stimulus males was randomly selected. When the next session of this stimulus condition arose, the stimulus fish for it was randomly selected from the two unused stimulus fish. For succeeding sessions the stimulus male which had not been used for the longest period of time was chosen. For a particular subject, the same stimulus fish was utilized for two 40 minute sessions, spaced 24 hours apart. Immediately upon the end of a session, the stimulus fish was put back into isolation.

Group C habituated stimulus males (three different ones were used) were housed separately in transparent battery jars that measured 13.7 cm. (length) by 7.1 cm. (width) by 14.5 cm. (height). Other than the 15 minutes it took to transport them to the laboratory, they had been maintained for over a month within full view of at least one other live male Betta. These stimulus males were chosen for a particular session in exactly the same manner as the unhabituated (Group B) stimulus males, and were as closely matched as possible to each other and the unhabituated

stimulus males in size, length, and color. It should be noted that the habituated stimulus males were always in full view of one another, since the battery jars were adjacent to one another with the long sides touching.

No control group utilizing an empty stimulus compartment was used, since in vacuo threat displays were non-existent in pilot work and in available literature. Other than the choice of the eliciting stimulus, the experimental procedure was identical for every subject in the experiment.

Each subject was placed in the test aquarium which was filled to 15.24 cm. in depth and covered by a .64 cm. translucent plexiglas sheet. The S was allowed to habituate to the surroundings for 10 minutes while an opaque sheet of gray plastic separated him from the stimulus which also had been placed in the other compartment. Observations were made during this period to detect any in vacuo displaying. The gooseneck lamp remained on throughout this acclimation period and the duration of the session. At the end of the acclimation period and when S was facing the partition, the experimenter lifted the opaque screen, revealing the stimulus compartment to the fish. At the same time, the timer was activated which automatically started the event recorder. Each session lasted 40 minutes with observations recorded for ten minute periods during the first, middle, and last ten minutes of the sessions. At

the end of the session, the recording equipment was automatically turned off by the timing circuit and the subject was netted and put back into his home jar. Netting the fish was always accomplished in less than two seconds. Then the entire aquarium was drained and flushed out with conditioned water. Water from the adjacent holding tank was then siphoned into the stimulus tank to a depth of 15.24 cm. For conditions involving live stimuli, the stimulus compartment was filled to an identical depth. No water was present in the stimulus compartment for the mirror or the cut-out conditions. Water temperature was recorded before and after each session. Each fish was given two 40 minute sessions spaced by 24 hours. Testing took place from October 6 to October 30, 1969. Sessions were conducted Monday through Saturday at 8:30-9:20 a.m., 9:50-10:30 a.m., 11:00-11:40 a.m., and 12:10-12:50 p.m. The order of subject testing was randomized across groups prior to the experiment.

As described above, 3 ten minute recordings, separated by 5 minutes were taken during each of the two sessions. Each S therefore was observed for 6 ten minute periods. During these observation periods, five components of the subject's threat display were simultaneously recorded:

1. Total gill cover erection duration (GD): total amount of time that the gill covers were erected during the 10 minute observation period.

2. Gill cover erection frequency (GF): number of times the gill covers were erected during the 10 minute period.

3. Total medial fin erection duration (FD): total amount of time that the medial fins were erected during the 10 minute period.

4. Medial fin erection frequency (FF): number of times the medial fins were erected during the 10 minute period.

5. Air gulping frequency (AG): number of times the fish came to surface to gulp air during the ten minute period.

AG was chosen as a measure because it is a purported activity level indicator (Simpson, 1968; Clayton and Hinde, 1968). This response was easily discernible and occurred in an all-or-none manner. The frequency and duration of a particular response were both recorded on one channel of the recorder by holding the push button down for as long as the response occurred. The operational definition of gill cover erection was taken from the extensive work of Simpson (1968):

Gill cover erection is a sudden increase in the distance between the distal edge of the operculum and the body, regardless of how far erect the operculum was to start with. The end of a gill raising bout is marked by a sudden decrease in this distance, even if the opercula are not completely closed thereby. In practice, such changes are clear-cut, although different individuals have different degrees of opening for

what are here recognized as "open" and "closed" positions. When the gill covers are erected the brachio-stegal membranes are usually protruded. Different degrees of protrusion were not distinguished (p. 16).

This response has been mentioned in nearly all descriptions of the Betta's threat and courtship displays. Some investigators use the frequency (GF) measure (Clayton and Hinde, 1968; Laudien, 1965), while others use some form of the duration (GD) measure (Adler and Hogan, 1963; Simpson, 1968). For the purposes of this study both frequency and duration measures were utilized in order to be able to evaluate the relationship between them.

The operational definition of medial fin erection was also taken from the work of Simpson (1968):

As a fish turns toward a display-eliciting stimulus for the first time, the vertical fins are spread . . . The dorsal is the last fin to be erected fully, probably because that is the fin that has to be lifted furthest against gravity. The criterion for fins spread is thus an erect dorsal. However, when a displaying fish approaches another one, the first few dorsal rays may be slightly lowered, but the remaining ones remain rigidly erect (p. 14).

Although this response has not been looked at as closely in the literature as gill cover erection, it is an integral part of the display and easily recorded. Previous investigators have broken this response into finer components (e.g. tail flashing, carouseling) but for the purposes of the present study, the above measurement was taken (Simpson, 1968).

Although there are other finer-grained components to the threat display, the above ones were chosen for their discreteness, wide usage in previous studies, reliability of elicitation, and accuracy with which they could be recorded.



RESULTS

The data analysis consisted of scoring each ten-minute observation period for each S in terms of each of the five dependent variables. Therefore, each S had six scores for each dependent variable (i.e. a total of 30 scores for each S).

Then the data were analyzed using a three-factor multivariate analysis of variance and a consequent three-factor repeated measures (Case I) univariate analysis of variance (Winer, 1962) for each dependent variable, separately. The data analyses could have been undertaken using only the five separate repeated measures three-factor analyses of variance, but the true overall alpha level would have been higher than that specified for each test. When using univariate tests, a single probability statement applicable to all variables jointly cannot in general be obtained from separate Fs (Bock and Haggard, 1968):

Because all . . . variables have been obtained from the same subjects, they are correlated in some arbitrary and unknown manner, and the separate F-tests are not statistically independent. No exact probability that at least one of them will exceed some critical level on the null hypothesis can be calculated. The multivariate tests, on the other hand, are based on sample statistics which take into account the correlations between variables and have known exact sampling distributions from which the required probabilities can be obtained (p. 102).

Preliminary inspection showed that the assumptions of homogeneity of dispersion and normality were not appreciably violated. Also, since an N of 10 is of moderate size and since all groups in the study had equal N s, mild violations of the above assumptions would not affect the true probability of making a type I error (Boneau, 1960; Hays, 1963). A level of significance of .05 was used throughout, with respect to both multivariate and univariate effects. If, in any case, the multivariate overall, with respect to a particular effect does not reach significance, the usual procedure is to dispense with the analysis of each dependent variable, separately. This procedure was followed in the present study.

The general organization of the results section will involve a brief discussion of the multivariate results and then a more complete discussion of each dependent variable, separately. Then the relation among the various dependent variables will be discussed. Finally, a further discussion of some selected dependent measures will be undertaken. Since the analyses become quite involved, a general summary will follow each section.

To begin with, it is quite clear (see Table 1) that the multivariate F for each and every effect reached significance. Therefore, a true overall alpha level of at least .05 was attained for all main effects and the various interactions. Since the prime purpose for using

A black and white photograph showing a close-up of a racing helmet. The helmet features a checkered pattern on the left side and a dark, curved opening on the right side. The helmet is positioned horizontally, and the background is dark and indistinct.

Effect	Multivariate Overall	Univariate Analyses				
		AG	GF	GD	FF	FD
Stimulus	$\frac{df}{F}$ 15/88.74	3/36	3/36	3/36	3/36	3/36
	$\frac{F}{p}$ 2.26	3.15	10.95	7.39	10.82	7.00
	$\frac{p}{\chi^2}$.01	.05	.0001	.001	.0001	.001
Time Period	$\frac{df}{F}$ 10/27	2/35	2/35	2/35	2/35	2/35
	$\frac{F}{p}$ 4.59	2.62	2.82	15.49	2.24	14.37
	$\frac{p}{\chi^2}$.001	N.S.	N.S.	.0001	N.S.	.0001
Stimulus x Time Period	$\frac{df}{F}$ 30/78.93	6/70	6/70	6/70	6/70	6/70
	$\frac{F}{p}$ 1.81	1.19	4.10	3.94	4.41	3.45
	$\frac{p}{\chi^2}$.05	N.S.	.01	.01	.001	.01
Session	$\frac{df}{F}$ 5/32	1/36	1/36	1/36	1/36	1/36
	$\frac{F}{p}$ 5.91	3.39	3.39	19.42	8.52	11.65
	$\frac{p}{\chi^2}$.001	N.S.	N.S.	.0001	.01	.01
Stimulus x Session	$\frac{df}{F}$ 15/88.74	3/36	3/36	3/36	3/36	3/36
	$\frac{F}{p}$ 2.84	2.39	3.26	1.97	.99	2.32
	$\frac{p}{\chi^2}$.01	N.S.	.05	N.S.	N.S.	N.S.
Time Period x Session	$\frac{df}{F}$ 10/27	2/35	2/35	2/35	2/35	2/35
	$\frac{F}{p}$ 3.51	.43	4.36	5.29	.94	4.45
	$\frac{p}{\chi^2}$.01	N.S.	.05	.01	N.S.	.05
Stimulus x Time Period x Session	$\frac{df}{F}$ 30/79.93	6/70	6/70	6/70	6/70	6/70
	$\frac{F}{p}$ 1.96	2.04	1.67	3.99	1.29	2.93
	$\frac{p}{\chi^2}$.01	N.S.	N.S.	.01	N.S.	.05

the multivariate analysis was to ensure the accuracy of the overall alpha levels, the presentation of results will move immediately into the treatment of each dependent variable, separately.

Air Gulping Frequency (AG)

From an inspection of the AG variable in Table 1 and Figure 2 which show the mean frequency per ten-minute observation for each stimulus group, it can be seen that only the Stimulus effect reached significance ($F = 3.15$, $df = 3/36$, $p < .05$). Across both sessions, the different threat stimuli elicited differential air gulping frequencies. Figure 2 shows that the unhabituated male stimulus (Unhab. male) was the strongest elicitor, followed by the mirror stimulus (Mirror), habituated male stimulus (Hab. male) and cut-out stimulus (Cut-out), respectively. A Newman-Keuls paired comparisons test uncovered no .05 differences between pairs of treatment means, although the Unhab. male-Cut-out and Unhab. male-Hab. male pairs approached significance.

Earlier in the data analysis, a multivariate analysis for the vector of all dependent variables at T_1 (first ten-minute observation) was undertaken. It proved to be highly significant ($F = 2.33$, $df = 15/88.74$, $p < .01$). A one-way analysis of variance was then performed on the AG data at T_1 . Again the effect was significant ($F = 4.76$,

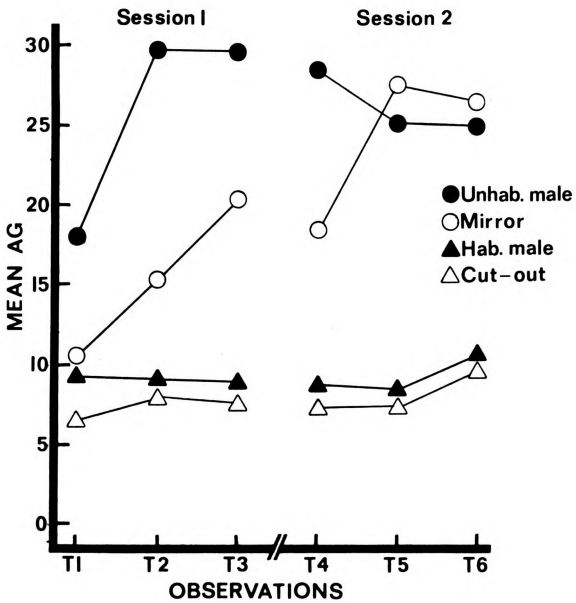


Figure 2. Mean air gulping frequency per ten minute observation period.

$df = 3/36$, $p < .01$). Using the Newman-Keuls test, it was found that the Unhab. male group had a significantly higher frequency of air gulping during the first observation (T_1) than did the Mirror, Hab. male or Cut-out groups. However, the other stimulus groups did not differ from one another (all Newman-Keuls reported at the .05 level).

No Time Period effect (habituation) nor Session effect was evident with respect to this particular dependent variable. Also, none of the interactions attained significance.

Summary of AG data analysis

In general, air gulping frequency was strongly influenced by the differential eliciting stimuli. At both T_1 (initial observation) and generally throughout the duration of the experiment, the Unhab. male group was the strongest elicitor, followed by the Mirror, Hab. male and Cut-out groups, in that order. No systematic habituation of the air-gulping response was evident during the present experiment. Also, no significant frequency differences were present between the two 40 minute sessions.

Gill Cover Erection Frequency (GF)

Table 1 and Figure 3 provide an overall picture of the GF data. There was a highly significant Stimulus effect ($F = 10.95$, $df = 3/36$, $p < .0001$). The Newman-Keuls

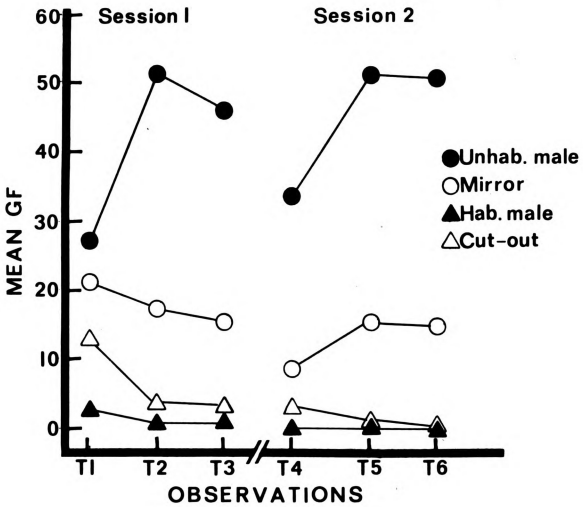


Figure 3. Mean gill cover erection frequency per ten minute observation period.

test showed that the Unhab. male group had a significantly higher GF during the experiment than the other three groups (which did not differ from one another). Notice from Figure 3 that the order of strength of eliciting stimuli is again Unhab. male, Mirror, Hab. male and Cut-out groups, in that order. A simple analysis of variance of the GF data at T_1 was highly significant ($F = 5.81$, $df = 3/36$, $p < .01$). The Unhab. male group had a significantly higher GF than the Cut-out group. The Mirror group was also significantly greater in response than the Cut-out group, as shown by the Newman-Keuls test. The other paired comparisons were not significant.

The Time Period effect was not significant for the GF data; therefore, no systematic decrement occurred when stimulus groups were pooled. However, the Stimulus x Time Period interaction was significant ($F = 4.10$, $df = 6/70$, $p < .01$), reflecting an increase in GF across time for the Unhab. male group and a decrement in response for the other three stimulus groups. Although there was no difference between sessions in GF level when treatments were pooled, a Stimulus x Session interaction ($F = 3.26$, $df = 3/36$, $p < .01$) reflected an increase in session 2 responding for the Unhab. male group while the other three groups showed a decrease. Adding to the complexity of results for the GF data was a significant Time Period x Session interaction ($F = 4.36$, $df = 2/35$, $p < .05$). The Mirror group showed a

response decrement during session 1, but an increment in responding during session 2. The Hab. male and Cut-out groups both showed more decrement in session 1 than in session 2. The Cut-out group data in session 2, however, reflects the lack of response for that particular group. The Unhab. male group increased in GF about the same amount in each session. For the FG variable, the Stimulus x Time Period x Session interaction was not significant.

Summary of GF data analysis

The Unhab. male group responded the most during the initial observation and the entire experiment, followed by the Mirror, Hab. male and Cut-out groups respectively. No systematic response decrement was evident for all groups across trials, with a response increment for the Unhab. male group being apparent during both sessions, and a session 2 increment for the Mirror group offsetting a general response decrement for the Hab. male and Cut-out groups.

Gill Cover Erection Duration (GD)

This dependent variable, as defined earlier, is the total amount of time that the gill covers are in an erected position during each ten-minute observation period.

As seen in Table 1, the Stimulus effect was highly significant ($F = 7.39$, $df = 3/36$, $p < .001$). Again, the order of the eliciting stimulus strengths was the Unhab. male, Mirror, Hab. male and Cut-out, respectively (see

Figure 4). The analysis of this effect using the Newman-Keuls procedure revealed a significant difference between the Unhab. male group and all the other groups. However, none of the other groups significantly differed from one another. A simple effects analysis of variance of the GD data at T_1 also showed significance ($F = 7.80$, $df = 3/36$, $p < .001$). A Newman-Keuls analysis resulted in the same profile as with the Stimulus main effect: the Unhab. male differed from the other three groups, which did not differ among themselves.

The Time Period effect ($F = 15.49$, $df = 2/35$, $p < .0001$) reflected systematic habituation with respect to the GD variable. However, different stimulus groups had different absolute amounts of decrement as evidenced by a significant Stimulus x Time Period interaction ($F = 3.94$, $df = 6.70$, $p < .01$). The greatest absolute decrement was shown by the Unhab. male group, followed by the Mirror, Hab. male and Cut-out groups, in that order. Care must be taken in interpreting this particular finding, since the great differences between groups in initial response level gave the Unhab. male group a greater potential absolute decrement than a group with a lesser initial level. The same argument applies to each other group and those groups above and below. A more equitable measure of decrement would be a proportional one, which equates the differential initial level of responding in some way. This issue will

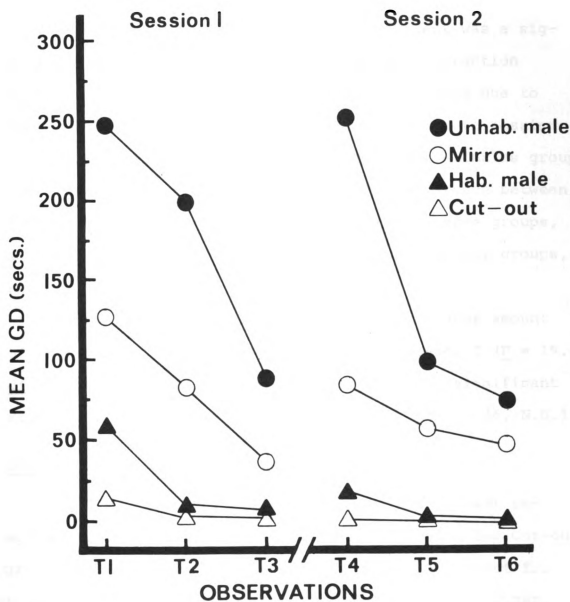


Figure 4. Mean total gill cover erection duration (seconds) per ten minute observation period.

be taken up in a later section. A significantly greater amount of decrement occurred during Session 1 than in session 2 as shown by the Time Period x Session interaction ($F = 5.29$, $df = 2/35$, $p < .01$). Also evident was a significant Stimulus x Time Period x Session interaction ($F = 3.99$, $df = 6.70$, $p < .01$). This effect was due to the greater decrement in session 2 as compared to session 1 for the Unhab. male group, while the other stimulus groups had a greater session 1 decrement. The difference between the session 1-session 2 decrement, in these three groups, was greatest for the Mirror, Hab. male and Cut-out groups, respectively.

Overall, there was a significantly higher amount of response in session 1 as compared to session 2 ($F = 19.42$, $df = 1/36$, $p < .0001$). However, there was no significant Stimulus x Session interaction ($F = 1.97$, $df = 3/36$, N.S.).

Summary of GD data analysis

The Unhab. male group again had the highest response level, followed by the Mirror, Hab. male and Cut-out groups respectively. There was a response decrement for every stimulus group with the strongest elicitor (Unhab. male) having the greatest absolute decrement, followed again by the Mirror, Hab. male and Cut-out groups respectively. Therefore, the absolute decrement was directly related to eliciting stimulus strength. Session 1 responding was significantly greater than that for session 2.

Fin Erection Frequency (FF)

Again, the Unhab. male stimulus was the strongest elicitor followed by the Mirror, Hab. male and Cut-out stimulus respectively (see Figure 5). This ordinal relationship of eliciting stimulus strength is the same as that for the other dependent variables. The Stimulus main effect was significant ($F = 10.82$, $df = 3/36$, $p < .0001$) and significantly interacted with Time Periods ($F = 4.41$, $df = 6/70$, $p < .001$). The breakdown of the Stimulus effect using the Newman-Keuls procedure showed that the Unhab. male group was significantly different from the other three groups, but they did not differ from one another. As with the other dependent measures, a one-way analysis of variance of the FF data at T_1 (initial observation) was highly significant ($F = 6.32$, $df = 3/36$, $p < .01$). Using the Newman-Keuls method, it was shown that at the first observation the Unhab. male group had a significantly higher response level than either the Cut-out or the Hab. male groups. The Mirror group responded significantly more than the Cut-out group, but the other three possible pairs did not reach significance. As seen in Figure 5, however, the order of eliciting stimulus strengths at T_1 was the same as that at every other observation period throughout the experiment.

Although the Time Period (habituation) effect was not significant ($F = 2.24$, $df = 2/35$, N.S.), the Stimulus

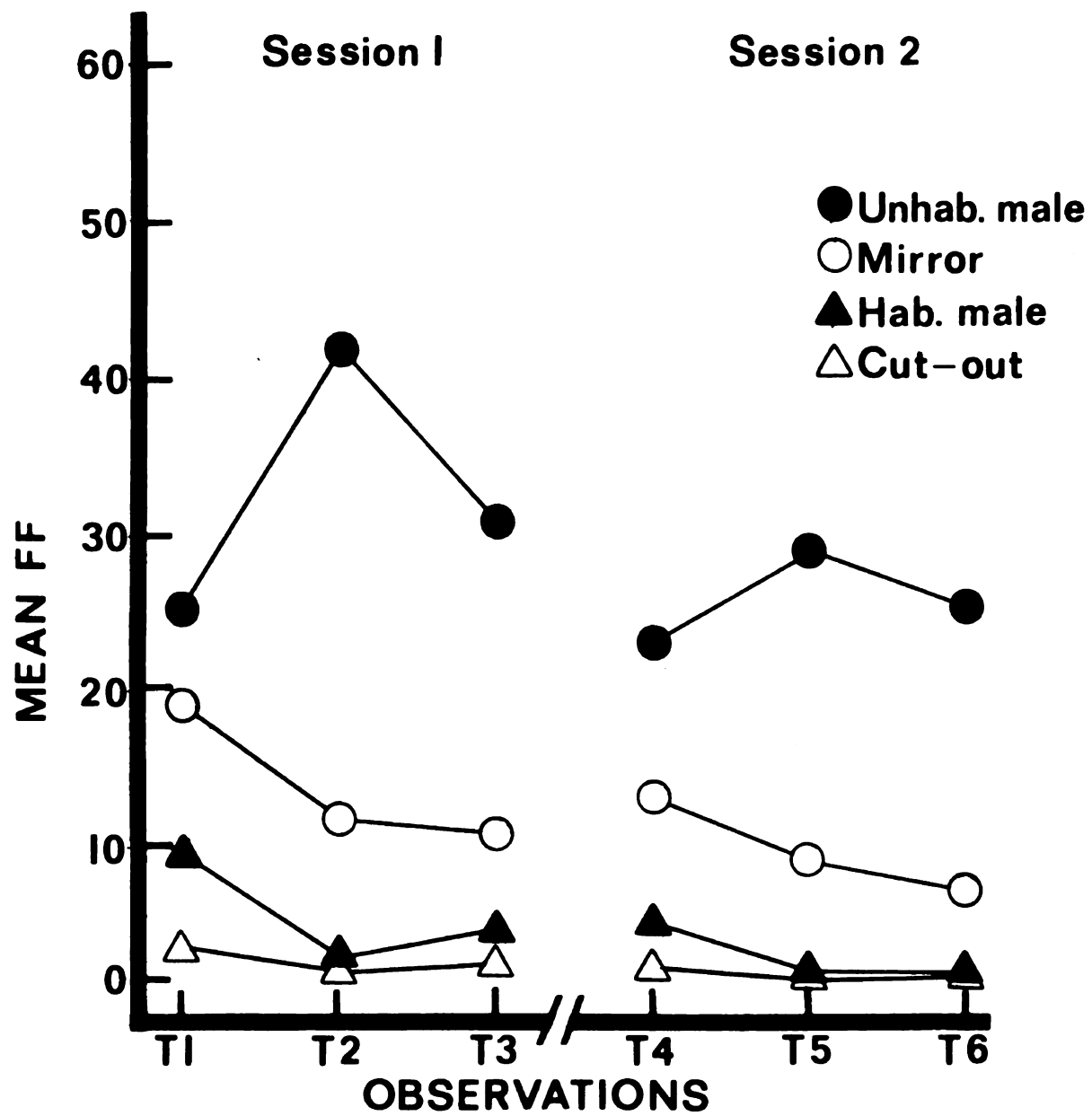


Figure 5. Mean fin erection frequency per ten minute observation period.

x Time Period interaction was significant, as mentioned above. This interaction was due to an increment in response level within and across sessions for the Unhab. male group, while the Mirror, Hab. male and Cut-out groups displayed a general decrement within and across sessions. In general, session 1 responding was greater than session 2 ($F = 8.52$, $df = 1/36$, $p < .01$). However, the Stimulus x Session, Time Period x Session, and Stimulus x Time Period x Session interactions all failed to reach significance (see Table 1).

Summary of FF data analysis

With respect to the FF data, the strongest elicitor again was the Unhab. male stimulus, followed by the Mirror, Hab. male and Cut-out stimuli, in that order. This ordinal relationship was maintained throughout the experiment. No systematic habituation was present, since the Unhab. male group displayed a response increment within and across sessions while the other three groups showed response decrements. The only other significant finding was an overall higher response level for session 1 data as compared to session 2.

Fin Erection Duration (FD)

This dependent variable, as defined earlier, is the total amount of time that the medial fins are in an erected position during each ten-minute observation period.

As with all the other dependent variables, the FD data supports the contention that the Unhab. male is the strongest elicitor followed by the Mirror, Hab. male and Cut-out stimuli, respectively (see Figure 6). The Stimulus main effect was highly significant ($F = 7.00$, $df = 3/36$, $p < .001$). The subsequent Newman-Keuls procedure revealed that the Unhab. male group was significantly different from the Cut-out group and the Hab. male group. The other pairs did not reach significance.

The various stimulus groups were more widely separated at T_1 (first observation) than for the whole experiment, although the ordinal strength of the elicitors was the same (see Figure 6). A one-way analysis of variance of the T_1 data was highly significant ($F = 6.77$, $df = 3/36$, $p < .001$). This time the Newman-Keuls procedure revealed significant differences for four of the six possible pairs. The Unhab. male group responded significantly longer during the first ten minutes than either the Hab. male or Cut-out groups. The Mirror group also had a significantly longer duration than either the Hab. male or Cut-out groups. The Hab. male-Cut-out pair and the Unhab. male-Mirror group did not reach the .05 level of significance.

There was an overall decrement of response during the sessions as reflected by a highly significant Time Period effect ($F = 14.37$, $df = 2/35$, $p < .0001$). This Time Period effect significantly interacted with the Stimulus

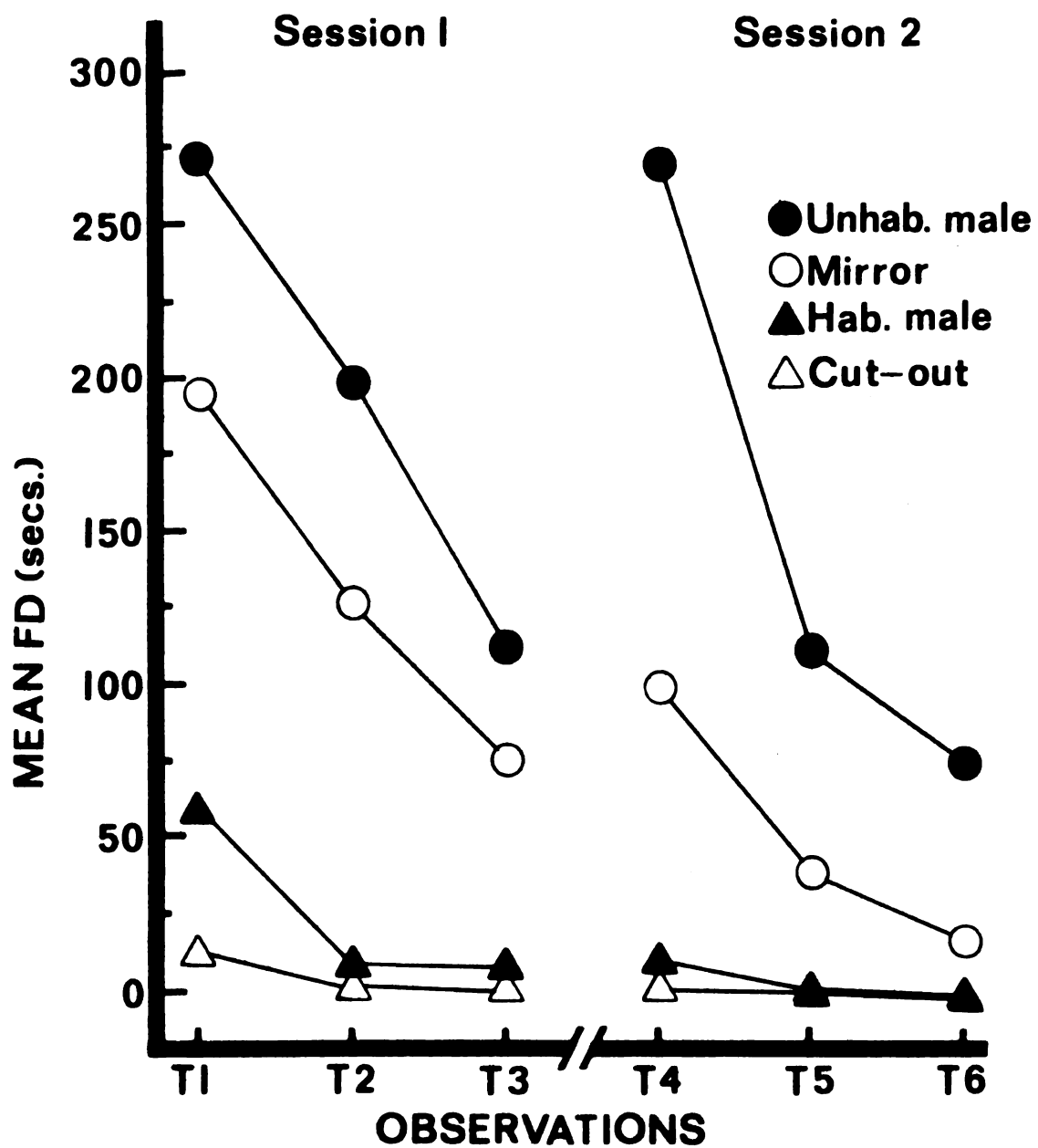


Figure 6. Mean total fin erection duration (seconds) per ten minute observation period.

effect ($F = 3.45$, $df = 6/70$, $p < .01$). The interaction was due to the fact that different stimulus groups had different absolute amounts of decrement (see Figure 6). The Unhab. male group had the highest mean amount of decrement followed by the Mirror, Hab. male and Cut-out groups, respectively. In other words, the stronger the elicitor, the greater the absolute amount of decrement.

There was an overall longer mean duration of response during session 1 as compared to session 2 ($F = 11.65$, $df = 1/36$, $p < .01$); this effect did not vary by stimulus group ($F = 2.32$, $df = 3/36$, N.S.). There was also a significant Time Period x Session interaction ($F = 4.45$, $df = 2/35$, $p < .05$) reflecting, in general, more response decrement during session 1 than in session 2. However, the greater response decrement in session 1 did not hold for all stimulus groups. The Unhab. male group had a larger response decrement in session 2 than in session 1, this being a partial explanation of a significant Stimulus x Time Period x Session interaction ($F = 2.93$, $df = 6/70$, $p < .05$). This interaction also reflected the larger session 1-session 2 differences in decrement for the Mirror and Hab. male groups, as compared to the Cut-out group.

Summary of FD data analysis

The Unhab. male stimulus again proved to be the strongest elicitor, followed by the Mirror, Hab. male and

Cut-out stimuli, respectively. Notice that this ordinal relationship holds up for all of the previously discussed dependent measures. The FD data reflected systematic habituation for all stimulus groups, although the Unhab. male group had the largest absolute decrement followed by the Mirror, Hab. male and Cut-out groups, in that order. Therefore, the stronger the elicitor (as measured by the response level at T_1), the larger the absolute amount of habituation. In general, there was a longer mean duration of response in session 1 than in session 2. Session 1 was associated with a larger response decrement than for session 2 data although this relationship varied with the different stimulus groups.

Intercorrelations

An intercorrelation matrix, averaged across stimulus groups is presented in Table 2. Separate matrices for each stimulus group may be found in the Appendix. Since the various correlational relationships involved in each separate stimulus group are generally similar to the other groups, the present discussion will focus on the combined data ($N = 40$). Table 2 data is organized by dependent variable and session number. For example, AG1 is the air gulping frequency data for session 1, while AG2 is the data for Session 2. It should also be noticed that some correlations are based upon three of the four stimulus groups, since there

Table 2.--Pearson rs for Dependent Variables in Session 1 and Session 2;
Stimulus_Groups are Combined ($N = 40$).

	AG1	AG2	GF1	GF2	GD1	GD2	FF1	FF2	FD1	FD2
AG1										
AG2	** .718									
GF1	.060	.174								
GF2	a .020	a .062	a ** .890							
GD1	-.014	.128	** .954	a ** .918						
GD2	a -.068	a -.052	a ** .750	a ** .952	a ** .926					
FF1	.046	.252	** .900	a ** .684	** .866	a ** .486				
FF2	.088	.288	** .906	a ** .896	** .918	a ** .876	** .888			
FD1	.154	.256	** .846	a ** .720	** .876	a ** .656	** .910	** .894		
FD2	.094	.232	** .852	a ** .782	** .890	a ** .852	** .792	** .974	** .932	

^aCut-out group did not respond, $N = 30$.

* $p < .05$

** $p < .01$

were no GF or GD responses for the Cut-out group during session 2.

Reliability

Product-moment correlations comparing the same dependent variable across sessions showed a high level of reliability for every measure. Although the correlations reported are derived from averaging across the stimulus groups, the reliability levels almost uniformly hold for each stimulus group separately (see Appendix). For those correlations based upon the combined groups, an r equal to or greater than .312 is significant at the .05 level for the first correlation used. An r equal to or greater than .404 is significant at the .01 level. Those measures (AG, FF, FD) based upon all four groups will be discussed first. The session 1-session 2 correlation for the AG variable was .718, reflecting a high degree of consistency of response across the two sessions. The r for the FF variable was .888. The FD measure was also extremely reliable across the two sessions ($r = .932$). These three dependent variables attained r s far beyond the .01 level of significance.

Since there were no GF or GD responses for the Cut-out group, the following r s are based upon the three remaining groups ($N = 30$). With this sample size, r s equal to or greater than .361 are significant at the .05 level for the first correlation used, while r s equal to or greater

than .463 are significant at the .01 level. The r for the GF data was .890, while the GD measure had a session 1-session 2 r of .926. Both of these measures are significant far beyond the .01 level.

In summary, every dependent variable proved to be highly reliable, reflecting both the ease and accuracy of recording and the relative constancy of the experimental situation from session to session.

Interrelationships among dependent variables

The following discussion is again based upon the data averaged across stimulus groups. However, as before, these general relationships hold up well when treating each stimulus group independently. First of all, it may be seen from Table 2 that there are significant positive intercorrelations among all of the following four dependent variables: GF, GD, FF and FD. For example, the correlation between the FF1 measure and GF1, GF2, GD1, GD2, FD1 and FD2 ranged from r_s of .486 to .910. The GD1 measure had a high degree of relationship with those variables mentioned above, as witnessed by correlations from $r_s = .866$ to .954. The point to be made here is that the four threat components used in the present study have high positive interrelationships with one another.

Looking again at Table 2, it is apparent that the AG variable is not significantly correlated with any of the

other four dependent variables in either session. The intercorrelations ranged from r_s of $-.014$ to $.288$, all being non-significant values. Very few of the values even reached an r of $.20$. Therefore, it was shown in a quantitative fashion that air gulping is not an integral part of the threat display, itself. This finding supports the contentions in previous sections. Further discussion will be deferred until the next section.

Further Analyses of GD and FD Data

Only two of the dependent variables, GD (Figure 4) and FD (Figure 6) showed systematic habituation for every stimulus condition. The other three variables reflected either no decrement at all (AG) or increments for certain treatment groups and decrements or no time changes at all for other groups (FF and GF). The probable reasons for these differences will be discussed later. The following discussion will focus solely on the GD and FD variables, for the reasons listed above.

In order to investigate further the relationship between initial eliciting stimulus strength and the degree of habituation, retention, and recovery of habituation the following analyses were performed for the GD and FD data. The procedure was identical for each measure. Proportions were used in this phase of the analysis in order to equate the initial response levels for the different stimulus

groups in some manner. It was already shown that the Unhab. male group had the highest initial level (T_1) of response followed by the Mirror, Hab. male and Cut-out groups, respectively. It was also shown that there was a positive relationship between the initial level of response (eliciting stimulus strength) and the absolute amount of decrement. The above relationships held for both the GD and FD data. An attempt was made, via proportions, to see if initial eliciting stimulus strength was related to the proportion of decrement, and retention and recovery of this decrement.

Only Ss which responded during the appropriate sessions were used in the following analyses. There were four fish in the Cut-out group, nine in the Hab. male group and ten in both the Mirror and Unhab. male group which responded during session 1. A chi-square analysis of this raw frequency data was highly significant ($\chi^2 = 17.10$, $df = 3$, $p < .01$). During session 2, the number of Ss which responded in each group were as follows: Unhab. male, nine; Mirror, six; Hab. male, five; and Cut-out, one. A chi-square analysis of this raw frequency data was also highly significant ($\chi^2 = 13.10$, $df = 3$, $p < .01$). Notice that there is a direct relationship between eliciting stimulus strength and the number of Ss which showed threat response: the Unhab. male group had the largest number responding in session 2, followed by the Mirror, Hab. male and Cut-out groups, respectively. A chi-square



analysis with the data pooled across sessions was not attempted, since there was no S which responded in session 2 that did not respond in session 1. In other words, the data for the pooled sessions was identical to that of session 1.

Proportional analyses of GD data

A session 1 decrement proportion was calculated for each S in each group using the formula $\frac{T_1 - T_3}{T_1}$ (first observation minus the third observation divided by the first observation). The data was analyzed with a Kruskal-Wallis analysis of variance by ranks, because of unequal cell sizes, small N, and violations of the assumptions for the parametric analysis of variance. The analysis did not reach the .05 level of significance: the four stimulus groups did not differ in the proportion of decrement during session 1 (see Table 3). A three-group analysis, without the Cut-out group also failed to reach significance.

Since the effect of initial eliciting stimulus strength on the degree of habituation might be made apparent with longer stimulus exposure, a proportion of across session decrement measure was calculated for each S using the formula $\frac{T_1 - T_6}{T_1}$. This time the Kruskal-Wallis test was significant ($H = 10.44$, $df = 3$, $p < .05$). Notice in Table 3 that the mean group rank is the largest (greatest decrement) for the Cut-out group, followed by the Hab. male,

Table 3.--Kruskal-Wallis H Test Summary Table for Four GD Proportional Variables (Proportion of Decrement in Session 1, Proportion of Across Sessions Decrement, Proportion of Retention, and Proportion of Recovery): Sum of Ranks and Mean Ranks for Each Stimulus Group.

GD Proportional Variables												
Stimulus Group	Proportion Decrement: Session 1			Proportion Decrement: Across Sessions			Proportion Retention			Proportion Recovery		
	Sum of Ranks	N	Mean Group Rank	Sum of Ranks	N	Mean Group Rank	Sum of Ranks	N	Mean Group Rank	Sum of Ranks	N	
												Mean Group Rank
Unhab. male	127	10	12.70	109.50	10	10.95	91	10	9.10	232	10	23.20
Mirror	169.50	10	16.95	157	10	15.70	181	10	18.10	121	10	12.10
Hab. male	158	9	17.56	196.50	9	21.83	181	9	20.11	125	9	13.89
Cut-out	109.50	4	27.38	98	4	24.50	108	4	27	50	4	12.50
p	N.S.			<.05			<.01			<.05*		

*Cut-out group was deleted from the analysis.



Mirror and Unhab. male groups, respectively. Post-hoc paired comparisons using the Mann-Whitney U test following the method of Lewis and Cotton (1958), and Peeke (1969), showed that the Unhab. male group had a significantly smaller proportion of across session ($T_1 - T_6$) decrement when compared to either the Hab. male or Cut-out groups. The other pairs were not significant at the .05 level, although the general trends show that the stronger the eliciting stimulus strength, the smaller the proportion of session 1 and across session decrement.

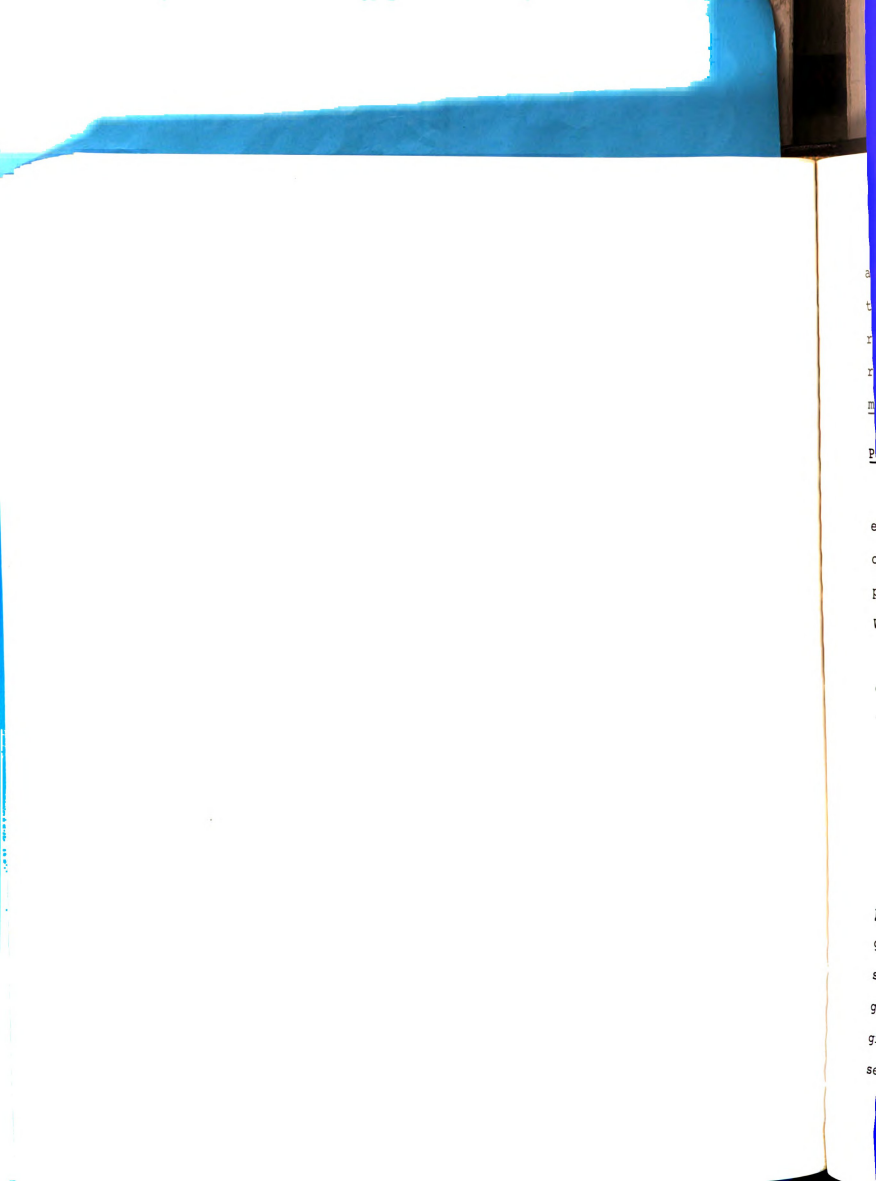
Next, a retention score was calculated for each S using the formula $\frac{T_1 - T_4}{T_1}$. A Kruskal-Wallis test was highly significant ($H = 12.85$, $df = 3$, $p < .01$). Post-hoc Mann-Whitney U tests showed that the Unhab. male group had a significantly smaller proportion of retention than either the Mirror, Hab. male or Cut-out groups. Table 3 shows that the mean group rank (proportion of retention) was smallest for the Unhab. male group, followed by the Mirror, Hab. male and Cut-out groups, respectively. The relation between the initial eliciting strength of the stimuli and the proportion of retention of habituation after a 24 hour rest period is thus a monotone decreasing one.

Finally, to investigate the proportion of recovery from the last observation of session 1 (T_3) to the first observation of session 2 (T_4), the following proportion was calculated for each S: $\frac{T_4 - T_3}{T_1 - T_3}$. This proportion gives

a rough ratio of the amount of recovery ($T_4 - T_3$) to the amount of decrement during session 1 ($T_1 - T_3$). Due to the small, unrepresentative sample for the Cut-out group ($N = 4$), this group was deleted from this part of the analysis. The three-group Kruskal-Wallis test reached significance ($H = 6.33$, $df = 2$, $p < .05$). The mean group rank (proportion of recovery) was the largest for the Unhab. male group followed by the Hab. male, Cut-out and Mirror groups, respectively. However, the post-hoc Mann-Whitney U tests showed that the only significantly different pairs were in the expected direction: the Unhab. male group had a significantly higher proportion of recovery than either the Mirror or Hab. male groups.

Summary of proportional analyses of GD data

Although conclusive data are not available due to the sample size of the Cut-out group ($N = 4$) in these analyses, there were some general relationships that were uncovered. The proportion of across session decrement was related to initial eliciting stimulus strength in a monotone-decreasing manner: the stronger the elicitor, the smaller the proportion of decrement. The proportion of decrement data for session 1 did not reach significance, although the trend was in the same direction. The proportion of retention of habituation after a 24 hour rest period was also strongly related to initial eliciting stimulus strength in



a monotone-decreasing manner: the stronger the elicitor, the smaller the proportion of retention. Proportion of recovery of habituation after a 24 hour rest period was related to initial eliciting stimulus strength in a monotone-increasing manner.

Proportional analyses of FD data

The analyses of the FD measures were dealt with in exactly the same way as the GD analyses above. The same calculations, alpha levels, and Mann-Whitney post-hoc comparison procedures were used throughout. The Kruskal-Wallis summary data is presented in Table 4.

A proportion of session 1 decrement measure was calculated for each S, again using the formula $\frac{T_1 - T_3}{T_1}$. The Kruskal-Wallis test did not reach significance for either the four-group analysis or when the Cut-out group (N = 2) was deleted (three-group analysis).

An across session decrement proportion was then calculated for each S using the formula $\frac{T_1 - T_6}{T_1}$. The Kruskal-Wallis test was significant (H = 9.42, df = 3, p < .05). Since there were only two Ss in the Cut-out group which could be used in this analysis, little conclusive data can be obtained for this particular stimulus group. In general, it can be seen that the Unhab. male group had the smallest mean rank (proportion of across session decrement), followed by the Mirror group. Although

Table 4.--Kruskal-Wallis H Test Summary Table for Four FD Proportional Variables
(Proportion of Decrement in Session 1, Proportion of Across Sessions Decrement, Proportion of Retention, and Proportion of Recovery): Sum of Ranks and Mean Ranks for Each Stimulus Group.

Stimulus Group	FD Proportional Variables											
	Proportion Decrement: Session 1				Proportion Decrement: Across Sessions				Proportion Retention			
	Sum of Ranks	N	Mean Rank		Sum of Ranks	N	Mean Rank		Sum of Ranks	N	Mean Rank	
Unhab. male	115	10	11.50		97	10	9.70		94	10	9.40	
									203	10	20.30	
Mirror	171.50	10	17.15		160	10	16		169	10	16.90	
									124	10	12.40	
Hab. male	138	8	17.25		172	8	21.50		162	8	20.25	
									80	8	10	
Cut-out	40.50	2	20.25		36	2	18		40	2	20	
									28	2	14	
p	N.S.				<.05				<.05			
									<.05*			

*Cut-out group was deleted from the analysis.

the Hab. male group had a larger mean group rank than the Cut-out group, the difference is negligible and the Cut-out data was based on an N of 2. The Mann-Whitney U tests showed that only one pair reached significance. The Unhab. male group had a significantly smaller proportion of across session decrement as compared to the Hab. male group.

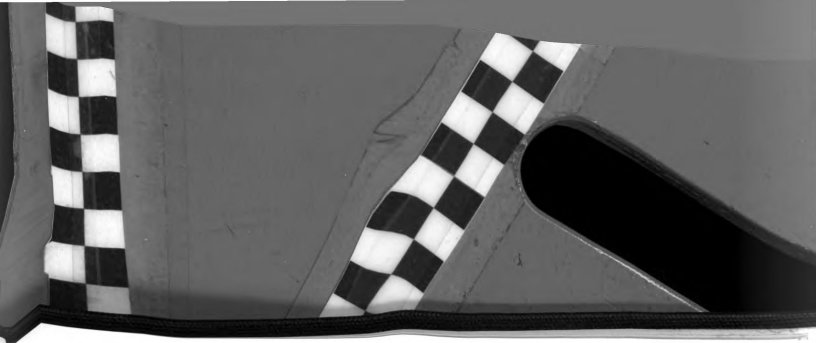
Then a proportion of retention was calculated for each S , again using the formula $\frac{T_1 - T_4}{T_1}$. The Kruskal-Wallis test was significant ($H = 8.57$, $df = 3$, $p < .05$). The Mann-Whitney U tests showed that the Unhab. male group retained significantly less than either the Mirror or Hab. male group. The other pairs did not reach significance. Any comparison with the Cut-out group was almost impossible to make due to the small sample size.

Finally, the proportion of recovery measure was calculated for each S , again using the formula $\frac{T_4 - T_3}{T_1 - T_3}$. A three-group Kruskal-Wallis test was performed. The Cut-out group data was discarded because of the small, unrepresentative sample ($N = 2$). The three-group analysis reached significance ($H = 6.17$, $df = 2$, $p < .05$). The Mann-Whitney U procedure on the remaining three groups showed that the Unhab. male group had a significantly higher proportion of recovery than either the Mirror or Hab. male groups. This trend is clearly shown in Table 4.

Summary of proportional
analyses of FD data

Again this part of the analysis suffered from the small sample size of the Cut-out group ($N = 2$). This particular stimulus was an overall poor elicitor. However, from the three remaining groups it is quite clear that eliciting stimulus strength strongly affects the degree of habituation, retention and recovery of habituation. There was a monotone-decreasing relation between initial eliciting stimulus strength and the proportion of across session decrement and the proportion of retention of habituation. The stronger the elicitor the less the decrement, and the poorer the retention of the decrement. There was a general monotone-increasing relation between initial eliciting stimulus strength and the proportion of recovery of habituation after a 24 hour rest period. The stronger the elicitor, the larger the proportion of recovery. Of course, the retention and recovery measures are strongly related in a negative fashion.

It is interesting to note that the above relations held up quite well for both the GD and FD analyses. The Unhab. male stimulus elicited the greatest initial level of response (eliciting stimulus strength) followed by the Mirror, Hab. male and Cut-out groups, in that order. This order of the strength of the elicitors was consistent for all investigated dependent variables. Finally, initial



eliciting stimulus strength was found to be strongly related to the absolute amount of habituation, the proportion of across session habituation, the proportion of retention of habituation and the proportion of recovery of habituation.

DISCUSSION

The present study provided strong evidence that components of the threat display of male Betta splendens are subject to habituation and that the degree of habituation and retention of habituation are strongly influenced by the initial strength of the eliciting stimulus.

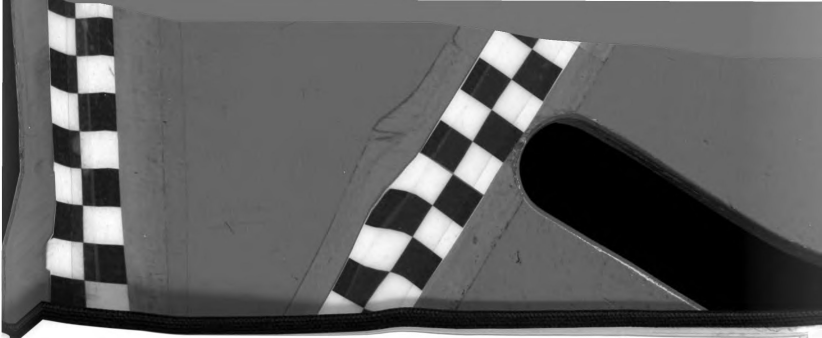
Eliciting Stimulus Strength

For all five dependent variables used in the study, the ordinal strengths of the four elicitors were the same. The group exposed to the Unhab. male stimulus responded to the greatest degree, followed by the Mirror, Hab. male and Cut-out groups, respectively. Why this particular ordinal relationship occurred may be explained by means of past literature and some speculation. That a live stimulus is a better elicitor than a stationary one (Cut-out) has been quite firmly established (Tinbergen, 1951; Martin and Melvin, 1964; Peeke, 1969). With respect to the Unhab. male, Mirror and Hab. male stimuli, the following argument is proposed. The Unhab. male stimulus provided movement and relatively prolonged, positive feedback to S, since the responding of both stimulus and subject in this particular group was quite consistent throughout the experimental

sessions. Although the Hab. male stimulus typically displayed and vigorously interacted with the subject for the first few minutes, the threat display and attention directed toward the subject waned extremely rapidly in this particular stimulus. Even though no quantitative measurements were taken, the differential responding of the Unhab. male and Hab. male stimuli was extremely evident beyond any question. Most Unhab. male stimuli were still vigorously responding to the subjects even at the end of the second session. The differences between the two live male stimuli (Unhab.-Hab.) therefore vary along a feedback dimension, including the intensity of the threat display, changes in body color, movement, etc. The Hab. male stimulus was, however, mobile, three dimensional and somewhat variable in its movements which made it a better elicitor than the two dimensional Cut-out stimulus.

The most difficult difference to explain is that between the Unhab. male stimulus and the Mirror stimulus. A Mirror gives invariable feedback of a subject's actions. That is, whatever the subject does is immediately reflected in the mirror. If the fish raises his gills at his "adversary," the "adversary" erects his gills at the same moment and in exactly the same way. As Peeke and Peeke (1970) state with respect to this simultaneous feedback situation:

While this might happen in a real encounter, it would certainly not be a frequent occurrence. If the behavior elicited in the animal is facilitated by having



his adversary perform the same act (e.g., if the probability of biting is increased by having just been bitten at) then the mirror image situation is one of perfect positive feedback which will increase the rate of the elicited response at a steeply accelerated rate (p. 233).

Another problem with the Mirror stimulus, especially with respect to the display of Betta splendens concerns the relative spatial orientation of two displaying fish. While the subject is broadside to the "adversary" in the mirror, the "adversary" is also broadside to the subject. Any changes on the part of the subject will bring about the exact same changes in his "adversary." This situation is extremely rare as Simpson (1968) demonstrated in his extensive research on the display of the Betta. He found that when two fish are displaying at each other, a frontal position in one fish usually elicits a broadside orientation in the other, and vice-versa. It is an extremely rare occurrence that both fish remain in a face-to-face position, or a broadside-to-broadside position. In general, as Gallup (1968) has stated, mirror image stimulation provides for many situations hardly ever encountered in the natural habitat.

The Unhab. male stimulus simulates most closely the type of adversary which would be encountered in a natural situation. It vigorously responds to a subject "adversary," but not in a perfectly invariant way as does the perfectly fed-back Mirror stimulus. The Unhab. male provides a source

of variable feedback in that it displays and interacts with the subject, but does not duplicate its every move. With regard to stimulus variability, Lovibond (1969) found that the degree of habituation of the orienting response (OR) to multiple stimulus sequences is a negative function of the uncertainty in the stimulus series. The relation between uncertainty of stimulus and the degree of habituation seems to be a curvilinear one. According to Sokolov's theory of habituation, a "neuronal model" of a stimulus which is variable in its attributes, is difficult to form as compared to some invariant stimulus (Lynn, 1966). Lorenz (1965) has also spoken on the problem, stating that the ease with which habituation of a response is attained in the laboratory as compared with a field situation is due to the relative constancy of the experimental situation, itself. The Mirror stimulus is a better elicitor than the Hab. male stimulus because the Mirror "adversary" responds back as long as the subject responds, providing positive feedback to the subject. The Hab. male stimulus responded only briefly, and usually appeared as rather innocuous (fins folded, pale color, and ignoring direct contact with the subject). Apparently the constancy of feedback inherent in the Mirror stimulus has some eliciting qualities, itself.

Habituation, Retention, and
Recovery of Habituation

Perhaps the most important finding in the present study was that the degree of habituation and retention of habituation is related to the initial eliciting strength of the stimulus. It should be mentioned here that for both of the threat components (GD and FD) that exhibited systematic habituation, the greatest absolute amount of habituation was associated with the Unhab. male group followed by the Mirror, Hab. male and Cut-out groups, respectively. That is, the greater the initial eliciting strength of a stimulus (as measured by the first 10 minute observation) the greater the absolute amount of habituation. The absolute amount of habituation is defined as the initial response level minus the terminal response level. This way of measuring habituation obviously does not take into consideration the different initial response levels to different elicitors. In other words, the response to a strong elicitor (measured by initial response level) has a greater potential absolute decrement than the responses elicited by stimuli of lesser initial strength (See Figure 6 for an example).

A proportional measure of decrement, using the initial response level as the anchor point, corrects for the different initial eliciting stimulus strengths. When these proportional measures of habituation were used in

the present study for GD and FD data, the relation to eliciting stimulus strength was different from that when the absolute amount of habituation was used as the measure of habituation. It was found that initial eliciting stimulus strength was inversely related to the proportion of across session decrement. That is, the stronger the initial response level, the smaller the across session decrement. The proportion of retention of habituation after a 24 hour rest interval was also related to initial eliciting stimulus strength: the stronger the initial level of response, the smaller the proportion of retention after 24 hours. The proportion of recovery of habituation after 24 hour rest was, therefore, positively related to initial stimulus strength.

A Theoretical Framework

The results of this study using proportional data, nicely fit an elicitation and competing response theory of habituation like that of Ratner (1970). According to this theoretical framework, the elicitation of a response is followed by a refractory period during which response strength diminishes. This refractory period is a consequence of temporary changes in sensory, transmission, and effector processes. Also affecting the originally elicited response are stimulus conditions that operate concurrently with the original eliciting stimulus. This concurrent

stimulation may facilitate or interfere with the originally elicited response, depending on the stimulus and the topography of the responses elicited by concurrent stimuli.

Habituation involves the intrusion of competing responses that arise from the action of stronger (more dominant) eliciting stimuli during the refractory periods. The dominance of the competing response may be temporary but if a number of such responses are elicited they may combine to equal the strength of the original response and thus cause habituation (Ratner, 1970, ch. 3).

Therefore, the greater the strength of the eliciting stimulus, the less the degree of habituation. This supposition follows from the argument that the greater relative strength of the elicitor will be dominant over other concurrent stimuli eliciting competing responses. This portion of the theory seems supported by the results of the present experiment: the greater the initial eliciting stimulus strength the smaller the proportion of habituation. As previously mentioned, however, increasing initial eliciting stimulus strength was associated with an increasing absolute amount of habituation. This finding concurs with the findings of much previous research involving many different organisms and S-R systems (Martin and Melvin, 1964; Miller and Murray, 1966; Askew, 1969; Melvin and Cloar, 1969; Peeke, 1969). Although Ratner's (1970) theory concerns itself with relative amounts of decrement, it might be restated as follows: the greater the initial eliciting stimulus strength, the greater the absolute amount of

decrement and the smaller the relative amount of habituation. These contentions obviously require further validation through research using different organisms and S-R systems. The proposition that greater eliciting stimulus strength is associated with a relatively smaller amount of retention of habituation also was supported by the data of the present study.

Non-Habituating Indices of the Display

A few comments are necessary, at this point, in order to explain the lack of systematic habituation for all stimulus groups when using GF or FF as the indices of decrement. Apparently the frequency measures operate along a different time dimension when compared to the quickly habituating duration measures (GD and FD). That is, if the experimental sessions were of longer duration, the frequency measures might have shown systematic habituation. Evidence for this supposition is available from Clayton and Hinde (1968). Using male Bettas, they found that gill cover erection frequency showed little systematic change during the first day (26 minute observation) of exposure to a mirror image, but showed a significant decrement as early as the second day of their ten day exposure period. What is of importance in the present experiment is the fact that different threat components were differentially reflective of habituation when the same test period length was used.

Therefore, whether or not habituation of a component occurs is related to both the duration of stimulus exposure and the particular way of measuring the component.

It was also noticed that there was an increment in both within and across session responding for the GF and FF data for the group exposed to the unhabituated male stimulus (Unhab. male). Since this stimulus was the strongest elicitor, the responses were much more resistant to habituation. Hinde (1954) has shown that habituation involves both incremental and decremental processes, with incremental processes predominating during the early phases of stimulus exposure. Apparently the Unhab. male group exhibited most conspicuously the incremental components of the habituation processes during the time span of sessions used in the present study.

Relation Among the Indices of the Display

There were large individual differences in responding within each stimulus group and for all measures used in the present study. These highly reliable individual differences are a general characteristic of the habituation process (Ratner, 1970). However, these individual differences were overshadowed by the group differences in responding associated with different stimulus conditions. For instance, air gulping frequency (AG) was strongly affected



by the different elicitors: the Unhab. male stimulus elicited the highest level of AG responding, followed by the Mirror, Hab. male and Cut-out stimuli, respectively. Perhaps of greater significance was the fact that no significant changes in the level of responding were noticed for this particular measure. This response is a purported measure of activity level (Simpson, 1968) and thus was not expected to show a decrement during the present experiment. The data confirmed this expectation. That AG is not an integral component of the threat display was shown by the uniformly negligible correlations with the other threat measures. However, the four other measures (GF, GD, FF, FD) were highly correlated in a positive direction, reflecting the integral relation among these components of the Betta's threat display.

Controls for Adaptation and Fatigue

The consistency of the AG data also provided evidence that the decrement in GD and FD responding was not due to the effects of general fatigue, since this component remained fairly constant throughout the duration of the experiment.

Other factors support the interpretation of the response decrement (GD, FD) in the present study as being due to habituation rather than sensory adaptation and/or general fatigue. First of all, significant retention of

habituation after a 24 hour rest period rules out these effects. Also, immediately upon the termination of session 2, any S which either had not displayed to the appropriate elicitor during the experimental sessions or had approached a near-zero level of responding, was exposed to an unhabituated male stimulus (Unhab. male) placed for 30 seconds in the same compartment as the S. Every S which fitted into the categories described above, responded immediately, completely and almost constantly during the 30 second post-experimental session. Therefore, as far as the Ss which did not respond at all during the experiment are concerned (almost all were in the Cut-out group) the lack of responding was not due to an inability to perform the complete threat display.

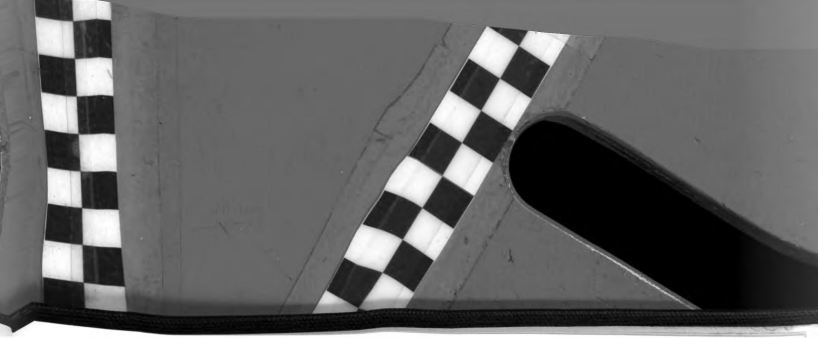
The Threat Display as a
Consummatory Response

Of particular interest is interpreting the results of the present experiment when the fighting sequence of the male Betta is placed in the appetitive, consummatory, and post-consummatory framework of Denny and Ratner (1970). The threat display probably fits somewhere in the middle of the consummatory sequence, culminating in direct attack (biting, tail-slashing, etc.). Although quantitative measurements were not taken, it is interesting to note that the only instances of biting at the partition between the

stimulus and S were noticed in Ss in the Unhab. male group and the Mirror group (the two strongest elicitors). Biting by the Unhab. male group was especially apparent. Stronger elicitors may elicit the complete consummatory sequence in less time than weaker stimuli. Perhaps weaker stimuli do not even elicit the late components of the consummatory sequence at all. These speculations are particularly amenable to experimental validation.

Conclusions

The threat display of male Betta splendens is an easily measured, highly reliable phenomenon, consisting of many different S-R components. It was found that certain components of the display are subject to habituation and that the decrement is retained over a 24 hour period. For those threat components that exhibited systematic habituation (GD, FD), there was a strong relation between the initial eliciting strength of the various threat elicitors and the absolute and relative amounts of habituation, and retention of habituation. Portions of Ratner's (1970) elicitation and competing response theory of habituation were supported.



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APPENDIX

Table A. --Pearson rs for Dependent Variables in Session 1 and Session 2; Unhabituated Male Stimulus Group ($N = 10$).

	AG1	AG2	GF1	GF2	GD1	GD2	FF1	FF2	FD1	FD2
AG1										
AG2	**									
	.858									
GF1	.240	.136								
GF2	.060	.048	**							
			.932							
GD1	-.018	-.080	*	**						
			.742	.778						
GD2	-.106	-.188	*	*	**					
			.660	.754	.924					
FF1	.132	.110	**	.746	.496	.352				
			.854	*						
FF2	.072	.094	**	**	*	.606	*			
			.866	.904	.738		.874			
FD1	.120	.098	*	**	**	*	.428	*		
			.694	.842	.800	.698		.724		
FD2	.028	-.098	.546	*	.620	* .688	.420	.594	**	.862
				.634						

* $p < .05$

** $p < .01$

Table B. --Pearson rs for Dependent Variables in Session 1 and Session 2;
Mirror Stimulus Group ($N = 10$).

	AG1	AG2	GF1	GF2	GD1	GD2	FF1	FF2	FD1	FD2
AG1										
AG2	**									
	.858									
GF1	.258	-.014								
GF2	.188	-.024	**							
			.876							
GD1	.226	.018	**	**						
			.920	.954						
GD2	.104	-.114	*	**	**					
			.744	.918	.872					
FF1	.414	.342	*	*	*	.420				
			.684	.652	.670					
FF2	.498	.416	*	*	.592	.448	*			
			.652	.686			.758			
FD1	* .682	.396	.338	.136	.080	.020	.414	*		
							.686			
FD2	.538	.408	.492	.356	.326	.244	.522	**	**	
							.844	**	.888	

* $p < .05$ ** $p < .01$

Table C. --Pearson rs for Dependent Variables in Session 1 and Session 2;
Habituated Male Stimulus Group (N = 10).

	AG1	AG2	GF1	GF2	GD1	GD2	FF1	FF2	FD1	FD2
AG1										
AG2	.556									
GF1	-.192	.188								
GF2	-.186	.162	**							
GD1	-.180	.156	**	.948						
GD2	-.198	.150	**	.994	**					
FF1	-.328	.112	**	.648	.830	*	.652			
FF2	-.200	.136	**	.966	.946	**	.992	.606		
FD1	-.280	.090	**	.874	.916	**	.902	**	.890	
FD2	-.194	.136	**	.966	.944	**	.990	**	.996	.880

*p < .05

**p < .01

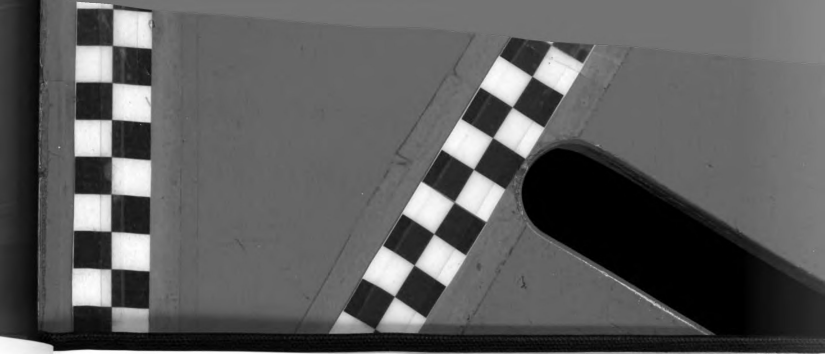
Table D. --Pearson r s for Dependent Variables in Session 1 and Session 2;
Cut-Out Stimulus Group ($N = 10$).

	AG1	AG2	GF1	GF2	GD1	GD2	FF1	FF2	FD1	FD2
AG1										
AG2	.402									
GF1	-.098	.374								
GF2	a	a	a							
GD1	-.080	.396	** .996	a						
GD2	a	a	a	a						
FF1	-.046	.414	** .990	a	** .992	a				
FF2	-.060	.468	** .990	a	** .994	a	** .988			
FD1	-.046	.410	** .988	a	** .990	a	** .998	** .988		
FD2	-.058	.440	** .990	a	** .994	a	** .988	** .998	** .988	

^aNo response.

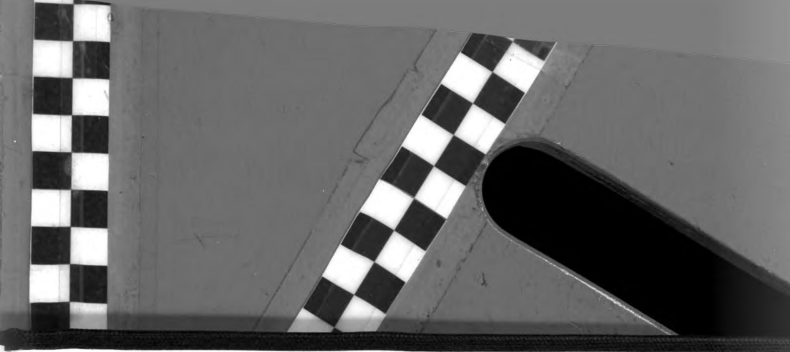
* $p < .05$

** $p < .01$









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