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The Maze of Personality:

Latency and electric organ discharge in a mormyrid fish,
Gnathonemus petersii Günther 1862 (Mormyridae, Teleostei)

by

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Submitted in partial fulfillment of the requirements for the degree of
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Abstract

Animal personality refers to individual differences in behavior that remain consistent across time and context. Research has categorized these behavioral syndromes into dimensions such as bold/shy, aggression, and exploration. We have investigated such dimensions, i.e. electric and locomotor activities in *Gnathonemus petersii*, an African freshwater fish during its trajectory in a 1-m diameter maze ($n = 24$). We tested three hypotheses: (1) Fish can be grouped into distinct slow and fast maze performers (latency), (2) fish can be separated into emitting low and high electric organ discharge (EOD) rates, and (3) testing the presence of a behavioral syndrome, i.e. latency and EOD rate are correlated regardless of context, i.e. while at rest or swimming. Our results showed a clear distinction between fast and slow latency values, and also lower and higher EOD rates, these distinctions were not tied to particular groups of fish but remained variable within each subject. Thus, our first two hypotheses were not supported. The correlation of each fish's latency with its associated EOD was significant for shorter latencies, thus partially supporting our third hypothesis.

Keywords: *Gnathonemus petersii*, behavior syndromes, personality, electric organ discharge, maze learning

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The Maze of Personality:

Latency and electric organ discharge in a mormyrid fish, *Gnathonemus petersii* Günther 1862 (Mormyridae, Teleostei)

The Terms of Animal Personality

Animal personality is an ever-growing field in Behavioral Ecology. Before one can take a deep dive into the many facets of this fascinating subject, including its development, one must first understand the meaning of the word. What is personality? There are many dimensions and connotations. When relating this word to the study of animals, an obvious problem arises in looking at the very root of the word. Many ecologists disagree with the use of the word personality because they believe it is anthropomorphic. When researching this field, one sees many terms containing subtle differences. Temperament is commonly used by animal researchers, potentially in an effort to not use the word personality which could be considered anthropomorphic. Behavioral syndromes are correlated behavioral types in individuals (bolder or shy, for example). To avoid any confusion, this paper will use the word personality as it is associated with its psychological definition, namely “behavioral differences between individuals that are consistent over time and across situations” (Dingemanse, Kazem, Réale, & Wright, 2010).

The Evolution of Personality Studies

Animal research has historically played a significant role in many areas of psychology. Some of the pioneers of psychology used animal-based experiments to better understand the human psyche. A century ago, Ivan Pavlov’s studies on dogs shed a light on the variations on different animals’ nervous systems. However, throughout most of the 20th century, research on animal personality was put on the back burner. Studies involving animal personality,

temperament, and behavioral syndromes have been rapidly rising (Sih, Bell, & Johnson, 2004). What could be the reason for this recent growth in interest? Evolutionary biologists are using the field of personality research to “explain differences in animal behavior over and above the ever-present variability among individuals that was first appreciated by Darwin as the essential basis for selection” (Trillmich & Hudson, 2011). Behavioral ecologists and theoretical biologists are also recognizing the likely evolutionary origins which contribute to fitness, with intra-species variation being the “raw material of evolution” (Mather, 1998). This recognition brings about questions such as: how does evolution play a role in the selection of behavioral traits? Approaches to studying animal personality are broadening. Researchers are looking to see if behavioral differences are determined during developmental phases, and what other factors could play a role establishing inter-individual differences. The factors include genetics, social environments, hormone levels, endocrine conditions, and individual niches within a litter or brood (Trillmich & Hudson, 2011).

Animal Personality in Literature

Gosling (2001) compiled an extensive review of the existing animal personality literature. His review shows that a wide array of taxa have been studied – ranging from ants and butterflies, to birds, canines, squirrels, and primates just to name a few. Through all of these studies, different personality “dimensions” have arisen. A majority of the papers Gosling compiled identified dimensions related to the reaction to a novel object or environment. These dimensions were referred to as reactivity, emotionality, or fearfulness. Another common dimension noted was exploration, or the willingness to investigate those novel environments or objects. Aggression is a dimension that has been measured by observing the latency to attack another individual. A fifth dimension that Gosling noted was the activity dimension. This is the animal’s

general activity level, such as the area covered by the animal within an enclosure, and the ranking of energy levels (Gosling, 2001).

One of the most complete studies of the ecological and evolutionary significance of a behavioral syndrome involves work with great tits by Verbeek, Drent, & Wiepkema (1994) and Verbeek, Boon, & Drent (1996). Researchers found consistent individual differences in exploratory behavior. Unlike their “slow” counterparts, “fast” explorers displayed more aggression, less fear of novel situations, and were more likely to form routines. This study demonstrated heritability of behavior and coping mechanisms by using artificial selection over four generations to produce fast, bold, and proactive birds versus slow, shy, and reactive ones. Interestingly, “slow” and “fast” birds also differed in hormone profiles. When investigating different exploratory behavioral strategies in the wild, the choice of strategy depended on the circumstances. When competition was intense, faster explorers had more success, while slower explorers performed better when the situation was more relaxed. The two strategies could be attributed to behavioral syndromes within the population (Sih et al., 2004).

It seems that with every study, new personality dimensions are added to encompass a broad range of witnessed behaviors in an effort to truly understand animal personality. If behaviorists and psychologists keep adding on to what could constitute personality, how will the scientific community ever narrow down its definition? Could there be a universal definition for these individual traits in all animals? With such a broad range of subjects, a definition must be broad to be able to satisfy every instance. Unfortunately, broad can also be vague. Personality is the characteristic of individuals that demonstrate patterns of feeling, thought, and behavior (Pervin & John, 1997). Most personality studies have addressed within-species research. To create a universal meaning of personality, there would need to be cross-species comparisons

between all species studied. To do this, however, would be a near impossible undertaking. The understanding of cross-species comparisons is important because these comparisons can aid in appreciating the significance of the adaptations of certain traits (Gosling, 2001). By learning about what is similar about species that share traits and what is dissimilar about species that do not, the evolutionary biologists could begin to understand from where these differing traits originate. Behavioral syndromes could help form a connection between mechanisms – such as genetics and development – and evolution and ecology (Sih et al., 2004). This understanding of where individual traits stem from could aid in creating a universally accepted definition of personality in animals.

Much of this research can be applied to other species. For example, Verbeek's studies on strategy selection in great tits could be applied to other bird species. Once patterns across those species are established, strategy selection research could potentially be expanded to other vertebrates like fish. Gaining knowledge of one species could open doors to the understanding of others.

Gnathonemus petersii

Gnathonemus petersii of the family Mormyridae is a weakly electric fish found in the freshwater rivers and lakes of Africa. Although nocturnal, these fish have eyes, so they are able to see in their blackwater habitats (Hopkins, 1981; Moller, 1981; Moller, 1995; Kramer, 1996; Ciali, Gordon, & Moller, 1997). *G. petersii*'s visual system is based on a grouped retina formation, in which rods and cones are bundled, allowing these fish to see in low contrast environments (Landsberger et al., 2008; Kreysing et al., 2012).

G. petersii possess an electric organ located in the caudal peduncle that generates electric pulses, electric organ discharges (EODs). Each electric organ discharge creates an electric field

around the fish (Bullock & Heiligenberg, 1986; Kramer, 1990; von der Emde, 1993; Moller, 1995; Schumacher, Emde & Perera, 2016). The mormyrid's body surfaces contains three types of electroreceptors, which can detect distortions of the self-generated electric field (mormyromasts) and thus facilitate object location and spatial orientation (Bullock & Heiligenberg, 1986; von der Emde & Bleckmann, 1998), *knollenorgans* are tuned to foreign, conspecific EODs and thus facilitate social communication (Bell et al., 1993; Bullock & Heiligenberg, 1986; Kramer, 1990; von der Emde, 1993; Moller, 1995; Kramer, 1996; Turner et al., 1999; von der Emde, 1999; Moller, 2002; Crampton, 2019). Passive electrosensing is mediated through ampullary cutaneous receptors that respond to direct current and low frequency electric potentials (Schluger & Hopkins, 1987). Electrosensing is the fish's primary means of interacting with its environment. The perceptual range of active electrosensing is limited to approximately 10-20 cm during object recognition (Moller, 1995; von der Emde & Bleckmann, 1998; Fechler & von der Emde, 2013).

Related Studies

Maze learning has always been a common tool in investigating spatial orientation and exploring how animals use both egocentric (internal cues such as learned motor routines, cognitive maps) and allocentric (external cues; such as landmarks) orientations (Tolman, 1948; O'Keefe & Nadel, 1978; Mittelstaedt, 1985; Gould, 1986). Walton & Moller (2010) investigated maze learning in the weakly electric fish, *G. petersii* and found that electrosense, vision, and lateral line input were hierarchically organized when the fish navigated the maze. Fish followed a memorized course independent of visual landmarks (path integration; motor routine), or in the presence of an "electric map" used that instead.

Rojas & Moller (2002) established that these fish can use all sensory modalities synergistically when maintaining shelter proximity. When one sense was inhibited, the fish was at first not as successful but improved its performance upon repetition of the task and daily exposure to the exercise. This suggested that learning could form a sort of sensory substitute or expectation. Von der Emde & Bleckmann (1998) found that individual fish use different combinations of sensory modalities when foraging for food. In the dark, the majority of fish use active electrolocation while some utilize passive electrolocation. If lighting conditions permit, some individuals switch to vision as their dominant sense (von der Emde & Bleckmann, 1998).

A fish's performance to either swim straight for shelter or end up in blind alleys could land them on a multitude of personality dimensions (maze dull and maze bright fish, following Tryon, 1940). The individual's use of various combinations of sensory inputs can result in different personalities (von der Emde & Bleckmann, 1998).

Kareklas, Arnott, Elwood, & Holland (2018) presented *G. petersii* with three objects differing in conductivity and scored mean latency to approach the object and mean inspection times. Fish approach objects in different ways as Toerring & Belbenoit (1979) reported, for example *va-et-vient*: positioning the body parallel to the object and exhibiting rapid back-and-forth movements. Kareklas et al. (2018) found that approach latency and inspection time were negatively correlated, i.e. the faster fish approached the object the longer they explored it (designated as boldness). With bolder fish showing lower avoidance and greater exploration tendencies. These correlations helped create a median score which sorted subjects into two groups: above-median were bold, and below-median were timid.

Fish positioned themselves to the novel object during *va-et-vient* depending on their personality types (bold or timid). Bolder fish were closer to the object on their left side, and

timid fish explored the object closest with their right side. Electroreceptors on each side of the body project to the contralateral hemisphere within the brain (Lazar, Libouban, & Szabo, 1984). The fish's preference is supported by the fact that its right hemisphere is associated with a higher tendency to approach, and the left hemisphere associated with a higher tendency to avoid (Barth et al., 2005; Dadda et al., 2010). Therefore, Kareklas et al. (2018) surmised that electrosensing is lateralized depending on the personality phenotypes of these fish.

While Kareklas viewed inter-individual differences in behavior based on electrosensing habits, other studies have looked into different areas of fish physiology to try to answer some questions on personality. Careau, Thomas, Humphries, & Réale (2008) explored “linkages between personality and energetics” by creating a performance model testing the organism's resting metabolic rate. This model states that resting metabolic rate determines how much energy is available to an individual, and that individuals with a higher MR are able to allocate more energy into activity. In their literature review, Careau et al. (2008) found that the performance model is supported, with studies showing the more aggressive fish having a higher standard metabolic rate (Careau et al., 2008). Kareklas et al. (2018) focused on one particular aspect of the fish's behavior, namely its response in the presence of novel objects.

Here, we will consider whether its performance in a maze also reflects personality types. We will test three hypotheses: (1) Fish can be grouped into distinct slow and fast maze performers, (2) fish can be distinguished by low and high EOD rates, respectively, and (3) testing the presence of a behavioral syndrome, i.e. latency and EOD rate are correlated regardless of context, i.e. while at rest or swimming. We will also test three related alternative hypotheses to explore whether EOD rate and Latency may be decoupled across different contexts: (1) maze performance times regardless of the individual fish can be grouped into distinct slow and fast

performances, (2) EOD rates can be distinguished as low and high EOD rates, again regardless of fish, and (3) testing for consistent ties between latency and EOD rate.

Methods

Subjects

The subjects of this study were 24 subadult *Gnathonemus petersii* fish ranging in size from 110.1 ± 16.1 mm. All fish were imported and obtained through the local trade from Ali Kahn Tropical Fish in South Richmond Hill, New York, and housed and maintained in a 662-liter holding tank in our lab at Hunter College. Fish were maintained under a 12:12 hour light-dark regimen with lights on at 800 h.

Experimental Parameters

The maze used in this experiment was a round one-meter diameter maze constructed of clear plastic sheet and contained within an all-glass square tank. Turns and walls of the maze were labeled with numbers (1-12) to aid in describing the fish's trajectory. Even numbers refer to correct passages and odd numbers refer to blind alleys. This was used to calculate the number of errors committed during a trial. The correct path without any errors totaled at six turns, the sequence being 2, 4, 6, 8, 10, and 12. We defined any time the fish strayed from the aforementioned trajectory sequence as an error. The goal box was covered with an additional layer of black Plexiglas to provide a dark environment, serving as incentive to these nocturnal fish. A tall piece of clear Plexiglas was used as a "door" and was placed at the entrance of the goal box once the fish entered. The maze was aerated and heated between experiments. Maze

water was maintained at a comparable temperature to the fish's holding tank ranging from 22 to 24° Celsius. Water chemistry was maintained within limits: 300 to 400 $\mu\text{S}/\text{cm}$ for conductivity, and 7.00 to 7.75 for pH.

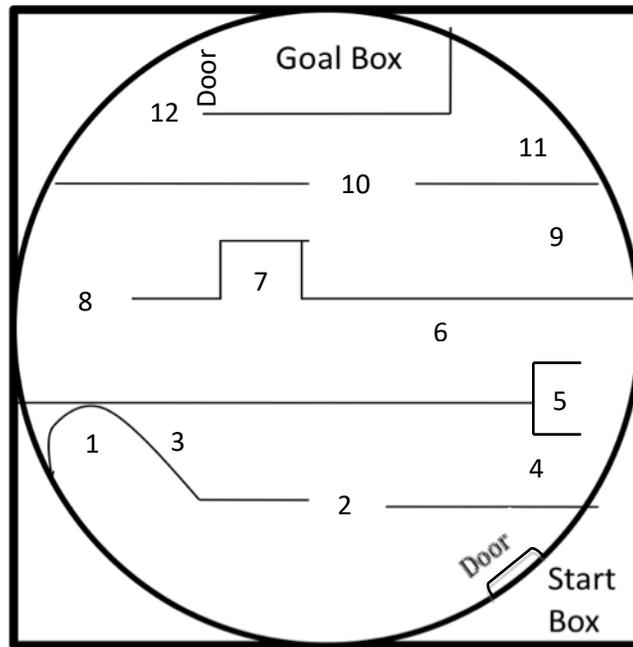


Figure 1. Sketch of the maze (not to scale). Even numbers represent correct passages, odd numbers represent blind alleys.

To measure the trajectory of the fish within the maze, each trial was filmed with a Sony HDR-CX900 HD Handycam Camcorder. EODs were monitored only when the fish was at rest in the goal box and recorded with a pair of stainless-steel electrodes installed at the narrow ends of the goal box. EODs were digitized and saved to a disk using g-Prime, a data collection and analysis software created by Gus Lott at Cornell University in 2007.

Procedures

The variables measured in this experiment include maze completion time (latency), the path trajectory, the number of errors, the amount of time spent resting in the maze, the number of nudges used (see below), and EOD rates.

A fish was transferred from its communal tank and placed into the darkened goal box where it acclimated for five minutes. EOD activity was recorded for 3 minutes following acclimation. The fish was then removed from the goal box and introduced into the start box and released into the maze. When the fish had not found the goal box within 10 minutes, the trial was terminated, and the time recorded as “max time”. When fish were in the maze resting for more than three minutes (time out), it received a small “neutral” nudge with a net, i.e. not directing it towards the goal. Once the fish successfully completed the maze and entered the goal box, performance time was recorded, and another 3-min EOD recording in the goal followed. The fish was then transferred back into the start box and a new trial was started. This procedure was repeated for a total of 7 goal readings and 6 trials. EOD activity was analyzed using g-Prime (Lott, 2007) to generate time series of fish discharge intervals. G-prime data was converted to establish descriptive statistical measures (means, SD, correlations). The time series displays (scattergrams) sometimes showed ‘unusual’ long inter-discharge intervals (faux IDIs) (Fig. 2) that clearly fell outside the fish’s EOD activity. The source of these ‘outliers’ was due to the fish’s position with regard to the recording electrodes. Faux IDIs exceeding 160 msec due to missed true EODs were eliminated from our computations.

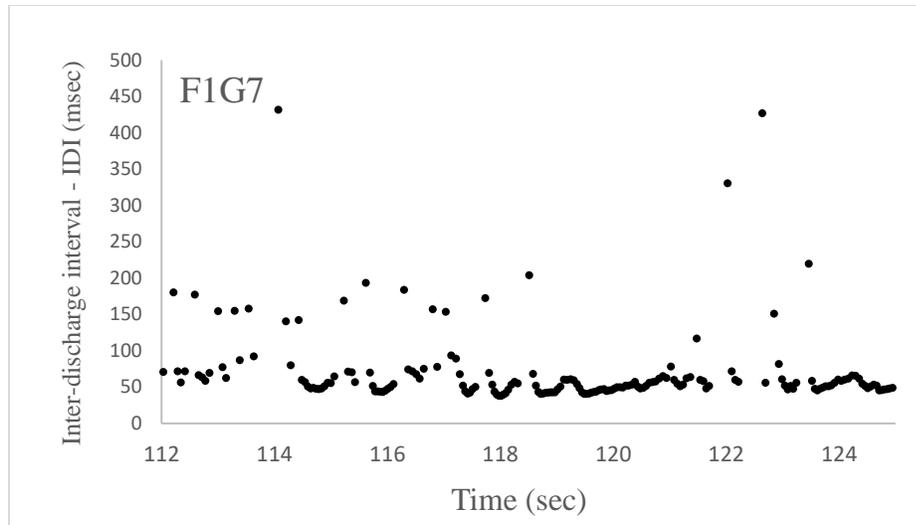


Figure 2. Example of a scattergram illustrating faux IDIs (> 160 msec) due to unfavorable positions of the fish with regard to the recording electrodes. F1G7 – fish identifier.

Statistical Procedures

This study hypothesized that the ranked performances of subjects can be divided into two groups of fast and slow swimmers, and also high and low EOD rate emitters. To test for such a distinction, we subjected the data sets to test for normalcy using one-sample Kolmogorov-Smirnov tests. Deviation from normality would suggest, but not prove skewed or multimodal distributions, which in turn might indicate an apparent personality divide. Paired and multiple data sets were compared using non-parametric statistics, i.e. Mann-Whitney U (M-W U), Kruskal-Wallis tests (K-W), and Wilcoxon-Paired Ranks tests, respectively. An a-priori power analysis assessing effect size, mean and SD differences could not be performed for lack of published or accessible comparable data.

We established a criterion for exclusion: data obtained from fish 8, 23, and 24 were removed from statistical analysis because they reached the maximum time (600 s) on four or more of the six trials. All procedures were approved by the Hunter College IACUC Committee on October 17th, 2018 (PM-Maze Learning 9/21).

Results

Maze performance

Overall Median Latency. Figure 3 illustrates the median performance time over six consecutive trials. The apparent decline in latency over trials was not significant (comparison of trials 1 & 6: Mann-Whitney U, $p = 0.289$ (2-tailed), $z = -1.060$, and across all six trials Kruskal-Wallis test, $\chi^2 = 5.696$, $df = 5$, $p = 0.337$).

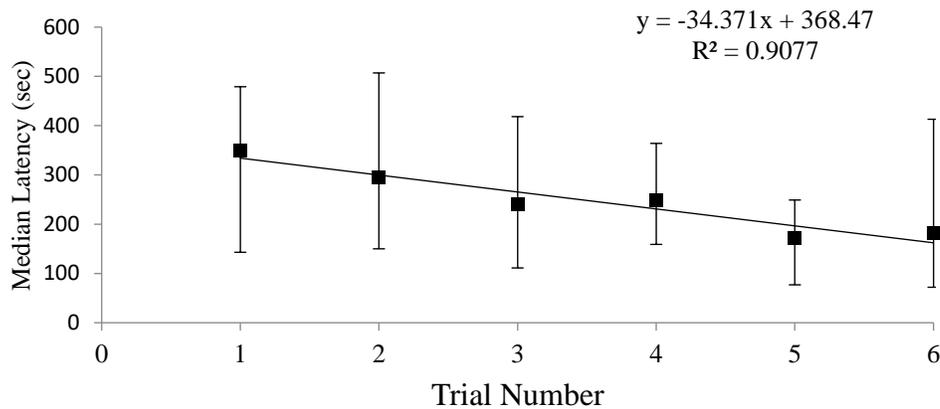


Figure 3. Median maze performance time (black squares) and interquartile ranges for trials 1-6. Squares represent median maze performance time for each trial. Whiskers represent first and third quartiles. The apparent decline in latency was not significant.

These results allowed us to continue using average latency values across all trial and for each fish separately. To support this approach further, we also determined the number of fish that increased or decreased their performance times across trials. Of 19 fish, 13 decreased and 6 increased latency values (fish with “max time” values are not included). The proportion of ‘increase/decrease’ was not significant (Pearson χ^2 , $p = 0.225$). The individual performance times are illustrated in Fig. 4, and a breakdown of changes in individual performance times in Fig. 5.

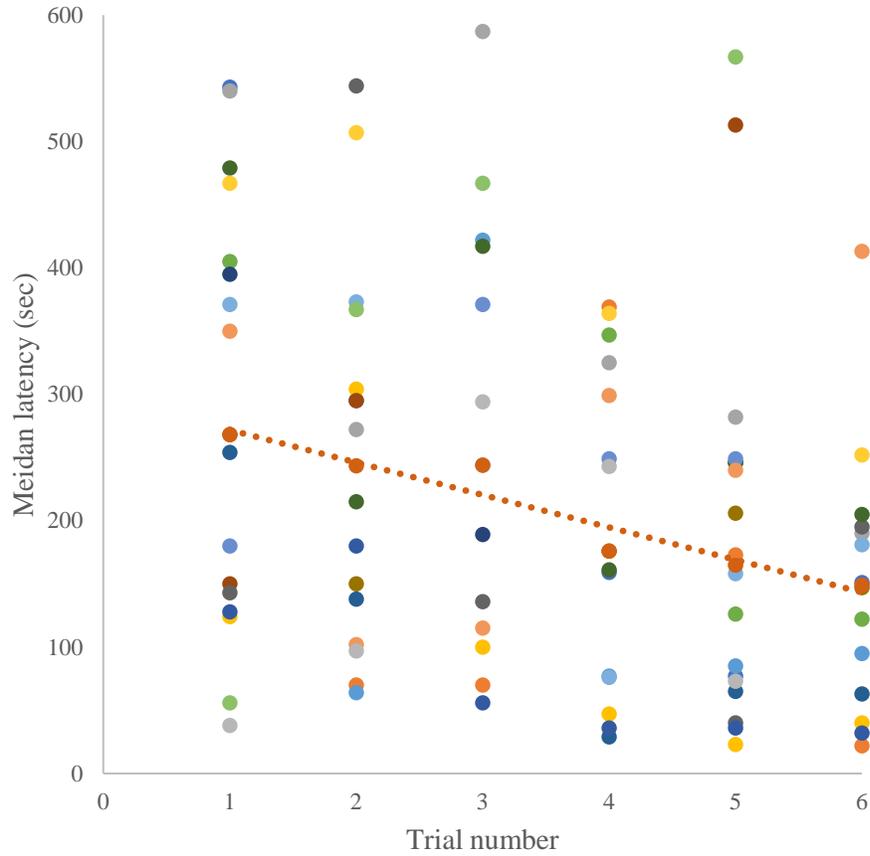
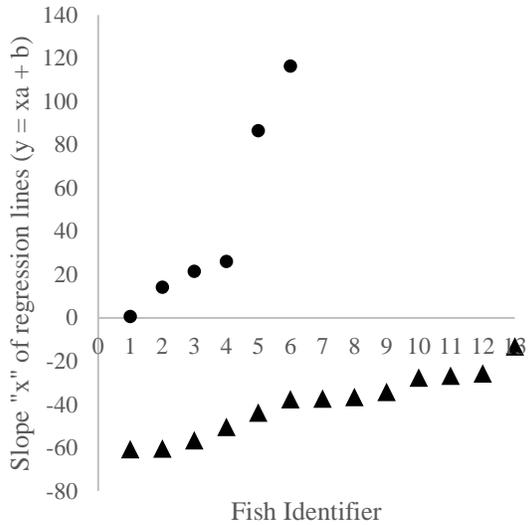


Figure 4. Median latencies of 19 fish on trials 1 through 6. Maze performance decreased in 13 and increased in 6 fish (fish with “max time” values are not included). The proportion of increase/decrease was not significant (Pearson χ^2 , $p = 0.225$). Stippled line represents the averaged median, also shown in Fig. 3).



Fish #	Slope	Fish #	Slope
143	-60.7	109	0.7
126	-60.36	121	14.26
108	-56.6	123	21.6
89	-50.37	92	26.08
127	-43.8	108b	86.57
118	-37.6	96	116.49
95	-37.25		
118	-36.48		
120	-34.2		
108a	-27.5		
88	-26.63		
112	-25.67		
86	-13.09		

Figure 5. Breakdown of individual performance times across 6 trials illustrating ranked ascending positive and negative slopes representing fish that increased (black dots) and decreased latency values (black triangles).

Table 1. Slopes (a) of individual regression lines ($y = ax + b$) from Fig. 4.

Ranking latency and K-S tests. We ranked performance times across all six trials from slowest to fastest to test whether the distribution was normal or deviated from normalcy (excluding “max time” 600 sec values, see Material and Methods). The distributions are illustrated as trial average performance times (Fig. 6) and as individual performance times (Fig. 7). We found that the distribution of average times did not deviate from normalcy (K-S test; $n = 21, p = 0.059$) whereas the individualized distribution did (K-S test; $D = 0.094, n = 96, p = 0.038$). The best-fit function was polynomial (see insert in Fig. 7). (We wish to note, however, that the trial average distribution showed a “break” between 178 and 233 sec, reflecting the near significance level). The corresponding distributions for each trial are shown in Appendix A1-6.

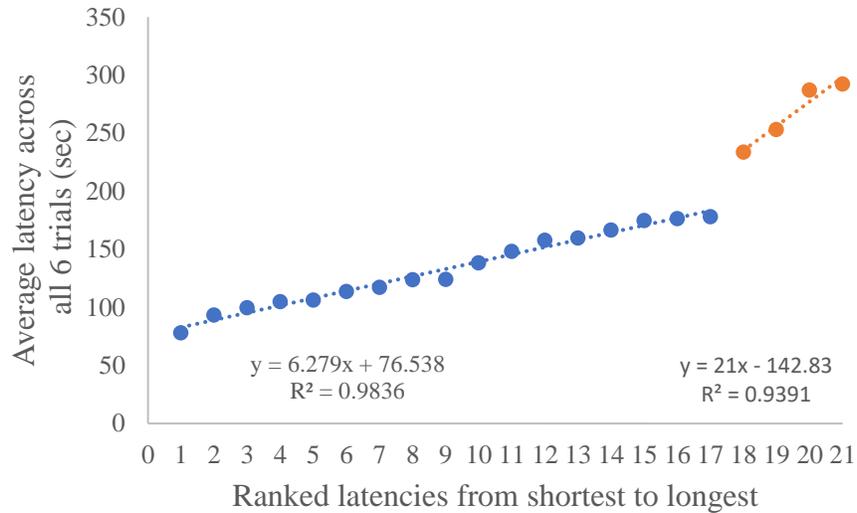


Figure 6. Average latencies and regression lines (21 fish) ranked from shortest to longest for all 6 trials combined. Although the distribution suggested a “break” between 178 and 233 sec, the distribution did not significantly deviate from normalcy (K-S test; $n = 21$, $p = 0.059$).

A deviation from normalcy would suggest a skewed distribution or the presence of two or more separate populations. The “break” in the distribution between 215 and 238 sec (Fig. 7) and the apparent one between 178 and 233 sec (Fig. 6) was suggestive of either possibility. We therefore plotted the occurrence of latencies in successive 50-sec bins to assess the nature of the distribution (Fig. 8). The fish’s maze performance times appeared to be skewed towards shorter latencies, but obviously were separated in shorter and longer latencies. The difference between these two groups (11-215 sec and 238-587 sec) was significant ($p < 0.001$; Wilcoxon-Signed-Rank test). These results indicate that maze performance times separate into two groups, fast and slow latencies. What they did not indicate was whether these two characteristics are typical of individual fish.

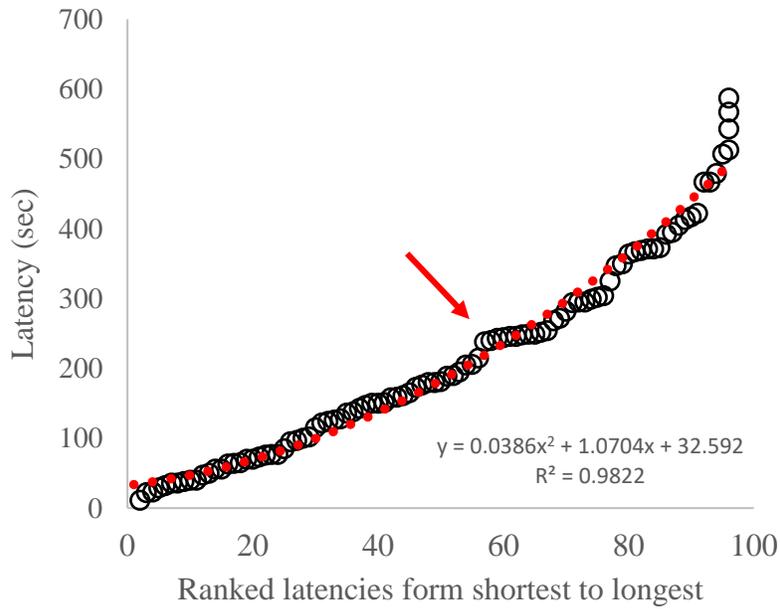


Figure 7. Latency and regression (red dotted line) of all individual fish ranked from shortest to longest for all 6 trials combined. The ranked distribution deviated from normalcy (K-S test; $n = 0.97, p = 0.038$). Red arrow points to a “break” in the distribution between 215 and 238 sec.

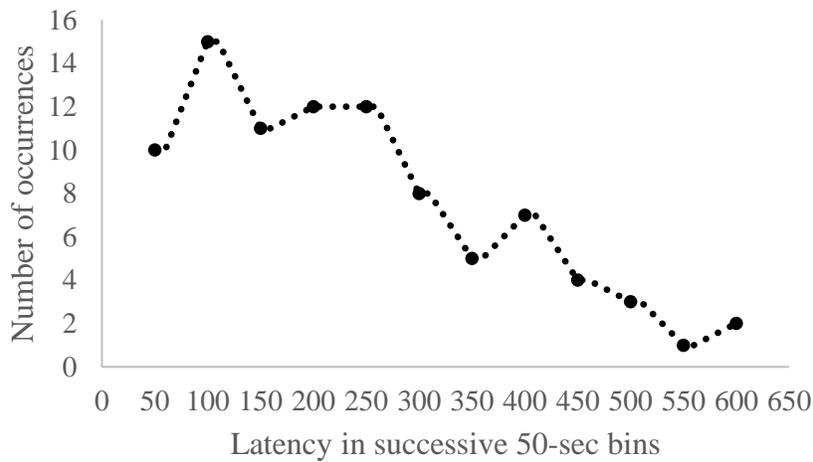


Figure 8. Distribution of latencies in successive 50-sec bins. Latencies appear to be skewed towards longer values, but also reflect a “break” (see Fig. 7) separating latencies in shorter and longer values.

Errors, Time Outs. An errorless “perfect” trajectory would be passages through positions 2, 4, 6, 8, 10 to 12. Table 1 lists the trajectories for trials 1 and 6 for each fish together with the number of errors and time-outs. The median amount of errors for fish in trial 1 was 6 and 5 for trial 6. The median amount of time spent resting in the maze (time-out) for fish in trial 1 was 56 sec and 10 sec for trial 6. The number of errors did not differ between trial 1 and 6 (K-W: $H = 2.617$, $p = 0.106$), and neither did the times fish paused during their trajectory through the maze (K-W: $H = 1.095$, $p = 0.307$).

Fish #	Trial 1 Errors	Trial 6 Errors	Trial 1 Time-Outs (sec)	Trial 6 Time-Outs (sec)
1	6	9	181	0
2	27	0	12	0
3	11	7	141	15
4	5	1	0	0
5	4	2	195	69
6	18	3	89	62
7	20	29	0	10
9	10	3	0	0
10	6	6	0	0
11	10	3	102	12
12	9	9	166	34
13	6	5	109	0
14	9	5	66	67
15	2	4	53	184
16	4	2	0	0
17	8	8	61	168
18	2	14	0	0
19	13	9	121	24
20	6	6	56	10
21	6	12	0	217
22	5	2	9	0

Table 2. Trial 1 & 6 errors and time-outs

Table 2 and Fig. 8 illustrate the occurrence (number) of errors (A) and duration of “time outs” (B) in trials 1 and 6. Although the figure might suggest a decrease in the number of errors in trial 6, the difference was not significant (K-W: $H = 2.617$, $p = 0.106$). The time fish paused during their trajectory through the maze did not differ between the two trials (K-W: $H = 1.095$, $p = 0.307$).

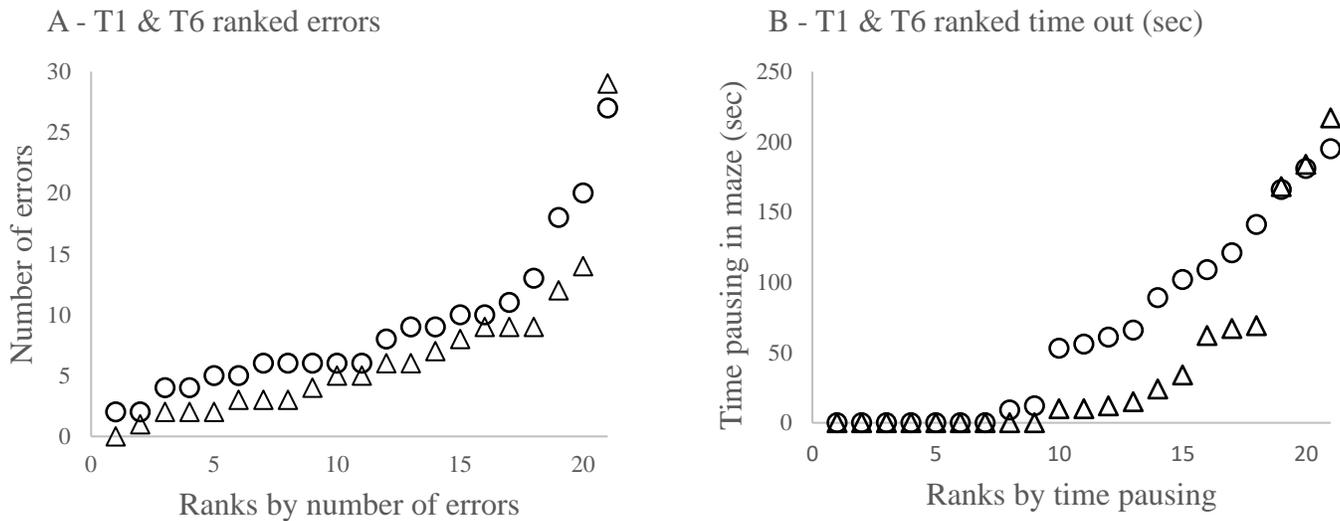


Figure 8. Occurrence of errors (A) and “time outs” (B) in trials 1 (open circles) and 6 (triangles). Figure A displays fish in ranked order from fewest to most errors within the maze for both trials. Figure B displays fish ranked from shortest amount of time spent without movement to the most (in seconds) recorded from all fish.

Neutral nudges. During the course of the experiment eight fish had to be nudged at one time or another with a total of 20 nudges, all of which resulted in “max time” scores of 600 sec. Fish were given a nudge when they were in the maze without movement for at least 180 sec. As fish learned the maze trajectory fewer nudges were needed to make the fish move again (Fig. 9). “Max time” scores were eliminated from the latency analysis (see Material and Methods).

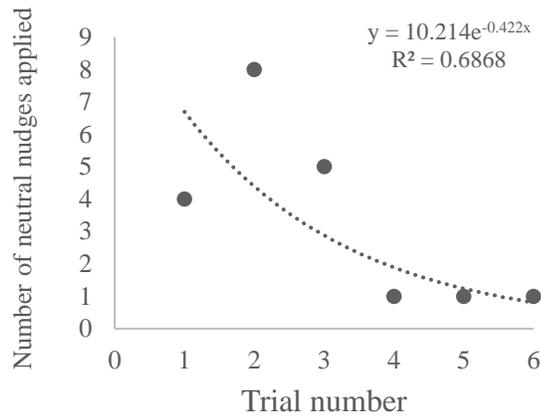


Figure 9. Relationship between trial number and nudges needed to reactivate a resting fish. In all, 20 nudges were needed during the course of the experiment.

Chosen trajectories in trials 1 and 6. A comparison between the fish's chosen trajectory at the start and the end of the experiment was created to help understand whether fish improved their performance by swimming through correct passages and avoiding blind alleys. The trajectory matrices for trials 1 and 6 (Tables 3, 4) show that in both trials, fish would leave the start box swim to passage "2" but instead of passing, return to the start box and out to "2" again. In Tables 3 and 4, fish show improvement indeed from trial 1 to trial 6 as indicated by an increase of successful passages from point 2 to 4, 4 to 6, and 6 to 8. Appendix B lists the complete trial 1 and 6 trajectory sequences for each fish.

Table 3. Trial 1 Maze Trajectory Matrix

	1	2	3	4	5	6	7	8	9	10	11	12
1		<u>78</u>	16	6								
2	<u>56</u>		33	11								
3	9	9		<u>74</u>		2		5				
4	4	9	30		13	44						
5				<u>63</u>		37						
6				24	18		<u>39</u>	6	13			
7						26		<u>74</u>				
8						7	23		3	67		
9						22		11		<u>56</u>	11	
10								18	4		39	39
11										27		73
12												

Table 3. Matrix of Trial 1 maze trajectories as percentage of occurrence. The left side column represents “from” maze locations, and the top row represents “to” maze locations. Numbers within the squares are the percentage of trajectories from one location to the next. Bold numbers represent the “perfect” trajectory. Underlined numbers indicate the highest percentage for that row. Note: some moves scored in this matrix do not seem possible (e.g. from 1 to 3). Multiple times, the same fish managed to squeeze itself behind the plastic sheet to reach post 3.

When comparing tables 3 and 4, one can see that the percentage of visit occurrences along the perfect trajectory (bold sequence) increases at all but one position from trial 1 to trial 6. This shows that by trial 6, more fish have learned the correct path. This explains why our data shows shorter latencies by trial 6.

Table 4. *Trial 6 Maze Trajectory Matrix*

	1	2	3	4	5	6	7	8	9	10	11	12
1		<u>64</u>	22	14								
2	<u>40</u>		36	24								
3	20	37		<u>43</u>								
4	10	10	6		6	68						
5				<u>83</u>		17						
6				29	8		<u>33</u>	27	3			
7						45		<u>55</u>				
8						13	19		3	<u>65</u>		
9						17		33		<u>50</u>		
10								15	11		30	44
11										<u>50</u>		<u>50</u>
12												

Table 4. Matrix of Trial 6 maze trajectories as percentage of occurrence. The left side column represents “from” maze locations, and the top row represents “to” maze locations. Numbers within the squares are the percentage of trajectories from one location to the next. Bold numbers represent the “perfect” trajectory. Underlined numbers indicate the highest percentage for that row.

Electric Organ Discharge

Similar to our latency data we first ranked the duration of all average inter-discharge intervals (IDIs) from shortest to longest to test whether these distributions were normal or showed discontinuities, i.e. were skewed, or contained more than one population. We excluded in this distribution those IDIs recorded prior to fish’s first trial (Figure 10). Appendix C1-6 illustrate these distributions for all individual six trials. We found that the distribution deviated from normalcy (K-S test; $D = 0.09$, $n = 143$, $p = 0.006$).

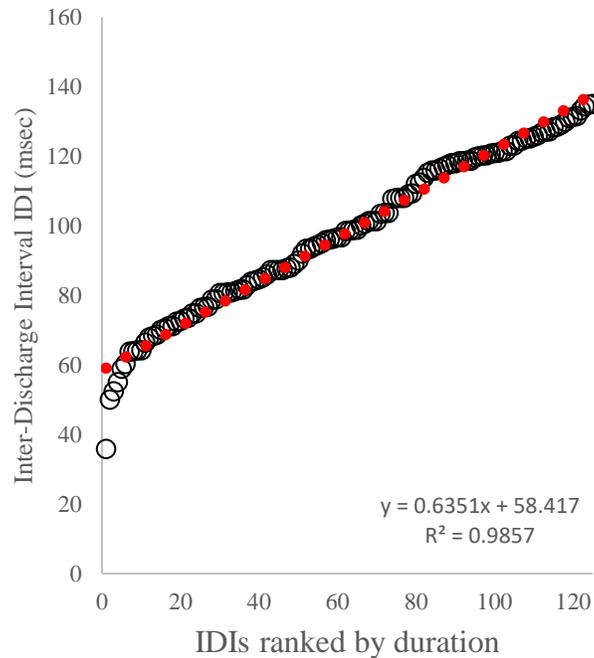


Figure 10. Ranked distribution of all recorded inter-discharge intervals from shortest to longest (six goal recordings combined). Regression (red dotted line). The ranked distribution deviated from normalcy (K-S test; $D = 0.09$, $p = 0.006$).

While combined distributions of IDIs across all goal readings significantly deviated from normalcy, when testing distributions for individual goals, K-S tests revealed that only goal 1 ($D = 0.196$, $p = 0.035$) and goal 6 ($D = 0.204$, $p = 0.029$) significantly deviated from normalcy (Appendix C).

As we did for the latency data, to test whether the data were skewed or distributed along two populations we plotted the IDI data in successive 5-second bins from 30 to 150 seconds. We found that IDIs comprised of two populations with modes at 85 and 120 msec (Fig. 11). In the figure, this is indicated by the presence of two peaks. The distribution is bimodal, meaning there are two modes present within the distribution. The results indicated that EOD intervals (IDIs) fell into two distinct groups, but again did not show whether a specific EOD activity was tied to individual fish.

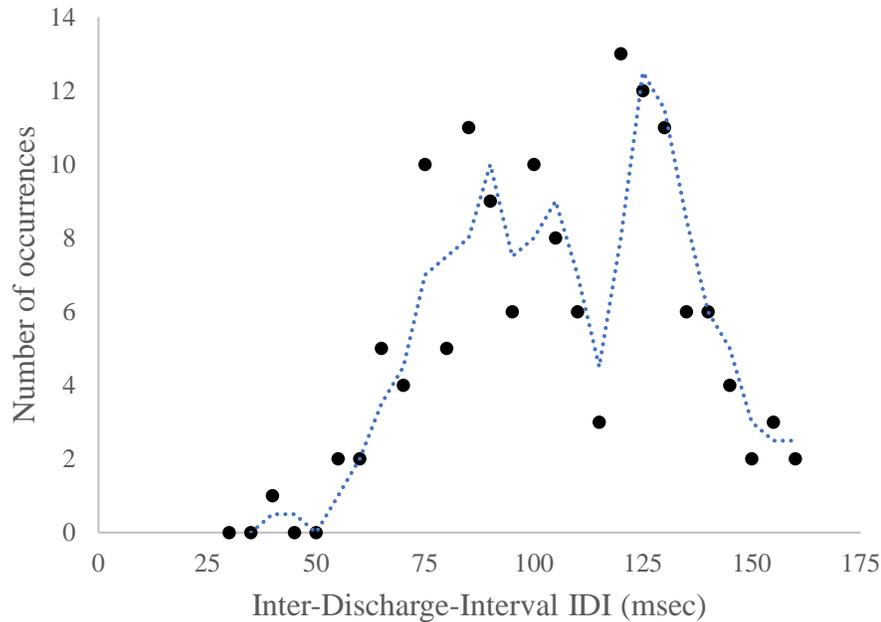


Figure 11. Distribution of Inter-Discharge-Intervals (IDIs) as a function of duration. The distribution comprises of two modes (85 and 120 msec) suggesting the existence of two distinct sets of EOD activity characterized by lower (8 Hz) and higher frequencies (12 Hz), respectively. Stippled line - moving average.

Correlating Locomotor and Electric Behavior

Our results on latency and inter-discharge intervals have only shown a separation into distinct groups, i.e. sets of two, but did not correlate these two traits with particular fish. Thus, the ultimate test finding confirmation of the behavior syndrome hypothesis was contingent on a significant correlation between latency and associated EOD rate. Now, do fish with faster performance times emit higher EOD rates when at rest, and fish with slower latencies emit lower EOD rates when at rest in the goal? We have correlated, separately, the latency data for all individual fish in each of the two identified latency groups with their associated inter-discharge intervals (IDIs) (Fig. 12).

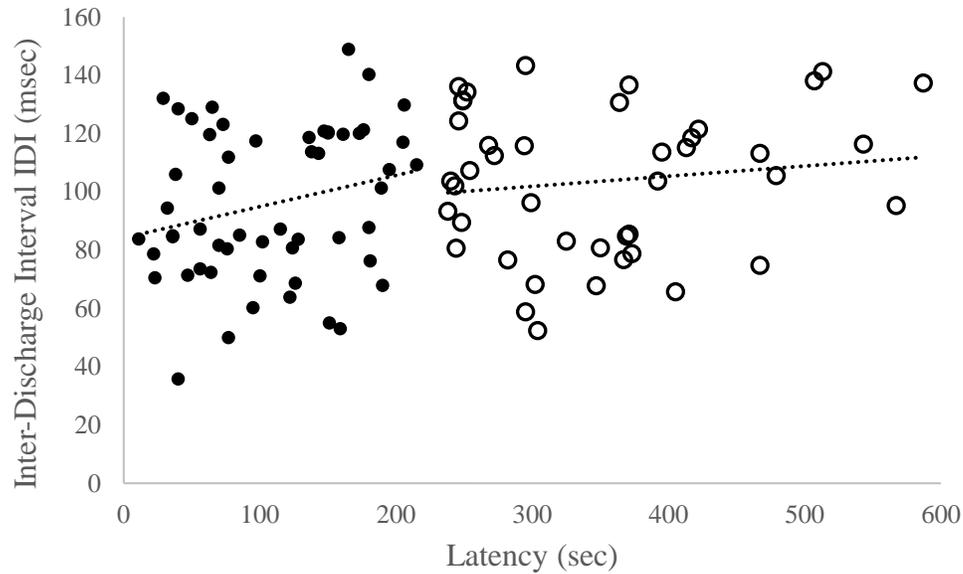


Figure 12. Correlation between IDIs and latencies for all six trials. Shorter latencies up to 215 s were significantly correlated with their respective IDIs ($r = 0.241$, $n = 55$, $t = 1.814$, $p = 0.0376$ one-tail), and latencies above 215 sec were not ($p = 0.194$ one-tail).

Considering the distinction of two latency groups, we have illustrated the correlation between latencies and inter-discharge intervals separately for each group (Figure 12). We see two clusters with the shorter latencies (< 215 sec) significantly correlated with their corresponding IDIs ($r = 0.241$, $n = 55$, $t = 1.814$, $p = 0.0376$ one-tail), and the longer latencies (> 215 sec) not correlated ($p = 0.194$). Fish whose performance time exceeded 215 sec maintained an average IDI of 94.05 ± 23.8 msec corresponding to about 10 Hz. Our third hypothesis relating latency and IDI as a behavioral syndrome was thus only partly supported for shorter latencies.

Discussion

This study hypothesized that a population of *G. petersii* could be divided along two traits into two groups, i.e. fast and slow maze performers, and slow and high EOD frequency emitting fish, suggestive of a personality divide. And while it has long been established that mormyrid fish increase their EOD rate when swimming and slow down when at rest (review Moller, 1995), we further hypothesized that the fish's EOD activity while at rest in the goal box is correlated with its EOD activity, with latency and EOD activity comprising a behavioral syndrome (Sih et al, 2004; Dingemanse et al., 2010).

While our results showed a divide between fast and slow latency values, and also lower and higher EOD rates, these distinctions were not tied to particular groups of fish but remained variable within each subject. Thus, our first two hypotheses were not supported.

To explore the behavioral syndrome hypothesis, we correlated each fish's maze performance times with its associated EOD activity (duration of inter-discharge intervals) by splitting the data into two groups along the divide apparent in our latency distribution (see Fig.7). The results partially supported our hypothesis that maze latency and EOD activity represented a behavioral syndrome, with shorter latencies correlating with the emission of shorter IDIs, i.e. higher EOD rates. This is all the more remarkable as short-latency fish maintained their elevated EOD rate in a restricted environment (goal) that does not allow sufficient space for fast displacements, which in mormyrids is typically associated with increased EOD activity.

Could EOD rate indicate a personality dimension that is present irrespective of the context? Our results were ambiguous. We have shown that the notion of a behavioral syndrome may be applicable over a small range of latencies. As Sih et al. (2004) explained, when trying to find evidence of consistent personality traits across different contexts, there is a chance that some

traits studied are simply domain specific. For example, Coleman and Wilson's (1998) study on pumpkinseed sunfish found consistent individual differences within specific contexts that did not correlate across situations. They further stated that personality dimensions such as shyness and boldness may not even lie on a one-dimensional continuum within a single context. We are asking the question of whether behavioral syndromes exist across contexts: swimming and at rest. While it seems as if a behavioral syndrome may be applicable to a select group of latencies, more studies are needed to assess if personality dimensions are apparent across other domains.

A possible context to be explored in a future study could be the fish's "motivational state" while negotiating the maze. On several occasions, the fish paused midway to the goal. We had to gently nudge the animal to get it swimming again. Interestingly, more nudges were needed during the first three trials than in the following three. With a large enough (powered-up) sample size we could learn whether exploratory eagerness or hiding (as motivational indicators) are compatible traits adjoining latency and/or EOD rate as a behavioral syndrome.

References

- Barth, K.A., Miklosi, A., Watkins, J., Bianco, I.H., Wilson, S.W., Andrew, R.J. (2005). Zebrafish show concordant reversal of laterality of viscera, neuroanatomy, and a subset of behavioral responses. *Current Biology*, 15 (9), pp. 844-850.
- Bell, C.C., Hopkins, C.D., Grant, K. (Eds.), (1993). Contributions of electrosensory systems to neurobiology and neuroethology. Proceedings in honor of the scientific career of Thomas Szabo, *Journal of Comparative Physiology A*, 173, 657–763.
- Bullock, T.H., Heiligenberg, W. (Eds.). (1986). Electoreception. John Wiley & Sons, New York.
- Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5), 641–653.
- Ciali, S., Gordon, J., & Moller, P. (1997). Spectral sensitivity of the weakly discharging electric fish *Gnathonemus petersii* using its electric organ discharges as the response measure. *Journal of Fish Biology* 50, 1074–1087.
- Coleman, K., Wilson, D.S. (1998) Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, 56, 927-936.
- Crampton, W. (2019). Electoreception, electrogenesis and electric signal evolution. *Journal of Fish Biology*, 95(1), 92-134. Doi: 10.1111/jfb.13922
- Dadda, M., Domenichini, A., Piffer, L., Argenton, F., Bisazza, A. (2010). Early differences in epithalamic left–right asymmetry influence lateralization and personality of adult zebrafish. *Behavioural Brain Research*, 206 (2), pp. 208-215.

- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B*, 365, 3937-3946.
- Fechler, K., & Emde, G. V. (2013). Figure-ground separation during active electrolocation in the weakly electric fish, *Gnathonemus petersii*. *Journal of Physiology-Paris*, 107(1-2), 72-83.
- Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychology Bulletin*, 127, 45-86.
- Gould, J. L. (1986). The locale map of honeybees: do insects have cognitive maps? *Science* 232, 861-863.
- Hopkins, C. D. (1981). On the diversity of electric signals in a community of mormyrid electric fish in West Africa. *American Zoologist*. 21, 211-222.
- Kareklas, K., Arnott, G., Elwood, R. W., & Holland, R. A. (2018). Relationships between personality and lateralization of sensory inputs. *Animal Behaviour*, 141, 127-135.
- Kramer, B (1990). *Electrocommunication in teleost fishes: Behavior and experiments*. Springer-Verlag, New York.
- Kramer, B. (1996). Electoreception and communication in fishes. In *Progress in Zoology*, vol. 42, pp. 1-119. Stuttgart: Gustav Fischer Verlag.
- Kreysing, M., Pusch, R., Haverkate, D., Landsberger, R., Engelmann, J., & Ruitter, J. (2012). Photonic crystal light collectors in fish retina improve vision in turbid water. *Science*, 336 (6089), pp. 1700-1703.

Landsberger, M., von der Emde, G., Haverkate, D., Schuster, S., Gentsch, J., Ulbricht, E. (2008).

Dim light vision–morphological and functional adaptations of the eye of the mormyrid fish, *Gnathonemus petersii*. *Journal of Physiology-Paris*, 102 (4), pp. 291-303.

Lázár, S. Libouban, T. Szabo. (1984). The mormyrid mesencephalon. III. Retinal projections in a weakly electric fish, *Gnathonemus petersii*. *Journal of Comparative Neurology*, 230 (1), pp. 1-12.

Lott, G. (2007). g-Prime [Computer Software]. Cornell University.

Mather, J. (1998) Individual differences. G. Greenberg & M. M. Haraway (Eds.), *Comparative psychology: A handbook* (pp. 134-137). New York: Garland.

Mittelstaedt, H. (1985). Analytical cybernetics of spider navigation. *Neurobiology of Arachnids* (F. G. Barth, ed.). Springer, Berlin, pp. 298-316.

Moller, P. (1981). Ecology and ethology of electric fish in West Africa. *National Geographic Society*. 1981, 519–526.

Moller, P. (1995) *Electric fishes: history and behavior*. Chapman and Hall, London.

Moller, P. (2002). Multimodal sensory integration in weakly electric fish: A behavioral account. *Journal of Physiology-Paris*, 96(5-6), 547–556.

O’Keefe, J. & Nadel, L. (1978). *The hippocampus as a cognitive map*. Clarendon Press, Oxford.

Pervin, L. & John, O.P. (1997) *Personality: theory and research* (7th ed.). New York: Wiley.

Rojas, R., & Moller, P. (2002). Multisensory contributions to the shelter-seeking behavior of a mormyrid fish, *Gnathonemus petersii* Günther (Mormyridae, Teleostei): The role of

- vision, and the passive and active electrosenses. *Brain, Behavior and Evolution*, 59(4), 211-221.
- Schluger, J., & Hopkins, C. (1987). Electric fish approach stationary signal sources by following electric current lines. *Journal of Experimental Biology*, 130, 359-367.
- Schumacher, S., Perera, T. B., & Emde, G. V. (2016). Object discrimination through active electrolocation: Shape recognition and the influence of electrical noise. *Journal of Physiology-Paris*, 110(3), 151-163.
- Sih, A., Bell, A. M., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *TRENDS in Ecology and Evolution*, 19(7), 372-378.
- Toerring, M.J. & Belbenoit, P. (1979). Motor programmes and electroreception in mormyrid fish. *Behavioral Ecology and Sociobiology*. 4: 369.
- Tolman, E. C. (1948): Cognitive maps in rats and men. *Psychological Review* 55, 189- 208.
- Trillmich, F., & Hudson, R. (2011). The emergence of personality in animals: The need for a developmental approach. *Developmental Psychobiology*, 53(6), 505–509.
- Tryon, R. C. (1940). Genetic differences in maze-learning ability in rats. *Yearbook of the National Society for Studies in Education*, 39, pp. 111-119.
- Turner, R.W., Maler, L., Burrows, M. (1999). Electrolocation and electrocommunication. *Journal of Experimental Biology*, 202, pp. 1167-1458.
- Verbeek, M. E. M., Drent, P., Wiepkema, P. (1994) Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*. 48, 1113–1121.

- Verbeek, M.E.M. Boon, A., Drent, P. (1996) Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*. 133, 945–963.
- Von der Emde, G. (1993). The sensing of electrical capacitances by weakly electric mormyrid fish: effects of water conductivity. *Journal of Experimental Biology*, 181, 157-173.
- Von der Emde, G. (1999). Active electrolocation of objects in weakly electric fish. *Journal Experimental Biology*, 202, 1205-1215.
- Von der Emde, G., & Bleckmann, H. (1998). Finding food: senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *The Journal of Experimental Biology*, 201, 969–980.
- Walton, A. G., & Moller, P. (2010). Maze learning and recall in a weakly electric fish, *Mormyrus rume probosciostris* Boulenger (Mormyridae, Teleostei). *Ethology*, 116(10), 904–919.

Appendix A. Individual Trial Latencies

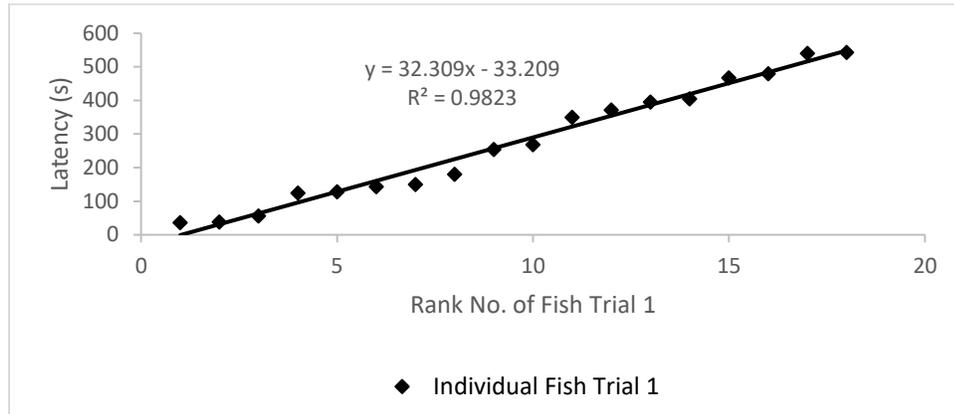


Figure A1. Latency of fish in the maze ranked from shortest to longest for trial 1.

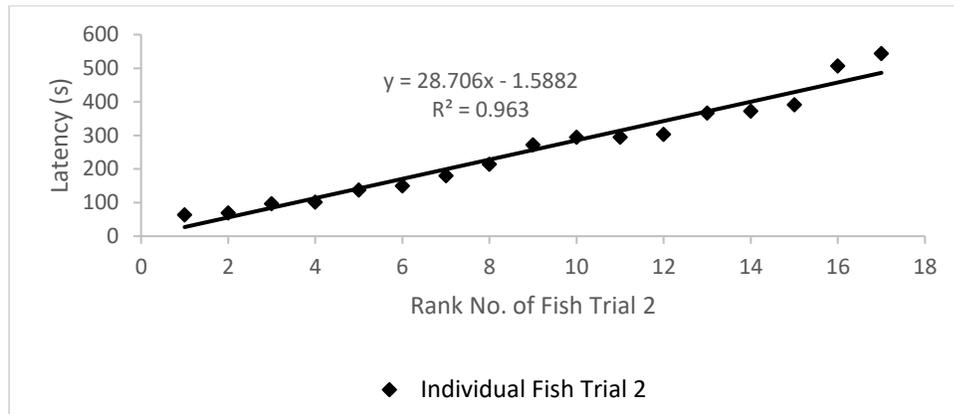


Figure A2. Latency of fish in the maze ranked from shortest to longest for trial 2.

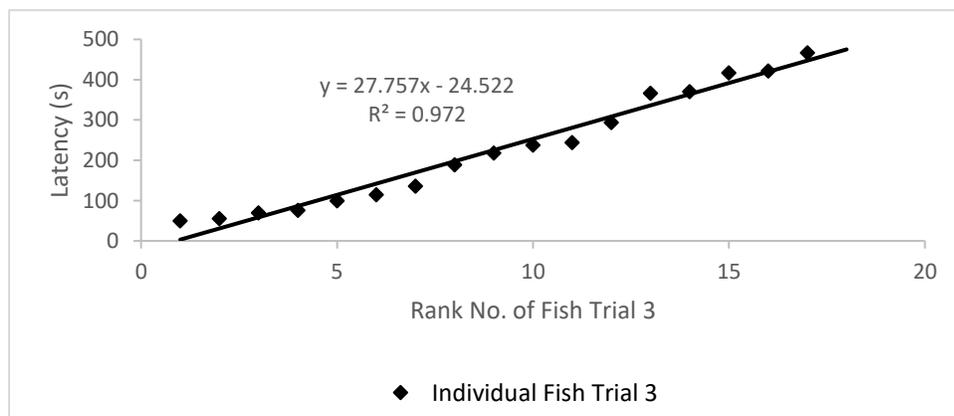


Figure A3. Latency of fish in the maze ranked from shortest to longest for trial 3.

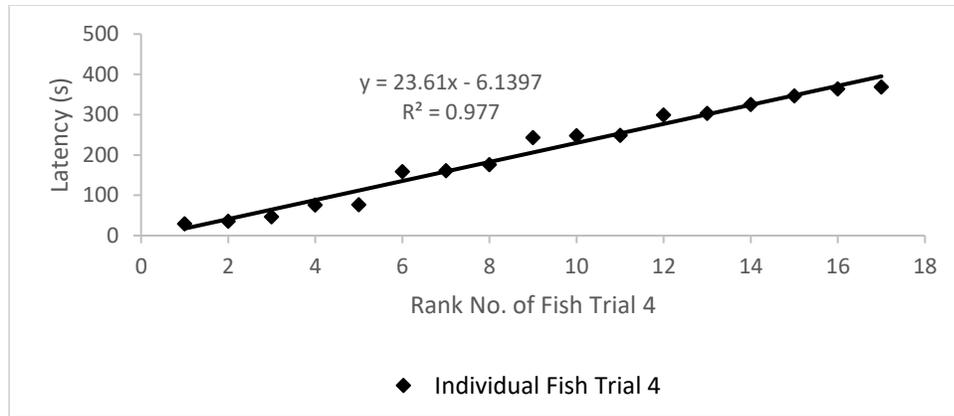


Figure A4. Latency of fish in the maze ranked from shortest to longest for trial 4.

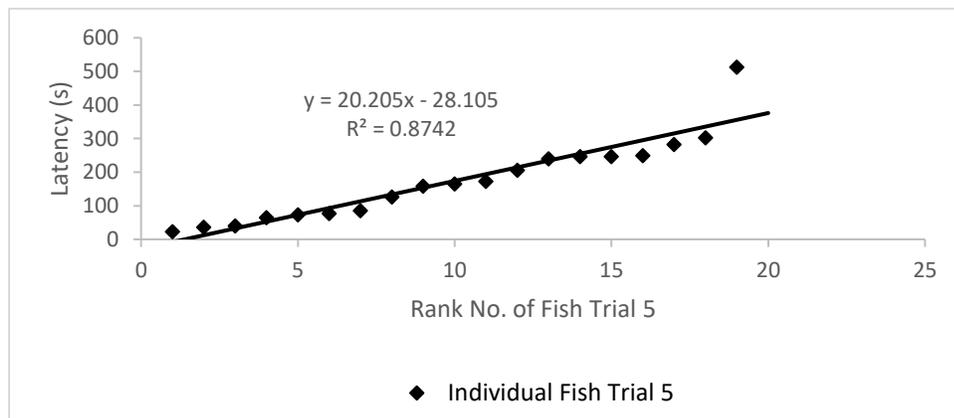


Figure A5. Latency of fish in the maze ranked from shortest to longest for trial 5.

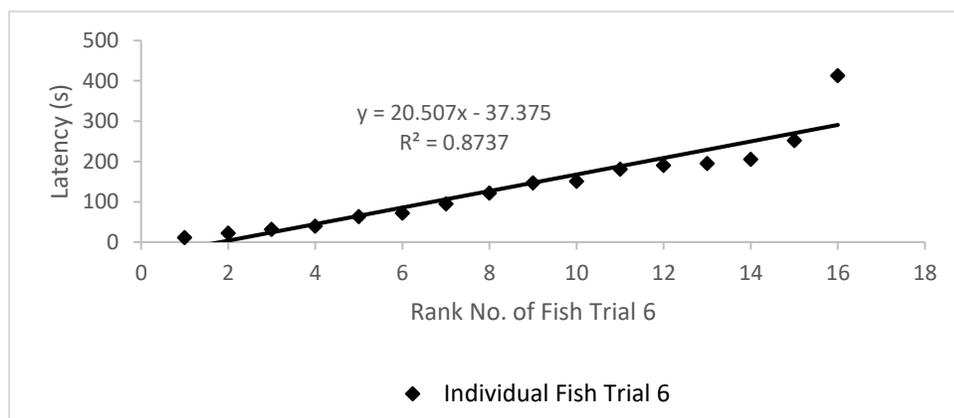


Figure A6. Latency of fish in the maze ranked from shortest to longest for trial 6.

Appendix B. Trial 1 and 6 Trajectory Sequences

Fish	Trial 1	Trial 6
1	2,1,4,3,4,3,4,6,7,8,10,8,10,8,10,12	2,3,2,3,2,3,2,1,2,3,4,6,8,7,8,10,12
2	2,3,4,3,4,5,4,3,4,5,6,5,4,2,1,2,3,4,5,6,5,4,3,2,1, 2,3,4,5,4,3,4,6,4,3,2,1,2,1,2,3	2,4,6,8,10,12
3	2,3,4,3,4,6,8,10,8,7,8,7,6,8,10,11,10,8,7,8,10,1 1,12	2,4,6,8,10,11,10,8,6,4,1,3,2,4,6,8,10,12
4	2,3,4,3,4,3,6,7,8,10,11,12	2,3,4,6,8,10,12
5	2,1,3,4,6,7,8,10,11	2,1,3,4,6,8,10,12
6	2,3,4,6,4,6,5,4,2,1,2,3,4,6,7,6,4,2,1,2,3,2,1,4,6, 5,6,4,3,4,6,7,8,10,12	2,1,3,4,6,7,8,10,12
7	2,3,2,3,4,3,1,2,3,4,6,5,4,3,1,3,4,6,5,4,3,1,3,4,6, 5,4,1,2,3,4,5,4,6,7,6,5,6,9,10,12	2,4,6,5,4,1,3,1,2,3,4,6,7,8,6,4,2,1,4,6,5,4,2,4,6,7,6,4,6,4 ,1,2,3,2,4,6,7,6,4,1,4,6,5,4,1,2
8	2,1,2,3,4,1,2	2,1,2,1,3,1,2,1,3,4,6
9	2,1,3,4,6,7,6,7,8,7,8,6,4,3,4,5,6,7,8,10,12	2,3,4,6,8,7,8,10,11,12
10	2,1,3,1,2,1,2,3,4,6,9,10,12	2,3,2,3,4,6,8,10,8,7,6,4,6,7,6,4,6,8,10,11,12
11	2,1,2,1,2,4,6,7,6,4,6,9,6,4,3,4,6,9,10,12	2,4,6,9,8,10,9,10,11,12
12	2,1,2,1,2,4,6,7,8,7,8,6,7,8,10,11,10,9,10,8	2,3,1,3,4,6,8,9,8,7,6,8,10,11,10,9,6,4
13	2,1,2,1,2,1,4,6,7,8,7,6,4,6,8,10,12	2,4,6,7,6,7,6,7,8,10,12
14	2,1,2,1,2,3,1,2,1,2,4,6,5,4,6,7,8,10,11,12	2,1,2,3,1,2,1,4,6,7,8,10,12
15	2,3,4,6,7,8,10,12	2,1,2,1,2,4,6,4,5
16	2,1,3,4,6,9,11,10,12	2,3,4,6,9,10,12
17	2,1,2,1,3,4,6,5,6,7,6,4,3,4,6,7,8,10,12	2,1,4,6,7,8,10,11,10,9,10,11,10,8,10,8,7,8,10,12
18	2,3,8,10,11,12	2,1,2,1,2,4,5,4,6,4,2,1,2,1,2,4,5,6,7,6,4,3,1,2,1,2

19	2,1,2,4,5,4,2,1,2,4,2,1,2,4,6,4,3,4,6,4,7,7,8,10,11,12	2,1,3,4,6,5,4,2,3,2,1,4,6,8,7,8,10,11,12
20	2,1,2,1,2,1,2,3,4,6,7,8,10,11,12	2,1,2,4,6,7,6,4,2,1,2,4,6,7,8,10,12
21	2,1,2,1,2,4,6,7,8,9,8,7,8,10,11,12	2,3,2,3,2,3,4,6,8,6,7,8,6,4,3,1,2,3,2,3,2,3
22	2,1,2,1,2,1,2,3,8,10,11,12	2,1,2,4,6,7,8,10,12
23	2,1,2,3,4,6,9,6,4,6,9,10,12	2,1,2,1,2
24	2,1,3,4,6	2,3,4,3

Appendix C. Individual Goal IDI Readings

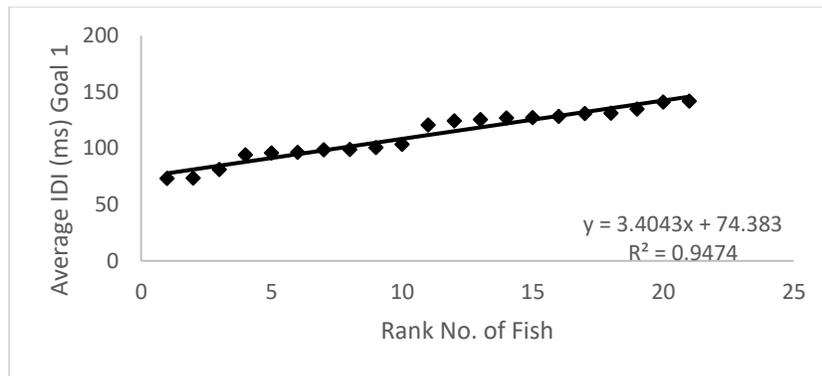


Figure C1. Inter-discharge intervals ranked from shortest to longest for goal 1 (prior to trial 1).

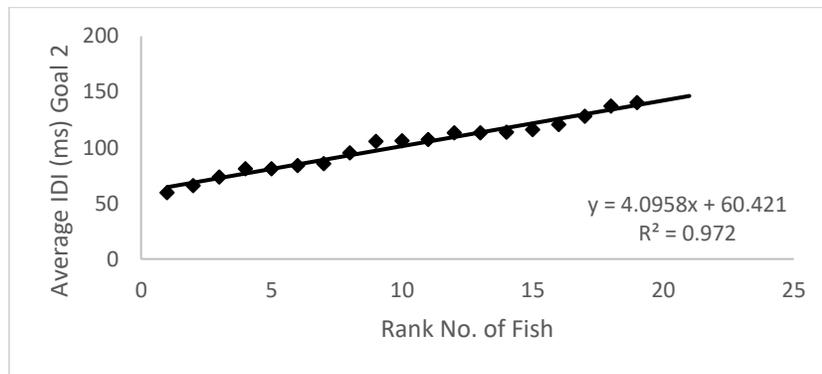


Figure C2. Inter-discharge intervals ranked from shortest to longest for goal 2 following trial 1.

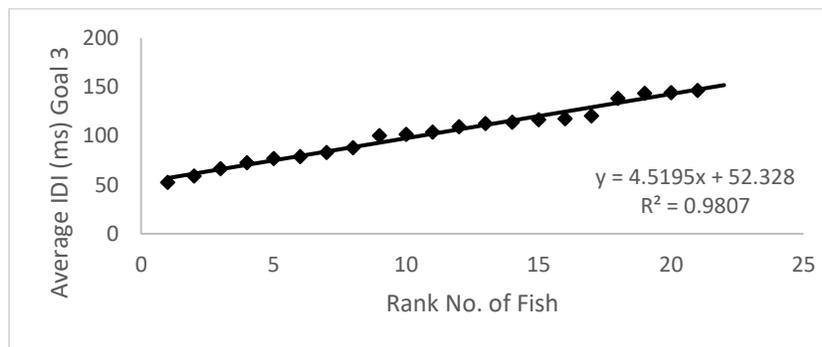


Figure C3. Inter-discharge intervals ranked from shortest to longest for goal 3 following trial 2

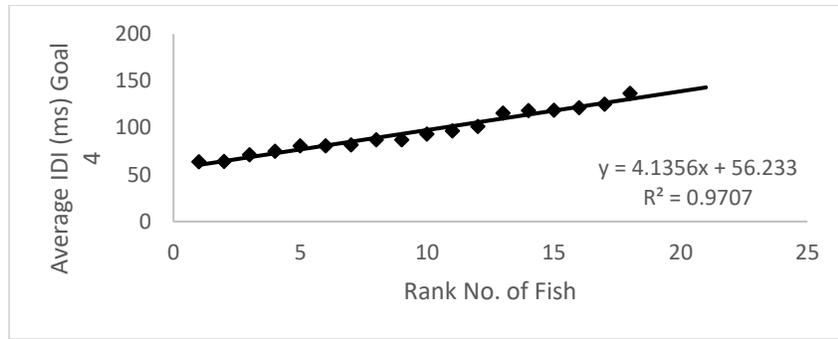


Figure C4. Inter-discharge intervals ranked from shortest to longest for goal 4 following trial 3.

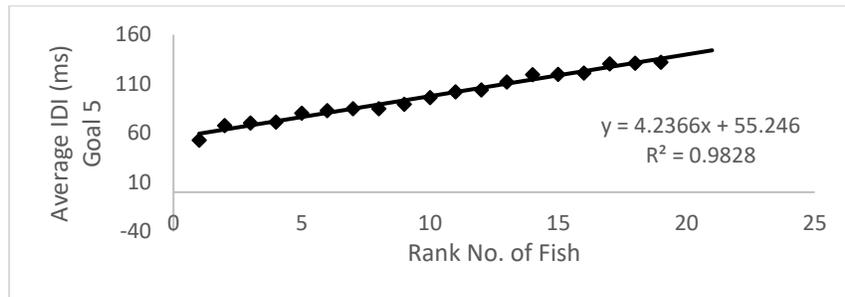


Figure C5. Inter-discharge intervals ranked from shortest to longest for goal 5 following trial 4.

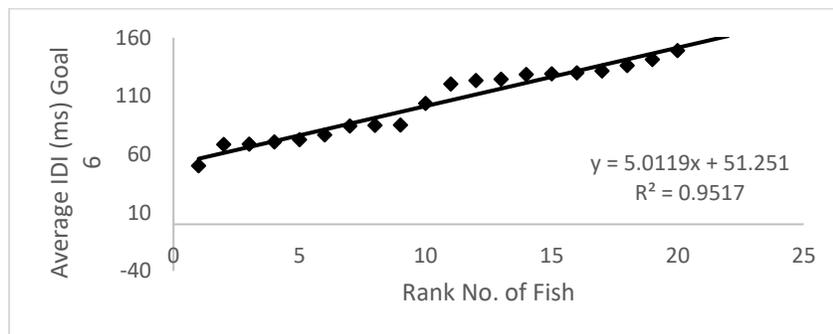


Figure C6. Inter-discharge intervals ranked from shortest to longest for goal 6 following trial 5.

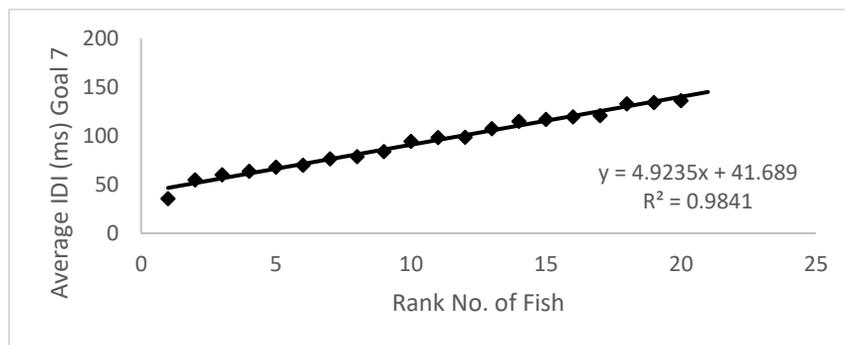


Figure C7. Inter-discharge intervals ranked from shortest to longest for goal 7 following trial 6.