Original Papers

Polish Psychological Bulletin
2012, vol. 43(2), 124-131
DOI - 10.2478/v10059-012-0015-4

Rafał Stryjek[*,**,***]
Klaudia Modlińska[**]
Wojciech Pisula[*]

Response to spatial and nonspatial change in wild (WWCPS) and Wistar rats

The purpose of the experiment was to investigate the effects of domestication on exploration in rats. The comparison was made between wild Warsaw-Wild-Captive-Pisula-Stryjek (WWCPS) rats and Wistar laboratory rats. The study used a purpose-built maze divided into zones connected with a corridor. Objects were placed in two out of four zones. Their location and shape were subject to experimental manipulation. Transporter used to move rats to the maze provided the opportunity for spontaneous exploration of the experimental arena. Rats were subjected to a series of 10 sessions (habituation), followed by a spatial or nonspatial change in the experimental arena, after which another 5 experimental sessions were conducted. The study revealed that wild rats had much higher exploration latency than their laboratory counterparts. At each analyzed stage, WWCPS rats spent much more time in the transporter than Wistar rats. Wistar rats spent much more time during the experiment on object interaction in the experimental arena. In post-manipulation sessions, however, it was wild rats that explored object zones relatively longer than laboratory rats. No differences in the animals' behavior depending on the type of change were observed. Results suggest that wild rats tend to explore much more cautiously than laboratory rats and are more sensitive to changes in their environment. The underlying cause of these differences is likely to be the higher level of stress in wild rats, resulting from threats in their natural habitat.

Keywords: *Wild rat, laboratory rat, domestication, exploratory behavior, neophobia*

Introduction

The aim of research on exploratory behavior is to understand the process of organism's adaptation to environmental change. Exploration involves collecting environmental information (Pisula, 2009). A new stimulus triggers the orienting response (see Sokolov, 1990), which may be followed by a whole range of exploratory behaviors (see Berlyne, 1960; Pisula, 2009).

A novel object in the wild rat's natural habitat not infrequently turns out to be poison or a human-set trap, therefore these rats respond with a higher level of fear (neophobia) than laboratory rats (Barnett, 1963/2009; Cowan, 1977). The traits which are adaptive in wild rats (e.g. high aggression, neophobia, fear of man, etc.) actually reduce fitness in laboratory conditions. And, conversely, the characteristics demonstrated by laboratory rats (e.g. submissiveness, low aggressiveness and fear, etc.) are maladaptive in the wild (Price, 1999). Thus, we are dealing with two contrasting habitats which stimulate the development of different adaptive traits.

To date, a number of differences between wild and laboratory rats have been identified. They include morphological changes (e.g. Castle, 1947; Keeler, 1947), and behavioral differences. Wild rats demonstrate significantly higher levels of aggression and vocalization (own experience; Barnett, Dickson, & Hocking, 1979; Barnett & Hocking, 1981). Despite systematic handling, wild rats still respond with fear and aggression to human contact (King, 1939; own experience). They also differ in their defensive behaviors (Blanchard, Flannelly, & Blanchard, 1986). E. O. Price (1999) reported that laboratory rats perform better at learning certain tasks. Other studies have shown, however, that learned responses extinguish faster in wild rats than in laboratory rats (Millar, 1975). Furthermore, wild rats are more sensitive to environmental changes early in life than their laboratory conspecifics (Huck & Price, 1975).

Laboratory rats have also been reported to demonstrate

* **Institute of Psychology, Polish Academy of Sciences, Warsaw, Poland**
** **Helena Chodkowska University of Management and Law, Warsaw, Poland**
*** **e-mail: rstryjek@wp.pl**

lower neophobia compared to their wild counterparts (Barnett, 1958; Calhoun, 1963; Cowan, 1977; Mitchell, 1976). J.B. Calhoun (1963) noted that wild rats tend to act tentatively towards novel objects appearing in a familiar environment. Their caution is not synonymous with avoidance. Wild rats repeatedly approach and flee from novel objects. The intensity of contact gradually increases as they become familiar with the new objects, construct a new cognitive map (Tolman, 1948), and stop perceiving them as potential threats (see Barnett, 1963/2009).

Unlike for laboratory rats, sensitivity to changes in the environment is of vital adaptive importance to wild rats, and as such it has been favored by the processes of natural selection. Nevertheless, besides unquestionable advantages, such as learning information about food, shelter, escape routes, etc., it comes at a cost: while exploring, the animal is at a risk of being attacked by a predator, straying from its group, sustaining an injury in an unfamiliar territory, etc. (Barnett, 1963/2009; Birke & Archer, 1983; Pisula, 2003). Exploration of a laboratory environment with rats housed in standard cages does not appear to bring any adaptive advantages. In the absence of threats, the costs are also low. Still, even the lack of direct advantages failed to extinguish this form of behavior. Despite hundreds of generations raised in a laboratory setting, laboratory rats are still willing to explore extensively. This may be explained by the stimulus-seeking behavior undertaken in order to maintain the optimum level of stimulation (Pisula & Matysiak, 1998; Pisula, 2009) and the effects of sensory reinforcement (Kish, 1955).

Shukitt-Hale, Casadesus, Cantuti-Castelvetri, and Joseph (2001) investigated the detection of novelty in spatial arrangement by exploring rats of various ages. Objects in their experiment were rearranged spatially (a familiar object was moved to a new location) or nonspatially (a familiar object was replaced with a novel one). Young (6 months old) rats detected both spatial and nonspatial changes, while old rats (at the age of 24 months) only noticed nonspatial changes. Cavoy and Delacour (1993) and Shukitt-Hale et al. (2001) claim that these differences may be explained by the presence of two distinct neural systems: one responsible for object recognition, the other for spatial arrangement recognition. If so, it behooves us to investigate the same phenomenon in wild rats. Perhaps the two processes of environmental change detection have not been altered by the potential changes in the rats' behavior due to domestication to the same extent. Identifying any differences in this area could be a good starting point for investigating their underlying mechanisms.

Since exploration of the wild rat's natural habitat is more risky, but also has a greater benefit potential, when planning our experiment we assumed that the higher level of fear in wild rats would delay the initiation of exploration and, probably to a lesser extent, decrease its subsequent intensity. Furthermore, it was likely that wild rats would be more sensitive to changes introduced during the course of the experiment in the test environment (arrangement of individual objects), which would lead to more intense re-exploration of the test arena. Since rats (and a number of other species) prefer complex environments (i.e. those that contain multiple elements) (Berlyne, Koenig, & Hirota, 1966) and taking into account that the study was conducted in a low-stress condition, we could reasonably assume that both strains under investigation would devote more time to exploring more complex zones of the testing space.

Method

Subjects

The sample consisted of 32 rats (8 WWCPS male and 8 WWCPS female wild rats, and 8 Wistar male and 8 Wistar female laboratory rats) aged 4 months. The WWCPS strain was derived in 2006 from genetic material obtained from 5 independent colonies of wild rats (Stryjek & Pisula, 2008, Stryjek, 2008, 2010). The experiment used the first laboratory-bred WWCPS generation (F1). The Wistar laboratory strain was chosen for comparison as one of the oldest and most popular laboratory rat strains.

All rats were housed in standard cages, 4 same-sex rats to a cage, with constant access to water and food. The day/night cycle was set at 12/12h.

Apparatus

The experiment was conducted in a maze with four separate 32 cm x 32 cm zones connected with corridors 15 cm in diameter (see Fig. 1). The height throughout the maze was 18 cm. The bottom and walls were painted with white emulsion paint. The space in the maze was arranged so that each zone was of equal area. All zone entrances were equidistant from the entrance to the maze (Fig. 1). The maze was covered on top with a mirror angled at 45 degrees, which meant that the recorded video was a mirror image of the experimental setting. The rats were moved from housing cages to the experimental setting using a purpose-built transporter with the base 16 cm in diameter and height of 35 cm. Rats were free to move inside the transporter, and a trapdoor raised by the laboratory technician enabled rats to enter the maze spontaneously.

The rats' behavior was recorded using a camera with infrared illuminator and, to minimize shadows, two separate infrared illuminators were positioned at different angles.

Procedure

Rats were moved to the maze individually, in the transporter. Each rat spent 1 minute locked in the transporter (adaptation phase). At the end of the adaptation phase, the transporter was opened and the animal was able to engage

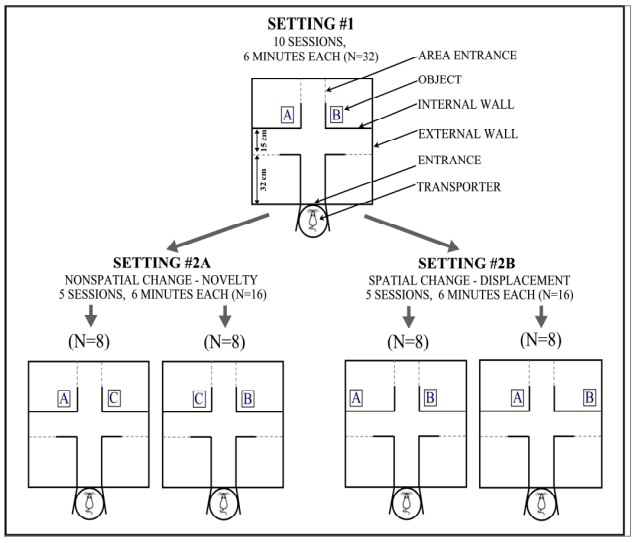

Figure 1. Experiment design diagram.

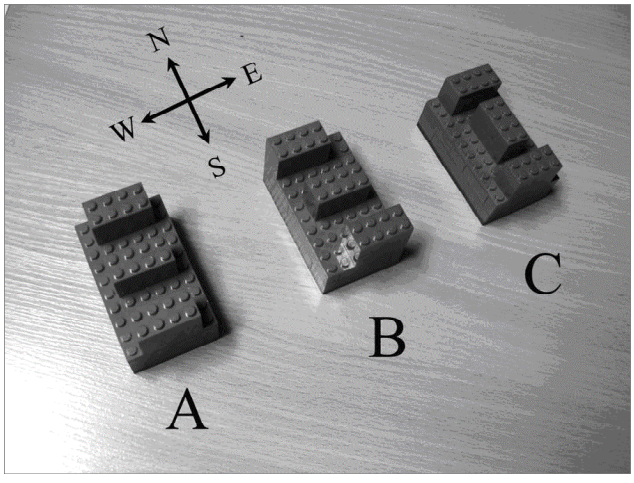

Figure 2. Objects placed in the experimental arena made of Lego blocks.

in spontaneous exploration. The lighting conditions were subjective darkness (weak red light). Two of each type of objects measuring 8 x 4.6 x 2 cm made of variously connected Lego blocks were selected and placed in the maze as shown in the diagram (Fig. 1 & 2). The study was divided into 15 daily sessions of 6 minutes each. Sessions no. 4, 5, 8, 9, 10, 11, 12, 14, and 15 were recorded and analyzed. The data file was built on the basis of videotape records using the EthoLog 2.2 observational software (Ottoni, 2000). After 10 sessions treated as the period of habituation to experimental conditions (cf. Pisula, Stryjek, & Nałęcz-Tolak, 2006; Pisula, 2009) a change was introduced in the arrangement of objects. The change was spatial for one half and nonspatial for the other half of the rats (Fig. 1). To avoid the effects of lateral bias and the resulting tendency to turn left or right, half of the rats experienced a given type of change in the right zone, and the other half in the left zone (Fig. 1). Animals were randomly selected to each experimental condition.

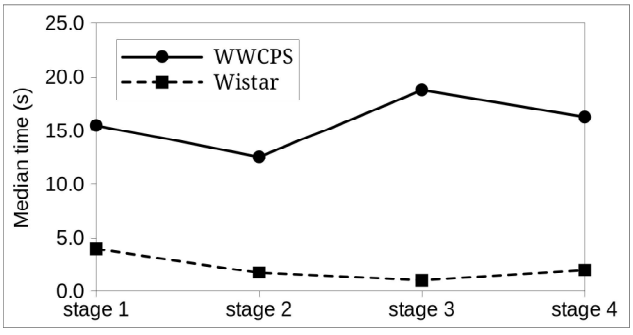

Figure 3. Median latency to exiting the transporter by experimental stage.

The rats were tagged at the start of the experiment to ensure consistent order of participation in successive sessions. At the end of a session, each rat was removed from the maze in the transporter and then placed in a new cage, with no contact with untested rats. The experimental apparatus was cleaned after each animal's run to remove fecal droppings, urine, and other sources of odor stimuli. At the end of the session all rats were moved to their housing cages.

Results

For the sake of clarity, outliers (i.e. outlying values in each measured variable) have been excluded using the Grubbs test (Grubbs, 1969). For the sample size (N=32) and the confidence interval of 95%, the outliers were considered to be the results above 2.745 SD in the sample. To account for the fact that comparisons were made between strains, rejections were made on the basis of SD values for each group rather than for the entire sample.

To reduce the risk of randomness in measurements, the data have been aggregated. Behavior in sessions 4, 5, 9, 10, 11, 12, 14, and 15 was analyzed. Sessions were aggregated by successive pairs. Following aggregation by drawing the arithmetic mean from 2 successive sessions, stage 1 (long before manipulation of objects in the maze) included sessions 4 and 5, while stage 2 (immediately before manipulation) consisted of sessions 9 and 10, while stages 3 (immediately after manipulation) and 4 (long after manipulation) of sessions 11 and 12, and 14 and 15 respectively.

The Kolmogorov–Smirnov test revealed deviations from the normal distribution. Sample size (N=32) did not warrant the additional use of multivariate analysis of variance. To avoid errors, standardize the analysis, and ensure result comparability, only non-parametric tests were used.

No differences in the animals' behavior depending on the type of change (relocation vs. novelty) were observed. Therefore the following analysis was based on the results observed in the two combined experimental groups.

Table 1
Comparison of Wistar and WWCPS rats in terms of the duration of object interaction and time spent in object zones of the experimental arena for each stage of the experiment. U Mann-Whitney test.

	Time of interaction with manipulated object			Time spent in manipulated zone			Time spent in non-manipulated zone		
	Median	U	p	Median	U	p	Median	U	p
	STAGE 1								
Wistar	20.25	35.0	.001	57.25	76.5	.052	52.75	86.5	.118
WWCPS	6.5			39.25			46.75		
	STAGE 2								
Wistar	23.5	24.0	<.001	45.0	56.0	.011	49.75	77.0	.089
WWCPS	8.5			35.75			32.5		
	STAGE 3								
Wistar	21.75	5.5	<.001	56.5	73.5	.04	54.25	34.0	.001
WWCPS	10.0			43.0			33.5		
	STAGE 4								
Wistar	22.75	6.0	<.001	42.0	99.0	.274	50.0	45.5	.002
WWCPS	7.75			32.0			30.75		

Initiation of exploration

Time in seconds from the start of each session (i.e. the moment the trap door of the transporter was opened) to the rat leaving the transporter was adopted as the index of latency (Fig. 3). Mann-Whitney U-test showed that the WWCPS rats demonstrated higher latency of exploratory behavior compared to Wistar rats at all stages under analysis (stage 1 – U=11; stage 2 – U=14; stage 3 – U=4; stage 4 – U=0; $p<.001$).

In the case of wild rats, Friedman test did not yield significant differences in the latency of leaving the transporter between the stages of the study [$\chi^2(3, N=13)=1.71$; $p=.635$]. There were significant differences in laboratory rats [χ^2 (3, N=14)=11.47; $p<.001$], and detailed analysis using Wilcoxon test revealed significant differences between the 1st and 3rd stages (Z=-2.78; $p=.005$), 1st and 4th stages (Z=-2.74; $p=.006$), and 2nd and 3rd stages (Z=-2.17; $p=.03$).

During the course of all stages of the observation, total time spent in the transporter was significantly longer in the case of wild rats: first stage U=18.5 (Wistar M=85.6; WWCPS M=146), second stage U=41.5 (Wistar M=78.9; WWCPS M=121.1), third stage U=31 (Wistar M=76.5; WWCPS M=152), and fourth stage U=53 (Wistar M=81.1; WWCPS M=141.3). The significance for all differences was $p<.01$. The analysis of variability of time spent in the transporter in various stages of the experiment yielded no significant differences between successive sessions for laboratory rats [χ^2 (3, N=16)=3.00; $p=.392$] or the wild rats [χ^2 (3, N= 15)=0.84; $p=.84$].

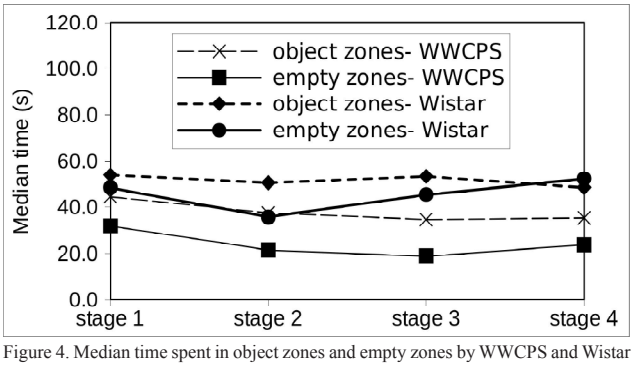

Figure 4. Median time spent in object zones and empty zones by WWCPS and Wistar rats by experimental stage.

Object interaction

In each of the experimental sessions under analysis, wild rats spent less time interacting with manipulated object than laboratory rats (Tab. 1). Length of interaction with manipulated object changed in the course of the experiment [χ^2 (3, N=30)=8.493; $p=.037$]. There was a clear increase in length between stages 1 and 2 in both strains (Wistar Z=-2.10; $p=.04$; WWCPS Z=-1.76; $p=.08$). Exploration time with the described object decreased between stages 3 and 4 in wild rats (Z=-2.02; $p=.04$).

Wistar laboratory rats spent significantly more time in the object zones during the 2nd and 3rd stages (Fig. 4 and Table 2). In the 1st and 4th stages of the study differences were not significant. Wild rats spent significantly more time in the object zones during stages 1-3 (Fig. 4 and Table 2). The differences in stage 4 were not significant.

Length of time spent in the zones with and without objects changed from one stage to another in both strains in the study. In Wistar rats, there was a significant drop-off after stage 3 (Table 3). Time spent in zones with no objects in the laboratory rats decreased after the first stage, and then increased significantly after the second stage (Table 3). In

Table 2
Comparison of time spent by rats in object zones and empty zones by strain of rats and stage of experiment. Wilcoxon test.

	Wistar			WWCPS		
	Median	Z	p	Median	Z	p
	STAGE 1					
Time spent in object zones	53.9	-1.42	.16	44.6	-2.59	.01
Time spent in empty zones	48.5			32.0		
	STAGE 2					
Time spent in object zones	50.5	-3.04	<.001	37.5	-2.73	.01
Time spent in empty zones	35.75			21.5		
	STAGE 3					
Time spent in object zones	53.25	-2.17	.03	34.75	-3.11	<.001
Time spent in empty zones	45.5			19.0		
	STAGE 4					
Time spent in object zones	48.5	-0.85	.40	35.4	-0.91	.36
Time spent in empty zones	52.25			23.75		

Table 3
Comparison of time spent by rats in object zones (part A) and empty zones (part B) by strain and stage of experiment. Medians are presented in Table 2.

		EXPERIMENTAL STAGE IN THE COMPARISON					
Part A		1-2	1-3	1-4	2-3	2-4	3-4
Wistar	Z	-0.63	-1.06	-1.06	-1.6	-0.82	-2.84
	p	.53	.29	.29	.11	.41	<.001
WWCPS	Z	-1.7	-1.25	-1.14	-0.06	-1.05	-0.8
	p	.09	.21	.26	.95	.29	.43
Part B							
Wistar	Z	-2.28	-0.85	-0.91	-2.51	-3.17	-1.34
	p	.02	.39	.36	.01	<.001	.18
WWCPS	Z	-1.88	-1.92	-0.87	-0.5	-1.61	-1.36
	p	.06	.06	.38	.62	.11	.17

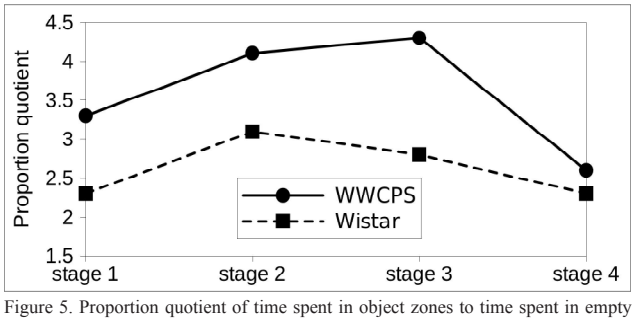

Figure 5. Proportion quotient of time spent in object zones to time spent in empty zones by experimental stage.

wild rats, there was a decrease (statistical tendency) in the time spent in object zones between stages 1 and 2 (Table 3). The time spent by WWCPS rats in empty zones decreased between the 1st and 2nd stages of the experiment, and then increased between stage 2 and 4 (statistical tendency) – Table 3.

The proportion quotient of time spent in object zones to the time spent in empty zones (i.e. preference of zones containing objects) differed significantly between strains only at the 3rd stage of the experiment (Mann-Whitney's U=64; p=.046) – Fig. 5.

The proportion quotient of time spent in the experimental zones varied over time: the value of Friedman's test was [χ^2 (3, N=28)=9.643; p=.022]. In Wistar rats there was a significant increase between sessions 1 and 2 (Z=-2.53; p=.01) and a decrease between stages 2 and 4 (Z=-2.64; p=.01). In the case of WWCPS rats, the decrease occurred between stages 2 and 4 (Z=-2.92; p<.001).

At all stages of the experiment, laboratory rats spent more time in the manipulated zone than wild rats. The differences are statistically significant for stages 1-3 (Table 1). Laboratory rats spent significantly more time in the non-manipulated zone during 2 stages (statistical tendency) 3 and 4 (Table 1).

There were no differences between the time spent in the manipulated and non-manipulated zone by Wistar rats. In WWCPS rats the difference was significant in the 3rd stage (Z=-2.54, p=.01).

Table 4
Comparison of the quotient of time spent in the zone with manipulated object to time spent in that zone by stage of experiment – Wilcoxon test. Mean values of the proportion quotient are provided in Figure 6.

		EXPERIMENTAL STAGE					
		1-2	1-3	1-4	2-3	2-4	3-4
Wistar	Z	-2,95	-2.22	-3.21	-1.93	0.34	-2.53
	p	<.001	.03	<.001	.05	.73	.01
WWCPS	Z	-2.5	-1.42	-1.19	-1.6	-0.83	-0.21
	p	.01	.16	.23	.11	.41	.84

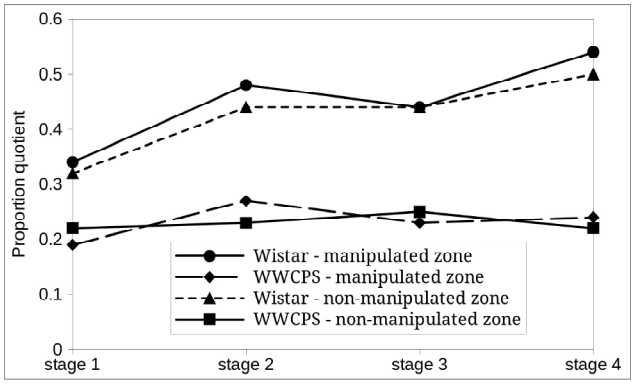

Figure 6. Proportion quotient of object interaction time to total time in a given zone by experimental stage.

As far as variability of time spent in the manipulated and the non-manipulated zones between the stages of the experiment, no statistically significant differences were found in Wistar rats. In wild rats there was an increase (statistical tendency) in the time spent in the manipulated zone between stages 2 and 3 (Z=-1.78; p=.07). Statistically significant differences (decreases) in the length of time spent in the zone with no object manipulation were observed between stages 1 and 3 (Z=-2.5; p=.01), 1 and 4 (Z=-2.64; p=.01), as well as 2 and 4 (Z=-2.42; p=.02).

At all stages of the study, Wistar rats devoted significantly more time spent in the manipulated zone on interaction with the manipulated object than WWCPS rats – Figure 6. The results were significant for each analyzed session (stage 1 – U=36; stage 2 – U=23; stage 3 – U=13; stage 4 – U=8; p<.001).

Friedman's test demonstrated the variability of the analyzed proportion over time [χ^2 (3, N= 30)=17.689; p= .001]. In Wistar rats there was a statistically significant increase in the proportion of interest following the first stage, decrease after the second stage and another increase after the third stage of the experiment (Table 4). In WWCPS rats the ratio increased significantly after the first stage and dropped after the second (statistical tendency) – Table 4.

In all analyzed stages Wistar rats devoted relatively more time spent in the non-manipulated zone to interaction with the non-manipulated object than WWCPS rats (stage 1 – U=55; stage 2 – U=21; stage 3 – U=12; stage 4 – U=6; p<.01) – Figure 6.

Friedman's test demonstrated the variability of the analyzed feature over time [χ^2 (3, N= 30)=10. 903; p=.012]. In Wistar rats, there was a statistically significant increase in the ratio of interest following the first (Z=-3.05; p<.001) and the third stage (Z=-1.96; p=.05). No significant differences between analyzed stages were found in WWCPS rats.

Discussion

Analysis of our results showed that wild rats started exploring much later than their laboratory counterparts. At each analyzed stage, WWCPS rats spent much more time in the transporter (70% more on average) than Wistar rats. Exploration latency and longer time spent in the relative safety (due to familiarity) of the transporter may be associated with a higher level of fear in wild rats. The low-stress environment and lack of external threats reduced the level of fear responses in laboratory rats (own experience; Barnett, 1958; Calhoun, 1963; Cowan, 1977; Mitchell, 1976). This may explain why, on average, 30% of laboratory rats left the transporter within a second of its opening. A wild rat in its natural habitat, before leaving its burrow, almost invariably first sticks out its head, freezes and, for some time, listens, sniffs and observes its surroundings (own experience, Calhoun, 1963). WWCPS rats in the study behaved similarly when exiting the transporter and before starting to explore the maze. Wild rats started exploring on average 20-50 seconds after the transporter was opened (depending on the stage of the experiment), while the mean for laboratory rats was 2-6 seconds. The caution of wild rats is of evolutionary origin and as such may serve an adaptive function, mitigating the risk of predatory attack in the wild (Barnett, 1963/2009; Cowan, 1977). A laboratory setting, by contrast, offers no threats of this type, which may explain the behavioral differences between the two strains.

Lower fear in Wistar rats is also evidenced by the fact that they spent more than 2.5 times as much time during the experiment on object interaction in the experimental arena. In post-manipulation sessions, however, it was wild rats to spend relatively more time in zones with objects (proportion quotient of time spent in object zones to time spent in empty zones). In each analyzed stage, Wistar rats

spent twice as much time in object zones interacting with objects placed in these zones. This could mean that wild rats employ a different strategy, focused on risk assessment (Ray & Hansen, 2004), whereby they minimize direct contact with objects and explore the surrounding zone instead. These differences may plausibly be explained, to some extent, by poor eyesight of albino laboratory rats (Prusky, 2002). With the lack of pigment in the iris of these rats (e.g. Wistar), overexposure of the retina to light results in eye impairment. Even though sight is not the basic sense in rats (the dominant ones are smell and hearing, supported by touch using vibrissae; Hartmann, 2003), it still is an important instrument of perception. During the experiment, the maze was illuminated with weak red light. The receptors (cones) in the rat's retina are not adapted to receive red light frequency waves (Szel & Rohlich, 1992; Jacobs, Fenwick, & Williams, 2001). Nevertheless, there is no certainty that the lighting conditions in the experimental arena ensured complete darkness for the rats. If not, wild rats may have been making better use of visual cues. Consequently, they were less dependent on direct interaction with objects than laboratory rats. To control for this possibility, our future studies on the behavior of rats and other nocturnal mammals will be conducted in complete darkness.

As hypothesized, both wild and laboratory rats spent significantly more time in the zones which contained objects. As we can see, preference for environment complexity (Berlyne et al., 1966) is common to both strains in the study.

No differences in the animals' behavior depending on the type of change (relocation vs. novelty) were observed. Perhaps both types of changes had a similar effect on the behavior of rats exploring the maze. The effect of experimental manipulation (regardless of the type of change) was more pronounced in wild rats. In their case the length of time spent in the transporter dropped after the 1st stage (habituation), and then increased considerably in stage 3 (i.e. directly after manipulation). Time spent by Wistar rats in the transporter remained constant throughout the study. The change in the experimental arena noticed by wild rats probably produced fear, leading to decreased exploration.

Following manipulation, WWCPS rats spent more time in the zone with the manipulated object and less time in the unaltered zone. No significant differences were found in this respect in Wistar rats. This is probably the result of wild rats' greater sensitivity to changes in their surroundings. Having noticed a change, they started staying more frequently close to the location where it had taken place. The increase in the time spent in the manipulated zone did not translate into longer interaction with the manipulated object: WWCPS rats explored the immediate surroundings of the object, perhaps examining it from a safer distance.

To conclude, the present study suggests that wild rats tend to explore much more cautiously than laboratory rats (greater latency of exploration, less frequent object interaction) and are more sensitive to changes in their environment. The underlying cause of these differences is likely to be the higher level of stress in wild rats, resulting from threats in their natural habitat. Perhaps the differences in the behavior of WWCPS and Wistar rats observed in the study could be interpreted by reference to the general environmental conditions in which these animals live. The rate of changes suggests their epigenetic nature (Jensen, 2010). If this hypothesis is correct, studies on differences in exploration among animals at various degrees of domestication would be important for understanding behavioral plasticity in general.

References

Barnett, S.A. (1958). Experiments on "neophobia" in wild and laboratory rats. *British Journal of Psychology*, 49, 195-201.

Barnett, S.A. (2009). The Rat. *A study in behavior.* New Brunswick and London: Aldine Transaction.

Barnett, S.A., Dickson, R.G., & Hocking, W.E. (1979). Genotype and Environment in the Social Interactions of Wild and Domestic "Norway" Rats. *Aggressive Behavior*, 5(2), 105-119.

Barnett, S.A. & Hocking, W.E. (1981). Further experiments on the social interactions of domestic "Norway" rats. *Aggressive Behavior*, 7, 259-263.

Berlyne, D.E. (1960). *Conflict, arousal and curiosity.* New York: McGraw-Hill.

Berlyne, D.E., Koenig, I.D.V., & Hirota, T. (1966). Novelty, arousal, and the reinforcement of diversive exploration in the rat. *Journal of Comparative and Physiological Psychology*, 62, 222-226.

Birke, L. I. & Archer, J. (1983). Some issues and problems in the study of animal exploration. In J. Archer & L. I. Birke (Ed.), *Exploration in animals and humans* (pp. 1–21). Cambridge, Endland: Van Nostrand Reinhold.

Blanchard, R.J., Flannelly, K.J., & Blanchard, D.C. (1986). Defensive behaviors of laboratory and wild Rattus Norvegicus. *Journal of Comparative Psychology*, 100, 101-107.

Calhoun, J.B. (1963). *The Ecology and Sociology of the Norway Rat.* U.S. Department of Health, Education and Welfare, Bethesda, MD.

Castle, W.E. (1947). The domestication of the rat. *Genetics*, 33, 109-117.

Cavoy, A. & Delacour, J. (1993). Spatial but not object recognition is impaired by aging in rats. *Physiology & Behavior*, 53, 527-530.

Cowan, P.E. (1977). Neophobia and neophilia: New-object and new-place reactions of three Rattus species. *Journal of Comparative and Physiological Psychology*, 91, 63-71.

Grubbs, F. (1969). Procedures for Detecting Outlying Observations in Samples. *Technometrics*, 11, 1-21.

Hartmann, M.J., Johnson, N.J., Towal, R.B., & Assad, C. (2003). Mechanical characteristics of rat vibrissae: resonant frequencies and damping in isolated whiskers and in the awake behaving animal. *Journal of Neuroscience*, 23, 6510-6519.

Huck, U.W. & Price, E.O. (1975). Differential effects of environmental enrichment on the open-field behavior of wild and domestic Norway rats. *Journal of Comparative and Physiological Psychology*, 89, 892-898.

Jacobs, G.H., Fenwick, J.A., & Williams, G.A. (2001). Cone-based vision of rats for ultraviolet and visible lights. *Journal of Experimental Biology*, 204, 2439-2446.

Jensen, P. (2010). Domestication, selection, behavior and welfare

of animals—Genetic mechanisms for rapid responses. *Animal Welfare,*19, 7-9.

Keeler, C.E. (1947). Modification of brain and endocrine glands, as an explanation of altered behavior trends, in coat character mutant strains of the Norway rat. *Journal of the Tennessee Academy of Science,* 22, 202-209.

King, H.D. (1939). Life processes in gray Norway rats during fourteen years in captivity. *American Anatomical Memoirs*, 17, 1-72.

Kish, G.B. (1955). Learning when the onset of illumination is used as reinforcing stimulus. *Journal of Comparative and Physiological Psychology,* 48, 261-264.

Millar, R.D. (1975). Free-operant comparisons of wild and domestic Norway rats. *Journal of Comparative and Physiological Psychology*, 89, 913-922.

Mitchell, D. (1976). Experiments on neophobia in wild and laboratory rats: A reevaluation. *Journal of Comparative and Physiological Psychology*, 90, 190-197.

Ottoni, E.B. (2000). EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. *Behavior Research, Methods, Instruments & Computers,* 32, 446-449.

Pisula, W. (2003). Costs and benefits of curiosity: the adaptive value of exploratory behavior. *Polish Psychological Bulletin,* 34, 183-186.

Pisula, W. (2009). *Curiosity and information seeking in animal and human behavior.* Boca Raton, Florida, USA: BrownWalker Press.

Pisula, W. & Matysiak, J. (1998). Stimulus-Seeking Behavior. In G. Greenberg, M. M. Haraway (Ed.), *Comparative Psychology – A Handbook* (pp. 198-202). New York, London: Garland Publishing, Inc.

Pisula, W., Stryjek, R., & Nałecz-Tolak, A. (2006). Response to novelty of various types in laboratory rats. *Acta Neurobiologiae Experimentalis*, 66, 235-243.

Price, E.O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behavior Science*, 65, 245-271.

Prusky, G.T., Harker, K.T., Douglas, R.M., & Wishaw, I.Q. (2002). Variation in visual acuity within pigmented, and between pigmented and albino rat strains. *Behavioral Brain Research*, 136, 339-348.

Ray, J. & Hansen, S. (2004). Temperament in the rat: Sex differences and hormonal influences on harm avoidance and novelty seeking. *Behavioral Neuroscience,* 118(3), 488-497.

Shukitt-Hale, B., Casadesus, G., Cantuti-Castelvetri, I., & Joseph, J. A. (2001). Effect of age on object exploration, habituation, and response to spatial and nonspatial change. *Behavioral Neuroscience*, 115, 1059-1064.

Sokolov, E.N. (1990). The orienting response, and future directions of its development. *Integrative Physiological and Behavioral Science*, 25, 142-150.

Stryjek, R. (2008). Devices for handling small mammals in laboratory conditions. *Acta Neurobiologiae Experimentalis*, 68, 407-413.

Stryjek, R. (2010). Transportation device for rats. *Lab Animal*, 39 (9), 279-281.

Stryjek, R. & Pisula, W. (2008). Warsaw Wild Captive Pisula Stryjek rats (WWCPS) – establishing a breeding colony of Norway Rat in captivity. *Polish Psychological Bulletin*, 39, 67-70.

Szel, A. & Rohlich, P. (1992). Two cone types of rat retina detected by anti-visual pigment antibodies. *Experimental Eye Research,* 55, 47-52.

Tolman, E.C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55, 189-208.