ABC 2022, 10(4):287-303
Animal Behavior and Cognition
DOI: https://doi.org/10.26451/abc.10.04.01.2023

Animals in Search of Stimulation and Information: A Review of over 10 years of our Research on Spontaneous Exploration in Rats as a Response to Novelty in Low-Stress Paradigm

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Citation – Pisula, W., & Modlinska, K. (2023). Animals in search of stimulation and information: a review of over 10 years of our research on spontaneous exploration in rats as a response to novelty in low-stress paradigm. *Animal Behavior and Cognition, 10*(4), 287-303. https://doi.org/10.26451/abc.10.04.01.2023

Abstract – This article comprehensively reviews our studies that analyzed novelty-related behaviors in rats. We developed and utilized techniques and equipment during these studies to ensure our findings' high ecological validity. We allowed rats to explore a testing apparatus freely, and after a long habituation phase consisting of multiple trials, we introduced non-emotionally arousing changes. The research shows that rats demonstrate enhanced abilities in processing and responding to heightened environmental complexity, as evidenced across various studies. Conversely, when environmental complexity diminishes, rats exhibit reduced exploratory behaviors and decreased cognitive effort despite the adaptive importance of such behaviors. Of particular interest is the observation that rats exhibit greater sensitivity to emerging opportunities in contrast to their limited responsiveness to diminishing ones, unveiling a novel facet of the animal mind that warrants further investigation. The influence of individual experiences before testing sessions on the processing of sensory input in terms of complexity is also determined. Our studies highlight the noteworthy impact of environmental unpredictability versus stability on cognitive development, affecting behaviors like food neophobia and exploration. Furthermore, the social environment during development holds wide-ranging implications for individual characteristics, necessitating continued research and refinement of our understanding in this domain. Moreover, the studies recognize strain and species differences in novelty-related behavior, primarily characterized by quantitative variations that do not overshadow the animals' coping strategies in response to environmental changes. Additionally, curiosity is portrayed as an active approach to seeking and processing environmental affordances, with exploratory behaviors fulfilling this cognitive and motivational need. The authors underscore the significance of ecological validity in test methodologies, particularly in designing environments that authentically invite and encourage pertinent behavioral responses. In summary, this research enhances our insight into rat cognition, underscores the role of curiosity, and underscores the imperative of ecological validity in experimental design, ultimately advancing our comprehension of animal behavior and cognition.

Keywords – Curiosity, Exploration, Reaction to novelty, Rats, Environmental enrichment, Environmental complexity, Social play, Learning

The landscape of animal research in psychology has undergone a transformation, moving away from the traditional "animal model" approach towards a more contemporary system that emphasizes processes, rather than specific species (Maestripieri, 2005). Vonk (2021) succinctly captures this shift by advocating for comparative psychologists to focus on understanding behavior development, function, and mechanisms across all species within a biological context. While this perspective extends to humans, it does not imply that exact parallel processes exist between humans and animals. It is important to recognize that a rat cannot serve as a model for a cat or a human in the way that models of airplanes or ships are utilized in the engineer's lab. There is no direct projection from rat behavior to human activity and *vice* *versa*; they are fundamentally different creatures. Nonetheless, research involving rat subjects can yield valuable insights and information concerning behavioral processes that are of interest to comparative and general psychology if several criteria of the proposed model are met, as discussed by Sjoberg (2017). This approach serves as the fundamental framework for the research projects discussed in this paper.

A primary objective of our research program is to understand how organisms adapt to changes in their environment. Such changes, perceived as a novelty by individuals, play a crucial role in facilitating adaptation to new circumstances. This process operates at multiple levels. Intense or biologically significant stimuli, such as predator-like events, often elicit stereotypical species-specific defense responses (SSDR) like freezing, tail autotomy in lizards, burying, emitting putrid odors, or fleeing (Fanselow & De Oca, 1998). Reactions to low-intensity stimuli that are not immediately vital for survival are less overt but equally significant, as they constitute a major part of the behavioral repertoire across many species. Since reflexive responses do not apply to this category of stimuli, their processing involves higher-level organizational phenomena, including cognitive or pre-cognitive processes (Pisula, 2020).

One behavioral response to novelty is exploration, which involves actively seeking information about the environment. It enables individuals to prepare for the future by avoiding predators, adverse weather conditions or ensuring food availability (Birke & Archer, 1983). Exploration encompasses various behavioral phenomena, including responses to novelty, risk assessment, arousal, locomotor activity, habituation, and memory. Furthermore, a novel stimulus, even without intrinsic rewards or biological benefits, can act as a positive reinforcer due to its potent motivational properties (Olsen 2011). The inherent interest in novelty displayed by organisms, a central component of exploratory behavior, is considered an evolutionary prerequisite for complex learning and guides organisms in acquiring adaptive behavioral repertoires (Farahbakhsh & Siciliano, 2021).

In our research, we have developed a protocol and specialized experimental apparatus designed to assess the phenomenon of free exploration in small laboratory mammals, including rats, mice, and opossums (Pisula & Modlinska, 2020). The apparatus is a purpose-built chamber with a volume of approx. 0.4 m^3 divided into three zones (Figure 1). The Central zone is empty and comprises the entrance to the apparatus. Two side zones serve as testing spaces. The changes associated with novelty take place in one of these two zones. Each testing chamber enables horizontal and vertical exploration, allowing animals to navigate the test arena freely and, if needed, seek refuge in a secure space (transporter).

Wooden tunnels are incorporated into the apparatus as objects for the animals to explore. It is only after the animals have become familiar with the experimental setup that novelty is introduced (Figure 2). Depending on the experimental configuration, this novelty can involve several changes to the familiar environment (Figure 2). In contrast to commonly used two-dimensional experimental setups, tunnels offer a complex three-dimensional environment. Our protocol examines small mammals' exploration of a new environment, habituation rates to it, and responses to innocuous and low-intensity novelty. We assess this by measuring the duration and frequencies of behaviors related to the objects in the test environment as well as the allocation of the behaviors in the apparatus.

Figure 1

Detailed Scheme of the Test Arena (A) and an Infrared Photo of the Test Arena (B)

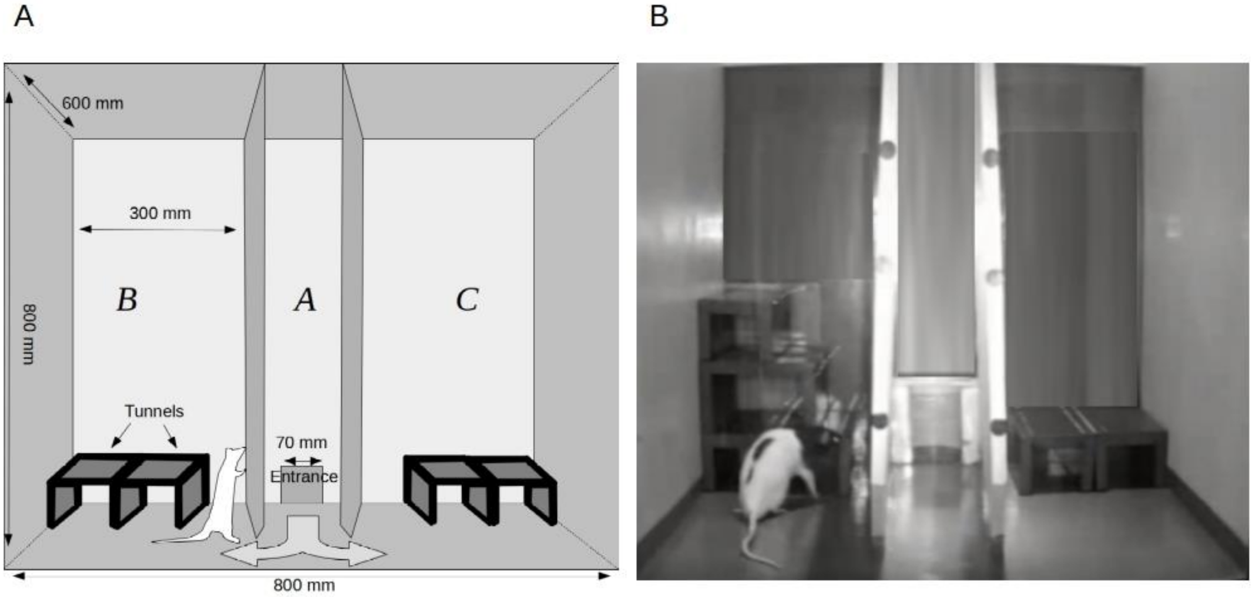
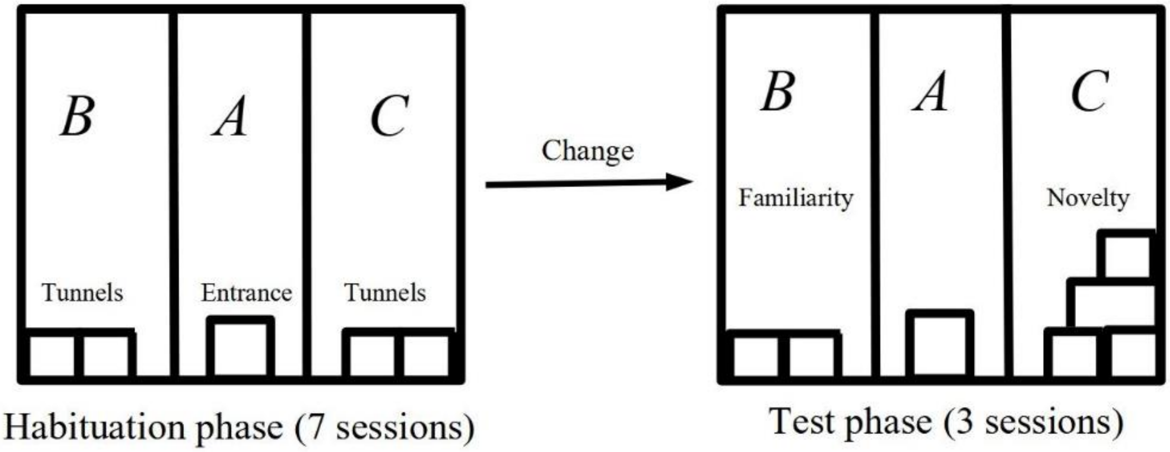


Figure 2

General Scheme of our Research Methodology and Testing Environment



Note. Animals are provided a several-trial-long habituation phase when they become familiar with the testing environment. Subsequently, at the beginning of the test phase, a change (novelty) is introduced to one of the apparatus chambers. The change may involve the addition of a novel object(s), an object with changed properties, a novel environmental condition (e.g., light), or the removal of a familiar object. The test phase lasts three sessions.

By investigating exploratory behavior, we aim to identify changes in overall behavioral characteristics. Our studies utilize the "free exploration" test (Pisula & Modlinska, 2020), which prioritizes maintaining a low-stress level in the studied animals, comprehensively analyzing how animals adapt to environmental changes. To ensure the high ecological validity in our analyses, we prioritize providing animals with low-stress conditions throughout the experiment. This is achieved by ensuring that rats can initiate exploration at any time and move freely around the apparatus, as well as by implementing a lengthy habituation phase before introducing low-intensity novelty. This approach also yields data for studying temporal behavioral dynamics. Unlike many other behavioral tests focusing on a single behavioral parameter, the free exploration test is grounded in the belief that rodents only demonstrate their complete behavioral repertoire in a rich testing environment (Lundberg et al., 2019).

Given the diverse forms of exploration, the approach aligns well with the theory of integrative levels (Pisula, 1998). According to this theory, the forms of exploratory behavior can be approached as successive levels of the qualitative evolution of behavior. The framework includes three levels of analysis: the level of behavior, the level of mechanisms, and the level of function. The level of behavior refers to the observable characteristics of exploratory behavior, while the level of mechanisms refers to the underlying physiological and neural processes that enable exploratory behavior. The level of function refers to the adaptive significance of exploratory behavior. The framework emphasizes the importance of considering multiple levels of analysis when studying behavior rather than focusing on a single level. This approach to exploratory behavior is a holistic one that considers the different levels of analysis, allowing for a more comprehensive understanding of the behavior. The integrative levels approach also allows the incorporation of various forms of interrelated exploratory behaviors into one hierarchically organized system, allowing one to grasp the key and common elements of distinct forms of exploration (Pisula, 1998, 2020). From this perspective, studying exploratory behavior enables the detection of behavioral changes occurring at higher levels of integration rather than being limited to measuring behaviors or their components at a lower level of organization.

This paper utilizes a broad understanding of novelty, defined as a change in stimulus conditions from prior experiences (Berns et al., 1997). This approach is based on the notion that the novelty effect only manifests when the organism can learn and compare previous and incoming experiences (Pisula, 2007; Staddon, 2016). Here, we provide a comprehensive review of our studies that have embraced this general approach to investigating novelty-related behavior in rats.

Environmental Complexity

Increased Complexity

Animals prefer complex environments compared to simplified or impoverished ones (Nissen, 1931; Pisula et al., 1992; Sackett, 1967). This preference is particularly evident when modifications to the environment increase its complexity. Increased environmental complexity evokes behavior changes linked to various changes in the brain (e.g., Benaroya-Milshtein et al., 2004; Hebb, 1946; Kolb & Whishaw, 1998; Lewis, 2004). Among other changes, environmental complexity increases novelty-seeking behavior (Fernandez-Teruel et al., 1997) and object exploration (Widman & Rosellini, 1990) while reducing anxiety-like behavior and increasing activity (Anderson et al., 2021; Bach et al., 2019). Our research indicates that laboratory rats show a positive response to novel objects that are more complex compared to the objects that they were familiarized before the introduction of novelty, especially under low-stress or non-stressful conditions (Pisula, 2003; Pisula & Siegel, 2005; Pisula et al., 2006; 2012; Tanas & Pisula, 2011). This positive response is characterized by increased exploration of the novel object and spending more time in the area where the change was made. For example, in a study with Lister Hooded rats (Pisula et al., 2019), we manipulated the tunnels in the experimental chamber to regulate environmental complexity. Introducing new tunnels resulted in a significant behavioral change, as evidenced by the rats spending more time near the novel objects, sniffing, touching, and climbing on the tunnels. These findings were further supported by a subsequent study (Pisula et al., 2022), where increased environmental complexity through adding objects stimulated more vigorous exploratory behavior in rats.

It is important to note, however, that not all modifications increasing environmental complexity positively impact exploratory behavior. When spatial complexity is combined with the moveability of novel objects (an object that can be moved/manipulated by the study subject), it seems to elicit increased caution toward the novelty after an initial inspection of the altered objects (Pisula et al., 2022). This suggests that the complexity of the novelty can evoke both attraction and aversion, depending on the predictability of the novel environment. Moreover, illumination appears to mediate responses, such that higher illumination of novel objects reduces level of object exploration (Pisula et al., 2022). Pisula et al. (2022) found that rats exhibited a response characterized by an extended stay in the area containing modified (illuminated) tunnels but without close contact to them. This effect is likely specific to nocturnal animals such as rats. Nevertheless, these findings demonstrate that certain environmental modifications can create a conflict between approaching and withdrawing, diminishing the attractiveness of a complex environment. Afterall, increased spatial complexity stimulates exploratory activity in a manner likely perceived as an incentivizing offer or reward. One may propose that spatial complexity correlates strongly with the practical opportunities to spot novel food sources or shelters (cf. Balcombe, 2006). Therefore, the perceptual systems' high sensitivity to environmental stimulation, such as light, seems to be adaptive.

Decreased Complexity

Understanding how animals respond to novelty resulting from changes in the stimulus field requires examining the interplay between the positive response to novelty and the shift in their preference for complex environments. To address this issue, we conducted experiments comparing rats' reactions to standard novelty (introduction of novel objects) and novelty induced by removing objects present during the habituation phase. Previous research by Pisula and Siegel (2005) demonstrated that the addition and removal of tunnels had similar effects on rat behavior. However, our more recent study (Pisula et al., 2019) found that removing the tunnels had less influence on rats’ behavior than adding tunnels. Discrepancies in findings may be attributed to differences in measurement techniques and behavioral coding. The only noticeable effect of the object removal procedure was an increased time spent in the transporter during the last test trial. This may indicate a gradual decrease in the attractiveness of the altered zone, leading rats to allocate more time to the comfortable and safe space provided by the transporter.

These findings underscore the importance of considering both the specific changes implemented and the level of complexity when manipulating environmental enrichment. Changes that result in environmental impoverishment should be recognized as distinctly different from environmental enrichment. They seem not to be the poles of the same dimension. The differential response to novelty arising from introducing or removing objects/qualities may also have implications for evolutionary and clinical human psychology (e.g., Burghardt, 2013; Woo et al., 2015). It may suggest that the evolution of cognitive processes was driven predominantly by the pressure of seeking novel opportunities rather than preserving knowledge about the existing ones (Gibson, 1988). Although the statement mentioned above does not exceed a speculative hypothesis's status, it seems attractive enough to provoke research on other species. This view fits well in modern analyses of the relationship between environmental complexity and cognitive evolution (Mikhalevich et al., 2017). However, further studies are needed to confirm the impact of this effect.

Environmental Enrichment - Increased Complexity in the Living Environment

In laboratory settings, researchers create a stimulating and complex environment by adding various objects (such as wooden blocks, spinning wheels, houses, and variable bedding) and increasing opportunities for social contact (Bloomsmith et al., 1991; Newberry, 1995). Studies have shown consistently that animals housed in enriched conditions exhibit higher levels of exploratory activity and lower anxiety (Gardner et al., 1975; Genaro & Schmidek, 2001; Pietropaolo et al., 2004; Thoré et al., 2020; Tatemoto et al., 2021). The increased complexity of the environment is associated with greater novelty-seeking behavior (Fernandez-Teruel et al., 1997) and object exploration (Widman & Rosellini, 1990). Furthermore, environmental enrichment has a significant impact on the nervous system of both young and mature animals (Frick & Fernandez, 2003; Kempermann, 2019), may contribute to the reversal of cognitive and emotional impairments (Dahlqvist et al., 2004; Forbes et al., 2020; Francis et al., 2002; Jankowsky et al., 2005), and positively affects animal welfare in captivity (Abou-Ismail et al., 2010).

To examine the influence of environmental complexity on animal behavior, Modlinska et al. (2019) conducted a study in which rats were housed in three different conditions before a behavioral test. One group of rats lived in a spacious enclosure with numerous enriching objects, another group lived in an identical enclosure where the objects were regularly rearranged, and the control group was kept in standard laboratory conditions (standard laboratory cages with basic enriching objects, e.g., wooden blocks and nest materials). The results showed that during the initial phase of the experiment, rats from the control group exhibited higher levels of exploratory behavior in zones containing objects. They spent more time exploring the objects and less time in other areas of the experimental setup. It suggests that the control group, housed in relatively unstimulating conditions, had a greater need for interaction with the novel environment (Fernandez-Teruel et al., 1997; Tanas et al., 2015). However, during the final habituation phase, activity levels became similar across all groups, indicating a comparable level of habituation to the experimental environment.

When new objects were introduced to one of the zones in our test apparatus (Figure 1), all groups showed a significant increase in exploration focused on novelty. However, it was observed that the control group spent the least amount of time in the modified zone and explored the new objects to a lesser extent (Modlinska et al., 2019). Nonetheless, they maintained a high level of exploration in subsequent test trials. In contrast, rats from the enriched environment quickly habituated to the change, resulting in a decreased level of exploration toward the new objects in subsequent trials. These findings suggest that environmental experiences significantly influence the development of regulatory mechanisms (as discussed by Moore, 2004) associated with habituation, as slower habituation to change within a familiar environment indicates a slower process of behavioral adaptation. These results are consistent with previous studies (Schrijver et al., 2002; Zimmermann et al., 2001) and support the idea that learning plays a crucial role in the mechanisms underlying adaptation to a changing environment. With this respect, we utilize a widely accepted learning definition proposed by Domjan (2015): "Learning is an enduring change in the mechanisms of behavior involving specific stimuli and/or responses that results from prior experience with those or similar stimuli and responses" (p. 14).

One may also put forward the notion of the relative value of the complexity of the sensory input. The individual's experience plays a modifying and mediating role when processing the actual sensory input in terms of complexity level (see Varga (2017) for an extensive conceptual discussion of the issue in question). This again brings us to the crucial role of acquiring experience (learning) in forming behavior regulatory mechanisms, also from a cross-domain perspective (Vonk et al., 2021). Learning itself, however, cannot be limited to the associative processes, as pointed out by Timberlake (1997): "...there seems little question that the complex learning abilities of animals exceed what would be expected from an extreme behaviorist approach" (p. 112). The role of experience may be observed and analyzed at various levels, beginning from the neural one (Kolb, 2018), but not limited to it. The particular mechanisms underlying the experience effects may be however distinct, as pointed out by van Duijn et al. (2006).

Environmental Changeability and Controllability

Contrary to controlled laboratory settings, wild animals reside in environments characterized by diverse levels of changeability and encounter a wider range of environmental stimuli. However, limited research has examined the role of environmental variability in animal behavior. The organism's exposure to environmental variability can influence its expectations toward the environment and ability to anticipate and regulate environmental changes (Fox et al., 1999). Given that the motivation to control environmental events is a crucial aspect of behavioral regulation, the generalized experience of unpredictability versus stability can significantly impact the organism's cognitive development (Bassett & Buchanan-Smith, 2007; Chorpita & Barlow, 1998; Cramer et al., 1997; Soames Job, 2002). The reaction to an increased influx of stimulation may involve habituation to emerging novelty, reducing the intensity of the emotional response to change. Conversely, the unpredictability of environmental changes and the lack of control can trigger a stress response (LaDage, 2015). Individuals with high reactivity may experience a decline in their capacity to adapt to environmental challenges (Carere & Locurto, 2011).

The changeability of the living environment also affects the development of animal expectations regarding the predictability and controllability of their surroundings based on their previous experiences (Zentall, 2002), which can influence animal behavior. However, the results of our studies (Modlinska et al., 2019, 2020) indicate no significant differences in the behavior of rats exposed in their living environment before the experiment to stable or changeable conditions. Thus, in a setting characterized by long-lasting environmental complexity, the changeability of the environment does not play a significant role, at least concerning the exploration, general activity, and the rate of habituation to novelty.

The impact of environmental variability on animal behavior may be observed in the context of food-related behavior, particularly food neophobia. Food neophobia (caution when encountering unfamiliar food, Barnett, 1958, 2009; Pliner & Hobden, 1992) is present in many species (for example, see Addessi et al., 2004; Barnett, 1958; Jones, 1987; Launchbaugh et al., 1997; Pliner & Hobden, 1992). It occurs mainly in omnivores, which need to distinguish between novel edible food and inedible novel food (generalist's dilemma: Rozin, 2000). Food neophobia manifests in initially avoiding novel food, followed by progressive food sampling (Barnett, 2009). If the new food does not evoke adverse bodily symptoms, its intake increases (Barnett, 2009; Mitchell, 1976). Contact with novel food elicits caution and an exploratory reaction toward the unfamiliar object (Hebb, 1946; Modlinska & Stryjek, 2016; Modlinska et al., 2015). However, it is hypothesized that rats inhabiting highly variable environments, such as landfills, often exhibit lower general neophobia and a relative absence of food neophobia (Barnett, 2005; Boice, 1971). It can be speculated that residing in an environment rich in stimuli and subjected to frequent changes lowers an animal's neophobia threshold, enabling it to consume foods with unknown properties. It might be proposed that building a more diverse representation of the environment creates a lower likelihood of producing a dissonance effect as an outcome of comparing the previous experience to a present input.

In a field study conducted on a neglected farm inhabited by a colony of wild rats, we discovered that even in such a changeable environment, a specific reaction to novel food could be observed (Modlinska & Stryjek, 2016). Introducing new food elicited a neophobic reaction, such as an increase in exploratory behavior; however, typical manifestations of food neophobia, such as sampling novel foods before eating or lower consumption rates, were not observed. This finding may be attributed to the highly complex and variable environment, coupled with interspecific competition for resources, leading the animals to exploit various food sources and attenuating their neophobic response towards novel foods. In a later experimental study examining the impact of environmental manipulations of varied complexity (Modlinska et al., 2019), we assessed the influence of living environment variability on subsequent exploratory behavior. Specific differences were observed in the level of exploratory behavior in rats housed in two enriched configurations (stable and changeable) before the experiment. Rats from the changeable living environment showed no significant changes in time spent exploring objects in the unchanged zones of the test arena. In rats from the stable environment, there was a notable decrease in the exploration of objects in the unchanged zone following the introduction of novelty in the second zone. However, this did not result in an increased amount of time devoted to exploring new objects, and the effect size of this increase was comparable in both groups.

The absence of specific differences between rats from stable and changeable environments suggests that complex but stable conditions, despite their lack of variability, were sufficiently stimulating for rats to independently manipulate the complexity and diversity of their environment, thus regulating the level of stimulation they received. The lack of differences in the level of exploratory behavior between animals from stable and changeable environments may also be attributed to the rapid extinction of the novelty value under constant change. Constant changes unrelated to reward or punishment make the animal habituate and lead to a decrease in the body's sensitivity to novelty stimulation (De Paepe et al., 2019). Even if we assume that constant change serves as intrinsic reinforcement leading to increased exploration, intrinsically reinforced unlearned behaviors such as curiosity can become habituated to constantly emerging novelty (Dissegna et al., 2021; Ueda et al., 2021). This assumption is supported by the fact that the animals lived in a complex environment for an extended period, where changes (such as frequent spatial rearrangement of familiarized objects), although frequent, were of similar intensity and nature (i.e., no introduction of new objects). Therefore, in an environment characterized by high complexity, the variability of the environment does not play a significant role, at least in terms of the reaction to novelty, level of exploratory behavior, general activity, and adaptation to changes encountered in the familiarized environment.

The ability to generate stimuli through individual activity seems to be a key feature of the environment (Helmchen et al., 2006; Videan et al., 2005). However, despite its intuitive significance, this aspect has yet to be systematically examined. The issue is highly relevant in the broader context of studying developmental mechanisms, as the ability to manipulate the environment allows animals to regulate the level of incoming environmental stimulation (Oudeyer & Smith, 2016). Furthermore, an individual's locomotor activity in the home environment is a significant source of environmental variability for other individuals. This aspect of the environment may play a crucial role in understanding the effect of enrichment on behavior.

Controllability refers to an animal's capacity to modify elements within its surroundings, such as moving or manipulating objects (Videan et al., 2005). When given a choice, captive animals tend to prefer objects that can be manipulated over unmovable ones (Markowitz & Line, 1989). Control over the environment can mitigate physiological stress responses (Hulme & Kvitsiani, 2019; Kearton et al., 2020). In fact, some researchers (Sambrook & Buchanan-Smith, 1997) suggest that the controllability of the environment is more crucial than complexity when it comes to providing environmental enrichment for captive animals. In the natural habitats of many wild species, changes, unpredictability, and consequent uncertainty are common. Therefore, controllability enables animals to cope with the challenges posed by an environment of low predictability, as their own actions can reduce the uncertainty of environmental events (cf. Inglis, 2000).

We conducted a study involving rats to investigate the hypothesis regarding the positive influence of controllable elements in the environment on animal behavior (Chrzanowska et al., 2022). After a habituation period, we introduced modified objects to the rats. One group received the same object as during the habituation phase, but one of the objects could be manipulated by the rats, functioning like a see-saw. The next group also received the movable object, which was placed on top of additional objects. The last group experienced novelty by introducing similar objects, but these objects remained stationary. We observed that while increased complexity led to greater novelty exploration, the object's movability resulted in increased caution following the initial inspection of the changed objects. Interestingly, the movable object, resembling the one used in the habituation phase, did not promote exploratory behavior when presented alone, suggesting that the complexity of the novelty can induce both neophilia and neophobia depending on the predictability of the new environment. Additionally, the movability of newly introduced objects appeared to be interconnected with other environmental properties, such as complexity and novelty, indicating its dependence on multiple parameters.

In conclusion, the experience of unpredictability versus stability can profoundly impact an organism's overall cognitive development and motivation to exert control over environmental events. While unpredictability and lack of control can elicit a stress response, habituation to emerging novelty can reduce the emotional response to change. The changeability of the living environment can also influence an animal's expectations regarding the predictability and controllability of its surroundings (Koolhaas et al., 2019). The effects of this influence can be observed in various aspects of behavior, such as food neophobia. Our research indicates that in complex environments, the variability of the environment may not play a significant role, as animals can independently manipulate the complexity and diversity of their surroundings. However, controllability, the ability to modify elements within the environment, appears to be a crucial factor in mitigating stress responses and providing environmental enrichment for captive animals (Koolhaas et al., 2019; Videan et al., 2005). Further research is needed to explore the specific mechanisms underlying the impact of environmental variability and controllability on animal behavior and cognitive development. The classic concept of sensory reinforcement may serve as a useful theoretical tool when tackling the cognitive processing of the environment’s controllability.

Exploration and Social Play – Complexity and Controllability of the Social Environment

Given the importance of physical and social environments in shaping an individual's growth, it is reasonable to expect that alterations in the social structure experienced during early development will have long-term effects on adult functioning. Social deprivation during the initial development period, particularly the lack of contact with the mother, can lead to disruptions in emotional, social, and cognitive performance later in life (Levy et al., 2003; Pellis et al., 2019; Pryce & Feldon, 2003). On the other hand, some studies suggest that social deprivation can lead to increased exploratory behaviors under certain conditions, which may be attributed to an increased need for environmental stimulation (Whittier & Littman, 1965). However, these studies primarily focus on complete social deprivation and do not consider scenarios where individuals are isolated from their mothers while maintaining contact with peers or isolated from peers while maintaining contact with their mothers (i.e., only partial social stimulation diverted from the typical social environment). Contact with peers provides animals with the opportunity to engage in social play, particularly play fighting, which, in rats, involves reciprocal attacks and defenses targeting the nape of the neck (Ham & Pellis, 2023; Pellis & Pellis, 2017). Engaging in social play requires animals to monitor their own actions and those of their playmates. While contact with the mother only during development ensures social stimulation, it typically deprives the young rats of the necessary level of social play.

The role of contact with the mother and siblings in the pre-adolescent period on rat cognitive development was analyzed in a study by Modlinska et al. (2018). Rats were assigned to one of three different social conditions at 14 days of age: a single pup housed with its mother, juveniles housed with peers but without maternal contact, and standard breeding conditions (i.e., the mother with her litter). When the animals reached adulthood, their cognitive development was assessed using a T-maze test to measure their response to a new environment, their level of exploratory behavior, and their learning efficiency. The results revealed that both socially impoverished groups exhibited lower levels of exploratory behavior and higher levels of anxiety compared to the control group in which pups were raised by their mother and in the presence of littermates. Furthermore, differences were observed between the groups in terms of the frequency and attempts to drink from water bottles, indicating differences in in the ability to decrease the uncertainty toward environmental information. Rats from the control group showed higher confidence in the information obtained and a higher level of adaptive effectiveness in an uncertain environment, as evidenced by their revisiting of previously checked places. In contrast, rats from the socially deprived groups displayed reduced interest in an empty bottle and longer periods of inactivity, suggesting higher emotional arousal and minimal effort spent on water intake. These findings highlight the significant impact of developmental experiences and social contacts, including both mother and peer interactions, on coping strategies and the ability to deal with environmental complexity. They also highlight the characteristics shared across mammalian linkage since similar effects are described in a much higher organized species (Bales, 2017; Harlow et al., 1965; Matsuzawa, 2021).

The observed variations in behavior under low-stress experimental conditions indicate that the developmental effects arising from the specific social environment can have broader implications for an individual's characteristics. These effects extend beyond social behavior alone and are evident in the specific interactions exhibited with the environment. However, a more comprehensive understanding of the specific impacts of the social environment related to the play behaviors involving the mother and the peer group requires further research and revision at the present stage.

Species and Strain Characteristics in Reaction to the Increased Complexity of the Environment

The individual's ability to benefit from environmental experience is likely dependent on emotional characteristics (e.g., Steimer & Driscoll, 2003). These characteristics may increase or reduce the probability of an individual getting the environmental stimulation by triggering withdrawal *versus* approach activity in confrontation with the actual environment. One of the avenues to address this issue is the selection of a rat line differing in emotional characteristics, such as Roman High Avoidance (RHA) and Roman Low Avoidance (RLA) rats (Steimer & Driscoll, 2003). RHA rats are described as low emotionally reactive and RLA rats as highly reactive. Results of the study on exploratory behavior between these two rat lines show that the RHA subjects show a more pronounced response to novelty, as evidenced by a significant shift toward the changed zone of the testing apparatus (Pisula, 2003). In this study (Pisula, 2003), the active exploration of RHA rats in response to novelty corresponded with the behavior pattern described in an earlier study (Pisula & Osiński, 2000) and with an active coping style in these rats (Steimer et al., 1997). In a study on general exploration in a novel environment between these two rat lines, Pisula and Osiński (2000) showed differences in sniffing (RHA scoring higher) and in immobility (RLA scoring higher), both persisting throughout all measurement periods. Males of both sublines were generally more active and exploratory than their respective females. Sequential data analysis of the rats' behavior revealed that during the first 5 min, RHA rats showed a less diverse but more exploratory repertoire as compared to RLA rats, while during the first 15 min, males of both sublines showed more behavioral sequences than females. This indicates that the Roman rat sub-lines could provide a valuable model to study the mechanisms of exploratory behavior.

Differences in reaction to increased complexity of the environment and resultant exploratory behavior are also observed between wild and laboratory rats. Domestication rarely significantly modifies an animal's behavioral repertoire and rarely leads to a complete disappearance of behavior typical of its wild cousins (Himmler et al., 2014; Modlinska et al., 2015; Modlinska & Pisula, 2020; Price, 1999; Stryjek et al., 2012a). Moreover, most domestication changes manifest themselves in a reduced frequency of certain behaviors, or an increase in the threshold at which a stimulus elicits a given response. However, there are differences between wild and laboratory animals in their reaction to novelty. In a comparative study on laboratory grey short-tailed opossums (*Monodelphis domestica*), wild-type Warsaw Wild Captive Pisula Stryjek rats (WWCPS; non-domesticated line of 1-3rd generation of rats born in captivity), and laboratory rats (Wistar) differences in behavior related to a novel object in a familiarized environment were found (Pisula et al., 2012). In the new environment, the sequence of neophobic behavior, investigation, and habituation was shortest in the opossum, longer in the laboratory rat, and longest in the WWCPS rat. The grey short-tailed opossums demonstrated the least delayed and most intense exploration of the new environment. When confronted with novel objects, both opossums and laboratory rats extended the time in proximity to the new object, whereas the WWCPS rat did not respond similarly. Additionally, both opossums and laboratory rats increased their interactions with the new object compared to the habituation phase, while WWCPS rats reduced such interactions. These behavioral patterns were arranged in distinct clusters for each species and rat line. The results also indicated a higher level of anxiety in both rat lines compared to opossums.

The observed behavioral differences between species and rat lines can be attributed to different ecological adaptations in rats and opossums and the impact of domestication on laboratory rats (Pisula et al., 2012). Another study comparing wild and laboratory under a similar protocol showed that wild rats responded to novelty by orienting their behavior toward the source of change, followed by rapid habituation of that response (Pisula et al., 2015). Laboratory rats responded similarly to wild rats immediately after the change, but their increased activity in that section of the test apparatus was not subjected to habituation. We propose that information-seeking is more important in regulating the behavior of wild rats not adjusted to the laboratory conditions than fully domesticated animals, while for domesticated rats it is stimulus-seeking (see Pisula & Matysiak, 1998) that dominates behavior regulation. Conversely, in another experiment involving wild and laboratory rats, Tanaś and Pisula (2011) showed comparable levels of experimental cage exploration and positive exploratory reactions to the novel object in both rat lines. However, the study employed a different protocol with a habituation phase in an empty experimental chamber and objects introduced only in the test trials. The lack of preexisting familiarization with the objects in the same category as the objects offered during the test phase may constitute a significant ecological difference in the rat's cognitive capacity to process environmental changes.

Ecological Validity and Affordances that Invite Behavior

The data gathered throughout our studies on exploration provide evidence for the existence of two primary components in rat curiosity: activational and informational dimensions (Gibson, 1979/2014). The activational aspects of curiosity in rats can be attributed to arousal processes associated with novelty, while cognitive processes are triggered over longer intervals in response to more intricate stimuli. In the framework of ecological psychology, which considers the relationship between organisms and their environment, it can be inferred that as the perceptual field becomes more complex or offers more affordances. The term "affordance" was described by Gibson (1979/2014) as a noun derived from the verb "to afford," indicating that the environment offers opportunities for an animal to engage in actions or behaviors. Consequently, affordances can be defined as emergent properties of an animal's environment that influence its behavior and present opportunities for action (Heft, 2018; Stoffregen, 2018; Turvey, 1992). The abilities of an organism to exploit the affordances presented by the environment and the affordances themselves are interconnected. This perspective seems promising also for primate behavior students (Koops et al., 2014). Consequently, it is plausible to hypothesize that cognitive and motivational mechanisms, such as curiosity, evolve through close interaction with the environment, which presents specific new opportunities and excludes others.

It appears that our studies have underscored a phenomenon known as "perceived affordance" (Norman, 1998) by the animal's perceptual and learning systems. The affordance itself is not an independent variable; the animal must be capable of recognizing it and processing its qualitative and quantitative properties.

Conclusions

Our studies with rats lead us to the following concluding remarks:

1. The cognitive system of rats seems to process increased environmental complexity intensely and effectively (Pisula, 2003; Pisula & Siegel, 2005; Pisula et al., 2006; 2012, 2019, 2022; Tanas & Pisula, 2011). On the other hand, reducing complexity in the environment triggers fewer exploratory behaviors and requires less cognitive effort, although the adaptive significance seems comparable to the former case since the knowledge about the closing option is equally important to the opening one (Pisula et al., 2019). The higher cognitive sensitivity of rats to emerging new affordances compared to their low sensitivity to disappearing affordances seems to be an interesting cognitive phenomenon revealing some new element of the structure of the animal mind. This phenomenon deserves further study.
2. The individual's prior experience before the testing session plays a role in modifying and mediating the processing of the actual sensory input in terms of complexity level (Modlinska et al., 2019).
3. The generalized experience of unpredictability versus stability profoundly impacts animal cognitive development, which can be observed in various behavioral aspects, such as food neophobia and exploration (Chrzanowska et al., 2022; Modlinska & Stryjek, 2016; Modlinska et al., 2019, 2020).
4. The developmental effects resulting from the specific social environment can have broad implications for an individual's characteristics, extending beyond social behavior and manifesting in specific interactions with the environment (Modlinska et al., 2018). However, further research and revision are needed to understand the impact of the social environment created by the mother and the peer group at this stage.
5. Strain and species differences in novelty-related behavior are evident (Pisula, 2003; Pisula & Osiński, 2000; Pisula et al., 2012, 2015). However, they primarily manifest as quantitative variations and do not overshadow an animal’s coping patterns with environmental changes.

In the context of our research findings, curiosity can be understood as an active approach to seeking and processing environmental affordances. Exploratory behaviors serve as a behavioral tool to satisfy this cognitive and motivational component. In light of this, we can consider what it means to establish an ecologically valid test situation. Placing the concept of ecological validity within the context of the animal's cognitive system is essential. Curiosity undoubtedly falls within the realm of cognitive mechanisms. Thus, ecologically valid tests should be relevant to the regulation of exploratory behaviors, as they directly relate to the desire for information or curiosity. At the beginning of our paper, we outlined the fundamental characteristics of our test methodology, which include free exploration (no forced activity) and low-stress conditions (involving a long habituation period), which results in no restrictions on the expression of spontaneous behavior. As we previously proposed (Pisula & Modlinska, 2020), these characteristics were designed to ensure the ecological validity of the test arena. However, the results from our subsequent works have led us to add an element to the ecological validity description: the test arena should invite/provoke/elicit/encourage relevant behavioral acts. This additional characteristic relates to the more recent concept of affordance: an affordance that invites behavior (Stoffregen, 2018).

During the course of running our studies, we have developed a measuring protocol allowing for spontaneous exploration and securing high ecological validity. In our mind, an ecologically valid test should encourage our animal subjects to exhibit ecologically relevant (adaptive) behavior in response to the test stimuli. In our laboratory settings, the tunnels emerged as the most valid element of the test environment. They genuinely invite rats to enter and explore based on their tactile (touch and vibrissae input) perception. Naturally, each test arena should be analyzed independently in terms of these considerations. However, researchers in animal cognition should always question the ecological validity of a test in relation to the behavior being investigated, especially concerning the test characteristics that invite the behavior in question. The reason for this is because comparative psychologists often deal with phenomena that are not context-free, as shown by (Uithol et al., 2014). The valuable guidelines are provided by the classic concept of "umwelt" as described by Bueno-Guerra (2018, p. 3). The goal also remains classic: "help researchers (and reviewers) not to forget any species' particularity that may mediate their design as well as it would enhance the strength of their conclusions" (Bueno-Guerra, 2018, p. 3). We believe our studies constitute a small step in the right direction.

Conflicts of interest: The authors declare no conflict of interest.

Author Contributions:
Wojciech Pisula: Conceptualisation, Formal analysis, Validation, Visualization, Writing original draft, Writing – review & editing; Klaudia Modlinska: Conceptualisation, Formal analysis, Writing original draft, Writing – review & editing.

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