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Lorents, A.L.; Ruitenbergh, M.F.L.; Schomaker, J.

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Review article

Novelty-induced memory boosts in humans: The when and how

A. Lorents^a, M.F.L. Ruitenberga,b, J. Schomaker^{a,b,*}^a Department of Health Medical and Neuropsychology, Institute of Psychology, Leiden University, the Netherlands^b Leiden Institute for Brain and Cognition, the Netherlands

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ABSTRACT

Novel information potentially signals danger or reward and behavioral and psychophysiological studies have suggested that the brain prioritizes its processing. Some effects of novelty even go beyond the stimulus itself. Studies in animals have robustly shown that exposure to novel stimulation can promote memory for information presented before or after this exposure. Research regarding effects of novelty on memory in humans is lagging, but in the last few years, several studies have emerged that suggest that memory-facilitating effects of novelty also exist in humans. Here, we provide a comprehensive overview of these studies. We identified several factors that have been shown to influence whether novelty promotes memory or not, including the timing between the novel experience and the learning events, the involvement with the novel material, and population characteristics (such as clinical diagnosis or age). Finally, we link the behavioral findings to potential neurobiological mechanisms and discuss the relevance of specific findings in light of potential clinical and educational applications that could leverage novelty to improve memory.

1. Introduction

Visiting a new place can promote memory. For example, you may remember a breakfast that you had during your summer vacation abroad but may struggle to remember what you had for lunch last week. This memory benefit may relate to the significance of learning in novel environments: When visiting a new place, it becomes particularly relevant to learn about that environment to avoid danger and seek situations with reward opportunities in the future. As novelty is a biologically significant signal, it may not be surprising that previous empirical work revealed that novelty can promote memory (see Ref. [1]). The beneficial effects of novelty on memory have been investigated quite extensively in animals, but work in humans is lagging, resulting in a knowledge gap between the two fields [2]. In animal studies, novelty often is manipulated by placing an animal in a novel compared to a familiar environment (e.g., a new cage with unknown elements [a novel condition] rather than the home cage [a familiar condition]). This type of novelty has been referred to as spatial or environmental novelty [3–7]. Earlier human research focused on stimulus novelty (e.g., including novel images, sounds, or vibrotactile stimuli) typically reported distraction from ongoing tasks when task-irrelevant novelty is presented [8–11].

Earlier studies thus examined novelty effects at the *stimulus level*, and research on the link between novelty and memory showed memory benefits for physically deviant items (as in the Von Restorff effect [12]; or isolation effect [13]), or better recognition for novel items (i.e., novelty effect [14–16]). Until a little over a decade ago, there were no studies in humans investigating *generalizable* effects of novelty on memory – i.e., effects beyond the novel stimuli themselves. Then, one study in humans, consistent with work in animals,

* Corresponding author. Department of Health Medical and Neuropsychology, Institute of Psychology, Leiden University, the Netherlands.
E-mail address: j.schomaker@fsw.leidenuniv.nl (J. Schomaker).

showed that exposure to novel compared to familiar scenes led to improved declarative memory (i.e., a type of memory that allows us to explicitly recollect events or facts), as evidenced by better word recollection and free recall [17]. This laid the groundwork for a new line of research investigating the effects of novelty on memory in humans, which started to bridge the gap between the human and animal literature [2]. In this narrative review, we discuss the studies that have investigated these generalizable effects of novelty on memory in humans in the last decade. We identify factors that may be crucial for novelty exposure to induce memory benefits, including the timing between the novel experience and the learning events, involvement with the novel material, age, and clinical aspects (see Fig. 1 for an overview). The aim of our narrative review is to present a comprehensive framework in which relevant factors underlying beneficial effects of novelty on memory are identified. By defining the specific requirements for novelty to promote memory, we put forward potential avenues for future research and discuss potential clinical and educational applications.

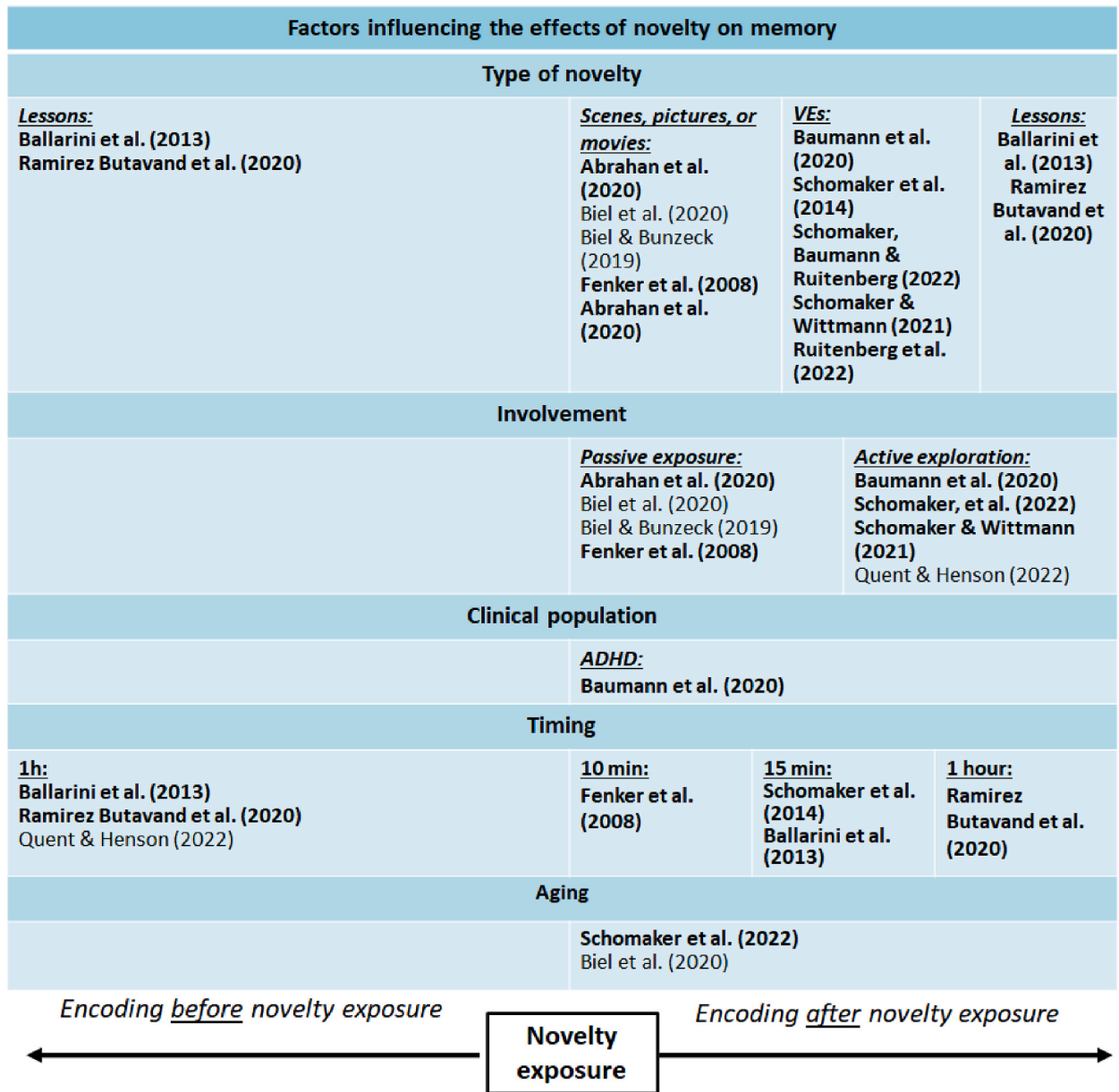


Fig. 1. Factors influencing the effects of novelty on memory. This overview shows factors that could drive or influence the effects of novelty on memory in humans. A distinction is made between studies in which encoding takes place *before* (i.e. with retroactive effects of novelty) or *after* (i.e., with proactive effects of novelty) novelty exposure. Studies that had conditions in which beneficial effects of novelty on memory were observed are printed in bold. If applicable, studies may feature under several headers. Lessons featured music- or science-themed content. Note: VE = virtual environment; ADHD = attention deficit hyperactivity disorder.

2. Search strategy and selection criteria

An electronic search was conducted between February and April 2021 using the PsycInfo and PubMed databases, and a new search was conducted in August 2022 to update the text with more recent articles. The search terms that were used were: “novelty”, “exploration”, “virtual reality”/“VR”, “novel experience”, “novelty mechanisms” and “novelty exposure” in combination with the terms “memory”, “learning”, “recollection”, “consolidation”, “recognition”, “hippocampus”, “dopamine”, and “ageing”/“aging”. We also checked the reference lists of the most crucial articles related to the effects of novelty on memory and the neural mechanisms to identify relevant work.

We used the following inclusion criteria for our narrative review: peer-reviewed studies, published in English language, experimental studies, and relevant reviews. We mainly selected publications from the last decade to highlight the most recent developments in the human literature, but older publications were also considered given the scarcity of relevant studies. Experimental and review studies of the current authors on the topic of novelty were also included, as they provide a theoretical framework for the effects of novelty on human memory.

3. The when: timing and conditions

3.1. Duration and timing of the effects

Rodent studies have shown that the beneficial effects of spatial novelty on memory may last up to 30 min and can also operate retrospectively, i.e., enhancing memory of material that was encountered *before* exposure to novelty [5]. Apart from the typically short-lived effects of stimulus novelty, with distracting and facilitating effects typically lasting less than a second, also relatively long-lasting effects of novelty on memory have been documented in humans (in the order of tens of minutes; [1]). The earliest study on the generalizable effects of novelty showed that word memory was improved when the encoding phase took place about 10 min after exposure to images of novel scenes [17]. More specifically, healthy individuals were familiarized with a list of words and scenes on a first day. On a subsequent day, participants were either exposed to pictures of novel or familiar scenes for 5 min. After another intermittent task (~5 min), participants studied a list of previously familiarized words. Memory performance was tested with a recognition and a free recall test immediately and the next day. Results from both experiments showed memory enhancements after novelty exposure on both the recognition and free recall test, suggesting that novelty may promote memory for events occurring in its close temporal vicinity. Similarly, results from a virtual reality study using *spatial novelty* showed that exploration of novel compared to familiar virtual environments improved recall for words that were presented up to about 15 min *after* novelty exposure [18].

While these two studies provide some insight into the timeline of the effects of novelty on memory, they did not experimentally manipulate the timing between novelty exposure and the learning events. Ballarini et al. [19] systematically varied the timing between exposure to a novel lesson and learning events in an educational setting. They exposed elementary school children to a novel or previously experienced (i.e., familiar) science or music lesson, either 1 h or 4 h *prior* to or 1 h or 4 h *after* being read a story. Results showed that students who experienced the novel lesson showed better memory of the story 24 h later when the lesson was experienced 1 h before or after the learning material, compared to students in a control condition. In the same study, students also showed improved long-term visual memory of the Rey-Osterrieth complex figure test [20] when a novel science lesson was given 1 h after the learning phase, suggesting that novelty boosted both verbal and visual memory [19]. In a follow-up study, high-school students that experienced a novel lesson 1 h but *not* 4 h before or after learning a complex figure, showed improved visual memory for that figure [21], further indicating that the effects of novelty on memory are time-restricted. Ramirez Butavand et al. [21] also observed that when the novel lesson was given 10 h after the learning phase, the beneficial novelty effects on memory were maintained 7 days later, suggesting that some of the effects of novelty presented after encoding are long-lasting.

In another study, typically developing children and children with attention deficit hyperactivity disorder (ADHD) aged between 9 and 15 years learned a list of words [22]. After a 45-min interval, they either explored a novel or previously familiarized virtual environment. Exploration of a novel rather than familiar environment led to better memory retention in the children with ADHD, but not in the typically developing children. In this study, the authors quantified memory retention as the percentage of words retained from short-term (immediate; i.e., with no delay or distractor task between encoding and retrieval) memory to long-term memory (~24 h later). The novelty-related memory improvements were observed even though patients explored the environment 45 min *after* the word encoding phase, suggesting that at least in this population of children with ADHD, the effects of novelty can also work retrospectively, i.e., on material that was presented tens of minutes prior. One other study, however, investigated the effects of novelty on memory for words that were presented *immediately* before novelty exposure, but failed to find positive effects on word memory [23]. In sum, the majority of findings in humans are in line with work in animals, suggesting that memory is promoted tens of minutes up to an hour around novelty exposure, but future studies are required to determine the exact timescale for different types of learning material or novelty.

3.2. Types of novelty and level of involvement

Whilst animal research consistently shows that exploring a novel environment facilitates memory performance, some studies on humans did not observe beneficial effects [24,25]. This discrepancy in findings in the human literature may depend on the degree of involvement with the novel material, as most studies involving active exploration of virtual environments have observed positive effects [22,26,27]. One recent study addressed the possibility that active exploration may be a requirement for novelty-induced

memory enhancements. In this virtual reality study, healthy young adults either actively explored a familiar and novel environment, or were passively exposed to the exploration behavior of another participant [26]. As such participants in both the active and passive conditions experienced the same visual and auditory stimulation, while the conditions differed in the level of involvement. After exposure to a novel or familiar environment, participants were presented a list of words. Participants who *actively* explored a novel environment remembered more words in a recall test after a short distractor task than those who were passively exposed to that same (familiar) environment. These findings suggest that active involvement may be a requirement for the beneficial effects of novelty on memory to be induced. Nevertheless, some studies using passive exposure (including no involvement [28]) to images or scenes requiring simple indoor/outdoor judgments (requiring minimal involvement [17]); still observed beneficial effects of novelty exposure on memory, and a study using active exploration failed to find effects [23]. Future studies should investigate whether involvement is a requirement and if so which type of involvement (e.g., semantic judgements or volition/active exploration) is sufficient for novelty-induced memory benefits to be elicited.

3.3. Different memory types and domains

Prior studies have reported beneficial effects of novelty on different types of memory, including explicit verbal (i.e., words or story) and visual memory for a complex figure (i.e., the Rey-Osterrieth complex figure [19]). Beneficial novelty effects may also depend on the type of memory *test* used. For example, some studies observed novelty-related memory enhancement on recall which is believed to be hippocampus-dependent, but not hippocampus-independent recognition [17,26,27]). One other study found that novel compared to familiar videos improved memory for visual and verbal emotional information [28]. Effects are not limited to explicit types of memory. One unique study reported beneficial effects of novelty exposure on motor memory [29]. Ruitenbergh and colleagues [29] had participants actively explore either a novel or previously familiarized virtual environment. Participants then performed an unrelated manual adaptation task, in which they had to adapt joystick movements to a visual perturbation. Results showed that participants in the novel condition were slower at de-adapting to removal of the perturbation, suggesting that they developed stronger sensorimotor representations than those in the familiar condition. This further suggests that the effects of novelty exposure are not limited to declarative memory and generalize to other types of memory as well.

Finally, studies also differ in the interval between encoding and assessment. Some studies used immediate tests assessing short-term memory (e.g. Refs. [19,28]), while others (also) assessed long-term memory after a short distractor task [18,26,27], and/or after a larger delay (e.g., 24 h later; [17,19,22,24,30]). Memory enhancements by novelty have been reported both for immediate and delayed effects, but one study reported detrimental effects of novelty for short-term retention (i.e., immediate recall), but positive effects one week later [28].

4. The how: Neural mechanisms and specific populations

4.1 Synaptic tagging hypothesis-behavioral tagging hypothesis

Exploration of novel environments can lead to enhanced brain plasticity in non-human animals [3–7]. Prolonged enhancement of synaptic plasticity can be the result of increased stimulation of hippocampal neurons; a process referred to as long-term potentiation

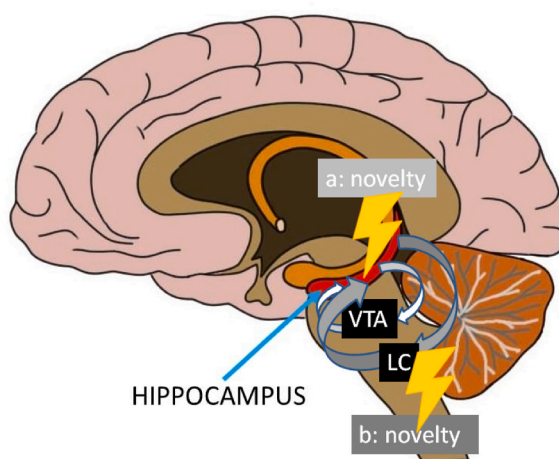


Fig. 2. Sagittal view of a human brain showing two potential mechanisms that may underlie novelty-dependent dopamine release in the hippocampus and beneficial effects of novelty on memory in the human brain [43]. Novelty can activate the ventral tegmental area (VTA) and locus coeruleus (LC). (a) Dopaminergic fibers of the VTA innervate the hippocampus, thereby promoting long-term potentiation (LTP; e.g. Ref. [48]), and lowering the threshold for learning. (b) Novelty-induced activation of the LC causes co-release of dopamine and norepinephrine into the dorsal hippocampus, also promoting hippocampal LTP (e.g. Refs. [42,44]). For a comprehensive and detailed discussion of the potential neural mechanisms see Ref. [35].

(LTP [31]). The process by which novelty can promote LTP can be explained by the so-called synaptic tagging and capture, and behavioral tagging hypotheses [31–34]. According to these hypotheses, a behaviorally significant event (such as experience of novelty, surprise, or emotion [35]) leads to the generation of a short-lasting ‘synaptic tag’ at a potentiated synapse that captures non-specific plasticity-related proteins (PRPs), maintaining input-specific LTP for a prolonged period, by turning early LTP (i.e., the first phase in which synaptic plasticity is increased) into late LTP (i.e., a more stable and long-lasting synaptic change; [31,33]). PRPs are thus associated with long-lasting plasticity and may underlie the beneficial effects of novelty on memory before and after exposure, with effects lasting for several tens of minutes, even after return to a familiar environment [4,5,34,36–38]. The beneficial effects of novelty in humans suggest that a similar behavioral tagging process exists in humans [2], with exploration of novel environments facilitating the PRPs to stabilize memories [39], but explicit evidence for this theory in humans is currently lacking.

4.1. Different neural pathways

Research in animals has uncovered two potential mechanisms by which novelty (and other salient events) can promote dopamine-release in the hippocampus (Fig. 2). A first mechanism was described by Lisman and Grace [40], who hypothesized that dopaminergic midbrain neurons in the ventral tegmental area (VTA) are functionally connected with the hippocampus via a bidirectional loop. New information is detected by the hippocampus, and a novelty signal travels through the subiculum, nucleus accumbens, and ventral pallidum to the VTA, where it induces novelty-related firing in dopaminergic neurons, making up one side of the loop. In the other direction, a dopamine signal travels back to the hippocampus, and early-LTP is promoted by lowering the threshold for learning [40]. Late-LTP is facilitated by dopaminergic promotion of protein synthesis [41].

For years, the VTA was recognized as the main source of novelty-related hippocampal dopamine, but more recent evidence points towards a second mechanism. Specifically, studies in animals have revealed that novelty-related hippocampal dopamine can also be signaled via noradrenergic fibers coming from the locus coeruleus (LC [42–44]). Results from optogenetic, behavioral, and pharmacological studies in rodents have demonstrated that noradrenergic neurons of the LC project to the dorsal hippocampus, co-releasing dopamine and norepinephrine. This pathway enhances spatial learning and memory, while LC activation alone mimics the beneficial effects of environmental novelty on memory and enhances synaptic transmission potentiating LTP in the hippocampus [42, 44]. Novelty-related hippocampal dopamine promoted by the LC thus provides another pathway through which novelty can enhance learning.

While both the midbrain (substantia nigra/ventral tegmental area [SN/VTA]) and LC can act as dopaminergic sources for the hippocampus and thus potentially drive the beneficial effects of novelty on memory, LC-TH+ fibers project more densely to the dorsal hippocampus while the VTA tyrosine hydroxylase-expressing neurons (VTA-TH+) project to the ventral hippocampus. This difference in anatomical connections may underlie differential functional effects. While VTA-TH+ fibers selectively target specific hippocampal synapses, LC-TH+ fibers may release dopamine non-selectively, resulting in a more widespread effect [42–44]. As a result, the effects induced via the VTA connection could be more specific to the novel material itself, while the LC-mediated effects may be more generalized, leading to more ubiquitous enhancements [45,46]. There is evidence suggesting that the two systems work collaboratively in signaling the hippocampus, as both VTA and LC fibers project to dopaminergic D1/D5 receptors [42,44,47,48]. A critical remark is that these specific mechanisms so far have solely been researched in rodents, making it unclear whether similar neural mechanisms exist in humans. So far, studies in humans have mostly focused on more generalizable effects (e.g., those of novelty exposure on an unrelated word learning task), suggesting that the LC rather than VTA connections may underlie the effects reported in the literature.

Although both mechanisms imply crucial involvement of the hippocampus, it is not known whether novelty effects could also occur via other dopaminergic pathways including the mesolimbic pathway. The mesolimbic pathway connects the VTA to the ventral striatum of the basal ganglia in the forebrain and could potentially be involved in the beneficial effects of novelty on other types of memory. For example, Ruitenberg et al.’s [29] findings that novelty benefited procedural memory in humans – and more specifically, motor learning after spatial navigation through a novel environment - from a study on humans suggests that novelty-induced dopaminergic effects in mesocortical and/or nigrostriatal pathways could underlie these novelty effects. This mechanism remains to be further investigated with neuroscientific methods.

4.2. Clinical populations

There is a currently unused potential for novelty to counteract memory issues in clinical populations. Empirical support suggesting that such interventions could be successful comes from Baumann et al. [22], who reported that children and adolescents with ADHD showed better recall on an unrelated word learning task after exploring a novel rather than familiar virtual environment, while no such benefits were observed in typically developing children. The authors hypothesized that these beneficial novelty effects may be the result of increased dopaminergic activity in the hippocampus, mimicking some of the common treatments of ADHD, such as methylphenidate, by improving selective attention underlying memory and spatial learning [22]. However, as the neural mechanisms were not directly investigated in this study and studies investigating the effects of novelty on memory in other clinical populations (e.g., patients with memory problems) are currently lacking, the clinical utility of novelty exposure remains to be evaluated in future studies [49,50].

4.3. Aging

Healthy aging is associated with memory decline, and memory issues are worsened by certain neurodegenerative diseases such as Alzheimer's and Parkinson's disease [51–53]. As memory issues progress, individuals become more homebound and consequently new experiences become increasingly rare. Potentially, novelty exposure would benefit individuals with memory issues. Nowadays, it has become easier to create 3D virtual environment and the use of virtual reality in research is increasing. An outstanding question, however, is whether the effects of novelty hold in an older healthy population. Structural and neuroimaging studies have suggested an age-related degeneration of the SN/VTA ([54]), a region that has been shown to drive the effects of novelty on memory in animals [40; 43]; see Fig. 2). The age-related degeneration of this region could potentially reduce the beneficial effects of novelty on memory, but so far only a limited number of studies have investigated the effects of novelty on memory over the lifespan. Furthermore, LC integrity has been reported to decline with age in humans, as measured with neuromelanin magnetic resonance imaging [55,56], and this region has been linked to memory facilitation by novelty in animal work [42–44]; also see Fig. 2). Both the changes in the dopaminergic system and the decrease in LC integrity could influence the effectiveness of novelty in facilitating memory in older age. A few studies have investigated whether novelty exposure promotes memory in older adults. One study that addressed the effects of novelty in a healthily aging population failed to observe positive effects of novelty [25]. In this study, the novel condition included *passive* exposure to novel nature videos, and the authors argued that active interaction with the novel material may be required (also see Refs. [24,26]). In another study, Schomaker et al. [27] recruited participants spanning a wide age range, including children (8–12 years), adolescents (13–18 years), younger adults (19–45 years) to older adults (>45 years). Participants actively explored either a novel or previously familiarized virtual environment, before they entered a word encoding phase. In an immediate memory test, word recall was found to be better after exploring a novel versus familiar environment for children, adolescents, and younger adults, but not older adults. Taken together, these findings suggest that there is a need for identification of the specific conditions under which novelty boosts memory in seniors, so it can be leveraged for clinical purposes [49].

The effects of age on the effects of novelty on memory thus remain underinvestigated: studies including a group of participants spanning a wide age range are scarce and there currently are no longitudinal studies. While the absence of beneficial effects of novelty exposure in older individuals may be explained by changes in habituation reduced dopaminergic signaling from the SN/VTA or decreased LC integrity in older individuals [57], it could also be explained by differences between designs (e.g., degree of involvement, the time between exposure and the learning events, delayed or immediate memory test, insufficient power, etc.). Although it has been argued that novelty exposure has the potential to counteract or slow-down age-related memory decline [2,54], it is currently unclear why several studies have failed to observe the beneficial effects of novelty on memory in older individuals, while similar designs yielded beneficial effects in younger individuals. Furthering our understanding of the when and how novelty promotes memory by systematically manipulating the factors identified in this review may provide novel insights regarding the potential of novelty exposure in promoting memory in older individuals.

5. Conclusion and future directions

Building on a rich literature in animals, empirical studies have suggested that novelty has generalizable positive effects on memory in humans as well. Here we reviewed those studies and identify crucial factors of when and how the memory-facilitating effects of novelty are most likely to occur. Recent evidence from optogenetic studies in animals suggests that the beneficial effects of novelty on memory are mediated by hippocampal dopamine, coming from two different sources (i.e., the VTA or LC). Behavioral studies in humans have led to identification of several critical factors, including the level of involvement with the novel material, the time between novelty exposure and the learning events, and the moment of the memory (delayed or immediate). The discussed findings suggest that the beneficial effects may be limited to children and young adults. These findings could be utilized in educational situations where novelty could potentially be used to promote declarative memory. A recent study in humans further suggested that the effects of novelty are not limited to hippocampus-dependent memory, as benefits were also observed in the motor domain (potentially via dopaminergic effects in mesocortical and/or nigrostriatal pathways). The neural mechanisms underlying the beneficial effects of novelty on memory, however, still need to be elucidated in humans. Insight into these mechanisms may also help in explaining why interventions have been less effective in older individuals and identifying the possibilities and limitations for clinical purposes.

Author contribution statement

All authors listed have significantly contributed to the development and the writing of this article. </p>.

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Data availability statement

No data was used for the research described in the article.

Declaration of interest's statement

The authors declare no competing interests.

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