Journal of Comparative Psychology
1998, Vol. 112, No. 1, 92–94

0735-7036/98/$3.00

BRIEF COMMUNICATIONS

Avoidance Learning and "Personality" in the Guppy (*Poecilia reticulata*)

Sergey V. Budaev and Alexander Y. Zhuikov
Russian Academy of Sciences

The authors examined the relationships between 2 "personality" dimensions (Approach and Fear Avoidance) and 2-way active avoidance learning performance in the guppy (*Poecilia reticulata*). Contrary to expectations (based on prior rodent studies), higher fearfulness facilitated both earlier appearance and acquisition of the shuttlebox avoidance responses, especially in the less exploratory and active fish. However, the overall maximum level of performance was not much affected by the 2 personality dimensions studied. Thus, the results emphasized the species-specific and interactional effect of fearfulness on the 2-way avoidance learning performance.

The companion study (Budaev, 1997) revealed consistent individual behavioral differences in the guppy (*Poecilia reticulata*) in a variety of test situations involving novelty, predator, and conspecifics. Two broad "personality" dimensions were identified: Approach (exploration and sociability) and Fear Avoidance (behavioral inhibition and active escape). The study also revealed discontinuous behavioral strategies in stressful situations argued to represent alternative coping styles.

A useful experimental paradigm for testing how personality and coping strategies translate to a nonsocial challenge is the two-way active avoidance learning task (e.g., see Benus, Bohus, Koolhaas, & van Oortmerssen, 1989, for mice). Many studies showed pronounced individual variability of fish of various species in this task (reviewed by Leschyova & Zhuikov, 1989), and there is a large body of evidence (but mostly for laboratory rodents) that subjects with different levels of fearfulness and coping strategies exhibit dissimilar performance in the active avoidance task, viewed as anxiety mediated (Benus, Bohus, Koolhaas, & van Oortmerssen, 1991; Brush, 1991; Gray, 1987). Thus, in the present investigation, we examined the two-way avoidance learning performance of guppies with known personalities and coping strategies.

Method

A complete description of the base population, experimental design, details of the preliminary data analysis, and definition of the personality dimensions are given in Budaev (1997), so we only briefly describe these issues here. The guppies were collected from a feral Moscow population living in an outlet of a sewage purification station. After a period of acclimation to the laboratory conditions, 29 adult males (standard length = 1.6–2.0 cm) were selected from a larger group. Each fish was tested in four tests representing two kinds of situations: (a) novel environments and predator inspection test, and (b) schooling tendency test and mirror test. In each trial of a particular test, the fish were selected in a randomized order to prevent sequential artifacts. Several behaviors were recorded in each of these situations: freezing, moving, skittering, escape, predator inspection visits, attempts to school, direct contacts with mirror image, and looking at the image. The latencies to enter an unknown area with a cichlid predator (*Cichlasoma nigrofasciatum*) behind a glass wall from a previously explored location were also measured. To reduce the large number of variables (83) to an interpretable number, we performed a data aggregation procedure, which resulted in a set of 21 composite measures (listed in Budaev, 1997). The data obtained in the inspection test were then subjected to principal-components analysis, and the component scores were computed for each fish. Two interpretable factors emerged: (a) Activity Exploration, with major loadings of locomotion in novel environments, predator inspection, and (negative loadings) freezing; and (b) Fear Avoidance, made up of freezing and escape (lower scores on this dimension indicate higher fearfulness). The former factor closely correlated with the tendency to enter a novel compartment. The length and weight of individual fish proved to be uncorrelated with the behavioral dimensions.

In the present analysis, we dichotomized both factors at the medians, thereby creating four distinct groups of individuals: (a) low Activity Exploration and low Fear Avoidance; (b) low Activity Exploration and high Fear Avoidance; (c) high Activity Exploration and low Fear Avoidance; and (d) high Activity Exploration and high Fear Avoidance.

Avoidance Training

The experiments on two-way active avoidance learning were conducted approximately 1 month after the ethological tests described above using the same subjects. Twenty-three subjects were selected in a way that included all possible combinations of the personality dimensions (i.e., high and low scorers on both; the above four groups consisted of 7, 5, 4, and 7 subjects, respectively). We used 12 shuttleboxes that measured 40 × 13 × 10 cm, each consisting of two identical compartments 20 cm long. These compartments were separated by a partition raised 2 cm above the

Sergey V. Budaev and Alexander Y. Zhuikov, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia.

This article represents the second part of the study of "personality" dimensions in the guppy.

Correspondence concerning this article should be addressed to Sergey V. Budaev, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect 33, Moscow, 117071, Russia. Electronic mail may be sent via Internet to sevin@glas.apc.org.

bottom, so that the fish were able to swim freely underneath. Uniform illumination of both compartments provided by two 6-V lamps was applied as the conditioned stimulus (CS). Electric shock—a series of 0.1-s pulses delivered at 2-s intervals along the aluminum walls of the shuttleboxes—was used as the unconditioned stimulus (US). We used a 9-V 50 Hz source to supply the shock, which was thereby of moderate intensity (0.69 V/cm) and had no apparent injurious effect on the guppies (see Woodard & Bitterman, 1973, for a similar experimental setup applied to small fish). One hundred trials were presented on a fixed-interval (10 min) schedule, 50 trials per day. During the CS-only interval (10 s), any transition to the opposite compartment was regarded as the avoidance response that consequently terminated the trial. If the fish failed to shuttle within a subsequent CS + US period (20 s), this trial was terminated to prevent unnecessary pain to the subjects. The fish were maintained in the shuttleboxes throughout the 2-day test period.

We calculated cumulative scores by collapsing the data into 10 blocks of 10 trials. The following learning measures were also recorded for each subject: (a) the number of trials until the first avoidance response was performed; (b) the maximum frequency of correct responding over the 10 blocks of trials; (c) the length of the longest series of consecutive avoidances; (d) the number of trials until two consecutive avoidances were performed for the first time; and (e) the number of trials until the longest series of consecutive trials was performed. Some fish did not reach the necessary criterion of learning (two consecutive responses), resulting in censored measures. In such cases, we ascribed them the maximum possible score of 100.

Statistical Analysis

A two-way analysis of variance was applied for the statistical analysis (Sokal & Rohlf, 1981). In some cases, logarithmic transformation was necessary to eliminate the correlation between means and variances and to equalize variances. The Tukey honestly significant difference (HSD) test for unequal samples (Spjotvoll–Stoline test) was used for multiple comparisons. The two censored measures were subjected to the survival analysis methods (Lee, 1992), specifically adjusting for the restriction of variability. The significance level was set at $p = .05$.

Results

Learning performance of individual guppies varied substantially. Some fish did not even reach 10 total avoidances, whereas other fish performed quite long series of consecutive avoidances (up to 43).

The second dimension, Fear Avoidance, significantly influenced the trial of the first avoidance, and the interaction between Fear Avoidance and Activity Exploration was also significant (see Table 1). As Figure 1 reveals, the effect of Fear Avoidance is pronounced for only the nonexploratory subjects (with low scores on Activity Exploration). The multiple comparisons indicated that the fearful and less exploratory group of guppies performed the first avoidance response significantly earlier than the bold and less exploratory group (Tukey HSD test for unequal *N*s, $p = .006$), as well as the bold and more exploratory group (Tukey HSD test for unequal *N*s, $p = .055$). Also, the bold and less exploratory guppies tended to perform the first avoidance significantly later, $t(14) = 2.21, p = .044$ (see Figure 1) than all exploratory subjects (bold and fearful) combined.

Both Fear Avoidance and Activity Exploration showed no significant effect on the length of the longest series of consecutive avoidances or on the maximum frequency of correct

Table 1
Relationships Between the Activity Exploration and Fear Avoidance Personality Dimensions and the Two-Way Avoidance Performance of Guppies

Effect	$F(1, 19)$	p
No. of trials until first avoidance response was performed[a]		
Activity Exploration	0.01	.921
Fear Avoidance	12.56	.002**
Interaction	7.25	.014*
Length of longest series of consecutive avoidances[a]		
Activity Exploration	0.05	.828
Fear Avoidance	1.17	.293
Interaction	1.18	.291
Maximum frequency of correct responding over 10 blocks of trials		
Activity Exploration	0.15	.699
Fear Avoidance	2.60	.123
Interaction	0.51	.485

[a]Logarithmic transformation was applied.
$^{*}p < .05$. $^{**}p < .01$.

responding (see Table 1). However, there was a nonsignificant ($p = .123$) trend for the more fearful fish to exhibit higher maximum frequency (the randomization test involving 5,000 random permutations revealed a similar $p = .125$).

The Activity Exploration dimension showed no significant influence on the number of trials until the criterion of two consecutive responses was reached: Cox's F test for censored measures, $F(16, 14) = 1.04, p = .47$. A different trend was indicated for the Fear Avoidance dimension: The more fearful guppies reached the criterion significantly earlier than bold guppies, Cox's $F(10, 20) = 2.84, p = .022$. Exactly the same pattern was observed for the number of trials until the longest series of consecutive avoidances: no effect of Activity Exploration, Cox's $F(14, 14) = 1.18, p =$

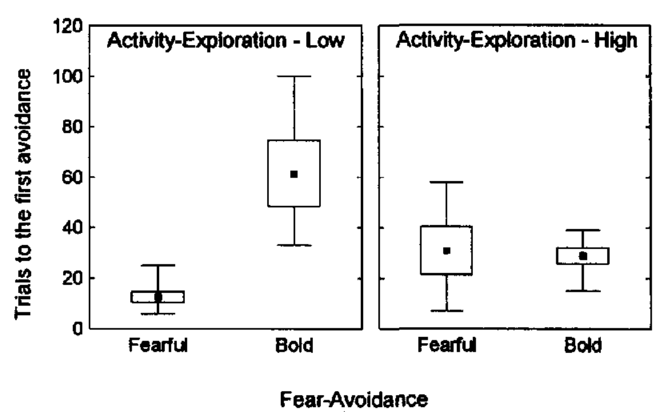

Figure 1. The number of trials until the first avoidance response was performed by individual guppies characterized by high and low scores on the Activity Exploration (exploratory and active when the score is high) and Fear Avoidance (bold when the score is high) personality dimensions. Means, standard errors, and minimums and maximums are presented.

.38, but a significant effect of Fear Avoidance, Cox's $F(8, 20) = 3.03$, $p = .021$, with the more fearful guppies exhibiting better performance. For both the number of trials until two consecutive avoidances and the number of trials until their longest run, a more complex Cox proportional hazard regression revealed no significant interaction between the Activity Exploration and Fear Avoidance dimensions ($t < 0.2$).

Discussion

The results of the present study suggest that higher fearfulness facilitates both earlier appearance and faster acquisition of the shuttlebox avoidance responses in the guppy, especially in the less exploratory and active group. However, the overall maximum level of performance was not much affected by the two personality dimensions studied.

These findings may seem puzzling because initial stages of two-way learning involve a bidirectional conflict in which behavioral suppression (conditioned fear) runs against active avoidance (the only appropriate response in this task) and impairs performance of fearful individuals (Benus et al., 1989; Brush, 1991; Gray, 1987). Nevertheless, higher fearfulness is known to facilitate performance in the one-way avoidance task (Gray, 1987; Huntingford & Wright, 1992) and in the fear-potentiated startle paradigm (Leaton & Borszcz, 1985; Young & Leaton, 1994). However, these patterns are based almost exclusively on studies of rodents.

One way to escape the impasse is to suggest that the adaptive stereotype of responding in the guppy is different from that in rodents, and guppies switch from freezing to active escape more easily. Unlike rodents, various fish species, including the guppy, exhibit jerking (series of startles) in response to threatening and aversive stimuli (including electric shock), which is mediated by the Mauthner neurons (Eaton & Hackett, 1984). In the present investigation, the electric-shock intensity was relatively low, not much greater than the jerking-response threshold. As a consequence, the less fearful subjects would not be much stressed by the shock and would not initially perform the overt escape (series of jerks), thereby leading to later responding. The more fearful subjects could be stressed more and began to emit this behavior earlier. Thus, the two-way avoidance task might bear some similarity with the fear-potentiated startle in the guppy and, perhaps, other fish species.

Because the fearful and nonexploratory guppies are passive copers (see Budaev, 1997), they could show a flexible behavior (Benus et al., 1991), switching between freezing and fleeing, so that the most appropriate response was finally reinforced. In addition, because the guppies stayed for the entire period of training in the shuttleboxes and explored them well, it seems reasonable to suppose (see Benus et al., 1991) that the passive copers were particularly attentive to important cues in this familiar environment (the effect of shifting to the opposite compartment, in this case).

The interaction between the Activity Exploration and Fear Avoidance dimensions is rather easy to understand as the more active subjects would have a higher probability to enter the opposite compartment earlier. They would also be less affected by the initial freezing. In this way, the nonexploratory and bold group is expected to show the worst performance, just as was the case in this study.

Thus, the present investigation emphasizes the potential advantage of the multidimensional personality approach (Budaev, 1997) and further highlights the need to define two distinct dimensions: Activity Exploration and Fear Avoidance. However, the multidimensionality of animal personality has not been appreciated in most rodent studies, and the description of avoidance learning performance has often been limited to only the gross number of avoidances. This obviously precluded careful examination of possible interactional effects of two or more dimensions and peculiarities of the test situation (e.g., the level of stress) on the learning performance.

In conclusion, although the present investigation is consistent with the common view that individual fearfulness and coping strategy play important mediating roles in the two-way avoidance learning task, it emphasizes species specificity and the interactional nature of this influence.

References

Benus, R. F., Bohus, B., Koolhaas, J. M., & van Oortmerssen, G. A. (1989). Behavioural strategies of aggressive and non-aggressive male mice in active shock avoidance. *Behavioural Processes, 20,* 1–12.

Benus, R. F., Bohus, B., Koolhaas, J. M., & van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia, 47,* 1008–1019.

Brush, F. R. (1991). Genetic determinants of individual differences in avoidance learning: Behavioral and endocrine characteristics. *Experientia, 47,* 1039–1050.

Budaev, S. V. (1997). "Personality" in the guppy (*Poecilia reticulata*): A correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology, 111,* 399–411.

Eaton, R. C., & Hackett, J. T. (1984). The role of the Mauthner cell in fast-starts involving escape in teleost fishes. In R. C. Eaton (Ed.), *Neural mechanisms of startle behavior* (pp. 213–266). New York: Plenum Press.

Gray, J. A. (1987). *The psychology of fear and stress.* Cambridge, England: Cambridge University Press.

Huntingford, F. A., & Wright, P. J. (1992). Inherited population differences in avoidance conditioning in three-spined sticklebacks. *Behaviour, 122,* 264–273.

Leaton, R. N., & Borszcz, G. S. (1985). Potentiated startle: Its relation to freezing and shock intensity in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 11,* 421–428.

Lee, E. T. (1992). *Statistical methods for survival data analysis* (2nd ed.). New York: Wiley.

Leschyova, T. S., & Zhuikov, A. Y. (1989). *Learning in fishes.* Moscow: Nauka. (in Russian)

Sokal, R. R., & Rohlf, F. J. (1981). *Biometry.* San Francisco: Freeman.

Woodard, W. T., & Bitterman, M. E. (1973). Pavlovian analysis of conditioning in the goldfish (*Carassius auratus*). *Journal of Comparative and Physiological Psychology, 82,* 123–129.

Young, B. J., & Leaton, R. N. (1994). Fear potentiation of acoustic startle and stimulus-evoked heart rate changes in rats. *Behavioral Neuroscience, 108,* 1065–1079.

Received February 28, 1996
Revision received April 26, 1997
Accepted April 28, 1997 ■