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OBJECT DISCRIMINATION IN A WEAKLY ELECTRIC FISH,
GNATHONEMUS PETERSII (MORMYRIFORMES)

City University of New York PH.D. 1979

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OBJECT DISCRIMINATION IN A WEAKLY ELECTRIC FISH, <u>GNATHONEMUS</u> <u>PETERSII</u> (MORMYRIFORMES)

by

ANTOINETTE DE FAZIO

A dissertation submitted to the Graduate
Faculty in Psychology in partial fulfillment
of the requirement for the degree of
Doctor of Philosophy, The City University
of New York.

1979

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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TABLE OF CONTENTS

Abstract

OBJECT DISCRIMINATION IN A WEAKLY ELECTRIC FISH, GNATHONEMUS PETERSII (MORMYRIFORMES)

by

Antoinette De Fazio

Advisor: Dr. Peter Moller

Gnathonemus petersii, a weakly electric African freshwater fish, was tested under a habituation-dishabituation procedure to determine if it could discriminate among different sized plastic cubes or spheres that were lowered into the aquarium. Each of 18 fish were presented with the same object for four 10 min. habituation trials. Changes in the electrical organ discharge (EOD) and the following motor activities were observed - touching the object with the head or the body, and swimming forward or backwards. Reliable decreases in activity, habituation occurred. On the fifth trial, the test trial, the same stimulus or a stimulus different in size from the habituation stimulus was presented. On this trial, an increase in activity, disinhibition,in the presence of a stimulus differing in size from the habituation stimulus was taken as evidence of discrimination. This was most clearly seen following habituation with a medium sized object. Differences in the EOD in response to a change in the size of the object were less clear, although statistically reliable differences were found in the EOD repetition rate when the first 20 sec. following the introduction of a stimulus into the aquarium were compared to a similar period during which an object was not introduced. This alteration appeared to be a startle or orienting response.

In three _G. petersii_ the electric organ was surgically rendered inoperative (electrically "silent" fish). Two additional individuals were sham-operated. The habituation-dishabituation technique was used before and after surgery to determine whether the fish could discriminate between small and large spheres. Subjects were tested in daylight, in dim light, and under a no light condition. Fish who were electrically silenced appeared able to discriminate between different sized objects only under dim light. Discrimination was not observed in the absence of light or in daylight. Sham-operated fish could discriminate under all three conditions. These results suggest that intact fish use both their visual and electrosensory systems in object discrimination.

ACKNOWLEDGEMENTS

It is impossible to express thanks to all those friends who helped me complete this thesis. When I was collecting data, two undergraduate students, Laine Jastrum and Annette Kirschgessner, gave many hours of their free time to observe fish with me.

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I would like to thank all the faculty of the Biopsychology Department, Hunter College, CUNY, for their support in developing my mind over the years. Also, the department deserved thanks for supplying financial support over many years.

Special thanks are due to my advisor, Dr. Peter Moller, who has provided guidance and support over the years I was a student. I thank Dr. Sheila Chase, Dr. P. H. Zeigler, Dr. C. Lavett Smith, of the Ichthyology Department of the American Museum of Natural History, and Dr. Phyllis Cahn of C. W. Post College for their advice and encouragement over the years.

Ultimately, the person who suffered the most during the production of this thesis was Dr. James Tyler, who lost sleep when I did, and worried when I did, but who now, I hope, will rejoice as I do.

LIST OF TABLES

LIST OF ILLUSTRATIONS

GENERAL INTRODUCTION

A small number of marine and freshwater fish families have developed the ability to generate electric discharges by means of specialized electrogenic tissue, so-called electric organs (reviewed by Fessard 1958; Bennett 1971a). While the powerful electric discharge volleys of the electric eel, Electrophorus electricus, the electric rays, Torpedo spp. and the electric catfish, Malapterurus electricus serve in the fish's predatory behavior (Bauer 1968, 1979; Belbenoit and Bauer 1972; Belbenoit et al. 1979) the weak electric impulses emitted by the neotropical gymnotids and the African mormyriform fish appear to serve only as social signals in communication, schooling and in electrolocation behavior (reviewed by Lissmann 1958; Scheich and Bullock 1974; Heiligenberg 1977; Moller 1976; Moller and Bauer 1973, 1979).

The mormyrid Gnathonemus petersii has been the subject of a number of studies investigating primarily the role of the electric organ discharges (EODs) as communication signals (e.g. Moller 1970; Moller and Bauer 1973; Bauer 1972; Kramer 1974; Bell et al. 1974; Russell et al. 1974). The present paper explores the discriminative capacities of the mormyrid G. petersii through a study of its motor behavior and changes in the EOD induced by the introduction of objects into its environment.

Most earlier studies on object discrimination and electrolocation in mormyrid fish have concentrated mainly on the involvement of the electrosensory system in the fish's discrimination behavior. None of these studies have attempted to include and investigate the contribution of other sensory modalities. In the present study, an attempt was made to examine the contribution of the EOD and vision to the ability of the fish to discriminate between objects of different geometrical configurations but the same electrical conductivity.

It is known that a variety of environmental stimuli such as the onset of aeration, mechanical disturbance of the substratum, of the walls, sound, electric current from recording electrodes, lightning or discharges from other electric fish, as well as the introduction into the aquarium of objects different in conductivity from water, all alter the EOD repetition rate. Such changes of EOD patterns have never been systematically examined in studies of object discrimination by these fish.

This research project had the following objectives:

Experiment I: A paradigm was developed to examine changes in *G. petersii's* motor behavior and EOD in response to stimuli differing in size, but not in conductivity.

Experiment II: This paradigm was used to examine the contributions of the electrosensory and visual systems to the discrimination among such stimuli by *G. petersii*.

EXPERIMENT I:

SIZE DISCRIMINATION IN G. PETERSII USING A HABITUATION-DISHABITUATION PARADIGM

The limited number of publications on object discrimination in *G. petersii* is partially due to the difficulty encountered when traditional methods of studying fish discrimination are used. (For a review of these methods, see Gleitman and Rozin 1971.)

For example, a high level of arousal is produced in *G. petersii* when food or other objects are introduced into the aquaria. When I attempted to shape lever pressing for a food reward, the fish avoided or bit the stick used to guide it to a lever which dispensed tubifex worms. Moreover, *G. petersii* ceased eating when stressed and often could not be induced to accept food even following accidental depression of the lever.

To avoid the above difficulties, a habituation-dishabituation paradigm was developed. The high level of arousal when an object was introduced could then be used to obtain behavioral responses. Orienting and exploratory behaviors which were discrete and mutually exclusive were sought. Behaviors studied here included touching the object with the head, body or tail, swimming backward or forward, and the EOD.

A habituation-dishabituation paradigm has been used by Bridger (1961) to study human neonate psychophysics and has recently been used in the study of tonal frequency discrimination in newly hatched chicks (Rubel and Rosenthal, 1975). In a habituation-dishabituation paradigm, the same stimulus is presented to the subject over a series of trials and the rate of occurrence of some behavior is recorded over trials.

Habituation - a response decrement over trials - can be described by the amount of decline in response over trials or by the number of presentations of the stimulus required to reach a zero level of response (Peeke and Peeke 1973; Figler, 1970). The former method was used in the present experiment. After habituation is obtained, a stimulus differing along some parameter (e.g. size) is introduced. An increase in response rate over that expected if the change had not been made may be taken as evidence that this stimulus change has been discriminated. Thus, dishabituation may be used as evidence of discrimination.

The electric organ discharge (EOD) had not previously been considered as a dependent variable in the study of discrimination by weakly electric fishes, although discrimination had been studied in these fishes (Lissmann 1958; Lissmann and Machin 1958; Belbenoit 1970; Harder 1972; Heiligenberg 1973, 1975). The adequate definition of a meaningful unit of behavior for the EOD had hindered exploration of this parameter, since the repetition rate of _G_. _petersii_ is variable. Researchers have used various statistical methods to show patterns of stability and changes in the EOD of _G_. _petersii_ over time. Bauer (1974), for example, claimed that _G_. _petersii_ emitted its entire discharge repertoire (temporal discharge pattern) in a three minute time period when stationary, and that the pattern of discharge was stable over days. Malcolm (1976) observed patterns of stability in _G_. _petersii_ such that fish produced patterns of discharges over days that were consistently skewed to the left or right or were bimodal in appearance with interval histograms.

In the present study, interval histograms that summarized activity over a three minute period were obtained when the fish was undisturbed, as well as when a stimulus was introduced into the aquarium. Changes in the number of responses over short periods of time were also analyzed.

Method

Subjects

Eighteen G. petersii, African freshwater, weakly electric, mormyrid fish were purchased from local suppliers. The fish ranged in length (tip of snout to fork of tail) from 16 to 20 cm, with a mean length of 18 cm. The fish were housed individually in 19 liter (five gallon) aquaria in the greenhouse of the American Museum of Natural History, New York. The ambient temperature in the greenhouse ranged from 23 to 43° C. Water temperatures ranged from 21 to 27°C with a mean temperature of 25° C. Water conductivity ranged from 275 to 500μS. cm^{-1}. Tubifex worms were available at all times as food in the aquaria.

Apparatus and Stimuli

Spheres and cubes of three sizes were used as stimuli. The spheres were 1.4, 2.6 and 3.3 cm in diameter, and the cubes were 1.2, 1.9 and 3.0 cm per facet. These clear plastic cubes and spheres will be referred to hereafter as small, medium and large. These objects were suspended from monofilament fishing tackle (5 lb. test) and lowered into the center of the aquarium to a level of 2 cm above the substream. The EODs of these fish were detected by carbon electrodes glued diagonally and opposite each other in the aquaria. The EODs were preamplified, recorded (Tandberg Series 6X tape recorder), and then analysed with a Synax desk computer.

Procedure

Prior to testing, each fish had been in an aquarium for at least 24 hours. Each fish was used for three sessions. A 10 minute recording of the EOD of the undisturbed fish was made before each session. A session consisted of five trials.

On the first trial, the habituation stimulus (H_1) was lowered into the aquarium for 10 minutes and the EOD as well as other behaviors were recorded by the experimenter. These behaviors included touching with the head and proboscis toward the object (TH), touching with the body (TB), touching with the tail (TT), backward swimming (BW) directed toward and past the object, and forward swimming (FW) directed toward and past the object. These behaviors were discrete and distinguishable to the experimenter.

After the introduction of the habituation stimulus for a 10 minute recording period, it was removed for a five minute intertrial interval during which data were not recorded. A session consisted of five such trials. Half of the fish were exposed only to cubes as stimuli; and the other half exposed only to spheres. In a habituation session, the same stimulus object was introduced five times (H_1 - H_5). In a test session, the same stimulus was presented four times (H_1 - H_4), and on the test trial, a test stimulus different in size was presented for 10 minutes. Six fish were exposed to the small cube or sphere, six were exposed to the medium cube or sphere, and six were exposed to the large cube or sphere as habituation stimuli. The habituation and test stimuli presented to each fish are listed in Tables 1 and 2, together with the shape and size of the objects. Stimuli for habituation and test sessions were presented in a partially randomized block to control for sequential effects.

TABLE 1

Size of the habituation (H_{1-5}) and test stimuli presented to each of 9 fish and the order of presentation of the sessions.

Size of Habituation Stimulus	Fish #	First Session	Second Session	Third Session
Cubes				
	22	3 cm H_{1-5}	3 cm H_{1-4} 1.9 cm Test	3 cm H_{1-4} 1.2 cm Test
Large (3 cm)	14	3 cm H_{1-4} 1.9 cm Test	3 cm H_{1-4} 1.2 cm Test	3 cm H_{1-5}
	30	3 cm H_{1-4} 1.2 cm Test	3 cm H_{1-5}	3 cm H_{1-4} 1.9 cm Test
	15	1.9 cm H_{1-4} 3 cm Test	1.9 cm H_{1-5}	1.9 cm H_{1-4} 1.2 cm Test
Medium (1.9 cm)	32	1.9 cm H_{1-5}	1.9 cm H_{1-4} 1.2 cm Test	1.9 cm H_{1-4} 3 cm Test
	27	1.9 cm H_{1-4} 1.2 cm Test	1.9 cm H_{1-4} 3 cm Test	1.9 cm H_{1-5}
	16	1.2 cm H_{1-4} 3 cm Test	1.2 cm H_{1-4} 1.9 cm Test	1.2 cm H_{1-5}
Small (1.2 cm)	24	1.2 cm H_{1-4} 1.9 cm Test	1.2 cm H_{1-5}	1.2 cm H_{1-4} 3 cm Test
	34	1.2 cm H_{1-5}	1.2 cm H_{1-4} 3 cm Test	1.2 cm H_{1-4} 1.9 cm Test

TABLE 2

Size of the habituation (H_{1-5}) and test stimuli presented to each of 9 fish, and the otder of presentation of the sessions.

Size of Habituation Stimulus	Fish #	First Session	Second Session	Third Session
<u>Spheres</u>	17	3.3 cm H_{1-5}	3.3 cm H_{1-4} 2.6 cm Test	3.3 cm H_{1-4} 1.4 cm Test
Large (3.3 cm)	20	3.3 cm H_{1-4} 2.6 cm Test	3.3 cm H_{1-4} 1.4 cm Test	3.3 cm H_{1-5}
	29	3.3 cm H_{1-4} 1.4 cm Test	3.3 cm H_{1-5}	3.3 cm H_{1-4} 2.6 cm Test
	26	2.6 cm H_{1-4} 3.3 cm Test	2.6 cm H_{1-5}	2.6 cm H_{1-4} 1.4 cm Test
Medium (2.6 cm)	31	2.6 cm H_{1-5}	2.6 cm H_{1-4} 1.4 cm Test	2.6 cm H_{1-4} 3.3 cm Test
	25	2.6 cm H_{1-4} 1.4 cm Test	2.6 cm H_{1-4} 3.3 cm Test	2.6 cm H_{1-5}
	19	1.4 cm H_{1-4} 3.3 cm Test	1.4 cm H_{1-4} 2.6 cm Test	1.4 cm H_{1-5}
Small (1.4 cm)	28	1.4 cm H_{1-4} 2.6 cm Test	1.4 cm H_{1-5}	1.4 cm H_{1-4} 3.3 cm Test
	33	1.4 cm H_{1-5}	1.4 cm H_{1-4} 3.3 cm Test	1.4 cm H_{1-4} 2.6 cm Test

Results

Figure 1 shows the mean percent of the total number of responses (TNR) for three different sized cubes used as habituation stimuli. TNR includes touching with the head, body or tail and backward and forward swimming. This information for the nine fish that were presented with three different sized spheres is given in Figure 2. The summaries of data for each fish were obtained by summing the total number of responses in each 10 minute trial for each fish. There were three sessions for each of the 18 fish. Trials H_1 - H_4 were the same for an individual fish on both habituation and test sessions. Therefore, there were three sets of data for trials H_1 - H_4. The TNR on H_5 was used only for the session on which this stimulus was the same as the habituation stimulus.

For each trial, the percent of the total number of responses was found, in order that fish showing different rates of response could be compared. Figures 1 and 2 also show the results on test trials for each fish. The total number of responses on each trial was treated similarly for touching with the head (TH), touching with the body (TB), and backward swimming (BW), as seen in Figures 3, 5 and 7 for cubes and 4, 6 and 8 for spheres.

Figures 1-8 provide a descriptive summary of the course of habituation and dishabituation with cubes and spheres for 18 fish. Inspection of these figures suggests that habituation occurred. This was confirmed by an analysis of variance performed on the total number of responses from trials H_1 - H_4. Table 3 shows the results of this

Figure 1. Mean percent of the total number of responses for H_1 - H_4 and test for three sizes of cubes used as habituation stimuli. Large = ● , medium = ■ , small = ▲ .

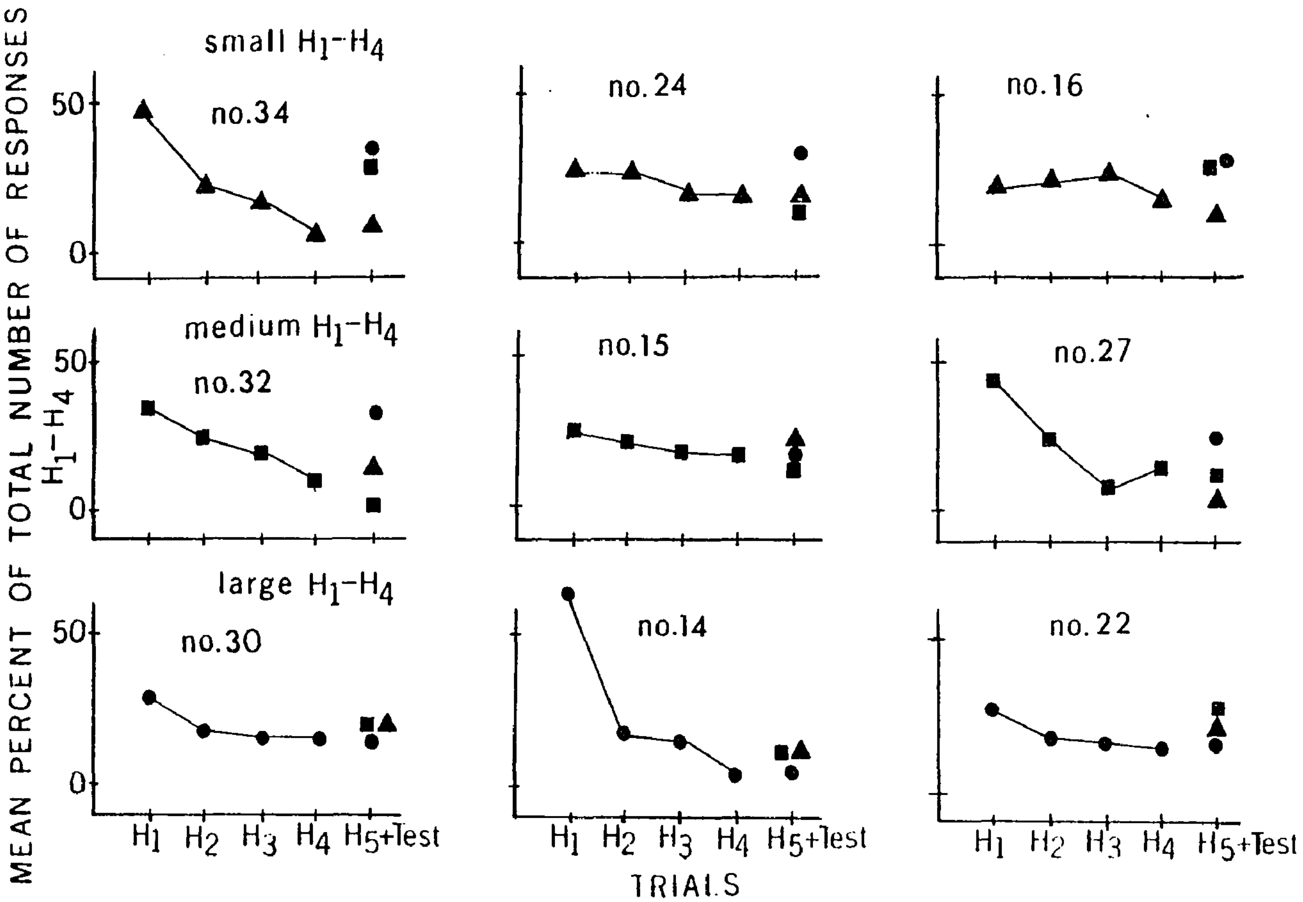

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
H_1–H_4
small H_1–H_4
medium H_1–H_4
large H_1–H_4
no.34
no.24
no.16
no.32
no.15
no.27
no.30
no.14
no.22
50
0
H_1 H_2 H_3 H_4 H_5+Test
TRIALS

Figure 2. Mean percent of total number of responses for H_1 - H_4 and test for three sizes of spheres used as habituation stimuli. Large = ●, medium = ■, small = ▲.

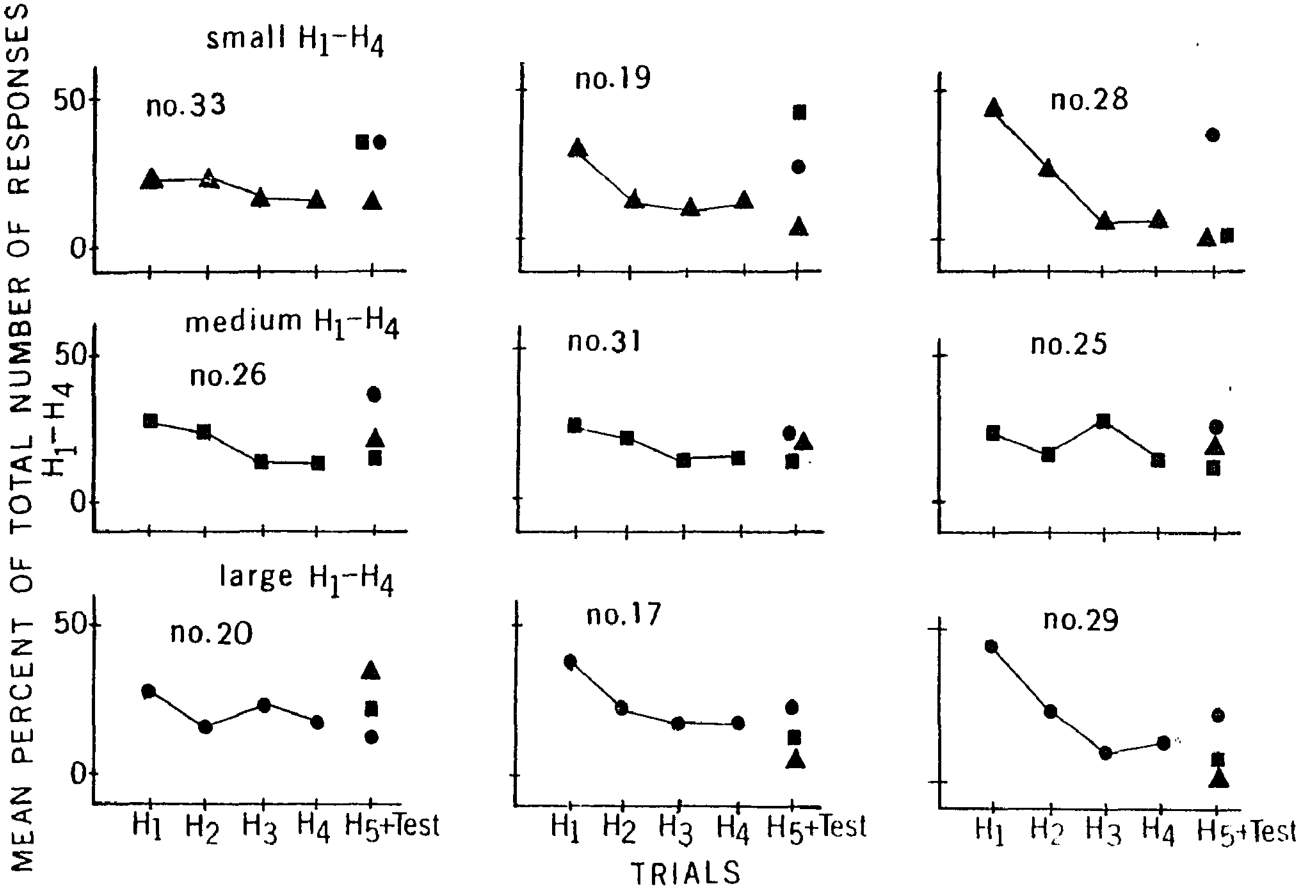

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
H1-H4
small H1-H4
medium H1-H4
large H1-H4
no.33
no.19
no.28
no.26
no.31
no.25
no.20
no.17
no.29
50
0
H1 H2 H3 H4 H5+Test
TRIALS

Figure 3. Mean percent of total number of touching with the head for H_1 - H_4 and test for three sizes of cubes used as habituation stimuli. Large = ●, medium = ■, small = ▲.

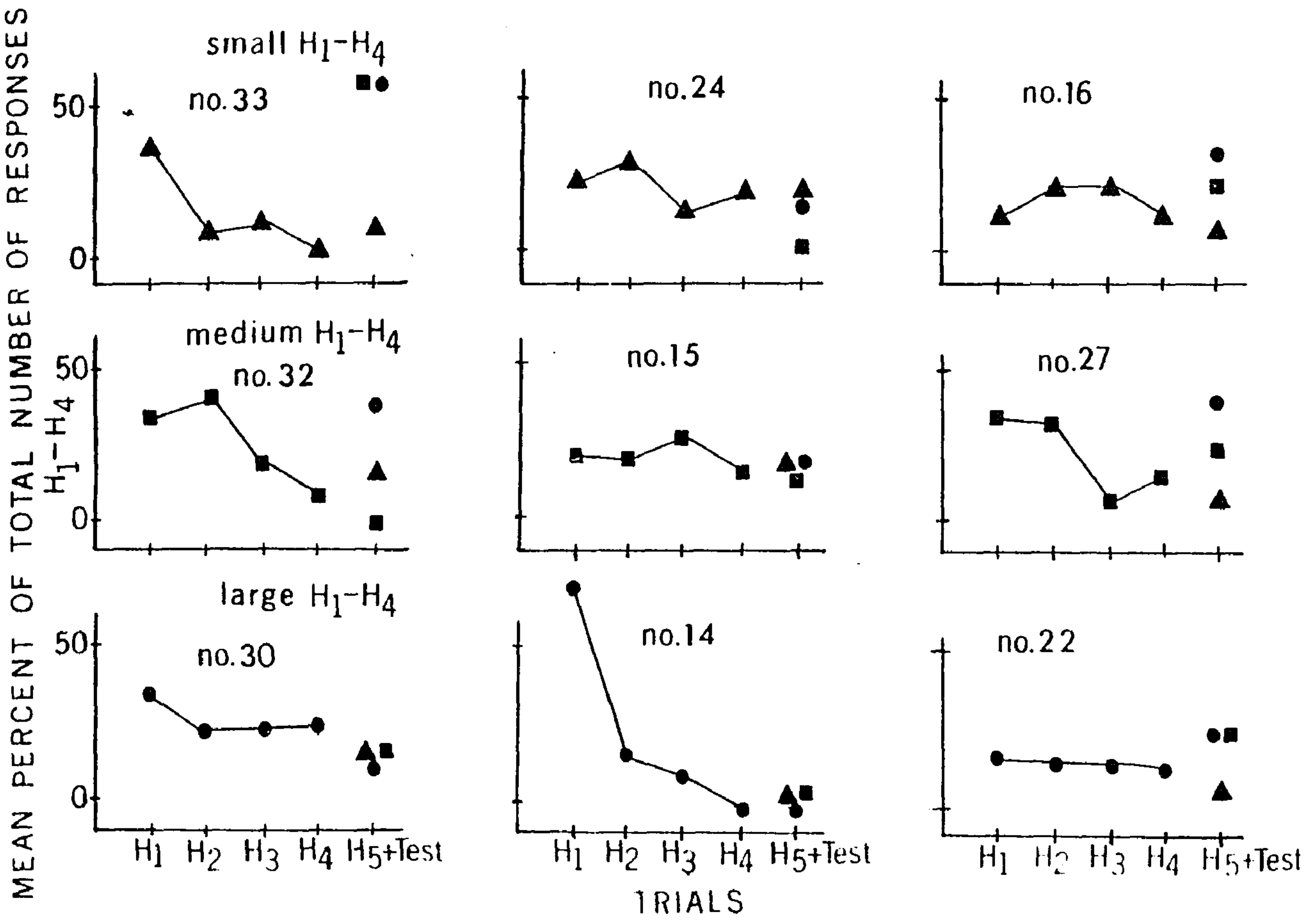

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
H1-H4
small H1-H4
no.33
medium H1-H4
no.32
large H1-H4
no.30
no.24
no.15
no.14
no.16
no.27
no.22
50
0
H1 H2 H3 H4 H5+Test
TRIALS

Figure 4. Mean percent of total number of touching with the head for H_1 - H_4 and test for three sizes of spheres used as habituation stimuli. Large = ● , medium = ■ , small = ▲.

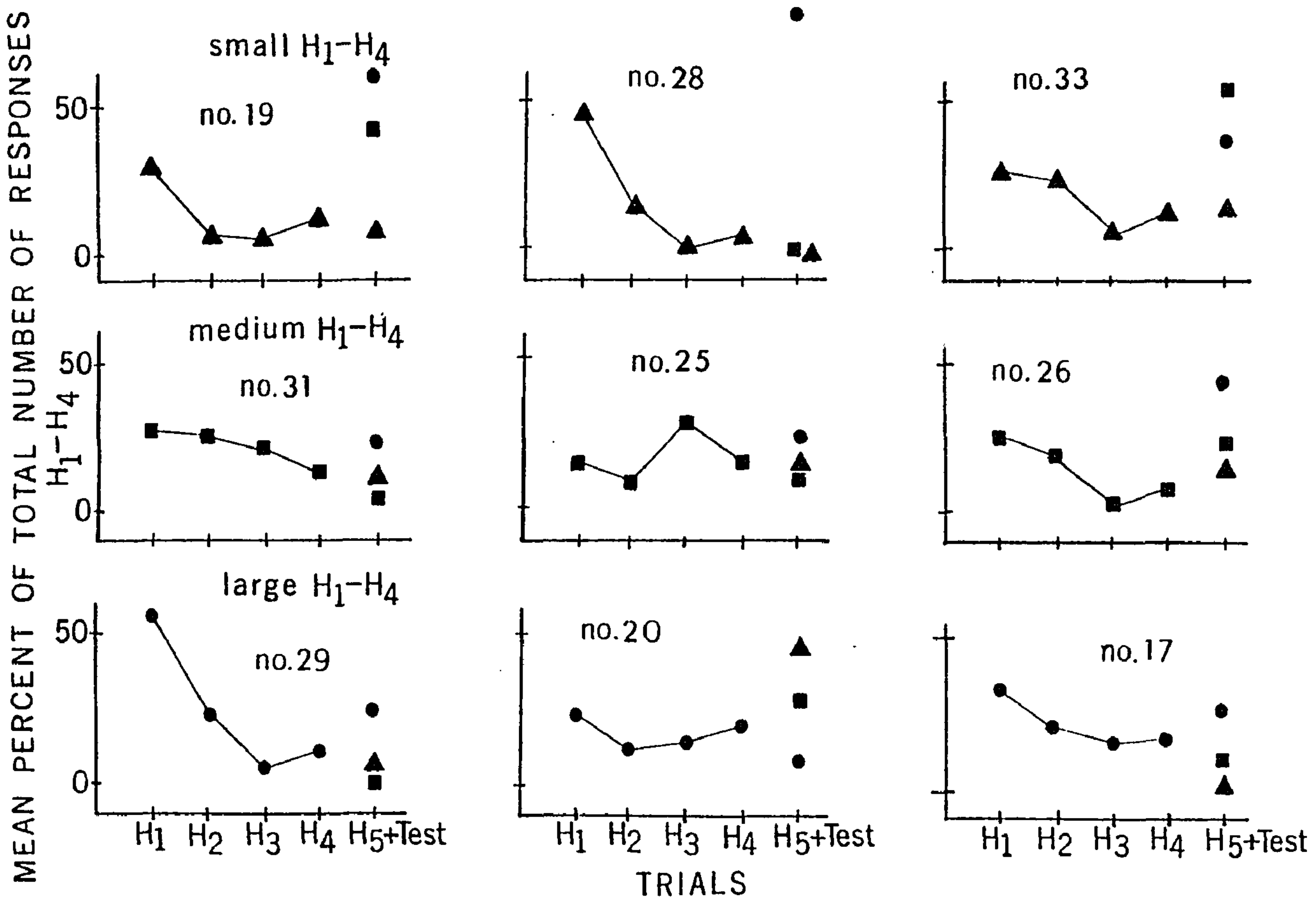
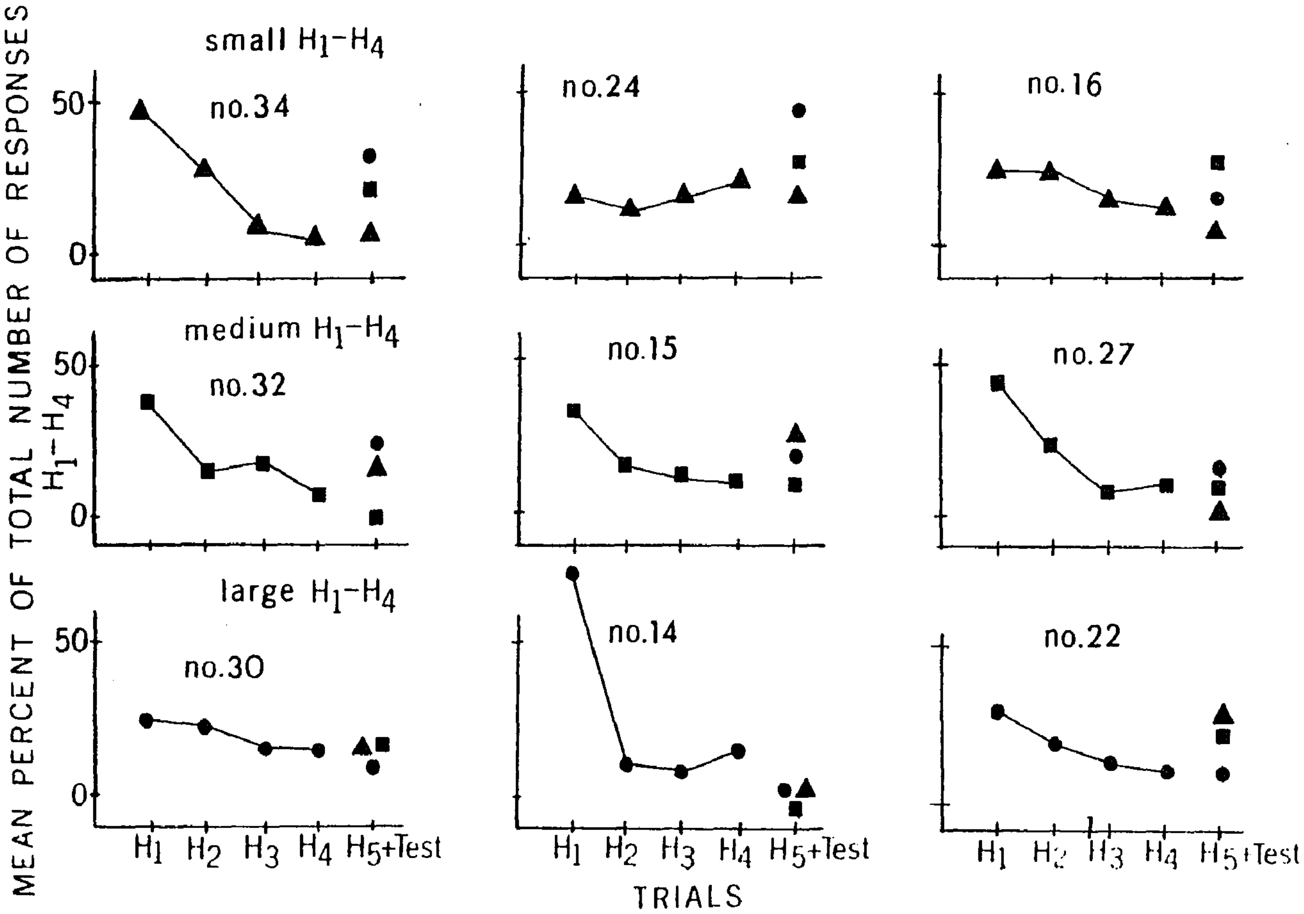

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES H_1–H_4
small H_1–H_4
no. 19
no. 28
no. 33
medium H_1–H_4
no. 31
no. 25
no. 26
large H_1–H_4
no. 29
no. 20
no. 17
50
0
H_1 H_2 H_3 H_4 H_5+Test
TRIALS

Figure 5. Mean percent of total number of touching with the body for H_1 - H_4 and test for three sizes of cubes used as habituation stimuli. Large = ●, medium = ■, small = ▲.



MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
small H_1–H_4
medium H_1–H_4
large H_1–H_4
H_1–H_4
50
0
no.34
no.24
no.16
no.32
no.15
no.27
no.30
no.14
no.22
H_1 H_2 H_3 H_4 H_5+Test
TRIALS

Figure 6. Mean percent of total number of touching with the body for H_1 - H_4 and test for three sizes of spheres used as habituation stimuli. Large = ●, medium = ■, small = ▲.

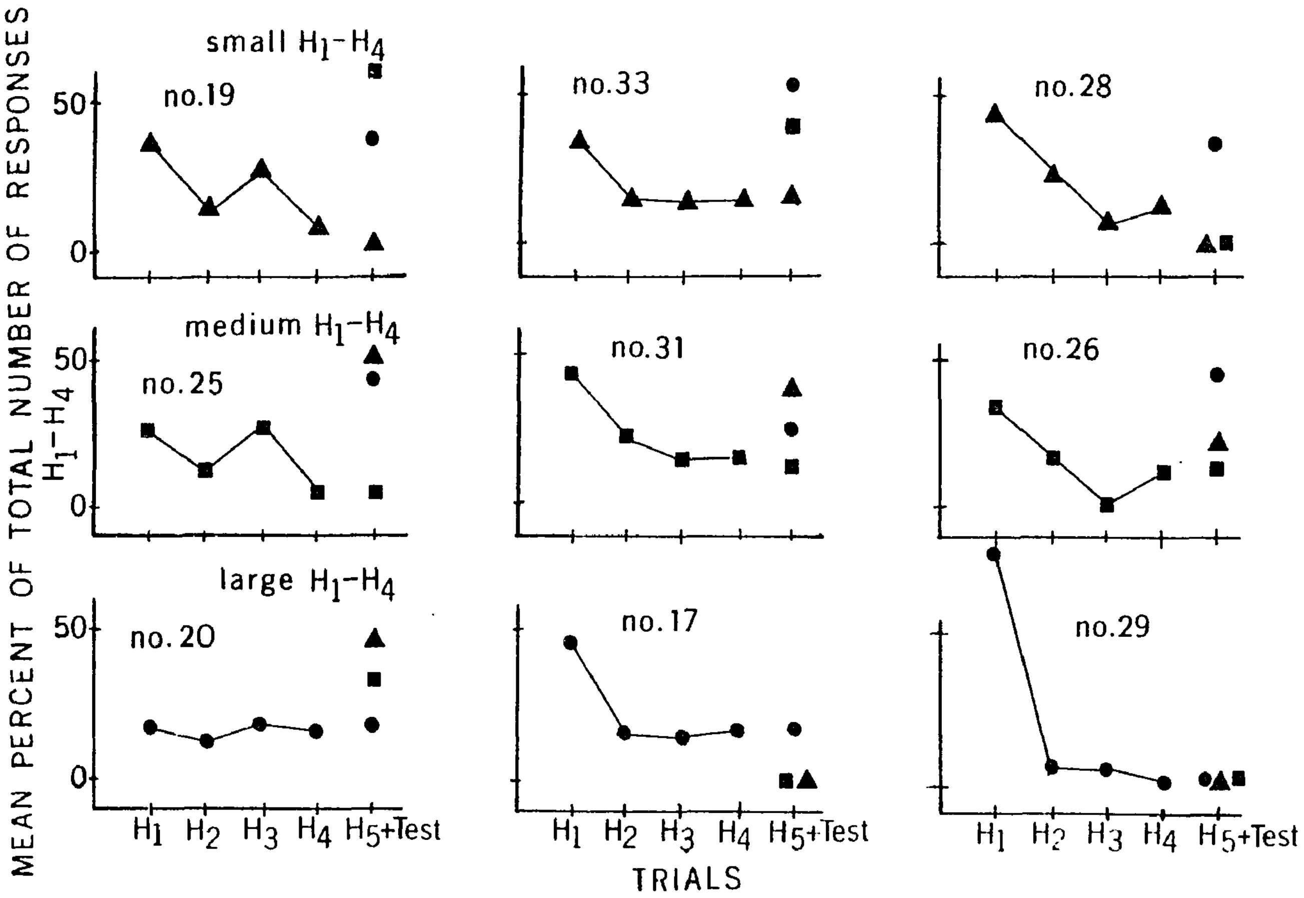

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
H_1-H_4
small H_1-H_4
no.19
no.33
no.28
medium H_1-H_4
no.25
no.31
no.26
large H_1-H_4
no.20
no.17
no.29
50
0
H_1 H_2 H_3 H_4 H_5+Test
TRIALS

Figure 7. Mean percent of total number of backward swimming for H_1 - H_4 and test for three sizes of cubes used as habituation stimuli. Large = ●, medium = ▬, small = ▲.

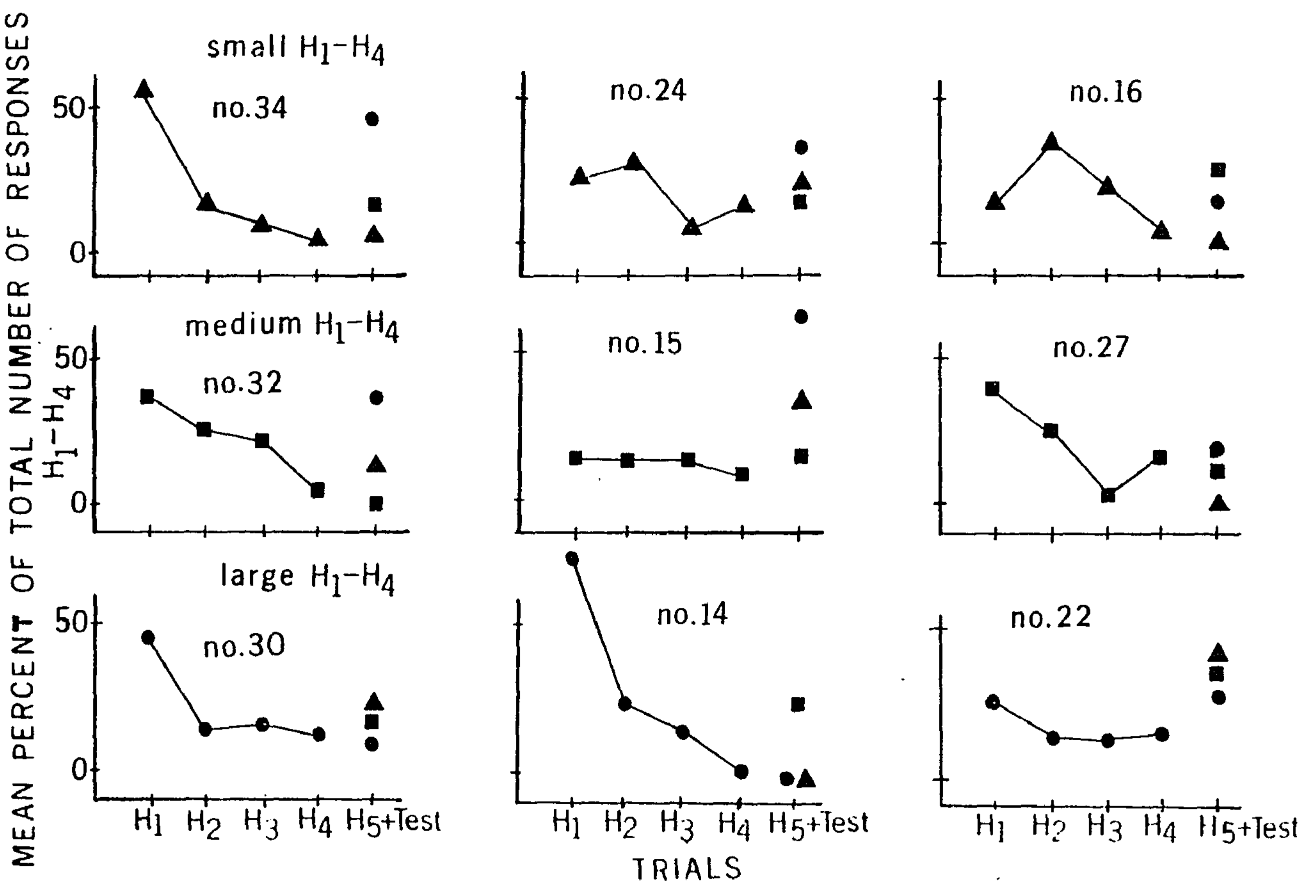

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
small H1-H4
no.34
no.24
no.16
medium H1-H4
no.32
no.15
no.27
large H1-H4
no.30
no.14
no.22
H_1-H_4
0
50
H1 H2 H3 H4 H5+Test
TRIALS

Figure 8. Mean percent of total number of backward swimming for H_1 - H_4 and test for three sizes of spheres used as habituation stimuli. Large = ● , medium = ■ , small = ▲ .

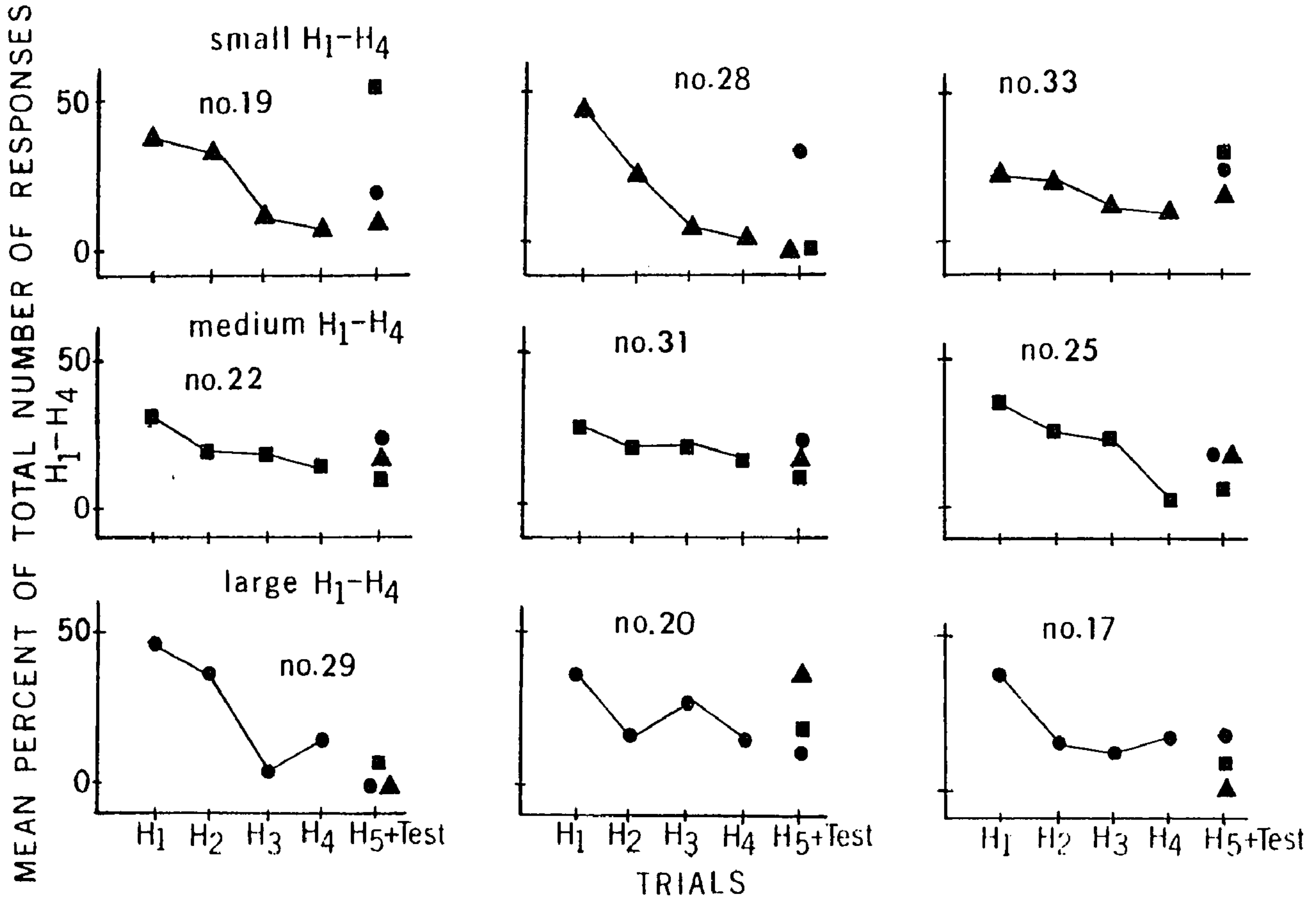

MEAN PERCENT OF TOTAL NUMBER OF RESPONSES
H_1-H_4
small H_1-H_4
medium H_1-H_4
large H_1-H_4
no.19
no.28
no.33
no.22
no.31
no.25
no.29
no.20
no.17
50
0
H_1 H_2 H_3 H_4 H_5+Test
TRIALS

Table 3

A three factor mixed design analysis of variance with repeated measures on one factor on the total number of responses on each of four trials (H_1 - H_4) for 18 fish for three sizes of cubes and spheres.

Source	SS	df	ms	F	p
Total	1033078.1	71			
Between Subjects	787864.1	17			
Shape (cube/sphere)	27848.1	1	27848.1	.45	
Hab. Size (S, M, L)	13591.01	2	6795.5	.11	
Shape X Hab. Size	14912.5	2	7456.2	.12	
Error_b	731512.5	12	60959.3		
Within Subjects	245214	54			
Trials	178568.4	3	59522.8	60.57	***
Trials X Shape	11525.07	3	3841.69	3.90	*
Trials X Hab. Size	10692	6	1782	1.81	
Trials X Shape X Hab. Size	9049	6	1508.1	1.53	
Error_b	35380	36	982.7		

* $p < .05$

*** $p < .001$

analysis. The significant effect of trials ($p < .001$) on the total number of responses emitted by the fish shows that habituation occurred. There was also a significant effect of shape on response rate ($p < .05$). The fish exposed to cubes as habituation stimuli made significantly more responses than those exposed to spheres.

The analysis of variance did not indicate what form these differences assumed as a function of trials or shape. Table 4 shows the results of a test for linear quadratic and cubic components of trend over $H_1 - H_4$ for the 18 fish. This orthogonal analysis showed that 80% of the effect of trials on response rate could be attributed to linear components, and 19% to quadratic components. The results of the trend analysis show that the significant differences found over trials were due to orderly changes in the number of responses over trials.

A further analysis was done on the data for the three fish that were presented the same habituation and test stimuli. The response rate of each fish on each trial was pooled, and a mean response for three fish was calculated from $H_1 - H_5$ and for test trials. For $H_1 - H_4$, nine scores from three fish contributed to each data point. For H_5 and test trials, one score from each fish contributed to the mean score. Each of six groups with a different sized sphere and cube as the habituation stimulus was formed.

From these data, a linear regression equation which roughly summarized the course of habituation from $H_1 - H_5$ for each cube and sphere size was obtained for TNR, TH, TB and BW. Table 5 lists these equations, the coefficient of determination, r^2, and the standard error of y around x (Sy.x) for small, medium and large cubes used as habituation

Table 4

Test for linear, quadratic and cubic components of trend over trials (H_1 - H_4), size, and shape of stimuli used for habituation for 18 fish.

Source	SS	df	ms	F	p
Within Subjects	257289	54			
Trials					
Linear	146692	1	146692	88.72	***
Quadratic	34936	1	34936	39.57	***
Cubic	645	1	645	.79	
Trials X Shape					
Linear	10.05	1	10.05		
Quadratic	9987	1	9987	11.31	***
Cubic	480	1	480	.59	
Trials X Size					
Linear	4374	2	2178		
Quadratic	8979	2	4489	5.08	*
Cubic	155	2	76	.09	
Trials X Size X Shape					
Linear	2762	2	1381	.84	
Quadratic	7874	2	3937	4.46	*
Cubic	169	2	84	.10	
$Error_w$	40227				
Linear	19839	12	1653		
Quadratic	10603	12	883		
Cubic	9785	12	815		

* $p < .05$ *** $p < .001$

TABLE 5

Linear regression equations, Sy.x and r^2 based on the mean percent of responses for TNR, TH, TB and BW for three fish in a group which were presented the same habituation and test stimuli. Small, medium and large cubes were used as habituation stimuli. The probability of test stimuli falling along the regression line is given and the significance level.

D.V.	Habituation Stimulus (Small)	Size of Test Stimulus	p	Habituation Stimulus (Medium)	Size of Test Stimulus	p	Habituation Stimulus (Large)	Size of Test Stimulus	p
Total Number of Responses	$y=.33-.05x$	M	***	$y=.43-.08x$	S		$y=.37-.06x$	S	
	$r^2=.91$	L	***	$r^2=.80$	L	*	$r^2=.70$	M	
	Sy.x=.03			Sy.x-.07			Sy.x=.08		
Touching with the Head	$y=.33-.05x$	M	***	$y=.37-.06x$	S		$y=.42-.08x$	S	
	$r^2=.94$	L	***	$r^2=.84$	L	***	$r^2=.75$	M	*
	Sy.x=.97			Sy.x=.04			Sy.x=.07		
Touching with the Body	$y=.37-.07x$	M	*	$y=.32-.05x$	S	*	$y=.37-.07x$	S	
	$r^2=.84$	L	***	$r^2=.80$	L	***	$r^2=.47$	M	
	Sy.x=.05			Sy.x=.05			Sy.x=.14		
Backward Swimming	$y=.30-.04x$	M	***	$y=.36-.06x$	S		$y=.43-.08x$	S	
	$r^2=.87$	L	***	$r^2=.77$	L	*	$r^2=.73$	M	
	Sy.x=.03			Sy.x=.06			Sy.x=.07		

* $p < .05$
*** $p < .001$

TABLE 6

Linear regression equations, Sy.x and r^2 based on the mean percent of response for TNR, TH, TB and BW for three fish in a group which were presented the same habituation and test stimuli. Small, medium and large spheres were used as habituation stimuli. The probability of test stimuli falling along the regression line is given and the significance level.

D.V.	Habituation Stimulus (Small)	Size of Test Stimulus	p	Habituation Stimulus (Medium)	Size of Test Stimulus	p	Habituation Stimulus (Large)	Size of Test Stimulus
Total Number of Responses	$y=.34-.06x$	M	***	$y=.27-.03x$	S	***	$y=.34-.05x$	S
	$r^2=.82$	L	***	$r^2=.84$	L	***	$r^2=.55$	M
	Sy.x=.05			Sy.x=.02			Sy.x=.06	
Touching with the Head	$y=.37-.08x$	M	***	$y=.26-.03x$	S	*	$y=.36-.06x$	S
	$r^2=.73$	L	***	$r^2=.83$	L	**	$r^2=.63$	M
	Sy.x=.08			Sy.x=.02			Sy.x=.08	
Touching with the Body	$y=.37-.07x$	M	***	$y=.35-.06x$	S	**	$y=.44-.08x$	S
	$r^2=.77$	L	***	$r^2=.86$	L	**	$r^2=.49$	M
	Sy.x=.07			Sy.x=.05			Sy.x-.15	
Backward Swimming	$y=.39-.07x$	M	***	$y=.33-.05x$	S	*	$y=.39-.07x$	S
	$r^2=.82$	L	***	$r^2=.89$	L	*	$r^2=.06$	M
	Sy.x=.06			Sy.x=.03			Sy.x=.06	

* $p < .05$
** $p < .01$
*** $p < .001$

stimuli. The data for spheres are shown in Table 6. Ths Sy.x may be used to estimate the probability that the behavior observed on the test trial was merely a continuation of the trend shown by the regression line. A significant deviation from the regression line in the presence of the test stimulus suggests that this stimulus is perceived as different from the habituation stimulus. The probability that the deviation from this trend is significant can be estimated by treating Sy.x as a normal deviate (z-score); i.e., .68 of responses for that measure can be expected to fall within ± 1 Sy.x, .95 can be expected to occur within ± 2 Sy.x, and .99 can be expected to occur within ± 3 Sy.x of the regression line.

As seen in Tables 5 and 6, when small cubes and spheres were used as habituation stimuli, in all cases there were significant differences found between habituation and test stimuli. That is, when medium or large stimuli were introduced on the test trial, there was a significant change in TNR, TH, TB and BW. When medium cubes and spheres were habituation stimuli, there were significant changes in the TNR, TH, TB and BW when the test stimulus was large and for spheres when the test stimulus was small. When small cubes were used as test stimuli, following habituation with a medium cube, only TB showed a significant deviation from the regression line. In all but one case, when large stimuli were used in habituation, behavior in the presence of the test stimuli did not significantly deviate from the regression line. This may reflect the fact that a straight line does not provide a good fit for these data rather than a failure of discrimination. Note that r^2 is smallest when the habituation stimuli are large.

A mixed factor analysis of variance (see Table 7) with repeated measures on one factor on the total number of responses on trial 5 was done to determine if TNR is influenced by stimulus size and shape, as well as the condition in effect on the four habituation trials. There were significant differences found as a function of the object used on the habituation or test trial ($p < .05$), as well as significant interactions between the size of the habituation stimulus and the size of the stimulus on trial 5. Inspection of Figure 9 shows the significant interaction to be due to differences in the effect of stimulus size on TNR as a function of size of the habituation stimulus. For small and large stimuli, TNR tended to increase as the size of the test stimulus increased while the function for the medium sized stimuli was V-shaped. Thus, disinhibition, an increase in TNR in response to stimulus change, was clearly seen only following habituation to medium size objects.

The EOD's of five of the fish which were presented with small cubes or spheres (H_1 - H_4) and large stimulus objects on test trials were selected for further analysis. The data for these fish were chosen for study since their behavior differed significantly on test and training trials (see Tables 5 and 6).

For each fish, an interdischarge interval histogram with a 5 ms time base was obtained, as well as the function showing the number of responses made in successive one sec. intervals for a 20 sec. period.

The EOD's were analyzed under the following experimental conditions: three minute recordings were obtained of each fish's EOD when undisturbed in the aquarium and on the first, fourth and fifth habituation trial, with either the small cube or sphere inserted into the

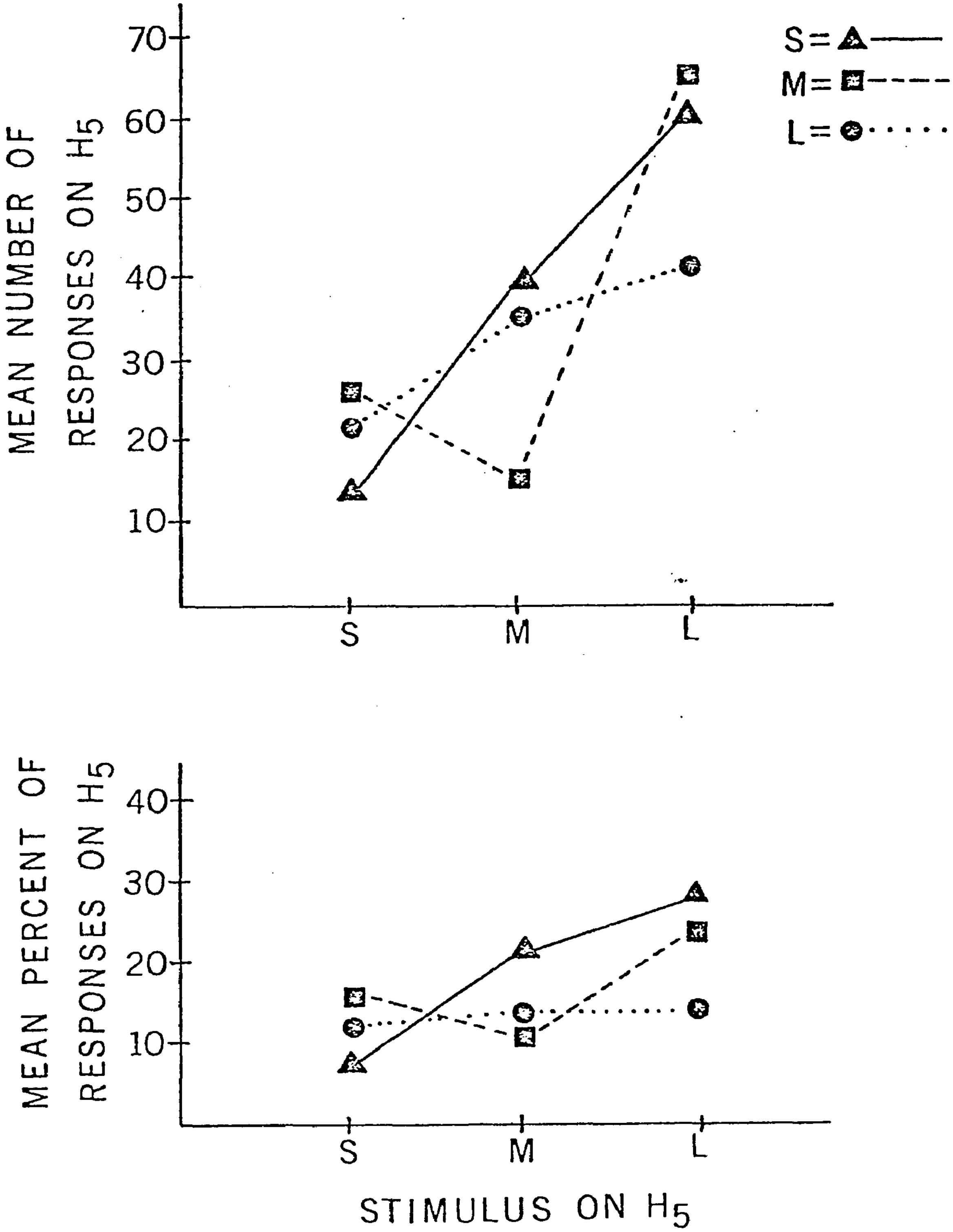
Table 7

A three factor mixed design analysis of variance with repeated measures on one factor on total number of responses on H_5 for 18 fish for three sizes of cubes and spheres.

Source	SS	df	ms	F	p
Total	214,883.21	53			
Between Subjects	93,761.87	17			
Shape (cube/sphere)	317.8	1	317.8	.04	
Hab. Size (S, M, L)	1,657.48	2	828.74	.11	
Shape X Hab. Size	5,349.93	3	1783.31	.23	
Error_b	86,436.66	11	7857.88		
Within Subjects	121,121.34	36			
Trials	19,334.26	2	9667.13	3.78	*
Trials X Shape	1,296.92	2	648.46	.25	
Trials X Hab. Size	34,403.3	4	8600.82	3.36	*
Trials X Shape X Hab. Size	4,722.85	4	1180.71	.46	
Error_w	61,364.01	24	2556.83		

* $p < .05$

Figure 9. Mean number of responses, and mean percent of responses on Trial 5 as a function of size of the habituation stimulus and the stimulus presented on Trial 5.


S = ▲ ——
M = ■ - - - -
L = ● · · · · ·
MEAN NUMBER OF RESPONSES ON H_5
70
60
50
40
30
20
10
S
M
L
MEAN PERCENT OF RESPONSES ON H_5
40
30
20
10
S
M
L
STIMULUS ON H_5

aquarium. Recordings were also made on the test trial with either the large cube or sphere.

Table 8 contains the mean, standard deviation, coefficient of skewness and kurtosis for inter-discharge interval histograms for the first three minutes of recorded EOD's under each of four conditions for six G. petersii. In the undisturbed condition, all but fish no. 19 produced a histogram that was skewed to the right. When an object was introduced into the aquarium, this skewness became more pronounced in all but fish no. 34. This indicated that the fish naturally produced a pattern of discharge that was biased in favor of smaller inter-discharge intervals. When an object was introduced, this response bias became more obvious.

The coefficient of kurtosis is sensitive to increases in scores above the mean. In all but one case (fish no. 34), there was less variation around the mean when objects were introduced. This trend was not seen as consistently when H_5 was compared with test scores.

Table 9 shows the total number of responses made in three minutes by undisturbed subjects compared to the number of responses made on H_1 for five fish. A Kolmogorov-Smirnov (K.S.) one sample test indicated that for fish nos. 16, 28 and 19, there were significant differences in the total number of responses between these conditions.

Table 10 shows the total number of responses for three minutes for H_5 and test for five fish. The K.S. test showed that for fish nos. 28 and 19, there were significant differences in the number of responses between these conditions. In three cases, however, no significant differences were found. A K.S. test with pairs of inter-

TABLE 8

Mean, standard deviation, coefficient of skewness and kurtosis for the distribution of each three minute interfish pulse interval histogram (5 ms time base) for each of six fish under the following conditions: undisturbed; H_1 (small cube or sphere); H_5 (small cube or sphere); and test (large cube or sphere).

Fish Number		$\bar{X}$	SD	Coefficient of Skewness	Coefficient of Kurtosis
Undisturbed					
	16	26.5	14.9	.21	2.14
cubes	34	12.5	9.0	1.87	6.3
	24	34.3	21.2	.07	1.7
	28	51.1	28.2	.07	1.9
spheres	19	26.3	13.1	-.24	2.1
	41	21.7	14.9	.65	2.2
H_1					
	16	10.1	7.4	3.8	22.8
cubes	34	18.4	13.7	.90	2.8
	24	38.7	28.4	.86	2.2
	28	48.9	24.9	.12	2.3
spheres	19	17.4	12.4	1.7	5.6
	41	12.3	8.3	2.1	7.7
H_5					
	16	17.4	15.7	1.8	5.2
cubes	34	21.9	14.7	.50	1.8
	24	30.5	13.7	.25	2.0
	28	20.6	16.9	1.3	3.8
spheres	19	44.3	35.3	0	1.3
	41	19.1	13.9	1.4	4.4
Test Trial					
	16	9.7	6.5	2.9	15.5
cubes	34	22.8	13.2	.64	2.6
	24	35.7	20.6	.01	1.8
	28	45.4	27.8	.19	1.8
spheres	19	14.6	12.4	1.3	4.1
	41	10.5	9.9	2.0	7.5

TABLE 9

Kolmogorov-Smirnov Test between the first three minutes of undisturbed compared with H_1 (small cube or sphere) for five fish. The number of EOD responses in a three minute interval for undisturbed and H_1 is given.

Fish Number	Number of Responses		p
	Undisturbed	H_1	
Cubes as H_1			
16	1048	3021	**
34	3064	1867	*
Spheres as H_1			
28	352	522	n.s.
19	1272	1494	**
41	1590	2876	n.s.

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

TABLE 10

Kolmogorov-Smirnov Test between the first three minutes of EOD in H_5 (small cube or sphere) and test stimuli (large cube or sphere) for five fish. The number of EOD responses in a three minute interval for H_5 and test are given.

Fish Number	Number of Responses		p
	H_5	Test	
Cubes as H_5 and Test			
16	1974	3401	n.s.
34	1613	1577	n.s.
Spheres as H_5 and Test			
28	1846	610	**
19	552	2253	**
41	1682	2790	n.s.

** $p < .01$

discharge histograms did not show consistent differences between experimental conditions sustained over a three minute interval when novel stimuli were introduced.

A change in the EOD of individual fish could be heard in the first 20 seconds after the introduction of a novel stimulus. The first 20 seconds of the undisturbed fish's discharge was compared with the first 20 seconds under H_1 conditions for each of six fish. In order to ascertain that the differences between these distributions were not random fluctuations, the first 20 seconds of the undisturbed period was compared with the second 20 seconds of the undisturbed period. Malcolm (1976) found that, if stimulus conditions remained the same, the fish produced stable and characteristic EOD patterns over time.

Figures 10, 11 and 12 contain the number of responses per second in a 20 second interval for each of six *G. petersii* under two conditions: undisturbed, and H_1. Table 11 shows the results of a t test for related samples between the fish's EOD in the undisturbed condition in the first 20 seconds compared with the second 20 seconds. There were no significant differences found between the means for six *G. petersii*, which indicated that there were stable patterns of EOD over a 40 second interval if no disturbance occurred in the aquarium. When the first 20 seconds of the fish undisturbed was compared with H_1 (small cube or sphere), there were significant differences found between the mean for four fish out of six comparisons. The data for these comparisons were taken from the sequential average frequencies per second (EOD repetition rate).

TABLE 11

Paired t test for dependent samples between undisturbed the first sequential 20 seconds compared with undisturbed the second sequential 20 seconds, and between undisturbed the first sequential 20 seconds compared with H_1 for the first sequential 20 seconds. H_1 = small cube or sphere for six fish.

Fish Number	Undisturbed vs Undisturbed			Undisturbed vs H_1		
	df	t	p	df	t	p
Cubes as H_1						
16	19	-1.82	n.s.	19	-7.64	**
34	19	1.65	n.s.	19	-2.37	*
24	19	.82	n.s.	19	7.50	**
Spheres as H_1						
28	19	-.19	n.s.	19	-1.66	n.s.
19	19	1.93	n.s.	19	-.56	n.s.†
41	19	.17	n.s.	19	-2.22	*

† For Fish 19 the first minute of H_1 was lost due to a bad recording. The second minute of H_1 was used, but obviously is not equivalent.

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

Figure 10. The number of responses in the first sequential twenty seconds of undisturbed and H_1 for fish no. 41, 19 and 28.

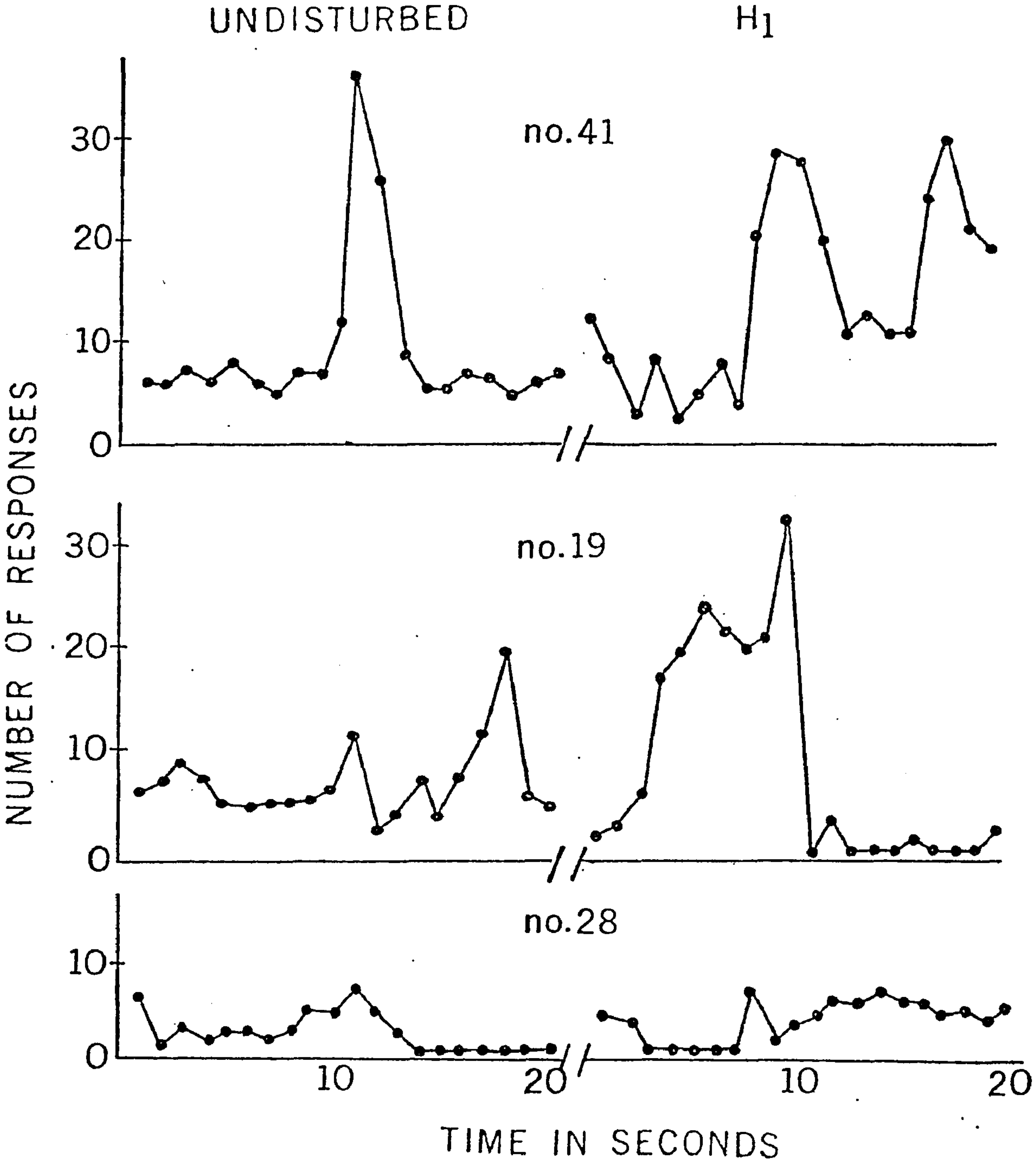

UNDISTURBED
H1
no.41
no.19
no.28
NUMBER OF RESPONSES
0
10
20
30
TIME IN SECONDS
10
20

Figure 11. The number of responses in the first sequential twenty seconds of undisturbed and H_1 for fish nos. 34 and 16.

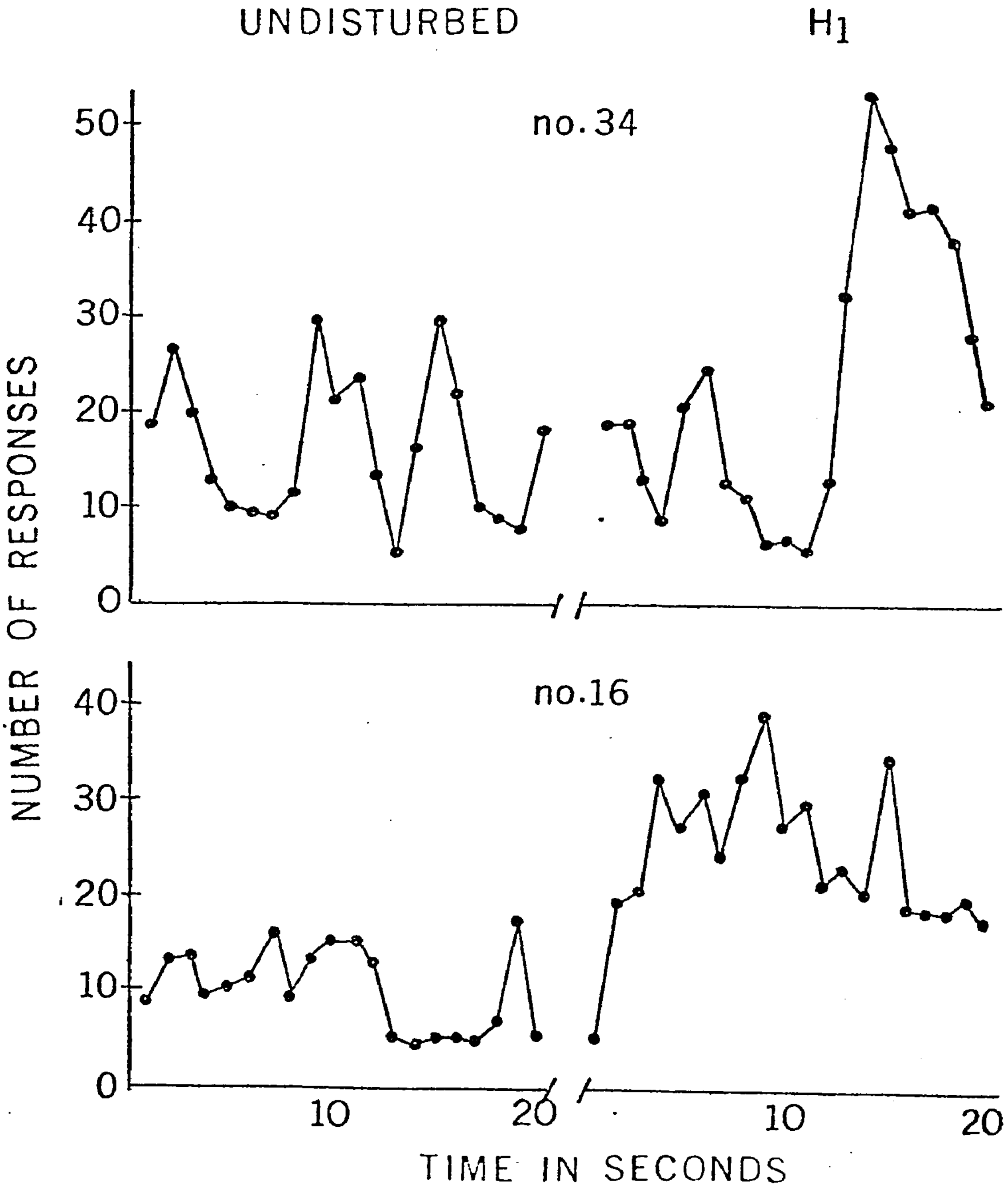

UNDISTURBED
H_1
no.34
no.16
NUMBER OF RESPONSES
50
40
30
20
10
0
40
30
20
10
0
10
20
10
20
TIME IN SECONDS

Figure 12. The number of responses in the first sequential twenty seconds of undisturbed and H_1 for fish no. 24.

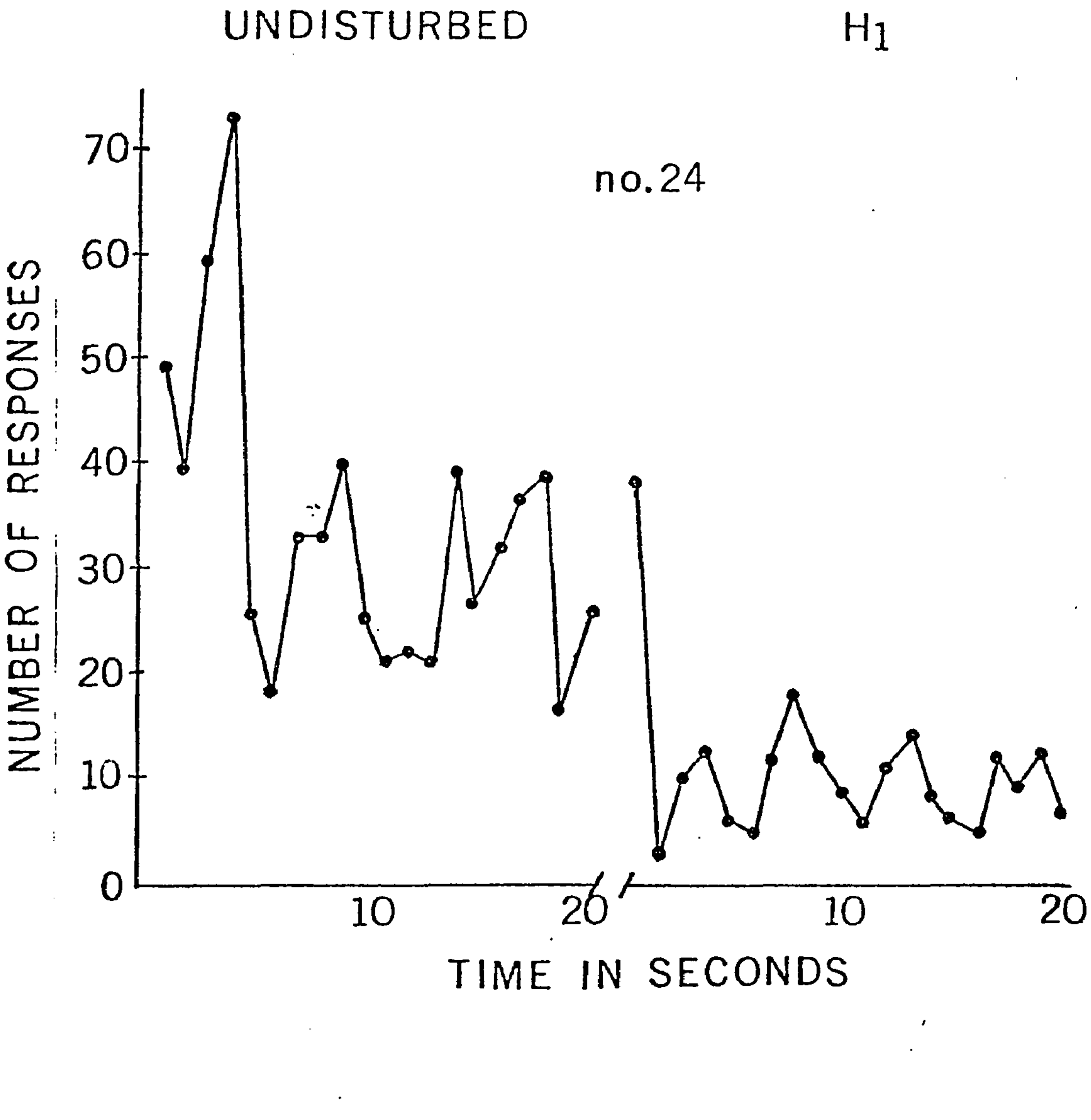

UNDISTURBED
H1
no. 24
NUMBER OF RESPONSES
70
60
50
40
30
20
10
0
10
20
10
20
TIME IN SECONDS

Table 12 shows the results of a paired _t_ test for dependent samples for six fish which were presented the largest stimulus objects on H_1. The following comparisons were made: undisturbed fish's EOD comparing the first 20 seconds to the second 20 seconds; the undisturbed fish's EOD compared with H_1 (large cube or sphere). In all but one case (fish no. 17), there were significant differences found between the EOD of the undisturbed fish and the H_1. Thus, comparing the undisturbed fish's EOD with that which occurred when a stimulus was introduced into the aquarium, there were nine significant differences found in 12 paired _t_ tests.

Comparisons were made between H_4 and H_5, H_4 and test stimuli, and H_5 and test stimuli . Small spheres and cubes were used as habituation stimuli, while the largest objects were test stimuli. Table 13 shows the results of a paired _t_ test for dependent samples between the first 20 seconds of H_4 and H_5. In all cases, significant differences were found between these two samples of the fish's EODs. Table 14 shows the results of a paired _t_ test between H_4 and test stimuli, and Table 15 shows the results of a paired _t_ test between H_5 and test stimuli. In all cases, the data used were from the sequential average frequencies per second.

TABLE 12

Paired _t_ test for dependent samples between undisturbed (the first sequential 20 seconds) compared with undisturbed (the second sequential 20 seconds), and between undisturbed (the first sequential 20 seconds) compared with H_1 (the first sequential 20 seconds). H_1 = large sphere or cube for six fish.

Fish Number	Undisturbed vs Undisturbed			Undisturbed vs H_1		
	df	_t_	_p_	df	_t_	_p_
Cubes as H_1						
30	19	-.82	n.s.	19	-3.15	**
14	19	-.82	n.s.	19	4.66	***
22	19	-3.56	**	19	-12.7	***
Spheres as H_1						
29	19	-.67	n.s.	19	-4.15	***
20	19	-.23	n.s.	19	-2.84	**
17	19	-1.35	n.s.	19	-1.27	n.s.

** $p < .01$
*** $p < .001$

TABLE 13

Paired t test for dependent samples between the first 20 seconds of H_4 (small cube or sphere) and H_5 (small cube or sphere).

Fish Number	Number of Responses		df	t	p
	H_4	H_5			
Cubes as H_4 and H_5					
16	328	95	19	4.04	***
34	155	290	19	3.64	**
24	49	1032	19	15	***
Spheres as H_4 and H_5					
28	92	220	19	4.44	***
19	204	383	19	11.33	***
41	307	127	19	4.75	***

** $p < .01$
*** $p < .001$

TABLE 14

Paired *t* test for dependent samples between the first 20 seconds of H_4 (small cube or sphere) and test (large cube or sphere).

Fish Number	Number of Responses		df	*t*	*p*
	H_4	Test			
Cubes as H_4 and Test					
16	328	387	19	.89	n.s.
34	155	193	19	1.17	n.s.
24	49	64	19	.66	n.s.
Spheres as H_4 and Test					
28	92	50	19	1.53	n.s.
19	204	243	19	1.29	n.s.
41	307	359	19	.41	n.s.

TABLE 15

Paired t test for dependent samples between the first 20 seconds of H_5 (small cube or sphere) and test (large cube or sphere).

Fish Number	Number of Responses H_5	Test	df	t	p
Cubes as H_5 and Test					
16	95	387	19	-3.64	**
34	290	193	19	3.92	***
24	1032	64	19	10.86	***
Spheres as H_5 and Test					
28	220	50	19	9.81	***
19	383	243	19	3.01	**
41	127	359	19	-3.33	**

** $p < .01$
*** $p < .001$

Discussion

This experiment showed that a habituation-dishabituation method could be used to study behavioral size discrimination in G. petersii. This technique deserves consideration for use with animals with which it is otherwise difficult to obtain discrimination data by operant or classical conditioning techniques.

The total number of responses on $H_1 - H_4$ was affected by trials and the shape of the stimulus objects. The effects of shape on trials is perhaps explainable by the greater deformation of an electric field produced by angles, since there was a larger number of responses emitted to the cubes compared with the spheres over trials. There was a significant interaction ($p < .05$) between the size of the habituation stimulus and the total number of responses made in the presence of small, medium or large objects on trial five. For the small and large stimulus objects as habituation stimuli, the TNR on trial 5 increased as the size of the stimulus on this trial increased. The function for the medium sized habituation stimuli, however, was V-shaped, providing the clearest evidence that discrimination occurred when either the small and the large stimulus was presented on test trials.

The number of responses over trials decreased in a predominantly linear fashion. These linear effects were also evident in the reasonably good fits obtained when straight lines were fitted to the mean percent of responses over trials for the total number of responses (TNR) and for the four components of behavior that were analyzed separately.

Since these behavioral measures showed orderly changes over trials, it was postulated that reliable alterations in the EOD could also occur. There were differences in the means and standard deviations in the frequency distribution of EODs obtained within and across subjects, but no consistent pattern emerged. In five out of six cases, the coefficient of skewness for the undisturbed fish's EOD was skewed to the right. When an object was introduced in the aquarium, the right skewness of the distributions became more pronounced, i.e. the fish tended to discharge at a faster rate. Recordings made when a test stimulus was introduced did not show an increase in the right skewness of the distributions when compared with H_1 or H_5 distributions. It appears that there is a greater increase in EOD frequency when an object is initially introduced than when an object of a different size, here a larger object after habituation with a smaller object, is introduced into the aquarium.

A change in the EOD rate was noticed when a novel stimulus was introduced. A comparison between the EOD obtained during the first 20 seconds following introduction of an object into the aquarium and the EOD obtained when the fish was undisturbed was made. Significant differences were found between 20 seconds during which the fish was undisturbed and the first 20 seconds after the introduction of H_1 (a small or large cube of sphere) on nine out of twelve $\underline{t}$ tests for dependent samples. In seven of these cases, an increase in the EOD occurred.

Difficulties were encountered when comparisons were attempted between H_5 and on the test trial. When trials close in time are compared (H_4 and test), the paired $\underline{t}$ test showed no statistical differences in the EOD. When EODs obtained on trials farther apart in time were compared (H_5 and test), significant differences were obtained.

EXPERIMENT II

THE SENSORY BASIS OF DISCRIMINATION IN A WEAKLY ELECTRIC FISH, *G. PETERSII*

The habituation-dishabituation method used in Experiment I provided evidence that *G. petersii* is able to detect changes in the size of stimuli introduced into the aquarium. This experiment did not provide information as to how these discriminations were accomplished.

G. petersii have an electric organ electroreceptor complex whose physiology has been described by Szabo (1974), an auditory system described by von Frisch (1938), a visual system whose physiology and histology has been described by McEwan (1938), as well as a lateral line system separate from the electric organ system. In the present experiment, an attempt was made to determine if the electrosensory and visual systems contribute to discrimination. Methods were sought that would separate the potential contribution of these two systems. Previous research suggests that a unisensory approach is limiting. Keeton (1969) and Keeton et al. (1974) have found, for example, that a complex series of integrations occur at the sensory level such that an adult pigeon has a variety of reliable sense impressions to guide its flight.

THE EOD of the fish was interferred with by severing the spinal cord anterior to that part of the caudal peduncle containing the electric organ (Moller 1976). This severing of the spinal cord rendered an experimental group of fish electrically "silent". These fish were tested before and after surgery to determine if there were deficiencies in exploratory and discriminatory behavior as a function of surgical intervention.

The fish in Experiment 1 were tested in daylight, and they discriminated between stimuli under these conditions. However, in the natural habitat (McEwan 1938; Moller 1976), these fish are nocturnal and it is likely that discrimination also occurs under reduced light intensities as well as in daylight. The histology and physiology of the mormyrid retina also indicate that the fish possess a nighttime visual system (McEwan 1938). In the present experiment, discrimination was studied in the absence of light, in dim light and in daylight.

The apparatus used in Experiment I was modified so that touching of the object could be recorded under daylight, reduced light and no light conditions. In daylight, all the behaviors recorded in Experiment I were noted in order to determine if there were alterations in the pattern of response under different experimental conditions. Touching with the head and body were found in Experiment I to be good indicators of discrimination under certain stimulus arrangements. One of these arrangements of the stimuli were chosen and used in all conditions. A small sphere was presented on habituation trials and on test trials a large sphere was presented. These stimuli were selected because in Experiment I there were clear differences in motor behavior when the larger object was presented following habituation with the smaller object.

In this experiment, fish were tested for their ability to discriminate between objects under daylight, dim light and no light conditions, with their EOD intact, and with the EOD surgically eliminated.

Method

Subjects

Six *G. petersii* were used as subjects. Three of the individuals were surgically rendered silent by severing the spinal cord anterior to the part of the caudal peduncle containing the electric organ (Moller 1976). Three subjects were sham-operated, i.e., an incision was made in the area where the electroplaques are located but the spinal cord was not severed. One sham-operated fish died after surgery, and data from that subject were discarded. Housing procedures were the same as described in Experiment I.

Apparatus

The apparatus used in Experiment I was modified as follows: two stimuli, small sphere (1.4 cm diameter) presented on H_1 - H_5 as a habituation stimulus, and the large sphere (3.3 cm diameter) used as a test stimulus, were suspended from glass rods. The free end of the glass rod was inserted through a smooth plastic sphere which rested in a smooth plastic circular opening above the aquarium. Responses were recorded whenever the fish displaced the stimulus sphere sufficiently to move the upper tip of the glass rod. A dim light condition was created by building a close fitting black cardboard box which was placed over the aquarium, leaving a 4 cm diameter circular opening through which stimuli could be presented. A no light condition was created by adding cresofuchsine and anilin dyes to the aquarium water. The water was considered to be impermeable to light when a beam of light produced by a flashlight held to the side of the aquarium did not penetrate the water.

Procedure

Before surgical intervention, all fish were tested in a partially randomized block to control for sequence under the conditions summarized in Table 16. In daylight, the five fish were habituated over five trials to the small sphere, and they were then tested in a discrimination session with H_1 - H_4 the small sphere, and the large sphere as the test stimulus. In dim light, the fish were tested with the large sphere as the test stimulus.

After the above conditions were presented, three experimental fish were rendered electrically silent, and three were sham-operated. Surgery was performed by Dr. Peter Moller. One sham-operated animal died and was not replaced. The recording electrodes were permanently glued into the aquarium and were used to determine that a fish was electrically inactive.

After surgical intervention, all fish were tested under the following conditions: in daylight, the fish were presented a discrimination test using the same stimuli as before; the same stimulus arrangement was presented in a discrimination session under dim light and a no light condition. Under all conditions, a pooled response measure of touching (T), including touching with the head, the body and the tail was recorded as the dependent variable. In daylight conditions, forward swimming (FW) and backward swimming (BW) were also recorded.

TABLE 16

CONDITIONS UNDER WHICH EXPERIMENTAL AND SHAM-OPERATED FISHES WERE TESTED

	DAYLIGHT	DIM LIGHT
WITH ELECTRIC ORGAN DISCHARGE	DAYLIGHT + EOD	DIM LIGHT + EOD
WITHOUT ELECTRIC ORGAN DISCHARGE	DAYLIGHT + NO EOD	DIM LIGHT + NO EOD

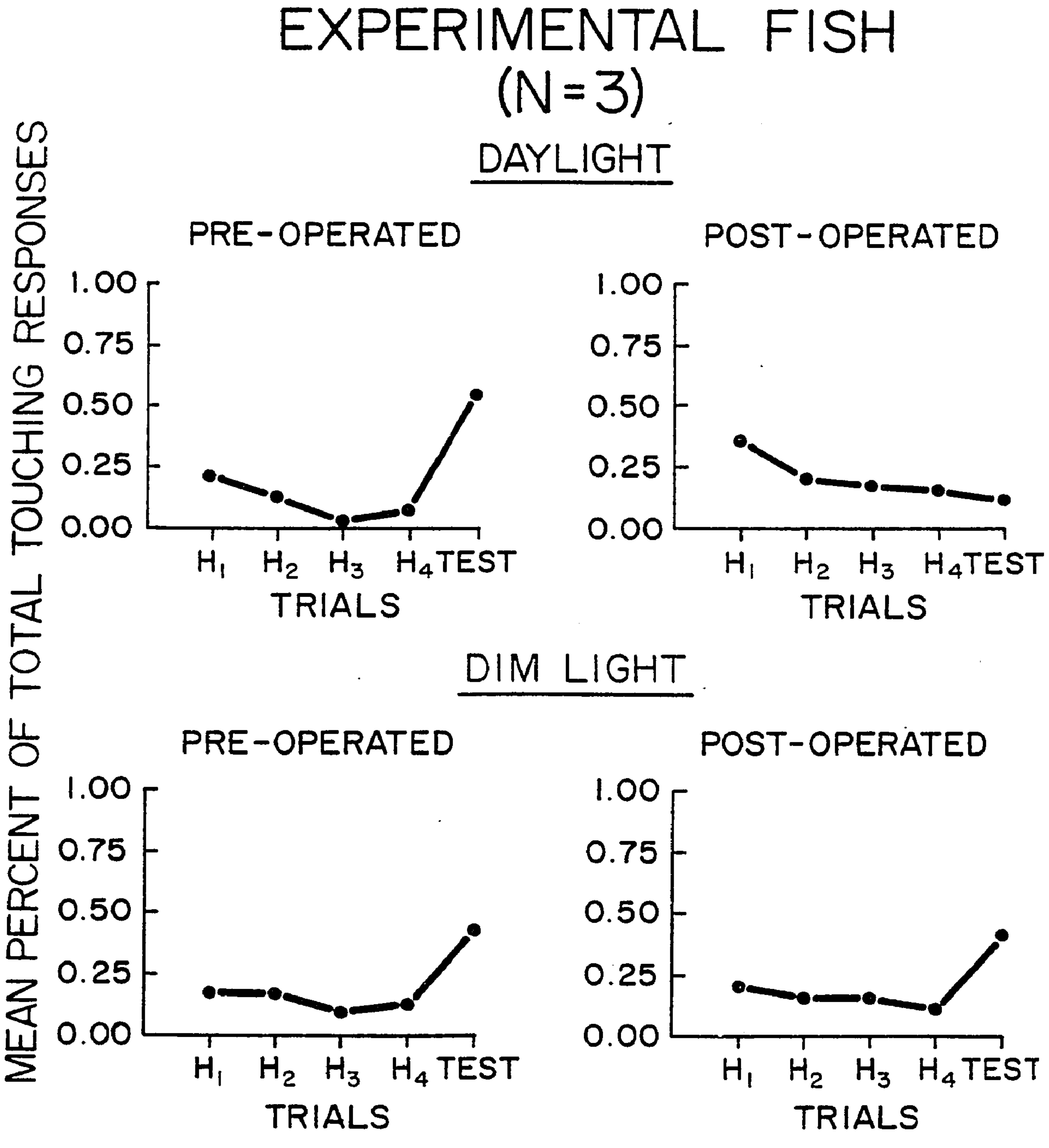
Results

Comparisons were made between experimental and sham-operated fish before and after surgical intervention under different light intensities. For each of the five fish, the number of touching responses was summarized for one session, and a percentage of the total response rate was calculated. Figure 13 contains the mean percent of touching (T) responses from H_1 - H_5 and Test for three experimental fish in daylight and dim light before and after surgical intervention. Figure 14 contains the information for two sham-operated subjects.

In order to further summarize the data, the mean percent response rate on each trial H_1 - H_5 was pooled for each fish group (experimental or sham-operated) across conditions. Therefore, a mean percent response rate from H_1 - H_5 was obtained for three individuals of the experimental group, and two sham-operated individuals. The mean percent response rate for each of the two groups was used to calculate individual regression lines from H_1 - H_5. Table 17 contains the calculated linear regression lines for experimental and sham-operated groups. The goodness of fit, as indicated by the coefficient of determination r^2, was .62 for the experimental and sham-operated subjects. The sample standard estimate of y on x (Sy.x) was also obtained. The interpretation of these statistics was described in Experiment I.

As seen in Figure 13 and Table 17, intact fish could discriminate between a small sphere and a large test sphere ($p < .001$) in daylight and dim light conditions. These three fish post-operatively were unable to discriminate between these objects in daylight. However,

Figure 13. The mean percent of touching (T) responses from $H_1 - H_5$ for three experimental fish in normal daylight and dim light conditions before and after surgical intervention.


EXPERIMENTAL FISH
(N=3)
DAYLIGHT
PRE-OPERATED
POST-OPERATED
DIM LIGHT
PRE-OPERATED
POST-OPERATED
MEAN PERCENT OF TOTAL TOUCHING RESPONSES
1.00
0.75
0.50
0.25
0.00
H1
H2
H3
H4
TEST
TRIALS

under dim light, the fish were able to discriminate between the stimuli ($p < .001$). As seen in Figure 14 and Table 17, before and after surgical intervention, in daylight or in dim light, the sham-operated fish discriminated between H_5 and test stimuli ($p < .001$) for all comparisons.

The surgically silenced fish appeared to be able to perform in dim light, a discrimination which they failed to make under daylight. In order to determine if G. petersii might be using vision under dim light conditions, both experimental and sham-operated fish were tested under a no light condition after surgical intervention. Figure 15 shows the mean percent of touching (T) responses from $H_1 - H_5$ and test conditions for experimental and sham-operated fish. Table 17 shows the calculated linear regression lines for this data. When most light was eliminated, experimental fish post-operatively could not discriminate between H_5 and test stimuli. Sham-operated fish did discriminate between the two spheres ($p < .001$).

The above interpretations of obtained results were based on the percent of responses on each trial. The absolute number of responses were examined under all conditions to determine if there were alterations as a function of stimulus conditions or surgical intervention. The absolute number of touching (T) responses under different conditions for experimental and sham-operated fish are presented in Figure 16. Before surgery, all but one fish (no. 34) emitted a higher rate of response (T) in dim light as compared with daylight. After surgery, the experimental fish continued to show this trend. However, after surgery, there was a drop in the absolute number of T responses emitted by experimental fish. This trend was not seen in the sham-operated fish, which tended to increase the number of touching responses post-operatively.

TABLE 17

Linear regression equations, Sy.x and r^2 based on mean percent of the total number of touching responses for experimental, electrically silenced fish (N=3) and sham-operated fish (N=2) under daylight, dim light and no light conditions. Small spheres were used as habituation stimuli from trials 1 to 5, and large spheres were used as dishabituation stimuli. The probability of the dishabituation stimulus falling on the regression line is given and the significance level.

Experimental					
Pre-operated			Post-operated		
Regression Equation	Dishabituation Stimulus Condition	p	Regression Equation	Dishabituation Stimulus Condition	p
y=.24-.03x	Daylight	***	y=.27-.04x	Daylight	n.s.
r^2=.62	Dim light	***	r^2=.63	Dim light	***
Sy.x=.07			Sy.x=.06	No light	n.s.
Sham-Operated					
y=.29-.05x	Daylight	***	y=.27-.05x	Daylight	***
r^2=.81	Dim light	***	r^2=.99	Dim light	***
Sy.x=.04				No light	***

*** $p < .001$

Figure 14. The mean percent of touching (T) responses from H_1 - H_5 for two sham-operated fish in normal daylight and dim light conditions before and after surgical intervention.

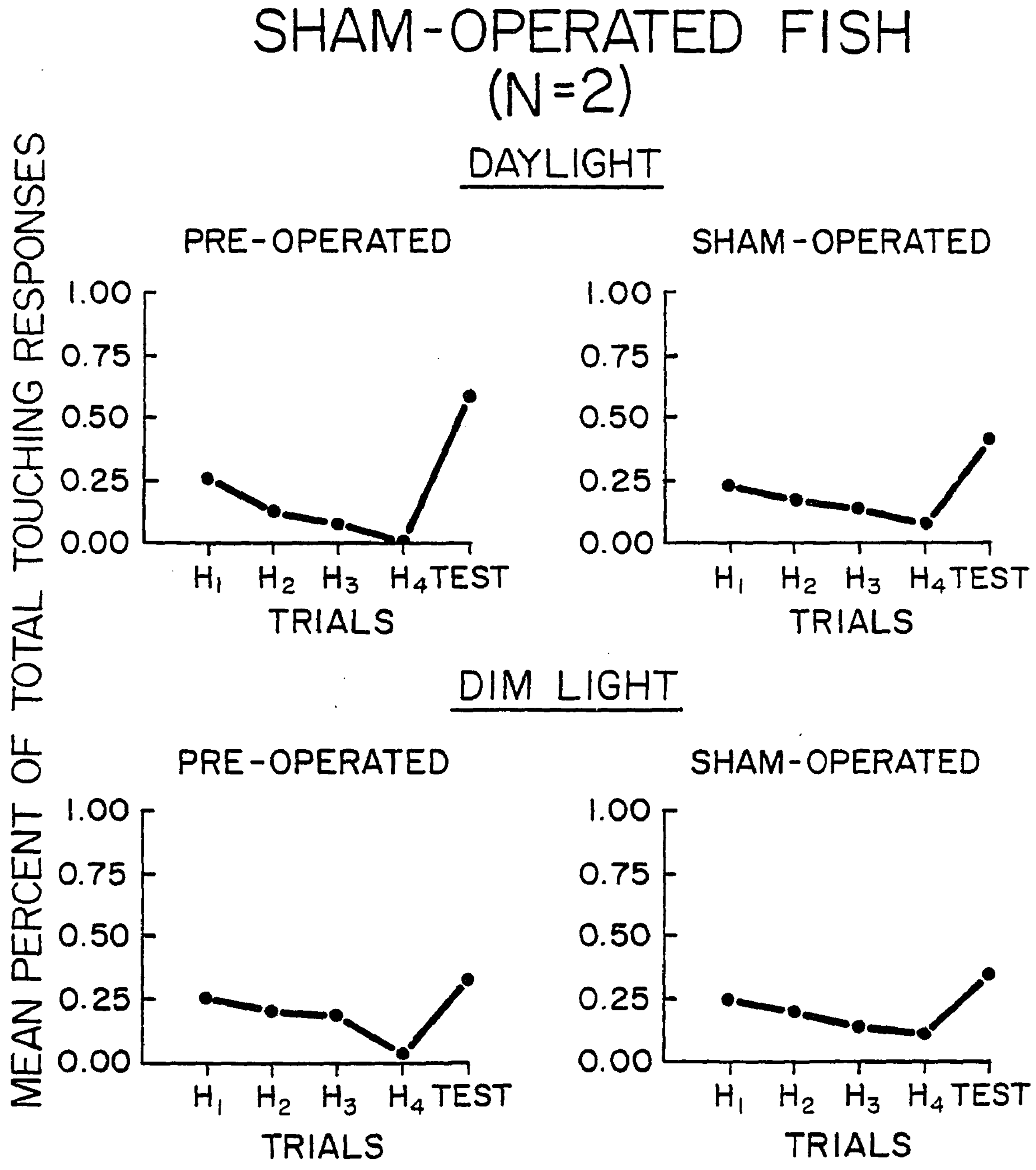

SHAM-OPERATED FISH
(N=2)
DAYLIGHT
PRE-OPERATED
SHAM-OPERATED
DIM LIGHT
PRE-OPERATED
SHAM-OPERATED
MEAN PERCENT OF TOTAL TOUCHING RESPONSES
1.00
0.75
0.50
0.25
0.00
H1 H2 H3 H4 TEST
TRIALS

Figure 15. The mean percent of touching (T) responses from H_1 - H_5 for experimental and sham-operated fish in a no light condition.

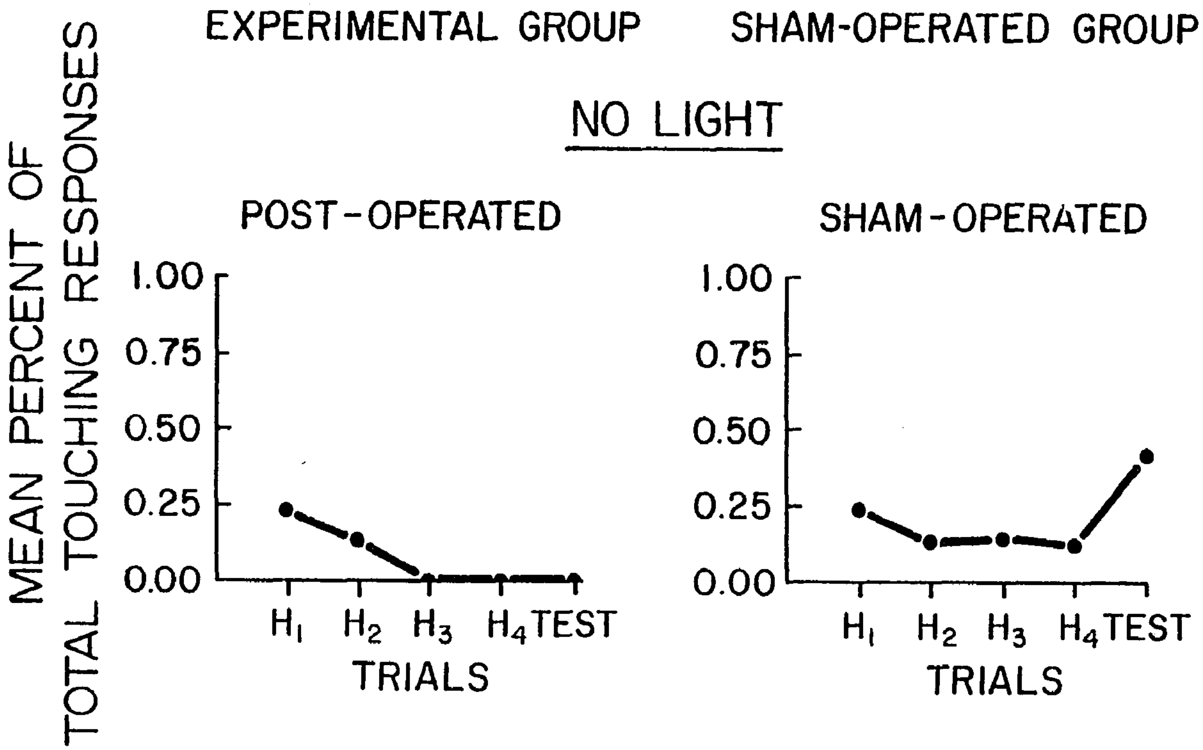

EXPERIMENTAL GROUP
SHAM-OPERATED GROUP
NO LIGHT
POST-OPERATED
SHAM-OPERATED
MEAN PERCENT OF TOTAL TOUCHING RESPONSES
1.00
0.75
0.50
0.25
0.00
H1
H2
H3
H4
TEST
TRIALS
1.00
0.75
0.50
0.25
0.00
H1
H2
H3
H4
TEST
TRIALS

Figure 16. The absolute number of touching (T) responses under different conditions for experimental and sham-operated fish.

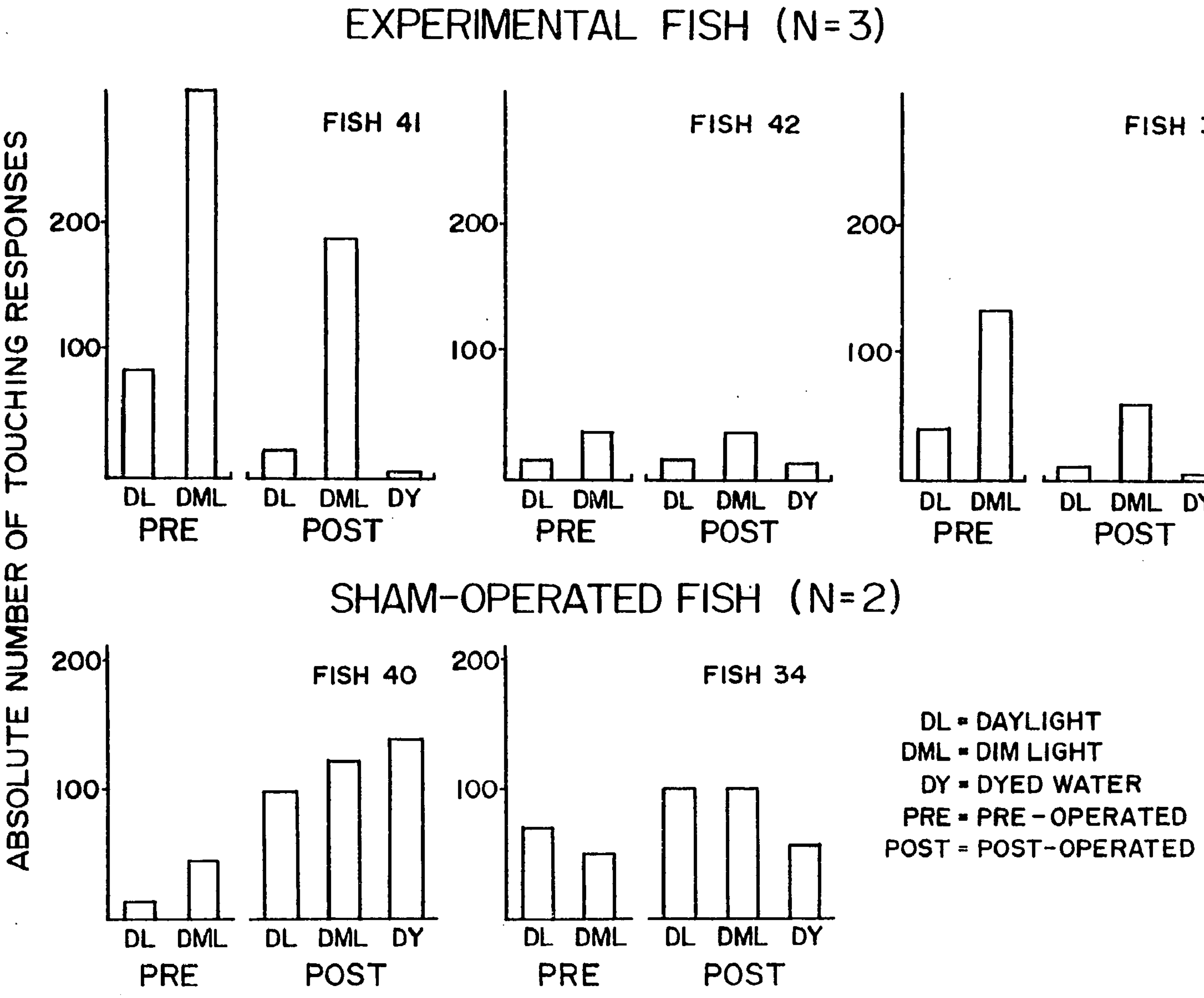
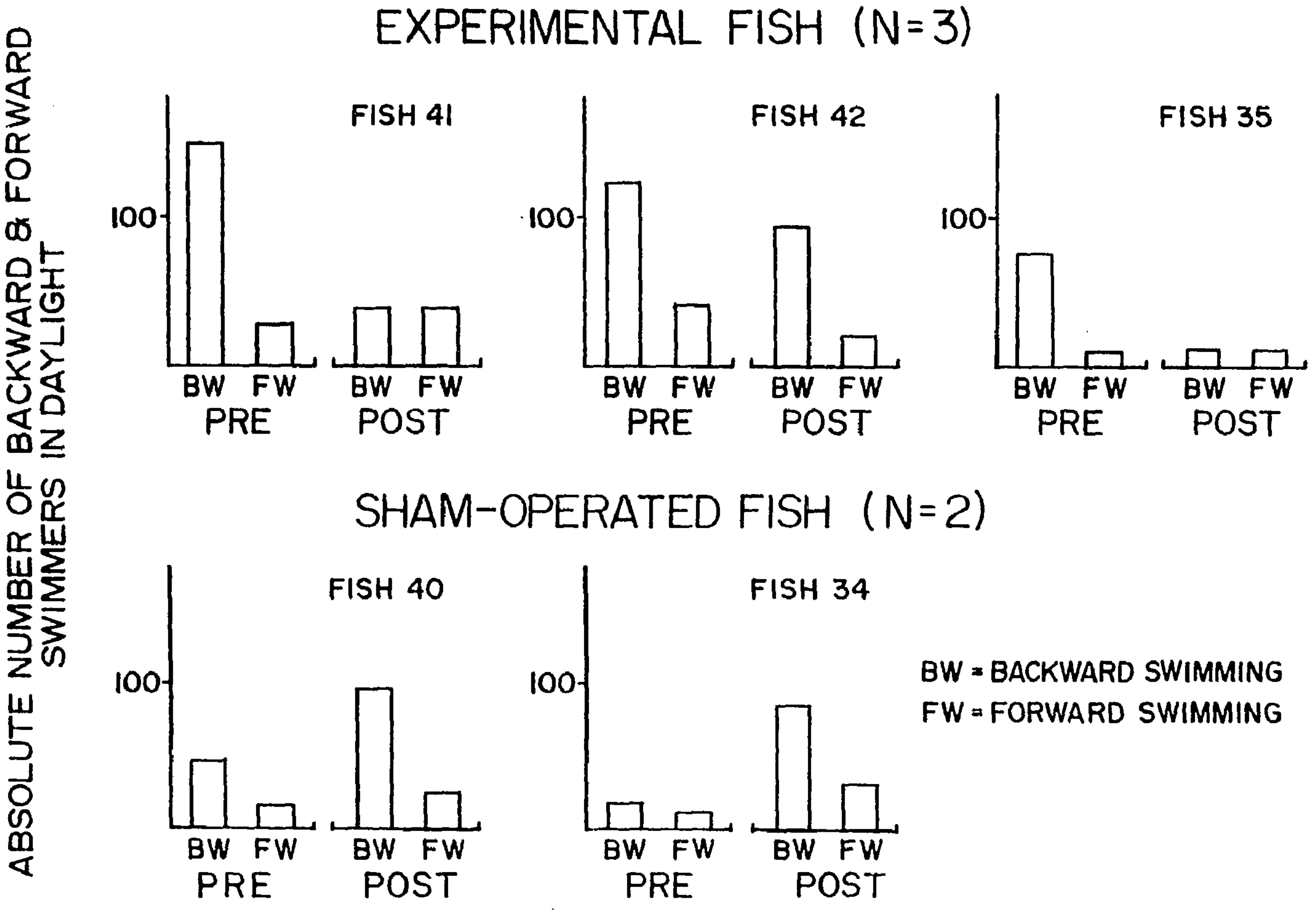

EXPERIMENTAL FISH (N=3)
ABSOLUTE NUMBER OF TOUCHING RESPONSES
FISH 41
FISH 42
FISH 35
200
100
DL
DML
DY
PRE
POST
SHAM-OPERATED FISH (N=2)
FISH 40
FISH 34
DL = DAYLIGHT
DML = DIM LIGHT
DY = DYED WATER
PRE = PRE-OPERATED
POST = POST-OPERATED

Figure 17. The absolute number of backward swimming (BW) and forward swimming (FW) responses under pre- and post operated conditions for experimental and sham-operated fish.


EXPERIMENTAL FISH (N=3)
SHAM-OPERATED FISH (N=2)
ABSOLUTE NUMBER OF BACKWARD & FORWARD SWIMMERS IN DAYLIGHT
FISH 41
FISH 42
FISH 35
FISH 40
FISH 34
100
BW
FW
PRE
POST
BW = BACKWARD SWIMMING
FW = FORWARD SWIMMING

In daylight, the number of responses for backward swimming (BW) and forward swimming (FW) were also recorded before and after surgical intervention for experimental and sham-operated fish. These data are presented in Figure 17. For experimental and sham-operated fish before surgery, there was a trend toward more BW than FW. Except for fish no. 34, there was more BW than T responses during daylight conditions (compare Figures 16 and 17). After surgical intervention, the experimental fish showed a decrease in the absolute number of BW. For example, fish no. 41 decreased the number of responses on BW from 152 to 39 after surgery. For the sham-operated fish, in contrast, there was an increase in the absolute number of BW. For example, fish no. 40 increased from 40 responses before surgery to 89 afterwards. The experimental fish appeared to alter their rate of FW randomly, while sham-operated fish increased the number of responses on this dependent variable after surgery.

In summary, intact fish emitted more T responses under dim light than under daylight conditions. Twenty-four hours after surgery, experimental fish without an EOD decreased the number of T responses under all conditions. However, this trend toward increases in response under dim light continued to appear. When the water was dyed to exclude most light, experimental fish emitted few responses. In contrast to experimental fish, sham-operated fish, twenty-four hours after surgery intervention, showed an overall increase in the number of responses emitted under daylight, dim light and dyed water conditions. Intact fish showed a high rate of BW in daylight. In all but one case, this rate of BW exceeded the rate of T in daylight. After surgery, the experimental fish showed a decline in the number of BW responses in daylight. The sham-operated fish, in contrast, increased the number of BW responses post-operatively in daylight. Trends for FW were not obvious in the experimental fish. The sham-operated fish increased the number of FW responses after surgery.

Discussion

The results of this experiment confirm that G. petersii has the capacity to use at least two different sensory systems - the visual and electrical - to discriminate between objects. Many other studies have shown that a variety of animals use multiple cues to orient in their environment. The white rat, for example, uses chemical as well as tactile and visual cues in maze learning (Southall and Long 1969); during courtship, the goldfish, Carassius auratus, relies not only on visual cues, but also on chemical signals from females (Patridge et al. 1976); bees use a variety of tactile, sun compass, and chemical cues to orient to pollen laden flowers (von Frisch 1967); and pigeons use a number of visual, electromagnetic and sun compass cues to orient home (Keeton 1969; Keeton 1971; Keeton, Larkin and Windsor 1974). In all these cases, special techniques were developed to unravel the contributions of different sense modalities to orientation.

In the present study, using the habituation-dishabituation method developed in Experiment I, in conjunction with surgical intervention and variations in light intensities, a number of conclusions could be reached: (1) G. petersii discriminated among objects in daylight primarily using its electrosensory system; (2) electrically silenced fish in daylight were unable under these conditions to discriminate among objects; (3) these same fish under dim light could discriminate between stimuli; (4) when vision was impaired by dyes placed in the water (no light condition), these silent fish were unable to discriminate; (5) sham-operated fish who received similar surgical interventions but who were not surgically silenced could discriminate among objects in daylight, dim light and no light conditions.

Under dim light conditions, G. petersii appears to use both its electrosensory system and its visual system to discriminate. The evidence for this lies in the absolute number of responses emitted by the fish under different light intensities. An inspection of Figures 9 and 10 shows that in all but one case the absolute rate of response (T) under dim light conditions was twice and even three times as high as that seen under daylight conditions. After surgical intervention, electrically silent fish continued to show an increase in T in dim light, although there was a general decline in the absolute number of responses compared to pre-operated levels. Sham-operated fish post-operatively did not show this decline, but did show an increase in T that contrasted sharply with the behavior of the experimental fish. Surgically silent fish under no light conditions emitted very few responses absolutely.

The rate of BW and FW were recorded in daylight pre- and post-operatively for all subjects. BW, as used in Experiment I,was sensitive to changes in stimulus condition and, therefore, was a good indicator of discrimination. In daylight, when G. petersii was using the electrosensory system as a major source of information, intact fish emitted a higher rate of BW than T for all but one fish. Post-operatively, however, the rate of BW for an electrically silent fish declined. Sham-operated fish contrasted with experimental animals; they increased their rate of BW post-operatively. These results suggest that BW could be correlated with the electric organ discharge of the fish. Heiligenberg (1975) noted that the electric fishes do not have a structure analagous to a lens in the visual system which can serve as an image focuser. One way that a fish can increase stimulation of its electroreceptors is to get close to the object. BW occurred close to the stimuli presented in the aquarium.

The histology and physiology of the mormyrid retina (McEwan 1938) indicated that the fish probably have a functional visual system under low light intensity: in daylight, the fish would effectively be blinded. This data also correlates with what is known of these fishes in their natural habitat. They tend to feed in schools in the evening, and hide in crevices along the banks of rivers in Africa during the day (McEwan 1938; Moller 1976).

GENERAL DISCUSSION

Advantages and Uses for the Habituation-Dishabituation Method

The methodology and data analysis used in these experiments can be applied to a variety of problems in animal behavior. For example, many species of animals do not operantly or classically condition easily, or at all (Shettleworth 1961). Gnathonemus petersii is representative of a species that has been difficult to condition. However, using the habituation-dishabituation methodology easily obtainable, consistent results were produced from individual G. petersii on a number of dependent variables. Individual fish that responded at a high rate in one session continued to respond at that same high rate over all sessions. The ANOVA showed that interfish differences were not significant over H_1 - H_4 and test trials. All fish used in this study responded to stimuli introduced into their aquarium with touching with the head, body, tail, swimming forward and backwards and alterations in the EOD repetition rate.

Consistent results were also obtained on stimulus pairs; for example, all G. petersii discriminated between small stimuli on habituation trials and large and medium stimuli as test objects. There was a consistent failure to discriminate when large habituation stimuli were contrasted with small and medium test stimuli.

This failure to obtain discrimination, when the large objects were the habituation stimuli, has been found by other researchers (Davis and Wagner 1968; Bernstein 1968) to be an intensity problem. They found that when high intensity auditory stimuli are used on habituation trials, the response to less intense stimuli is reduced. These researchers speculate that habituation to larger stimuli is shorter and more complete, and that subjects failed to respond because they are more habituated by the time the less intense stimulus is presented. Data from this study do not support this theoretical position. Both the ANOVA over trials H_1 - H_4, and the correlation coefficients indicated that habituation did occur, and that, as seen in the slopes of the linear equations, habituation was neither more nor less complete with the large stimulus objects.

The linear correlation coefficients did show, however, that the goodness of fit was poorer with larger stimuli. Also, fish, when presented with the large stimuli, increased the intensity of their behavior by audibly biting and butting the stimulus. Intensity of behavior was not recorded in these experiments. It is possible that if the intensity of response had been recorded, more of a continuum of response rates could have been observed in relation to the different sized stimuli.

The small and medium sized objects in this experiment were area equivalent, and, therefore, it was unexpected to find that there were significant differences in the number of responses emitted to cubes and spheres over trials H_1 - H_4 (ANOVA, $p < .05$). Cubes elicited significantly more responses than spheres over trials. If these results accurately reflect the behavior of the fish, it may be that distortion of the electric field produced by angles is more pronounced than that produced by spheres. This increased distortion could lead to increased stimulation of the electroreceptors.

A preliminary experiment to determine if fish treated area equivalent objects similarly was considered unsuccessful and discarded because differences were found in only one direction (preliminary research conducted by the author). Since the fish consistently could discriminate spheres as habituation stimuli from cubes as test stimuli, it was puzzling to find that discrimination did not consistently occur in the opposite direction. If the intensity of stimulation is greater with the cubes than with the spheres, it is possible that area equivalence is not an important criterion for discrimination in these fish, but angles may be. Rats, for instance, discriminate shape on the basis of degree of angles (Lashley 1938), and, therefore, this mechanism is not unknown.

Both the neotropical gymnotids and the unrelated African mormyrids have developed strikingly similar electrogenic tissue, electric organs, and electrosensory systems (Szabo and Fessard 1974; Scheich and Bullock 1974). These convergent systems are used for electrolocation and social behavior. However, few comparative studies on the species-specific functioning of these sensory systems have been accomplished. A habituation-dishabituation method would relatively rapidly produce information about species specific adaptations of the electrosensory system, and contribute to the understanding of the ethology of both the mormyrids and the gymnotids.

The EOD as a Novelty or Orienting Response

If the alteration in the repetition rate of the EOD when a novel stimulus is introduced is reliable, it is possible that the fish is emitting an orienting or novelty response. Thompson, et al. (1968) found a transient alteration in the EOD repetition rate in the first 15 seconds after the fish received an electric shock. It is suspected that both the presence and and absence of a stimulus can be signaled with this novelty response. However, experimental and temporal conditions were confounded in this experiment, and it was not possible to compare H_5 and test trials. Malcolm (1976) and Bauer (1974) found long term stability in the histograms of the EOD of _G_. _petersii_. On a short term basis, data obtained on different days in this experiment yielded statistically dubious results.

At present, a more elaborate study of the EOD based on a system which equates the variation in rate and pattern (Moller 1970) over days is needed. If the absolute number of responses in a 20 second interval is too variable over days or trials, then it is possible that the percent response over a 20 second time interval could be used and compared across trials and days. Once these methodological difficulties are overcome, it seems likely that orderly changes in the EOD will be found over all trials. All other dependent variables, such as touching with the head, the body, the tail, and swimming backward and forward, showed similar patterns habituation-dishabituation over trials. While it is possible that the EOD does not correlate well with these other dependent variables (Clayton and Hinde 1968), evidence from Experiment II suggests that the electrosensory system is associated with behaviors such as touching and backward swimming.

Visual and Electrosensory Integration

Experiment II definitely showed that the EOD is involved in the discrimination of size in _G_. _petersii_. The dependent variable used throughout this last experiment was touching. "Touching", in this context, is not associated with the cutaneous senses. This touching response, for instance, was reduced or absent when electrically silent fish were tested for their ability to discriminate in daylight. In dim light, these impaired fish resumed touching the stimulus objects and were able to discriminate. Touching, therefore, seems to be a general exploratory response, which appears when the fish is presented with an environment in which his sensory systems are functional.

The ways in which an organism processes and integrates information can vary considerably. For instance, the results of the present study suggest that the fish use both visual and electrical information to discriminate. When both systems were intact, sensory summation occurred under dim light and, if one system was damaged, the number of responses in the trials decreased by approximately 50%.

There are other ways of accomplishing the recovery of a behavioral function after intervention. For example, an animal can take in sensory information through all channels at once, and, if one system fails, the animal can probably compensate. Another alternative occurs when an animal has a definite preference in modality (for instance, movement in the cat visual system) and when this information is absent, the data previously available through that channel is centrally transposed into another channel (von Frisch 1967, visual angle information transposed into geotactic information in bees; Keeton 1974, electromagnetic cues transposed into optic cues). The techniques provided in this paper can help to separate and explore these phenomena further.

From this study, it is evident that the fish use a dual process sensory system when it is available to them. However, it is unknown what central mechanisms could account for this phenomena. The

EOD processing of intensity changes have been thought to occur in both the lateral lobes and the cerebellum of G. petersii. Szabo and Fessard (1974) have suggested that the lateral line lobes receive and process information about transient alterations in the electrical environment, while the cerebellum is expected to process long term changes. No information is available on the central processing of visual information since there are no previous behavioral studies involving vision in these fish.

It remains to be determined precisely what light intensities are useful to this animal. A group of animals could be electrically rendered silent, and a stimulus could be introduced into the aquarium under decreasing and increasing light intensities over trials. Electrically silenced fish, on the basis of results of this research, would fail to respond to non-conductive stimuli in daylight. Over trials, the light intensity could be decreased until the fish did respond to the stimulus. At the other end of the spectrum, the fish could be tested under dim light initially, and then the light intensity could be increased until a response (such as touching) no longer occurred. This light intensity data, under laboratory conditions, would have to be correlated with information from the habitat about the variation in light intensity shortly before dusk, at dusk and after night had fallen, to determine if the laboratory results were valid over the range when the fish was active in the wild.

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