LOCOMOTOR BEHAVIOUR OF THE BLACK BULLHEAD, *ICTALURUS MELAS* (RAFINESQUE) AND BROWN BULLHEAD, *ICTALURUS NEBULOSUS* (LE SUEUR)

by

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ABSTRACT

The locomotor patterns of black and brown bullhead were studied in an electronically monitored fish tank and cinematographically under constant environmental conditions. The size of turns, handedness, turning frequency, distance between turns, and velocity were computed and compared where possible with existing information for goldfish and other species. Two areas of the tank were considered--the central region and a strip around the periphery. Turning frequency and velocity were the least stable of the parameters studied and therefore perhaps the most useful as indicators of locomotor response to external stimuli. Handedness became more pronounced as the subjects approached the tank walls and as velocity increased, turn size decreased.

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INTRODUCTION

To date, the literature contains few analyses of fish locomotor behaviour which are quantitative in their approach. The work of Kleerekoper et al. (1970) provides the only comprehensive review of the subject, although single aspects of locomotion have received attention. Swimming speeds, for instance, are known for many fish (Stringham, 1924; Fry and Hart, 1948; Kerr, 1953; Gray, 1953, 1957; Bainbridge, 1961; Walters and Fierstine, 1964; Beamish, 1970; Olla et al., 1970; Brett, 1965, 1971, and Brett et al., 1958). The energetic advantages of burst swimming have been examined by Weihs (1974), and Tsukamoto et al. (1975) have formulated an index for comparing the swimming abilities of different species. Turning behaviour has been studied in elasmobranchs (Kleerekoper, 1967a,b) and in teleosts (Kapoor and Kleerekoper, 1970; Westlake and Kleerekoper, 1970); exploratory behaviour has been investigated by Welker and Welker (1958), Russell (1967), Amouriq (1969), Kleerekoper (1969), and Kleerekoper et al. (1974), and logarithmic spiral components of locomotor patterns have been discussed by Kleerekoper et al. (1973). In addition, it has been shown that changing environmental factors such as light conditions, magnetic fields, dissolved oxygen concentrations, temperature, and pollutants affect locomotor activity (Davy et al., 1972; Griffiths and Alderdice, 1972; Kleerekoper, et al., 1972; Hill, et al., 1973; Kleerekoper et al., 1973; Petrosky and Magnuson, 1973; Kelso, 1974; Otto and O'Hara Rice, 1974;

Varanelli and McCleave, 1974). Matis *et al.* (1973, 1974b) have suggested that these responses to external cues may be superimposed upon endogenous oscillations in orientation and locomotion.

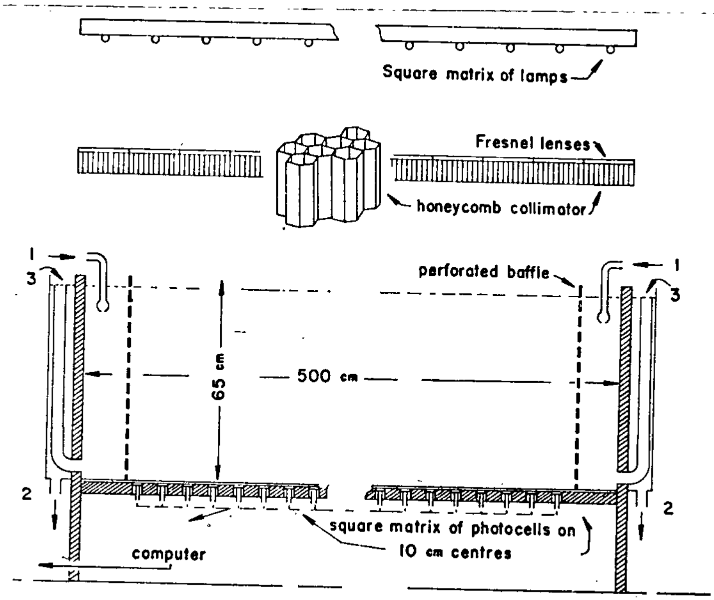
The aim of the present study is to provide a quantitative analysis of some of the parameters of catfish locomotion under controlled environmental conditions and to investigate the usefulness of these parameters as indicators of locomotor responses to external stimuli.

METHODS

The monitor tank (5.0 x 5.0 x 5.0 m) used in the initial experiments at Texas A & M University has been described elsewhere (Kleerekoper, 1967a; Kleerekoper et al., 1969, 1970). A square matrix of 1936 photoconductive cells embedded at 10 cm. centres in the tank floor received collimated light from above. Interception by a fish of the light impinging on a cell resulted in increased cell resistance. An electronic logic interface with an on-line digital computer determined the address of the changed cell and the time elapsed between successive cell intercepts. Storage of the information on magnetic tape allowed computations to be made on an IBM 360 computer. The response time of the system was sufficient for accurate velocity analysis and the angular resolution for the size of fish used was not less than 4^{o} (Fig. 1).

In a second series of experiments conducted at the University of British Columbia, a Plexiglass tank (thickness, 12 mm; dimensions, 1.83 x 0.76 x 0.39 m), similar in design to that used by Kleerekoper (1967a) for studies of locomotor behavior in the nurse shark, was constructed (Fig. 2). The clear tank front provided a view of the vertical movements of the subjects, while horizontal movements were reflected by a mirror (1.83 x 0.91 m.) on a wooden frame mounted 12 cm above the tank at a 45^{o} angle. Dechlorinated city water entered the tank through a Plexiglass pipe placed across one end and perforated on the lower surface by a row of holes (diameter, 5 mm.). A vertical overflow pipe

FIGURE 1. Cross-section of the Texas monitor tank and block diagram of the data processing system. (1) Water inlet; (2) water outlet; (3) standing pipe for water level regulation. From Kleerekoper *et al.* (1970).


Square matrix of lamps
Fresnel lenses
honeycomb collimator
perforated baffle
1
3
65 cm
500 cm
2
square matrix of photocells on
10 cm centres
computer

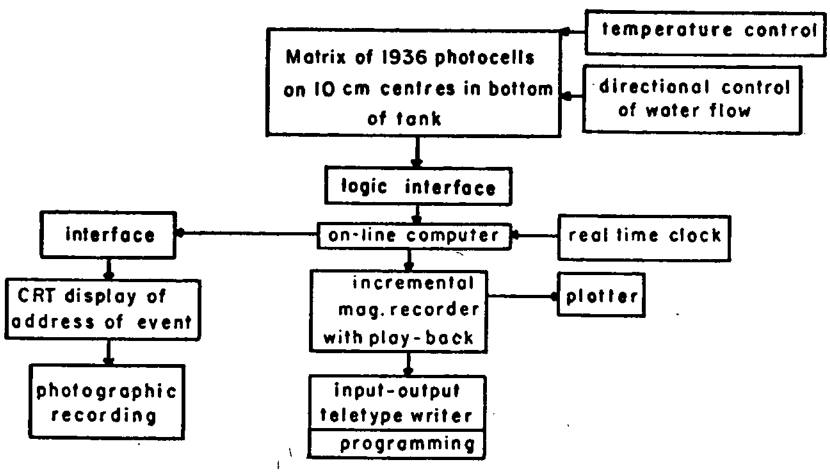
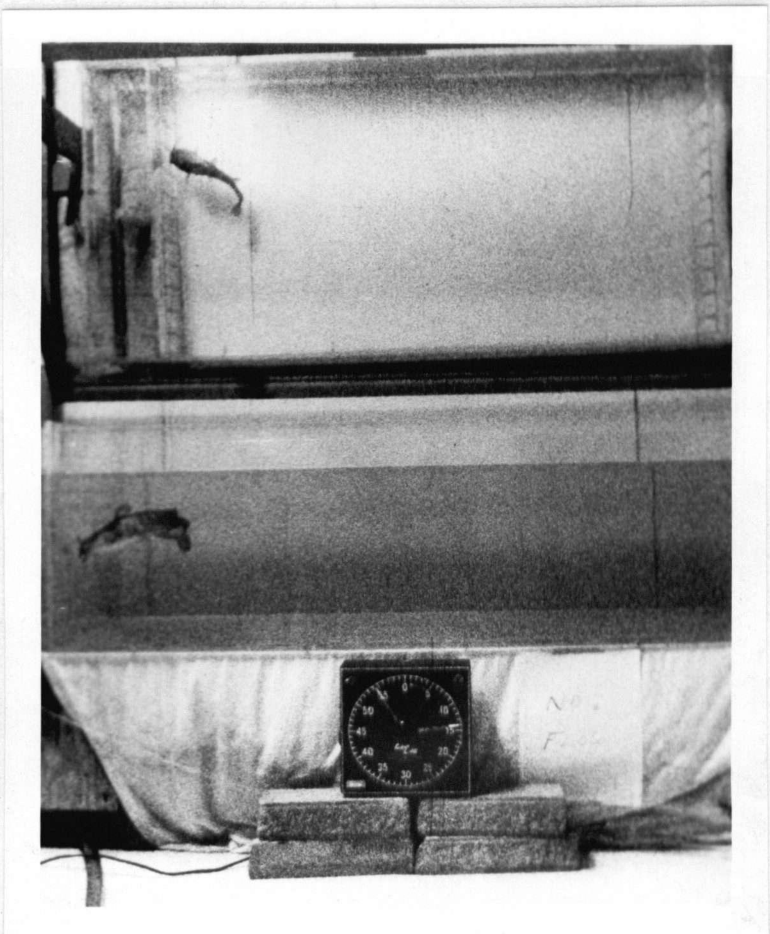

Matrix of 1936 photocells on 10 cm centres in bottom of tank
temperature control
directional control of water flow
logic interface
interface
on-line computer
real time clock
CRT display of address of event
incremental mag. recorder with play-back
plotter
photographic recording
input-output teletype writer
programming

FIGURE 2. U.B.C. experimental tank for cinematographic recording



(inside diameter, 2.54 cm.) at the opposite end provided the outlet. Uniform flow was achieved by inserting two Plexiglass baffles, each with 10 rows of holes (diameter, 8 mm), between inflow and outflow, 17 cm. from either end.

A 16 mm. Bolex movie camera (H 16 Standard) 2.5 m. directly in front of the tank recorded the fish movements. Manual advancement of the film at one frame/sec was maintained by triggering an external cable to the camera in synchrony with the second hand movements of a Gra-Lab Universal Timer (Model 168) placed in the photographic field. Development of the films (Kodak, 4x reversal 7277, 4xR 455) was handled commercially by Bellevue Pathé (B.C.) Limited.

The whole apparatus was housed in a Bill-Craft Industries Limited controlled-environment room (Model 2002) maintained at 20°C by a Sherer Camless Programmer Temperature Regulator. The walls of the room were uniform white and the lighting consisted of two fluorescent ceiling lights encased in frosted glass covered with several layers of cheesecloth to eliminate glare.

Movements in the horizontal plane recorded by this monitoring system were subjected to analysis on a Vanguard Motion Analyzer (Vanguard Instrument Corporation, Melville, N.Y.). For each frame of film, the position of the snout on the X and Y axes of the analyzer and the orientation angle of the body of the fish were transferred to punch tape for further calculations on a PDP-11 computer.

The subjects in the study were five black bullhead, Ictalurus melas (Rafinesque), average total length 20 cm., from Lake Bastrop, Texas and seven brown bullhead, Ictalurus nebulosus (Le Sueur), average total length 25 cm., from Deer Lake, Burnaby, British Columbia. Both groups were maintained in communal tanks prior to recording and fed with beef liver. Each fish was given only one recording session.

In Texas, the water temperature of the monitor tank at the start of recording fluctuated between 27^{o} and 31^{o}C. This was slightly higher than the 19^{o} to 24^{o}C range of the retaining tanks. Water flow through the tank was shut off immediately before the introduction of the subject and monitoring of a single animal was maintained over 20 to 24 hours.

At UBC, all fish were monitored at their acclimation temperatures since both monitor and retaining tanks were supplied with dechlorinated city water from the same central system. These temperatures varied from 6^{o}C in the winter to 19^{o}C in the summer. The fish in this second group of experiments were left undisturbed in the monitor tank for two to three hours prior to filming to avoid recording exploratory behavior. Fifteen minutes before recording began, the water supply was turned off. Monitoring of a single animal was divided into one hour filming periods during which recording was halted whenever the subjects stopped moving. Each fish received as many as three periods in one day resulting in a total of 650 ft. of film from the seven fish.

RESULTS

Five parameters of the locomotor pattern traced by a fish are considered in this paper: size of turns, direction of turning, turning frequency, distance between turns, and swimming velocity. A turn in the monitor tank is defined as a change in the direction of forward progression indicated by three consecutive photocell intercepts (Texas) or by three consecutive orientation angles on the motion analyzer (UBC).

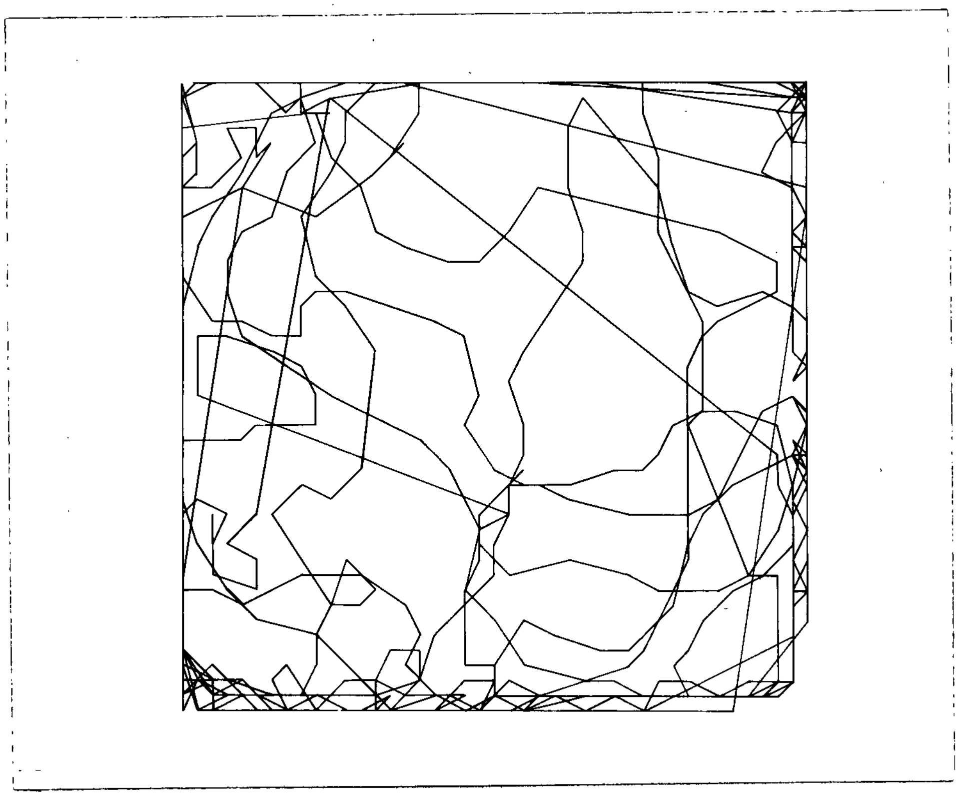
Kleerekoper _et al_. (1970) and Kleerekoper and Timms (1970) have shown that goldfish approaching a barrier such as the wall of a tank, alter the size of turns, turning frequency, and velocity of locomotion. In order to investigate these alterations in the catfish, the computer programmes divided the tanks into two sections--A, the central portion, and B, a strip around the periphery, 30 cm. wide in the Texas tank and 10 cm. wide in the UBC tank (Fig. 6 and 9).

While the parameters investigated in the two series of experiments are the same, the results are not strictly compatible since the Texas data is subject to the spatial limitations of the photocell grid and the UBC approach is limited by the filming speed of the camera. The results from each monitor tank, therefore, are presented separately. For several parameters, the initial Texas data provided the basis for a more detailed analysis of the UBC results.

General Locomotor Patterns - Texas

The locomotor pattern shown in Fig. 3 represents 1000 photocell intercepts made by Fish No. 32 and recorded by a plotter on-line to the

FIGURE 3. Locomotor pattern traced by Fish No. 32 in the Texas monitor tank. Plot represents 1000 photocell intercepts.



monitor tank computer. It is typical of the movements made by all five subjects.

General Locomotor Patterns - UBC

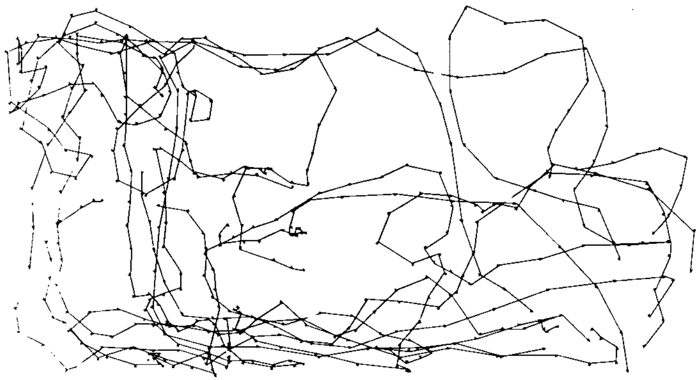
While the film itself provided a visual record of the locomotor pathways, a plot of the type shown in Fig. 3 for the Texas work is a much more useful display. Such plots were produced at UBC by a plotter on-line to the PDP-11 computer which transcribed successive X, Y addresses from the punch tape. Plots for four fish are shown in Fig. 4; each plot representing approximately 30 minutes of recorded movements. Activity was spread over most of the tank area in Experiments 1, 6, 18(B), and 20(B). In two hours of recording, the fish of Experiment 11 rarely ventured away from the walls, while the subjects of Experiments 7, 10, and 14(A) were most active around the walls but made occasional trips to the rest of the tank.

Differences between fish, however, are not as great as the differences between locomotor patterns for the same fish at different times during the recording period. Fig. 5 contains representative five to ten minute segments from each hour of Experiment 6. In the first hour, movement was restricted to the tank walls. In the second and third hours, activity shifted to the centre. In the fourth hour, the fish showed a preference for one corner of the tank.

Size of Turns

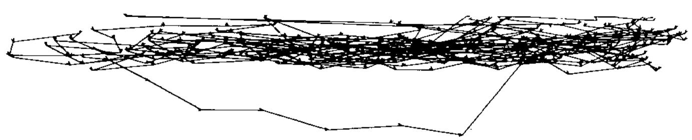
The frequency distributions of size of turns in degrees was computed for each subject for all turns, left and right, throughout the recording period.

FIGURE 4. Locomotor patterns traced by four fish in the U.B.C. monitor tank. Each plot represents approximately 30 minutes of recording.

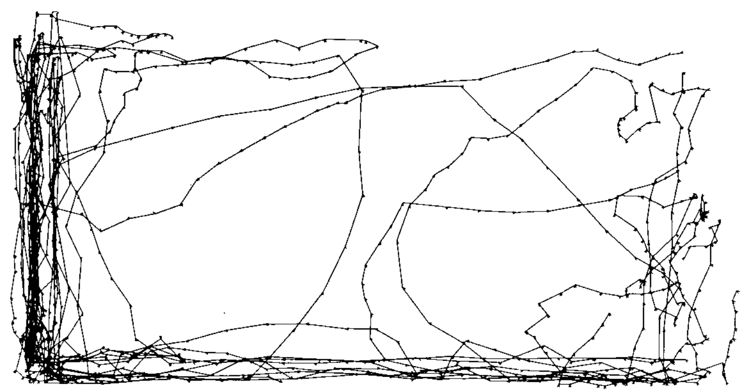


Experiment No. 1

Experiment No. 6

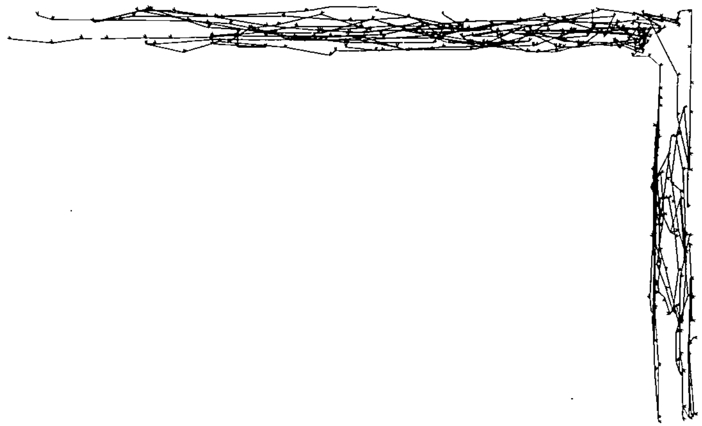


Experiment No. 11

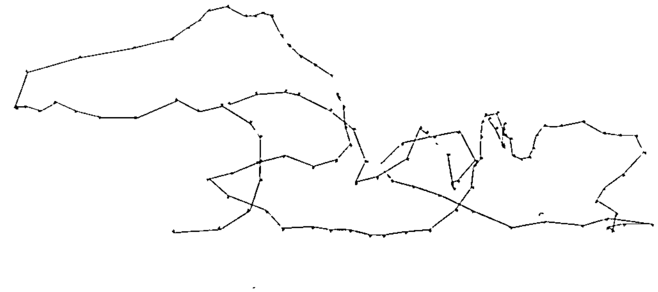


Experiment No. 14(A)

FIGURE 5. Representative locomotor patterns from successive hours of Experiment 6, U.B.C. Each plot is 5-10 minutes in duration.



Hour 1



Hour 2

Hour 3

Hour 4

Texas

A Kolmogorov-Smirnov test of these individual distributions indicated significant variations between certain fish ($p \leq .001$). Pooling the data from those subjects whose turning patterns were similar ($p > .05$) resulted in the three distributions of Fig. 6. Although all fish demonstrated a preference for angles of 10-20° in the centre of the tank (area A), Fig. 6 shows that the strength of the preference varies from slight (Fish No. 24 and No. 32) to very strong (Fish No. 45 and No. 62). The degree of preference for smaller turns is also illutrated by the mean angles of the three groups (Table 1). Near the walls of the tank (area B), the mean angle of turning became larger as the proportion of turns in the 10-20° class decreased (Table 1 and Fig. 6). In all cases, the frequency distribution of turns in regions A and B were significantly different (Kolmogorov-Smirnov, $p \leq .001$).

Two of the five fish exhibited significant differences between the magnitude of turns made to the right and those made to the left (Fig. 7), but the differences were less than those between individuals ($p \leq .05$ cf. $p \leq .001$).

UBC

Fig. 8 shows the frequency distributions of turn sizes in 10° classes for the whole tank over the full recording period of each fish.[1] A X^2 test indicated significant differences between the distributions of all individuals ($p \leq .05$) except for Experiments No. 7 and 14(A) ($p > .05$).[2]

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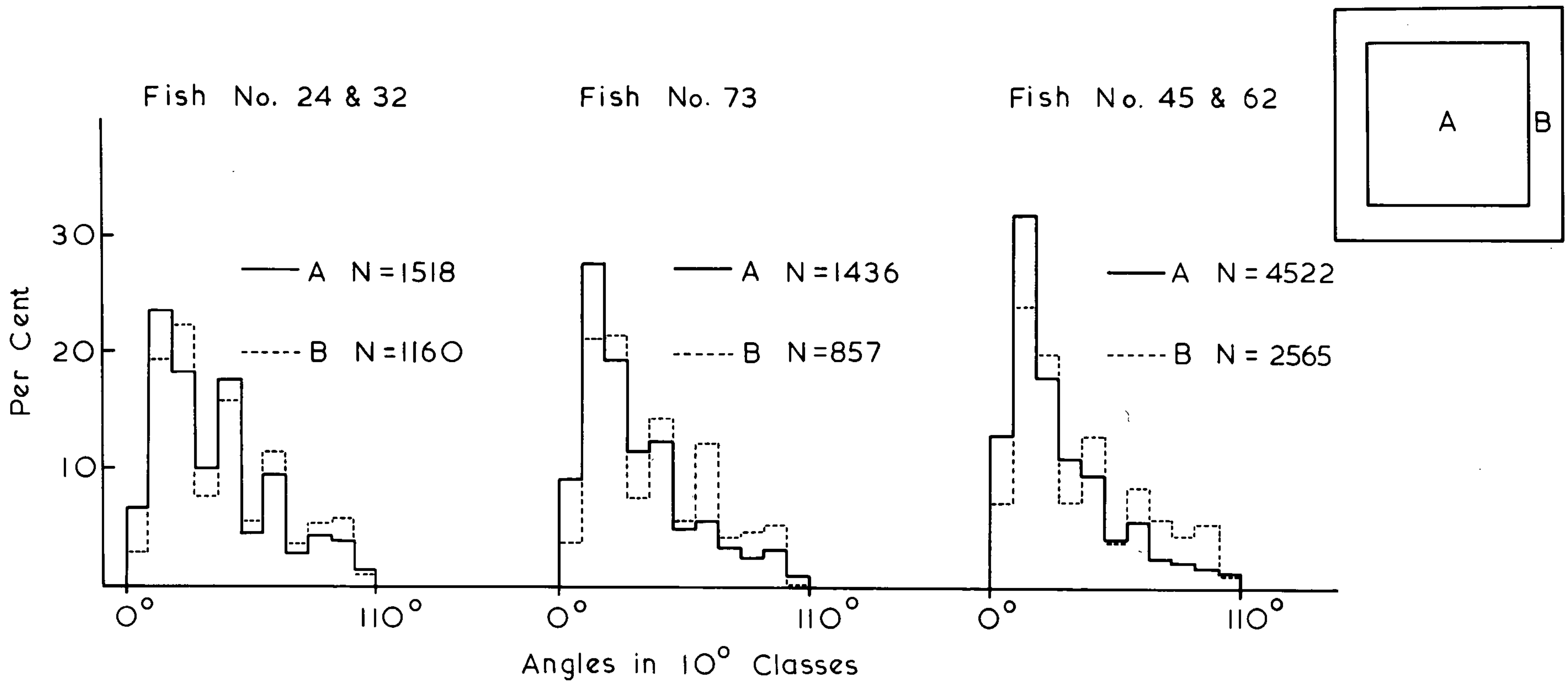
[1] All turns have been corrected for the presence of the mirror and therefore represent the true turning direction of the subjects.

[2] Since the X^2 test is not sensitive to interdependence of data, it was applied to the UBC results in preference to the Kolmogorov-Smirnov test.

FIGURE 6. Frequency distributions of size of turns in tank areas A and B, Texas data. Left and right turns pooled. Data of fish with statistically similar distributions are pooled ($p < .05$). Distributions shown are significantly different at .001 level. Insert shows tank floor divided into areas A and B.

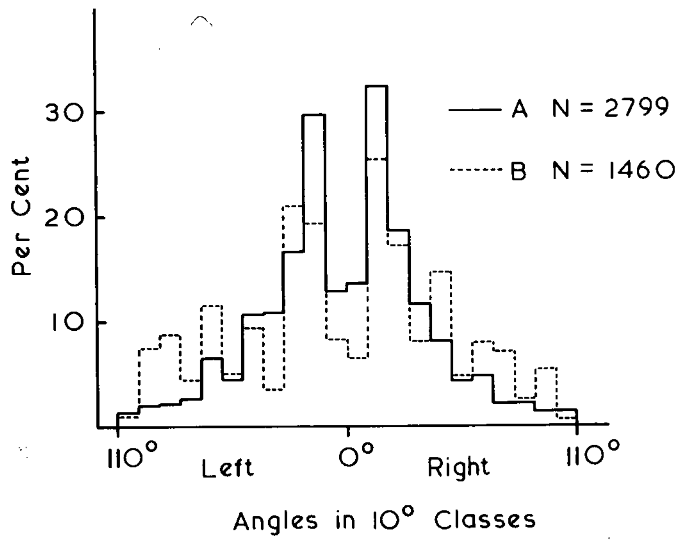


Fish No. 24 & 32
Fish No. 73
Fish No. 45 & 62
A
B
Per Cent
30
20
10
A N=1518
B N=1160
A N=1436
B N=857
A N=4522
B N=2565
0°
110°
Angles in 10° Classes

TABLE 1. Mean and standard deviation of turning angles for the centre (A) and walls (B) of the Texas tank

	Tank Area A		Tank Area B	
Fish No.	Mean Angle in Degrees	SD	Mean Angle in Degrees	SD
24 & 32	37.78	24.58	42.22	25.44
73	33.38	23.32	41.03	25.17
45 & 62	30.19	22.88	39.18	26.66

FIGURE 7. Frequency distribution of left and right turns in tank areas A and B for Texas Fish No. 62. Left and right turns are significantly different at .05 level.


Per Cent
30
20
10
A N = 2799
B N = 1460
110°
Left
0°
Right
110°
Angles in 10° Classes

The data for these two subjects were pooled (7 + 14(A)). All subjects showed a preference for turns in the 0-10^{o} category, but the degree of preference varied with the individual, as was also suggested by the Texas results. In Fig. 8, the experiments are arranged in order of increasing specificity for turn size. The means of the distributions are included in Table 4, Column 1.

The frequency distribution of left turns was significantly different from the distribution of right turns in Experiments 1, 6, and 7 + 14(A) (X^2: $p \leq .05$).

The turns in tank areas A and B were then computed separately and the resulting frequency distributions for each experiment (Fig. 9) compared using a X^2 test for goodness of fit. Significant results ($p \leq .01$) were obtained for Experiments 6, 10, and 20(B), but not for Experiments 1, 18(B), or 7 + 14(A) ($p > .05$). Experiment 11 was excluded from this type of analysis because the subject made too few trips through the tank centre (ref. Fig. 4). Means and standard deviations for the distributions of Fig. 9 are included in columns 1 and 2 of Tables 5 and 6. A t test of the means of combined left and right turns for each individual indicated that turns in the tank centre (area A) were significantly larger ($p \leq .01$) than those occurring next to the walls (area B) in those experiments for which a significant X^2 was obtained (Table 2).

Handedness

In initiating a turn, an animal in an open field situation may move either to the left or to the right. If there were a bias in turning behavior (handedness), left and right turns would appear with unequal

FIGURE 8. Frequency distribution of size of turns for the whole U.B.C. tank. Data of fish with statistically similar distributions are pooled ($p > .05$). Distributions are arranged in order of increasing preferences for turns of 0-10 degrees.

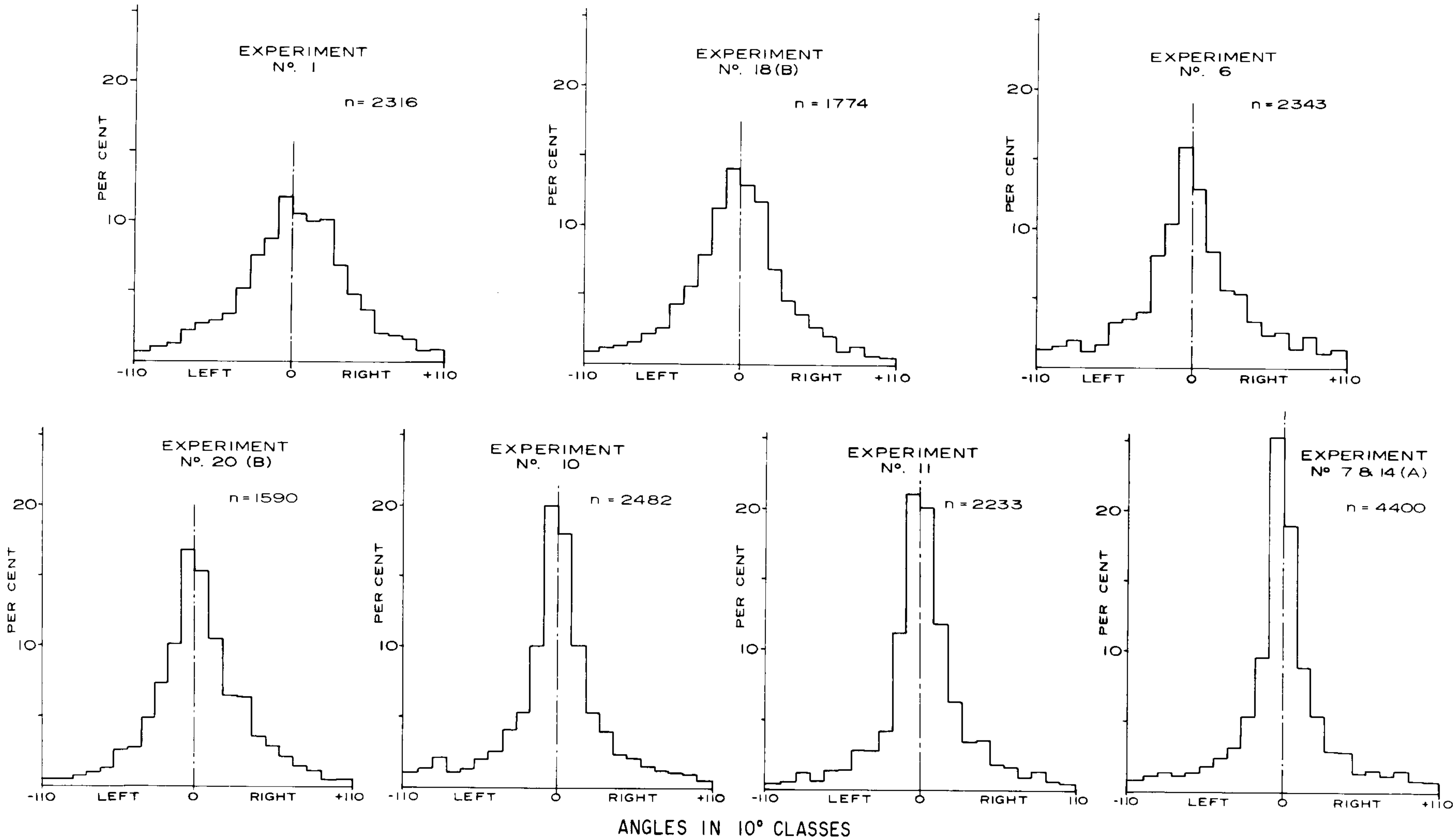

EXPERIMENT N°. 1
n= 2316
EXPERIMENT N°. 18 (B)
n = 1774
EXPERIMENT N°. 6
n = 2343
EXPERIMENT N°. 20 (B)
n = 1590
EXPERIMENT N°. 10
n = 2482
EXPERIMENT N°. 11
n = 2233
EXPERIMENT N° 7 & 14 (A)
n = 4400
PER CENT
10
20
-110
LEFT
0
RIGHT
+110
ANGLES IN 10° CLASSES

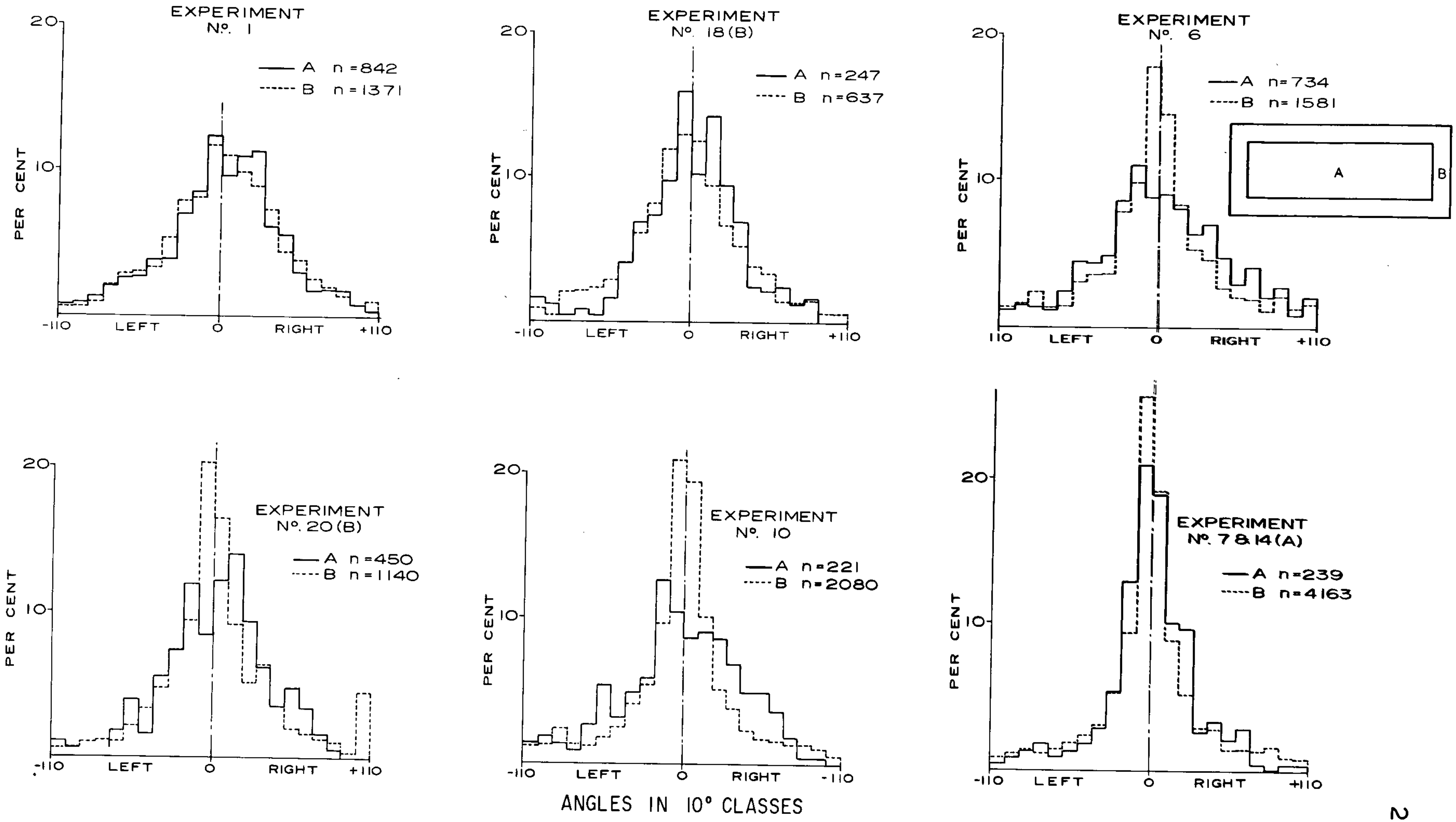
TABLE 2. t test of mean turning angles for the centre (A) and walls (B) of the U.B.C. tank; left and right turns pooled

	Tank Area A		Tank Area B			
Experiment No.	Mean Angle	Var.	Mean Angle	Var.	t	sig.[1]
1	31.06	615.3	31.56	628.1	0.46	---
6	35.03	710.5	29.95	815.4	4.17	.01
10	32.60	612.9	25.51	713.0	4.02	.01
18(B)	26.70	531.2	29.74	625.3	1.72	---
20(B)	28.62	512.2	24.90	553.5	2.92	.01
7 + 14(A)	22.32	502.0	23.82	665.6	1.00	---

t test modified for non-homogeneity of variances. Critical value $t_{.05,\infty} = 1.65$

[1]level of significance

FIGURE 9. Frequency distribution of size of turns in tank areas A and B, U.B.C. data. Data of fish with statistically similar distributions are pooled ($p > .05$). Distributions are arranged in order of increasing preference for turns of 0-10 degrees. Insert shows tank floor divided into areas A and B.


EXPERIMENT
Nº. 1
A n=842
B n=1371
EXPERIMENT
Nº. 18(B)
A n=247
B n=637
EXPERIMENT
Nº. 6
A n=734
B n=1581
A
B
EXPERIMENT
Nº. 20(B)
A n=450
B n=1140
EXPERIMENT
Nº. 10
A n=221
B n=2080
EXPERIMENT
Nº. 7 & 14(A)
A n=239
B n=4163
PER CENT
20
10
-110
LEFT
0
RIGHT
+110
ANGLES IN 10° CLASSES

frequency and/or magnitude.

Texas

In the Texas group of experiments, the turns of the five catfish were analyzed for handedness solely in terms of the frequency of left and right turns using a Z test (Table 3). Areas A and B of the tank were considered separately. In the vicinity of the walls, three fish were handed--two, left and one, right ($p \leq .001$). Only Fish No. 62 demonstrated handedness in the central portion of the tank ($p \leq .001$). This animal was very strongly right handed.

UBC

As shown in Table 4, Column 1, the mean of the frequency distribution of turns for any individual carries a bias to the left or right. This deviation from a mean of zero (no bias) represents a direct measure of handedness since it is subject to the influence of both the number and relative size of left and right turns. Of the eight fish, four had means which were significantly different from zero when the tank as a whole was considered (Z test; $p \leq .05$). Two subjects were biased to the left; two to the right (Table 4, Columns 1, 4, 5, 13). When the two componentssof handedness were treated individually, it was found that the subjects of Experiments 1, 6, and 7 + 14(A) made significantly more turns in one direction (Z test; $p \leq .01$) (Table 4, Columns 6-8), but only the two fish of the combined Experiments 7 and 14(A) showed a significant difference between the means of left and right turns (t test; $p \leq .01$) Table 4, Columns 9-12).

TABLE 3. Z test for handedness (turning bias) in the Texas tank. LT/ΣT represents the ratio of left turns to the total number of turns made during the recording session

	Tank Area A					Tank Area B				
Fish No.	LT/ΣT	ΣT	Z	Sig.	TB[1]	LT/ΣT	ΣT	Z	Sig.	TB
24	.49	1,591	.68	---		.55	1,684	3.95	.001	L
32	.48	517	.84	---		.45	209	1.53	---	
45	.52	1,975	1.73	---		.55	1,520	4.10	.001	L
62	.42	3,093	9.22	.001	R	.27	1,828	14.16	.001	R
73	.51	1,684	.88	---		.49	1,178	.54	---	

H_o: LT/ΣT = .50; H_1: LT/ΣT ≠ .50. Critical value $Z_{.05}$ = 1.96

[1]Turning bias.

TABLE 4. Summary table for handedness (turning bias) over the whole U.B.C. tank. Z test for bias in the mean turning angle (Columns 1-5); Z test for bias in the number of left and right turns (Columns 6-8), LT/ΣT represents the ratio of left turns to the total number of turns made during the recording session; t test of the mean left and right turning angles (Columns 9-12).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Experiment No.	Mean Angle in Degrees	SD	ΣT	Z	Sig	LT/ΣT	Z	Sig.	Mean of Left Turns	Mean of Right Turns	t	sig	TB[2]
1	+2.78[1]	39.83	2316	+3.35	.01	.47	-3.32	.01	30.58	31.82	1.20	---	R
6	-0.612	42.16	2343	-0.703	--	.53	-2.58	.01	30.49	32.64	1.85	---	
10	-1.48	37.15	2482	-1.99	.05	.52	-1.69	--	23.77	25.43	1.65	---	L
11	+1.81	30.11	2233	+2.84	.01	.48	+1.84	--	21.34	23.22	1.91	---	R
18(B)	-2.23	37.61	1774	-2.50	.05	.52	-1.80	--	29.58	27.57	1.72	---	L
20(B)	+0.748	34.72	1590	+0.859	--	.50	+0.15	--	25.30	26.60	1.11	---	
7 + 14(A)	-0.580	34.92	4400	-1.10	--	.54	-4.76	.01	22.68	24.87	2.82	.01	

H_o: $\mu = 0$; H_1: $\mu \neq 0$, H_o^1: LT/ΣT = .50; H_1^1: LT/ΣT $\neq$ .50. Critical Value $Z_{.05} = 1.96$

t test modified for non-homogeneity of variances. Critical Value $t_{.05,\infty} = 1.65$

[1] + bias to right
- bias to left

[2] Turning bias

Handedness was also computed for tank areas A and B. When only movements in the centre (area A) were considered, the significant bias shown by experiments 1, 10, and 18(B) in the mean of the frequency distribution of turns for the whole tank disappeared (Z test; $p > .05$) (Tables 4 and 5, Columns 1, 4, 5, 13). Along the walls (area B), it was maintained ($p \leq .05$) (Table 6, Columns 1, 4, 5, 13). Similarly, the significant difference observed in the magnitude of left and right turns for fish 7 and 14(A) in the whole tank was associated only with the walls (t test; $p \leq .01$) (Table 6, Columns 9-12). No significant differences were recorded in the central portion ($p > .05$) (Table 5, Columns 9-12). Two subjects, Experiments 1 and 20(B), turned significantly more often to one side in the centre (Z test; $p \leq .05$) (Table 5, Columns 6-8), but only one, 20(B), failed to exhibit this tendency in the vicinity of the walls as well (Table 6, Columns 6-8). In Experiment 18(B), a preference for a greater number of left turns appeared near the walls which was masked in the analysis of movements in the whole tank ($p \leq .05$) (Tables 4 and 6, Columns 6-8).

The preferred direction of turning may change with time. During the first two hours of Experiment 1, the animal turned more often to the left along the walls, and in the last four hours, more often to the right. The preference was significant in hours two, four and five (Z test; $p \leq .05$) (Table 7, Columns 6-8).

Turning Frequency

The term "turning frequency" refers to the number of turns made by each fish per metre travelled.

TABLE 5. Summary table for handedness (turning bias) in the U.B.C. tank centre (A). Z test for bias in the mean turning angle (Columns 1-5); Z test for bias in the number of left and right turns (Columns 6-8), $LT/\Sigma T$ represents the ratio of left turns to the total number of turns made during the recording session; t test of the mean left and right turning angles (Columns 9-12).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Experiment No.	Mean Angle in Degrees	SD	ΣT	Z	Sig	$LT/\Sigma T$	Z	Sig.	Mean of Left Turns	Mean of Right Turns	t	sig	TB[2]
1	+2.62[1]	39.68	842	+1.91	---	.46	+2.27	.05	30.85	31.23	0.22	---	
6	+1.35	44.01	734	+0.823	---	.50	-0.221	--	33.41	36.68	1.66	---	
10	-0.973	40.98	221	-0.353	---	.51	-0.202	--	33.13	32.06	0.27	---	
18(B)	+0.182	35.31	247	+0.081	---	.50	+0.064	--	26.63	26.77	0.05	---	
20(B)	+2.78	36.41	450	+1.63	---	.44	+2.64	.01	29.52	27.92	0.73	---	
7 + 14(A)	+0.460	31.65	239	+0.224	---	.50	0.00	--	21.75	22.90	0.40	---	

H_o: $\mu = 0$; H_1: $\mu \neq 0$, H_o^1: $LT/\Sigma T = .50$; H_1^1: $LT/\Sigma T \neq .50$. Critical Value $Z_{.05} = 1.96$

t test modified for non-homogeneity of variances. Critical Value $t_{.05,\infty} = 1.65$

[1] + bias to right
- bias to left

[2] Turning bias

TABLE 6. Summary table for handedness (turning bias) at the U.B.C. tank walls (B). Z test for bias in the mean turning angle (Columns 1-5); Z test for bias in the number of left and right turns (Columns 6-8), LT/ΣT represents the ratio of left turns to the total number of turns made during the recording session; t test of the mean left and right turning angles (Columns 9-12).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Experiment No.	Mean Angle in Degrees	SD	ΣT	Z	Sig	LT/ΣT	Z	Sig.	Mean of Left Turns	Mean of Right Turns	t	Sig.	TB[2]
1	+2.70[1]	40.22	1371	+2.48	.05	.47	+2.35	.05	30.81	32.22	1.04	---	R
6	-1.56	41.36	1581	-1.49	---	.54	-3.19	.01	29.17	31.12	1.36	---	
10	-1.77	36.89	2080	-2.19	.05	.52	-1.63	--	26.35	24.61	1.49	---	L
18(B)	-3.15	38.75	637	-2.05	.05	.54	-2.10	.05	30.36	29.01	0.68	---	L
20(B)	-0.053	34.27	1140	-0.052	---	.52	-1.48	--	23.91	25.99	1.49	---	
7 + 14(A)	-0.619	35.11	4163	-1.14	---	.54	-4.87	.01	22.66	25.01	2.92	.01	

$H_o: \mu = 0$; $H_1: \mu \neq 0$, H_o^1: LT/ΣT = .50; H_1^1: LT/ΣT $\neq$ .50. Critical Value $Z_{.05} = 1.96$

t test modified for non-homogeneity of variances. Critical Value $t_{.05,\infty} = 1.65$

[1]+ bias to right
 - bias to left

[2]Turning bias

TABLE 7. Hour by hour analysis of handedness (turning bias) at the tank walls (B) for U.B.C. Experiment 1. Z test for bias in the mean turning angle (Columns 1-5); Z test for bias in the number of left and right turns (Columns 6-8), LT/ΣT represents the ratio of left turns to the total number of turns made during the recording session; t test of the mean left and right turning angles (Columns 9-10).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Hour	Mean Angle in Degrees	SD	ΣT	Z	Sig	LT/ΣT	Z	Sig.	Mean of Left Turns	Mean of Right Turn	t	Sig	TB[2]
1	-0.337[1]	41.40	163	-0.104	---	.54	-1.02	---	27.84	31.93	0.92	--	
2	-5.49	41.78	82	-1.19	---	.62	-2.21	.05	30.88	36.29	0.91	--	
3	+4.25	40.40	240	+1.62	---	.46	+1.29	---	30.82	33.92	0.99	--	
4	+4.57	39.02	397	+2.33	.05	.44	+2.56	.05	30.32	29.29	0.40	--	R
5	+2.76	38.95	263	+1.15	---	.43	+2.28	.05	32.88	29.60	1.11	--	
6	+2.88	42.01	226	+1.03	---	.47	+0.798	---	31.82	34.08	0.65	--	

H_o: $\mu = 0$; H_1: $\mu \neq 0$, H_o^1: $LT/\Sigma T = .50$; H_1^1: $LT/\Sigma T \neq .50$. Critical Value $Z_{.05} = 1.96$

t test modified for non-homogeneity of variances. Critical Value $t_{.05,\infty} = 1.65$

[1] + bias to right
 - bias to left

[2] Turning bias

Texas

The mean of the hourly frequencies for each subject in each tank area is shown in Table 8. Turning frequency was significantly greater away from the walls in four of the subjects (test of least significant difference; $p \leq .01$). The average of all fish was 3.3 turns per metre in area A and 2.4 turns per metre in B with considerable individual variation.

UBC

Because of the smaller number of tracking hours in the UBC experiments, turning frequencies for these fish were based on the total number of turns and distance travelled. For six subjects, the amount of turning was higher in area B (Table 9). The average turning frequency for all experiments was 14.1 turns per metre in the centre and 17.3 turns per metre in the vicinity of the walls.

Distance Between Turns

Turns are separated by straight locomotor pathways of varying lengths. Fig. 10 illustrates the frequency distribution of distance between turns for the pooled data of two Texas fish. The mean distance between turns for these subjects was 40.62 ± 26.84 cm. with distances of 10-30 cm. accounting for 47% of the straight pathways.

Velocity - Texas

Kolmogorov-Smirnov analysis of frequency distributions of velocity revealed highly significant individual variation ($p \leq .001$) as well as significant differences between velocities in the centre and at the

TABLE 8. Frequency of turning. A comparison of the number of turns per metre travelled in areas A and B of the Texas tank. Level of significance refers to the results of a test of least significant difference of the values for each individual.

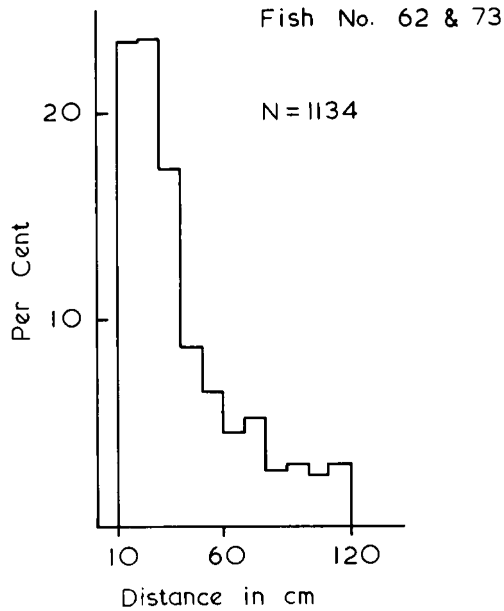
	Turns per Metre		Level of Significance
Fish No.	Tank Area A	Tank Area B	
24	4.16	3.06	.001
32	3.57	3.90	---
45	2.71	1.63	.001
62	2.92	1.58	.001
73	2.91	2.01	.01

TABLE 9. Frequency of turning. A comparison of the number of turns per metre travelled in areas A and B of the U.B.C. tank.

Experiment No.	Turns per Metre	
	Tank Area A	Tank Area B
1	13.4	15.9
6	15.4	21.0
7	6.2	11.7
10	14.2	15.3
11	--[1]	12.1
14(A)	10.8	17.7
18(B)	15.6	29.4
20(B)	23.5	15.4

[1]insufficient data

FIGURE 10. Frequency distribution of distance between turns, pooled data of two Texas fish.


Fish No. 62 & 73
N = 1134
Per Cent
20
10
10
60
120
Distance in cm

periphery of the tank ($p \leq .001$ for all but No. 32). In all cases, a shift toward lower velocities occurred as the animal approached the vicinity of the walls (Fig. 11). Table 10 lists the mean velocity and standard deviation for each fish in each tank area. In terms of body lengths per second, the mean velocity for a 20 cm. fish (No. 62) was 1.24 in area A and 1.16 in area B. Velocities up to 4.80 body lengths per second (L/sec.) were encountered at intervals.

Velocity - UBC

Since filming was carried out at a rate of one frame/sec., the distance travelled by the subjects between successive frames is also the swimming speed. Grouping all observed velocities for each individual into 2 cm/sec. categories resulted in the frequency distributions of Fig. 12 and the means and standard deviations of Table 11. As in the Texas study, the frequency distributions of velocity displayed considerable individual variation (X^2 test; $p \leq .01$). A maximum speed of 1.6 body lengths/sec. (L/sec) was recorded for four fish (25 cm TL; Experiments 7, 11, 14(A), 18(B). The mean velocity for these experiments was 1.25 L/sec.

Significant differences were found between the velocity distributions in tank areas A and B for 5 of 7 experiments (X^2 test; $p \leq .01$). The distributions for each area and the corresponding means and standard deviations are shown in Fig. 13 and Table 12. In three experiments, velocities recorded near the walls were significantly higher than those in the centre (Experiments 6, 10, and 20 (B)), while in two other

FIGURE 11. Frequency distributions of velocity in tank areas A and B, Texas data; class size, 5 cm/sec. Distributions are significantly different at .001 level.

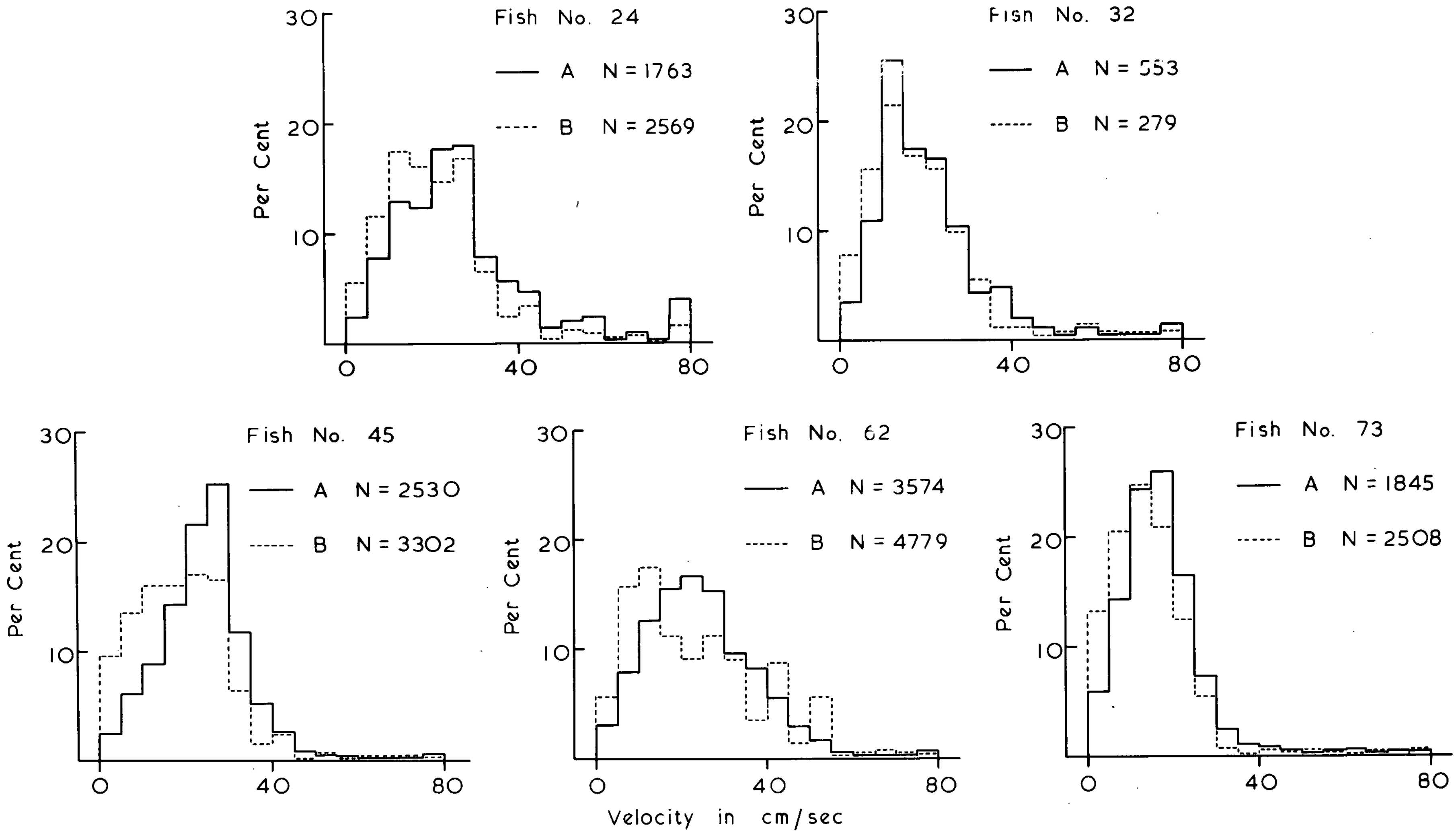
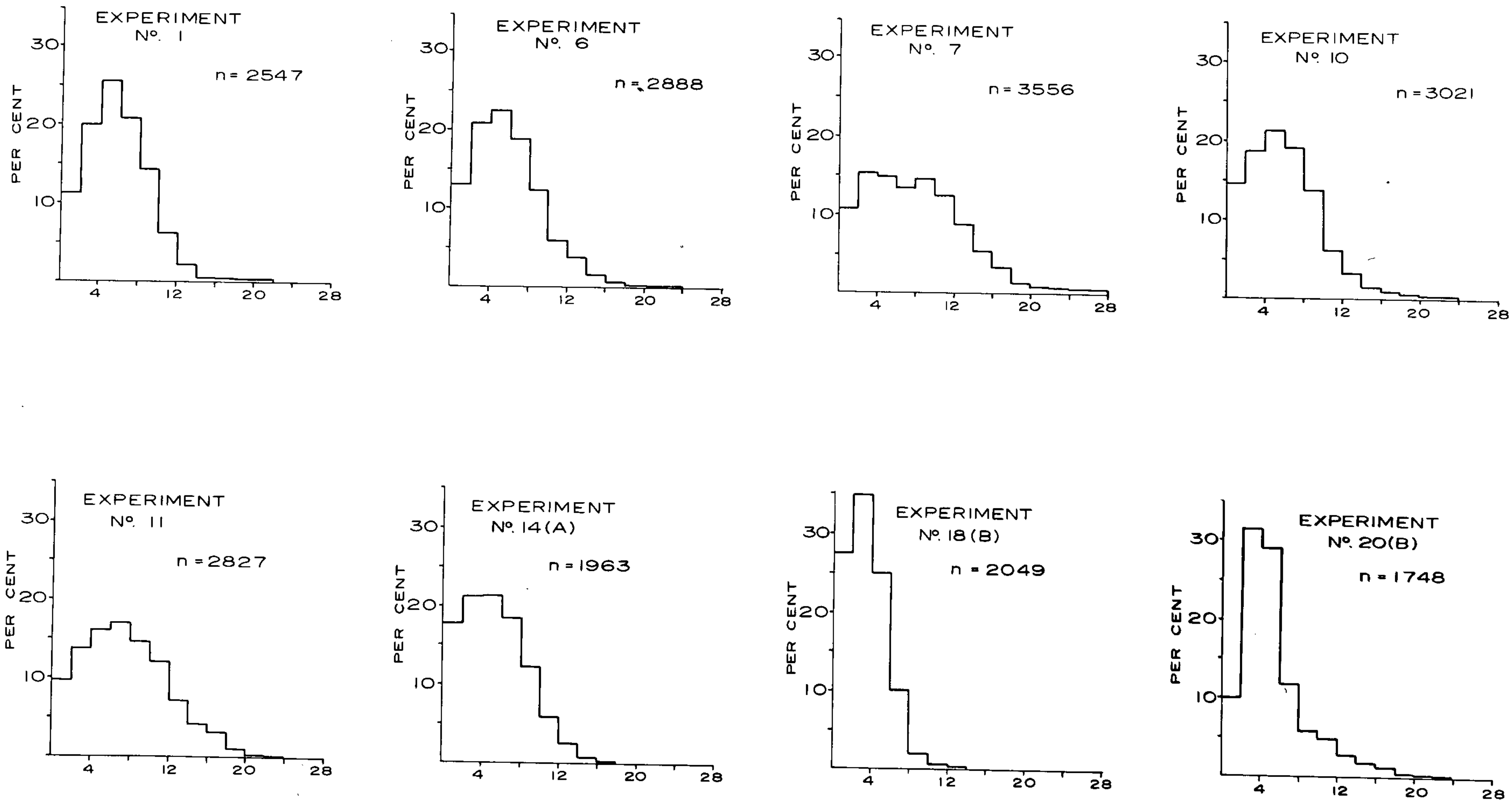

Fish No. 24
A N = 1763
B N = 2569
Per Cent
30
20
10
0
40
80
Fish No. 32
A N = 553
B N = 279
Per Cent
Fish No. 45
A N = 2530
B N = 3302
Per Cent
Fish No. 62
A N = 3574
B N = 4779
Per Cent
Fish No. 73
A N = 1845
B N = 2508
Per Cent
Velocity in cm/sec

TABLE 10. Mean and standard deviation of velocity for the centre (A) and walls (B) of the Texas tank

Fish No.	Tank Area A		Tank Area B	
	Mean Velocity (cm/sec)	SD	Mean Velocity (cm/sec)	SD
24	26.83	16.21	21.62	13.68
32	20.75	13.42	18.90	13.04
45	24.02	10.24	18.69	10.51
62	24.75	12.81	23.14	14.91
73	17.26	10.16	14.27	9.33

FIGURE 12. Frequency distributions of velocity in the whole U.B.C. tank; class size, 2 cm/sec. Distributions are significantly different at .01 level.



VELOCITY — CLASS SIZE 2 cm/sec

TABLE 11. Mean velocity and standard deviation of velocity for the entire U.B.C. tank.

Experiment No.	Mean Velocity (cm/sec)	SD
1	5.79	3.22
6	5.93	3.74
7	8.08	5.28
10	6.02	3.88
11	7.64	4.52
14(A)	5.40	3.44
18(B)	3.61	2.37
20(B)	5.50	4.05

FIGURE 13. Frequency distributions of velocity in tank areas A and B, U.B.C. data; class size, 2 cm/sec. Distributions are significantly different at .01 level.

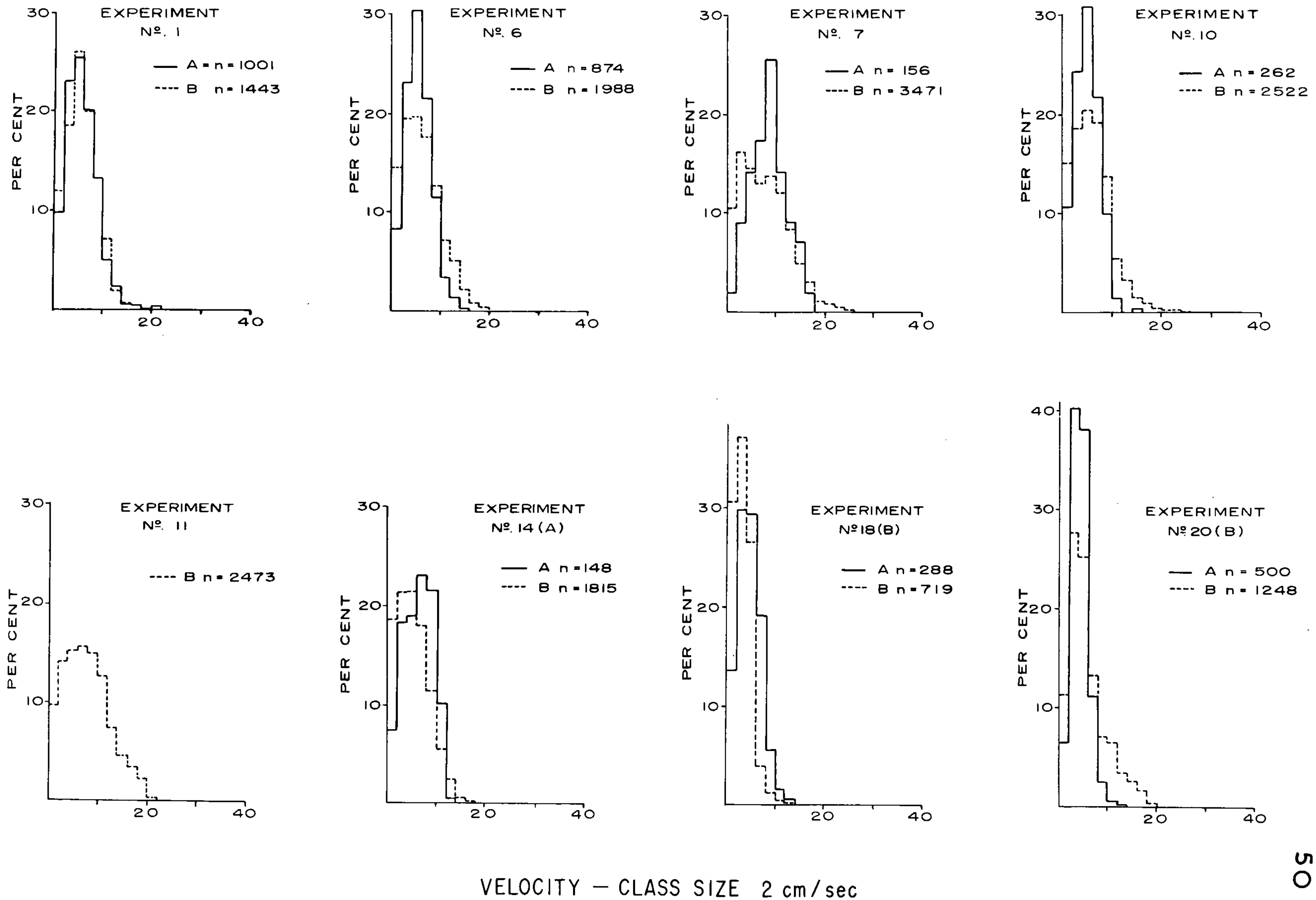

EXPERIMENT Nº. 1
— A = n = 1001
---- B n = 1443
EXPERIMENT Nº. 6
— A n = 874
---- B n = 1988
EXPERIMENT Nº. 7
— A n = 156
---- B n = 3471
EXPERIMENT Nº. 10
— A n = 262
---- B n = 2522
EXPERIMENT Nº. 11
---- B n = 2473
EXPERIMENT Nº. 14 (A)
— A n = 148
---- B n = 1815
EXPERIMENT Nº 18 (B)
— A n = 288
---- B n = 719
EXPERIMENT Nº 20 (B)
— A n = 500
---- B n = 1248
PER CENT
10
20
30
40
VELOCITY — CLASS SIZE 2 cm/sec

TABLE 12. t test of mean velocities for the centre (A) and walls (B) of the U.B.C. tank.

	Tank Area A		Tank Area B			
Experiment No.	Mean Velocity (cm/sec)	Var.	Mean Velocity (cm/sec)	Var.	t	Sig.
1	5.69	10.28	5.79	10.68	0.75	---
6	5.43	7.10	6.18	16.88	5.82	.01
7	8.62	13.12	8.00	29.55	2.04	---
10	5.05	6.10	6.04	15.14	5.79	.01
14(A)	6.32	8.68	5.32	12.02	3.91	.01
18(A)	4.63	5.96	3.20	3.73	8.89	.01
20(B)	4.46	7.49	5.92	19.33	8.36	.01

t test modified for non-homogeneity of variances.

experiments, (14(A) and 18(B)), velocities in the same area were significantly lower (t test; $p \leq .01$) (Table 12).

DISCUSSION AND CONCLUSIONS

Short segments of individual experiments, such as those depicted in Fig. 5, indicate that the bullhead explored the environment a portion at a time rather than traversing the whole tank at once. This type of behaviour has also been found in goldfish when it was shown to be non-random and persistent over a 20 hour period (Kleerekoper _et al_. 1974). In both the Texas and the UBC work, periods of high locomotor activity were often followed by extended periods of inactivity. There is evidence to suggest that in the long term, periods of activity and inactivity are related to oscillations in orientation which, in turn, may be dependent upon fluctuations in external factors such as the earth's magnetic field (Matis, _et al_., 1974b).

Kapoor and Kleerekoper (1970) have shown that the particular range of angles utilized in turning varies from species to species. The range may also differ among conspecifics of different stocks (Kleerekoper, _et al_., 1970). Presumably, the Texas and UBC experimental groups each represented a single stock, but here too, significant individual differences were exhibited in the frequency distributions of angles although the preferred angle of turning was always between 10° and 30° in Texas and 0^{0} and 10^{0} at UBC. The frequency distributions in both groups formed a continuum between a very low preference for a particular size of turn and a very high preference for such a turn. The range of turns used in locomotion may be part of the genetic make-up of the stock, but factors such as sex and physiological state could result in different degrees of preference for a certain angle in that range. While it is true that the subjects of this study represent two closely related but separate species, it is more probable that the preference for smaller turns shown by the UBC fish is due to the much smaller size of the UBC tank and to the differences in recording approaches than to species difference.

While handedness in the goldfish appears to be a stable characteristic of the individual (Spencer, 1939; Kleerekoper *et al.*, 1970), it may not always be so. *Diplodus sargus* (Linnaeus), *Mustelus mustelus* (Linnaeus), *Scylliorhinus stellaris* Blainville were found to vary their bias for turning direction with time and in the presence of olfactory stimulae (Kleerekoper, 1967a). Male *Ictalurus punctatus* (Rafinesque) circled consistently to the right in the presence of the odour of a female of the same species (Kleerekoper, 1972). Matis *et al.* (1973) found that both the number of turns and the size of turns in a given direction are oscillatory in nature but differ in period and are, therefore, often out of phase with each other. Hour by hour analysis of the present bullhead data indicates that there are fluctuations in handedness underlying the overall bias presented in Tables 3, 4, 5 and 6 (Ref. Table 7). However, the duration of the recordings was not sufficient to establish a pattern.

Of particular interest is the difference in handedness between tank areas A and B. Two of the Texas fish (No. 24 and No. 45) turned significantly more often to one side only at the tank periphery and a third (No. 62) greatly increased the degree of preference for right turns in the same area. A fourth fish (No. 32) slightly, although not significantly, increased the proportion of right turns in area B (Table 3). At UBC, despite the fact that three subjects were significantly handed in the vicinity of the walls (Experiments 1, 10, 18(B)), none displayed a significant bias in the tank centre. (Tables 5 and 6). This suggests that the animal, upon reaching a wall, tended to follow it in one direction. Breder and Nigrelli (1938), in very short-term recordings, found that five fish of different species made left turns resulting in counter-clockwise movements around the edge of a pan. The UBC results further show that considerable variability exists in the combined effects of turn size and number of turns on the bias of a given individual (Table 6). The bias may be due solely to a preference for more turns in a particular direction (Experiments 1 and 18(B)), or to a tendency for larger turns as well as a greater number of turns in the preferred direction (Experiment 10). The effect of a higher turning frequency in one direction may also be offset by fewer but larger turns in the opposite direction (Experiments 6 and 7 + 14(A)). This last phenomenon seems to imply that bullhead are capable of "compensating" or centrally cumulating left and right turns for a net straight line locomotion as proposed earlier for goldfish (Kleerekoper, et al., 1969, 1970). However, further research would be required to substantiate the results obtained here.

Turning frequency and the inversely related distance between turns are integral parts of the locomotor pattern. They may be characteristic of the group. The mean frequencies for Carassius in the Texas tank were 2.8 and 1.4 turns per metre for tank centre and walls respectively (Timms and Kleerekoper, 1970). Similar means for Ictalurus were greater at 3.3 and 2.4 turns per metre (Texas) and 14.1 and 17.3 turns per metre (UBC). Indications are that turning frequency in the bullhead is not constant in time but fluctuates with the diurnal activity of the individual.

Compared to certain other Ostariophysi, the bullhead is a slow swimmer. However, many of the recorded speeds involve forced swimming against a current and therefore are not strictly comparable to the results of the present investigation. *Cyprinus carpio* Linnaeus (13.5 cm.) attained a maximum velocity of 12.6 L/sec.; *Scardinius erythrophthalmus* (Linnaeus) (22 cm.), 5.9 L/sec., and *Leuciscus leuciscus* (Linnaeus) (18.5 cm.), 9.2 L/sec. (Gray, 1953, 1957). The maximum observed for *Ictalurus nebulosus* (Le Sueur) (25 cm.) was 1.6 L/sec. with a mean of 0.3 L/sec. Sustained swimming speeds of 1.9 L/sec. have been reported for *I. nebulosus* in the field (Kelso, 1974). In the Texas tank, *Ictalurus melas* (Rafinesque) (20 cm.) attained a maximum velocity of 4.8 L/sec. The mean for this species was 1.24 L/sec. in the tank centre and 1.16 L/sec. at the edge. In the same tank, *Carassius auratus* Linnaeus (30 cm.) averaged 0.8 L/sec. in the open and 0.5 L/sec. near the walls. The maximum velocity commonly observed was 2.0-2.6 L/sec. (Kleerekoper *et al.*, 1970). Gray (1957) reported a maximum speed of 13.0 L/sec. for *C. auratus* (13 cm.), while Bainbridge (1961) quoted a burst speed of 10.0 L/sec. and a sustained speed of 3.0 L/sec. in the same species (15 cm). A sustained speed of 7.9 L/sec. over a two hour period was recorded by Smit *et al*. (1971).

The UBC fish did not follow the turning frequency and velocity patterns of the Texas group. Turning frequencies in both tank areas A and B were not only much higher at UBC, but the tendency to turn more frequently in area B was a complete reversal of the Texas trend. Swimming speeds were considerably slower at UBC and the observed shift towards lower velocities as the Texas fish approached the walls was reversed in three UBC experiments. Two other UBC subjects failed to display any significant differences between velocities in the two tank areas.

The differences in the absolute values of these parameters in the two situations are explained by the small size of the UBC tank; however, this does not account for the contradictory reactions in areas A and B. The key to the problem lies in the basic construction of the two monitor systems. Vision in the Texas tank was restricted by the high black sides, the collimator overhead and the low light intensity in the room. To facilitate filming, the UBC tank was constructed of clear perspex and housed in a white room with high light intensity. In these surroundings, it is possible that the subjects were able to perceive their own movements in the tank sides and responded with increased turning frequencies and higher swimming speeds. Of 17 locomotor parameters studied by Matis *et al*. (1973), step length or distance between turns (the reciprocal of turning frequency) and velocity were the least stable and therefore the most subject to change in the presence of novel cues in the environment. These two aspects of locomotion have since been used to detect a response to odour in the nurse shark, Ginglymostoma cirratum (Gmelin) (Matis et al., 1974a). Timms and Kleerekoper (1970) have discussed the role of vision in the perception of barriers by goldfish. They found that vision was not required for alterations at the walls in the frequency distribution of size of turns, but was necessary for the observed changes in turning frequency and velocity. Whether, under natural conditions, vision plays a similar role in the bullhead which relies more strongly on tactile and chemical senses is not known.

The relationship between swimming speed and body length is well known (Gray, 1957; Beamish, 1970). Brett et al. (1958) have estimated that an increase in length of 1 cm. increases the cruising speed approximately 3 cm./sec. in coho and 2 cm./sec. in sockeye yearlings. Therefore, although the individuals used in the present study were within a very few centimetres of each other in length, some of the observed differences in velocity are likely to be the result of size variations.

In Texas, water temperature may also have influenced the recorded speed of locomotion, since the slowest mean velocity occurred during the summer when the water in the monitor tank rose to 30.8°C. (Fish No. 73).[1] Beamish (1970) found that for a given total length, Micropterus salmoides (Lacepede) reduced its maximum sustained swimming speed between 30°C and 34°C. Burst speeds, however, appear to be independent of temperature

[1] 35°C is reported to be the lethal temperature for Ictalurus (Cairns, 1956).

(Brett, 1971). At UBC, where the maximum reading was 19^{o}C, water temperature had no apparent effect on velocity.

Generalizing from the data of the thirteen bullhead, it would appear that during bouts of locomotion turn size decreases as velocity increases; handedness, or turning bias, increases as the animal approaches a barrier and follows it; and velocity and turning frequency, the least stable of the parameters studied, may increase or decrease in response to environmental conditions. Of the two monitoring systems, the Texas tank with its larger area and non-translucent walls is perhaps closest to natural conditions. In this tank,turns in the "open field" tend to be smaller, more frequent, and less biased directionally relative to turns made in the vicinity of the walls. These changes in turning behaviour are accompanied by an increased swimming velocity. Such a locomotor pattern could be of considerable biological significance if the elevated activity returned the animal to the shelter of rocks and vegetation or brought it into contact with food material.

Recent field data indicate that this is indeed the case. Ultrasonic tracking of I. nebulosus released near a thermal discharge and at a control site (Kelso, 1974) revealed a marked tendency on the part of the control fish to follow the shoreline. When these subjects did venture away from shore, turning frequency increased producing a locomotor pattern which would eventually bring them back to its vicinity. Further, in keeping with the laboratory finding that turning frequency and velocity are influenced by environmental conditions, fish released at the thermal discharge turned more often with a decreased swimming speed. Concommitant with the velocity drop, turn size increased.

The consistencies observed in the locomotor patterns of the two experimental groups and the similarity of the results with published field data would suggest that the analytical approach adopted here can provide a useful quantitative assessment of locomotor activity. Such an assessment is valuable when used as a basis for determining the locomotor responses of subjects to environmental influences such as sensory stimuli and pollutants which otherwise may not be directly observable. From the present data, it would appear that velocity and turning frequency have the greatest potential as indicators of such responses.

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