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Opinion

The curious interpretation of novel object recognition tests

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Novel object recognition tasks are commonly used to assess memory in rodents. These tests rely on an innate preference for exploring objects that are new or have been moved or changed. However, this preference, while normally seen in control conditions, is not immutable. Stressful experiences as well as lesions and genetic mutations can lead mice and rats to show clear preferences for exploring familiar objects and familiar locations. This opinion article discusses the evidence for changes in novelty preference, implications of this lability for assessing memory, and the significance of shifts in novelty preference as a readout of changes in curiosity with implications in approach–avoidance behavior and explore–exploit decision-making. Finally, we provide some recommendations for reporting and interpreting novelty preference task findings moving forward.

Highlights

Tasks involving exploration of novel and familiar objects, or objects in novel and familiar locations, are widely used to assess memory in rodents.

A critical underlying assumption of these object tasks is that animals always prefer novelty, such that failure to preferentially explore a novel item reflects impaired memory.

Emerging evidence suggests that animals exhibit significant preferences for familiar objects and places after stress exposure/experience, indicating that novelty preference is labile.

Novelty preference is an expression of curiosity, which plays important roles in approach–avoidance behaviors and explore–exploit decision-making.

We propose that changes in novelty preference be explicitly considered as alternatives to memory impairment in novel object exploration tests.

Novel object recognition tests

Understanding the neural basis of memory requires reliable tests. In humans, memory can be described through written or spoken words and, importantly, can be elicited with direct verbal requests to describe or indicate what is remembered. In other species, researchers must rely on carefully designed, often highly complicated behavioral tasks to study the neurobiological processes involved in encoding, storing, and recalling memories. Each task employs particular stimulus modalities, behavioral measures for assessing recall, and motivations for demonstrating the tested behavior. For example, a touchscreen delayed match (or nonmatch) to sample task, commonly used for memory testing in nonhuman primates and increasingly in rodents [1,2], involves viewing 2D images on a screen, touching a cue on the screen, and receiving food rewards for correct choices. These tasks are very flexible and can be run in numerous trials per day over long periods of time. However, they require food and/or water restriction as well as extensive training to learn the rules of the task, requiring days to weeks of experimental time prior to actual memory testing. Rodent tests of hippocampus-dependent memory frequently focus on spatial memory and use aversive motivation to elicit behavior, as in the Morris water maze and contextual fear conditioning tests [3]. The training for these tests is relatively short, but the tasks themselves involve stress, which can interact with memory processes [4]. It is not surprising, therefore, that novel object recognition tasks, which are minimally stressful and rely on natural behaviors requiring no pretraining, are growing in popularity as behavior tests, with over 5000 published studies to date.

The novel object recognition task was developed as a memory test for rats in the 1980s [5]. In this task, animals are placed in an arena with two identical 3D objects and given time to explore the objects. After a delay, the animals are tested by placing them back in the arena with a copy of the original object and a novel object. The time spent investigating each object is measured, and the relative amount of time spent with the novel object is expressed as a preference score,

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generally either a percentage of total exploration time or a difference index. The test takes advantage of animals' natural tendency to investigate novel items, thereby indicating that they recall the repeated (or now 'familiar') item from the previous exposure. Questions about whether object memory relies on the hippocampus [6] and interest in spatial memory as a hippocampal function have led to the development of alternative versions of the test, including one using objects that remain the same but are moved to a different location, often called the 'novel object location test,' and more complex versions with more than two objects and multiple changes in objects or their positions [7–9]. All of these tests rely on the preference of rats, mice, and other species [10] to spend more time investigating novel objects or locations than familiar ones. This novelty preference reflects an intrinsic drive for gathering information about new stimuli (i.e., curiosity) [11] rather than a preference for the item itself – rodents will also preferentially investigate novel aversive odors or aggressive animals if they can do so safely [12,13]. The specific parameters used in exploration tests are critical for eliciting the novelty preference. Key aspects of a successful preference test, including choosing equally preferred objects, avoiding objects animals can climb on, adjusting lighting and circadian cycles, choosing an appropriate interval between familiarization and testing, and so forth, have been discussed in several excellent validation studies and reviews [14–18]. Here, we discuss the interpretation of behavior in novel object exploration tests with a focus on the key underlying assumption of the test: that preference for novelty is fixed.

Novelty is not always preferred

Behavior differences in novelty exploration tests are interpreted as reflecting changes in memory, because failure to remember the initial investigation event would lead to the new and previously explored objects being treated as equally novel. But while impaired memory for investigation events would certainly alter behavior in these tests, the converse, that altered behavior in these tests indicates impaired memory, is not necessarily true. Many factors could affect exploratory behavior in this test, but a particularly notable one is a change in preference for novelty. In the most common scenario, control animals show a positive novelty preference score, indicating that they spent more time investigating the novel object and therefore must remember the previously investigated ('familiar') one, whereas experimental animals show no preference for the novel object. This decrease is generally understood to reflect a memory impairment, but a decrease in the animals' preference for investigating novel objects, or objects in novel locations, would produce identical behavior changes. An early discussion of this issue noted that the preference for novel objects 'is observed in almost all normal rats; it is well above the level of random variations of the exploration behavior' [5]. Even though this is true in naive control animals, it does not address the possibility that experimental or environmental manipulations might alter the novelty preference instead of, or in addition to, altering memory. And while many factors can be controlled for, preference for novelty is an integral assumption of the test that cannot be independently assessed, because it is the outcome measure.

Effects on novelty preference are more than just a theoretical possibility. Particular patterns of behavior in some novelty exploration experiments clearly demonstrate shifts in preference for novelty rather than memory. Specifically, several studies, discussed below, have reported preference ratios that are significantly below chance, a finding that is critically important for interpreting this test. If a test group shows a significant negative novelty preference, spending more time exploring the familiar object than the novel object (i.e., a familiarity preference), the animals are treating the two objects or locations differently and therefore must be able to distinguish between them, indicating that they remember the explored object. Their behavior, then, is not due to memory loss and instead is likely to reflect a shift in their preference for novelty.

Shifts from novelty preference to familiarity preference have been observed in several studies examining the effects of stress. After repeated daily restraint stress, male rats show preferences

for familiar and more recently investigated objects relative to novel or less recently investigated objects [19,20] (Figure 1A,B). (Familiarity preferences discussed here are either statistically significant according to the original authors or as determined from the original graphs.) Stressed female rats do not show the shift to familiarity preference, which is also blocked by estrogen in male rats [20], demonstrating an interaction effect between hormones and stress on novelty object preference. Baseline preferences for an object in a familiar location, where it was previously explored, have also been observed in rats bred for stress sensitivity [21] (Figure 1C). Taken together, these studies demonstrate a preference for familiarity in multiple types of tests, in multiple rat strains, at various ages, and with multiple forms of stress. They provide strong evidence that changes in novelty exploration tests can reflect effects on novelty preference rather than memory impairments.

Familiarity preferences have also been observed in transgenic mouse lines and following lesions and drug treatments. Mice with a knockout of the schizophrenia-associated gene *phosphorylation of eIF2a by PKR-like ER kinase* (*PERK*) [22] and a genetic Alzheimer's disease model line, 5xFAD [23], show preferences for a familiar object and for an object in a familiar location, respectively (Figure 2A,B). In wild-type male C57BL/6 mice, lesions of the medial prefrontal cortex and dorsomedial striatum lead to preferential investigation of familiar objects [7] (Figure 2C). And pharmacological blockade of NMDA receptors with MK-801 causes juvenile male mice to preferentially explore an object in a familiar location [24] (Figure 2D). Whether stress resulting from these experimental manipulations is responsible for the observed shifts in novelty preference remains unclear. However, the significant familiarity preferences shown in these studies indicate that a preference for novelty, although commonly observed in naive animals under control conditions, can be altered by genetic manipulations, circuit disruptions, pharmacological agents, and experience. This lack of preference stability makes interpretation of these seemingly simple exploratory behavioral tests significantly more complicated than generally acknowledged. Importantly, these shifts in preference for novel objects are not generally associated with changes in overall object exploration time [19,21,23,24], suggesting that additional components of exploratory drive such as hunger (foraging drive) and anxiety predominate in this measure [25]. Therefore, while assessing total exploration time is important for ruling out treatment effects on general exploratory drive, there seems to be no direct relationship between exploration time and preference shifts.

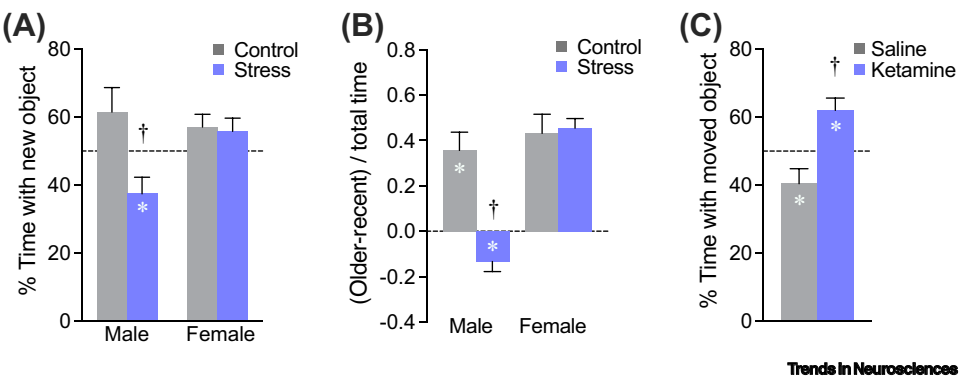

Figure 1. Experiments demonstrating preferences for familiarity in several rat stress models. (A) Adult male but not female rats show a preference for a familiar object after 1 week of restraint stress (adapted, with permission, from Figure 3b in [19]). (B) Adolescent male rats (~4 weeks old) show a preference for an object seen more recently after 1 week of restraint stress (adapted, with permission, from Figure 1a in [20]). (C) Males of the Wistar-Kyoto rat line, bred for stress sensitivity, prefer objects in familiar locations but prefer the displaced object following ketamine treatment (adapted, with permission, from Figure 5C in [21]). $^{*}P < 0.05$ relative to chance (marked with broken line); $^{\dagger}P < 0.05$ relative to control (closest gray bar).

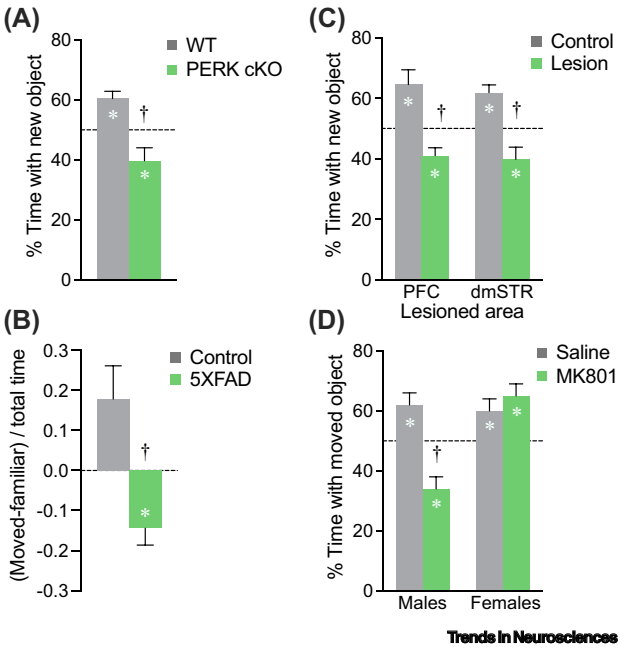

Figure 2. Experiments demonstrating preferences for familiarity in mice and rats following genetic mutations, lesions, or pharmacological treatment. (A) Male *PERK*-deficient mice prefer a familiar object (adapted, with permission, from Figure 3B in [22]). (B) Female mice with Alzheimer's disease–related mutations spend more time with an object that remains stationary than one that moves to a new location (adapted, with permission, from Figure 1I in [23]). (C) Male mice with lesions of the prefrontal cortex or dorsomedial striatum prefer a familiar object (adapted, with permission, from Figure 1C,E in [7]). (D) Juvenile male but not female rats prefer an object in a familiar location after MK-801 treatment (adapted, with permission, from Figure 1C in [24]). $^{*}P < 0.05$ relative to chance (marked with broken line); $^{\dagger}P < 0.05$ relative to control (closest gray bar).

One could argue that the cases in which animals show significant preferences for investigating familiar over novel items are relatively sparse in the literature. However, the lability of novelty preference has consequences for interpreting novel object exploration behavior in all studies, namely that preference shifts must be considered as alternatives to memory effects in all experiments involving novelty exploration behavior (Figure 3). For example, indifferent exploration of novel and familiar items might reflect impaired memory for the previously explored object, but indifference could also reflect a moderate decrease in novelty preference (i.e., a preference shift too weak to lead to a familiarity preference but sufficient to produce similar preferences for familiar and novel objects).

Several previous studies have made the point that changes in investigation of novel objects or locations cannot be assumed to necessarily reflect effects on memory [26–29]. In addition, a recent review comparing visual novelty exploration tests and rewarded matching tests in humans and nonhuman primates has pointed out that the two types of tests show contradictory effects of hippocampal damage, questioning the validity of novelty preference as a measure of memory [2]. However, numerous studies identifying behavior changes in object exploration tests continue to interpret these as indications of memory impairment (or improvement), without addressing the potential for shifts in novelty preference.

The relationship between novelty preference, curiosity, and memory

Memory is critically important for survival and for making sense of the world, so it is no surprise that it is the focus of a vast research effort. The value of studying the circuitry and synaptic or molecular mechanisms underlying memory is immediately understood, whereas experiments pointing to changes in novelty preference may seem less compelling in comparison. However, shifts in novelty preference, or neophilia, likely reflect changes in curiosity, a highly adaptive motivational drive that is not well understood at the cellular or circuit level [11]. Curiosity has been less widely studied in rodents than some other components of cognition, perhaps because of the risk of anthropomorphizing [30]. But while some aspects of curiosity may be fundamentally human, exploration of novelty in animals is broadly agreed to reflect curiosity [11,30,31].

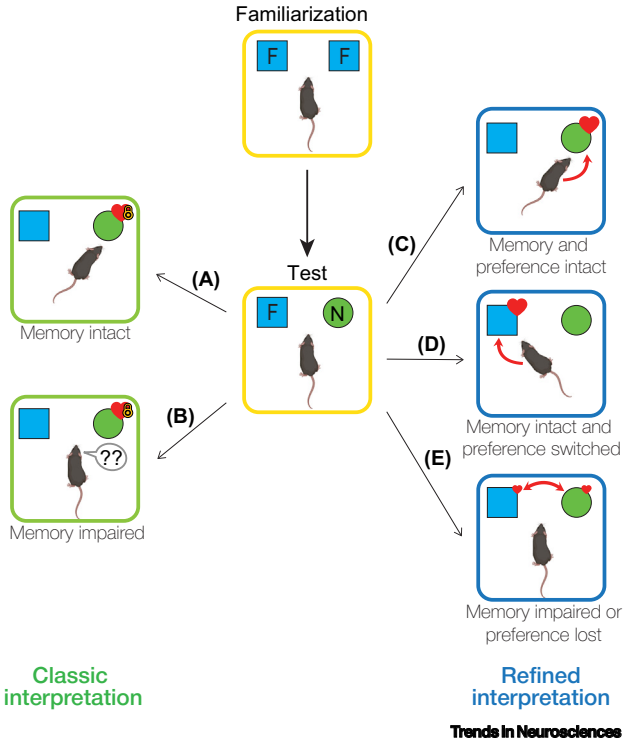

Figure 3. Interpreting novel object exploration behavior. In the novel object preference test (yellow outlines), mice (or rats) are allowed to freely explore two identical objects (familiarization, top) and after a delay are placed back in the arena with a copy of the now familiar object and a novel object (test, center). In the classic interpretation (green outlines), animals that spend more time exploring the novel object (N) than the familiar object (F) demonstrate that they recall the familiar object, reflecting intact memory (A), whereas failure to preferentially explore the novel object reflects impaired memory for the familiar object (B), because preference for novelty is assumed to be fixed (heart with lock). However, evidence that novelty preference is labile suggests a refined interpretation (blue outlines) in which greater exploration of the novel item indicates intact memory and intact novelty preference (C), greater exploration of the familiar item indicates intact memory but altered novelty preference (D), and indifferent exploration could reflect either impaired memory or loss of novelty preference (E).

Interestingly, although novelty can generate curiosity-driven exploration of stimuli, it may also trigger avoidance, presumably because of the potential danger of the unknown, producing an inherent conflict described as approach–avoidance [32,33]. Approach–avoidance behavior toward novel stimuli is impaired in a wide range of psychological disorders [34] and is highly sensitive to emotional factors such as anxiety and anhedonia, which decrease novelty approach in humans and in rodent models of related behaviors [35–37]. Conversely, increased curiosity or engagement with novelty is associated with behavioral and endocrine signs of stress resilience in animals [38] and enhanced well-being in humans [39,40]. In addition to providing a readout of emotional factors, curiosity is important in decision-making, with increased investigation of novel items enabling organisms to identify and take advantage of the best rewards [41,42]. Like approach–avoidance behaviors, these explore–exploit decisions can be affected in a variety of neuropsychiatric disorders, including attention-deficit/hyperactivity disorder, addiction, and depression [43–47].

Several neocortical and subcortical areas, including the prefrontal cortex, zona incerta, amygdala, and striatum, have been identified as critical nodes in the circuitry supporting novelty exploration in the context of both novel item exploration and explore–exploit decision-making [7,42,48,49]. A small number of studies have also pointed to roles for the hippocampus and dentate gyrus in novelty exploration [7,28,50,55]. Studies in humans indicate that curiosity is critical for hippocampus-dependent memory [51], suggesting that shifts in novelty exploration that do not directly reflect altered memory may still predict impacts on memory through changes in attention, exploration, and information seeking. Moreover, curiosity is an important driver of incidental learning (i.e., unintentional learning about stimuli in the environment), which is a key feature of hippocampus-dependent episodic memory [51–54]. Incidental learning, therefore, may be an important bridge between curiosity and memory, and novel object exploration may predict both incidental learning and episodic memory abilities.

Concluding remarks

Novel object exploration is widely used as a memory test in mice and rats, taking advantage of animals' natural exploratory behavior and novelty preference. A key assumption of this test is that all animals prefer novel objects and that changes in preference behavior therefore reflect effects on memory (i.e., the ability to recognize the previously explored object). In this opinion article, we make the case that this assumption needs to be reconsidered. Studies in which experimental manipulations lead animals to show a preference for familiarity, without decreasing overall exploration, demonstrate that animals can remember previously explored items and yet fail to show a novelty preference. These shifts in novelty preference are seen after animals experience stress as well as with lesions, drug treatments, and genetic mutations. Although there is still much to learn about the contributions of novelty preference and memory to rodent exploratory behavior (see Outstanding questions), the plasticity of novelty preference suggests that the cognitive changes underlying behavioral effects in these tests must be carefully considered and not necessarily assumed to reflect effects on memory.

At the risk of being overly prescriptive, we have several recommendations for interpreting and reporting findings in novel exploration tests in light of the issues discussed in the preceding text. The first, and probably most important, is to consider whether any behavioral changes observed in these tests reflect altered memory or novelty preference and to discuss all possibilities. Second, we recommend comparing preference scores to chance levels across group comparisons and reporting total exploration times during training and testing to rule out potentially confounding changes in exploratory drive [50]. Third, we recommend that 'recognition' be dropped from the names of these tests of exploratory preference, because recognition is not directly tested and instead only inferred on the basis of preference. Instead, we suggest the terms 'novel object preference' and 'novel object location preference,' referring to measures that are directly calculated from the exploration times and describe the specific aspect of exploration that is assessed. Fourth, explicit matching tests may prove to be better measures of memory impairment in rodents as they are in nonhuman primates [2]. Finally, we suggest that changes in novelty preference should be further explored as windows into the mechanisms underlying curiosity and its roles in cognition and emotion.

Outstanding questions

In nonhuman primates, rewarded matching tasks are better tests of memory than novelty-driven preferential viewing tasks. Can matching tasks in rodents help separate memory effects from preference shifts observed in novel object exploration tasks?

Do all shifts in novelty preference reflect stress in some form, or are there stress-independent shifts?

Is it possible to disentangle memory deficits from weak preference shifts when indifference to novelty is observed? Could preference shifts be confirmed by increasing the strength or duration of the intervention until familiarity preference becomes significant?

What experiences and molecular targets alter novelty preference (curiosity)? Results from novel object preference testing may provide an opportunity to better understand the regulation of this important intrinsic drive.

What brain circuits drive curiosity? Is the hippocampus, which has been commonly studied using object exploration tests and is responsive to stress, a key component?

Can animal models help identify critical points of intersection between memory and curiosity? Is incidental memory one of these connections?

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Declaration of interests

The authors declare no competing interests.

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