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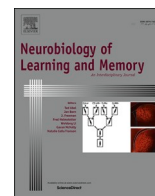
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Effects of active exploration on novelty-related declarative memory enhancement

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ABSTRACT

Exploration of novel environments has reliably been shown to enhance learning in rodents. More recently, these effects have been replicated in humans using virtual reality: Memory is enhanced after exploration of novel compared to familiar virtual environments. However, exploration of a novel versus familiar environment differs in another aspect. Navigating familiar territory can rely more on habits, while navigating new territory requires active decision-making. This difference in choices could contribute to the positive effects of novelty exploration on memory. In this study, we aimed to investigate this possibility. Participants familiarized with a virtual environment (day 1) and were exposed to this environment again (day 2 or 3) and to a novel environment (day 2 or 3). Participants either actively explored the environments or were passively exposed to the exploration behavior of another participant in virtual reality. After exposure to the environment, participants performed a word-learning task and filled out questionnaires regarding virtual presence and the novelty seeking personality trait. Mixed models suggested that memory performance was higher after participants actively explored versus were passively exposed to a novel environment, while these effects were reversed for a familiar environment. Bayesian statistics provided further weak evidence that memory performance was influenced by the interaction between novelty and exposure type. Taken together, our findings suggest that active exploration may contribute to novelty-induced memory benefits, but future studies need to confirm this finding.

1. Introduction

When making your way home after a day at work, you heavily rely on habits and may not think too much about the route you are taking or the landmarks that you encounter. In contrast, when finding your way to your hotel after you arrived at a new holiday destination, you will have to make active navigational choices and remember landmarks to find your way back at a later time. This example highlights the importance of learning when visiting a new place, but also exemplifies the differences between navigating familiar versus unknown territory (i.e., spatial novelty). Animal studies have reliably shown that exploring a new environment enhances long-term potentiation (e.g., Davis, 2004; Li, Cullen, Anwyl, & Rowan, 2003; Sajikumar & Frey, 2004; Sierra-Mercado, Dieguez, & Barea-Rodriguez, 2008), and work in humans using images of novel scenes (Fenker, Frey, Schuetze, Heipertz, Heinze, & Düzel, 2008) and virtual environments (VEs; Schomaker, van Bronkhorst, & Meeter, 2014) suggests that novelty promotes learning in humans (for a review see Schomaker, 2019). The current study aims to

investigate the effects of active decision-making during navigation of novel versus familiar environments on human declarative memory, using virtual reality (VR).

Research in animals, especially rodents, has provided insight into the exact neural mechanisms underlying these effects. Two influential theories have suggested that when novelty-triggered dopamine from substantia nigra/ventral tegmental area (SN/VTA) neurons is released in the hippocampus, it enhances plasticity by decreasing the threshold for late long-term potentiation (LTP) and thus promotes long-term memory consolidation (for reviews see, NOMAD framework: Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010; the “hippocampal-VTA loop”: Lisman & Grace, 2005; neoHebbian framework: Lisman, Grace, & Düzel, 2011; Otmakhova et al., 2013). The VTA was long believed to be the sole source of hippocampal dopamine associated with novelty-related hippocampal memory, but more recently optogenetic studies have suggested that some hippocampal dopamine may have its source in the locus coeruleus (Duszkiewicz, McNamara, Takeuchi, & Genzel, 2019; Kempadoo, Mosharov, Choi, Sulzer, & Kandel, 2016; McNamara &

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Dupret, 2017; Takeuchi et al., 2016; Yamasaki & Takeuchi, 2017). Irrespective of the source, exposure to novel environments positively influences neurogenesis (Olson, Eadie, Ernst, & Christie, 2006), and lowers the threshold for hippocampal late LTP (Davis, 2004; Li et al., 2003; Sajikumar & Frey, 2004; Sierra-Mercado et al., 2008; Straube, Korz, & Frey, 2003). These findings demonstrate that exposure to spatial novelty has a robust, beneficial effect on hippocampal memory consolidation.

These effects can be explained by the synaptic tagging and capture (STC) hypothesis. According to this theory, the formation of long-lasting memories depends on several interacting processes in the neuron. First a learning *tag* – a temporary structural state of the synapse – needs to be set at a potentiated synapse, and second, plasticity-related proteins need to be synthesized, which are then captured at the tagged synapse where they stabilize the increased synaptic strength (Frey & Morris, 1997; Frey & Frey, 2008). The STC framework further explains how weak, transient memory traces can become long-lasting memories when the encoded event occurs close in time with a behaviorally relevant event that triggers the synthesis of plasticity-related proteins. In addition to direct evidence for these synaptic changes, some studies have suggested a similar, behavioral tagging mechanism in animals and humans that is elicited by behaviorally relevant events such as reward and novelty exploration (Ballarini, Moncada, Martinez, Alen, & Viola, 2009; Kemp & Manahan-Vaughan, 2004; Moncada, Ballarini, & Viola, 2015; Moncada & Viola, 2007; Wang et al., 2010). For example, exposure to a novel science lesson (Ballarini, Martinez, Perez, Moncada, & Viola, 2013) and novel scenes (Fenker et al., 2008) have been shown to improve memory. The novelty-induced increase in neuroplasticity is not temporally restricted to the time of exposure to the new information, but has been detected up to thirty minutes afterwards (Li et al., 2003; Straube et al., 2003; Lisman, Grace, Düzel, 2011). Previous work in humans also suggests that the effects of novelty on memory are not limited to the novel event itself but extend to events occurring after exposure (Fenker et al., 2008).

While behavioral tagging and novelty-related dopamine release can explain the effects of novelty exploration on consolidation, it remains unclear what mechanisms drive an immediate novelty-related memory enhancement. Our previous work using VR suggested that exploring spatially novel environments can improve performance on a subsequent, unrelated word learning task immediately after exploration, that is without a consolidation period (Schomaker et al., 2014). Potential candidate mechanisms include the effects of novelty on attention or arousal (Schomaker & Meeter, 2012, 2014, 2015), as both increases in attention and arousal can lead to memory enhancements (Aly & Turk-Browne, 2016; Mather & Sutherland, 2011). As individuals differ in their tendency to seek out and appreciate novelty (Cloninger, 1986) and the effects of novelty on memory may depend on these differences (Krebs, Schott, Düzel, 2009), the current study also investigated the role of novelty seeking (NS).

2. The role of action

Early work investigating the NS trait and exploration behavior in animals already acknowledged the importance of discriminating between locomotor activity and exploration behavior (Mislin & Ropartz, 1981; Robbins & Iversen, 1973). Novel environments may induce a mode of exploration (Düzel et al., 2010) and facilitate actions (Koster, Seow, Dolan & Düzel, 2016), potentially increasing locomotor activity and thereby creating differences between novel and familiar conditions in studies employing spatial novelty. Although locomotion in animals can be controlled to some extent, another aspect of exploration behavior cannot: agency – the active decision-making involved in navigation. Exploring a novel compared to a familiar environment differs in the extent to which decision-making processes are taxed. Navigating familiar territory can rely on habits, while navigating a novel environment involves decision making. It is possible that the positive effects of

novelty on memory that have previously been observed depend on these differences in the nature of exploration, rather than novelty per se. One study that used VR found that a condition that required planning a route and motor control enhanced spatial memory, compared to a passive exposure condition (Plancher, Barra, Orriols, & Piolino, 2013), and recently similar results were obtained in a group of older adults (Meade, Meade, Sauzeon, & Fernandes, 2019). These findings suggest that active exploration compared to passive exposure is linked to higher memory performance for information encountered during travel. It remains unclear whether these effects are generalizable to other learning events, for example occurring after exploration. But recent findings suggested that active exploration may be required to induce benefits of novelty on memory, as passive exposure to novel videos failed to promote memory (Biel & Bunzeck, 2019). Similar effects of agency on memory encoding have been found in a reward-based task (Koster, Guitart-Masip, Dolan, & Düzel, 2015).

Interestingly, theta oscillations have been linked to volitional movement, spatial navigation and memory encoding (Kaplan, Doeller, Barnes, Litvak, Düzel, Bandettini, Burgess, 2012). This study showed that increases in hippocampal theta during the commencement of virtual movement were positively correlated with later memory success. This demonstrates the involvement of the hippocampus in both agency and memory encoding. The Storage, Recall, and Novelty Detection of Sequences (SOCRATIC) model has suggested that novelty elicits a theta state in the hippocampus that is associated with learning rather than recall (Lisman and Otmakhova, 2001). It may be through this pathway that active, but not passive exploration of novel environments could promote learning. Therefore, in the current study we aimed to investigate the role of agency in the effects of novelty on memory performance.

3. Current study

Participants familiarized with a VE (day 1) and were exposed to the same or a novel VE on day 2 or 3 in a counterbalanced fashion. After exposure on day 2 and 3 participants performed a word-learning task. The word lists were unrelated to the VEs, and memory performance was expected to be enhanced by exposure to a novel compared to a familiar environment (Schomaker, van Bronkhorst, & Meeter, 2014; Fenker et al., 2008). In a between-subjects design, participants either actively explored the environments or were passively exposed (yoked) to the audiovisual input of another participant in VR. We predicted that active exploration of novel environments would be more potent in enhancing memory performance than passive exposure.

Individual differences in the NS personality trait were quantified using the Tridimensional Personality Questionnaire (Cloninger, 1987; Cloninger, Przybeck & Svraki, 1991; Cloninger, Svrakic, & Przybeck, 1993). In addition to these personality measures, we asked participants to fill out a questionnaire regarding spatial presence in the VE, the Igroup Presence Questionnaire (IPQ; Schubert, Friedmann, & Regenbrecht, 2001). Since the subjective experience of presence has previously been found to be enhanced by novelty, and stronger presence is associated with higher memory performance (Schomaker et al., 2014), we expected that novelty would increase presence and further promote the beneficial effects of novelty on memory. The experience of presence could also be enhanced by active exploration compared to passive exposure. Exposure to novelty leading to enhanced declarative memory has potential practical and therapeutic applications aimed at enhancing memory (Schomaker, 2019). Understanding and taking into account influences of individual differences and choosing the appropriate type of novelty exposure (active/passive) will be critical when designing effective novelty interventions.

4. Methods

4.1. Participants

Forty-one students of Justus Liebig University, Giessen, or THM University of Applied Sciences volunteered for this study. Inclusion criteria were right-handedness, age between 18 and 35 years, no history of neurological, psychiatric or severe physical illness (including serious eye disease), and no drug or excessive alcohol use as indicated during an intake interview. Three participants were excluded because they failed to finish all tests in all three sessions, and an additional two participants were identified as outliers (>2 standard deviations from the mean). Analyses were performed on the remaining 36 participants (25 female; $M_{Age} = 24.9$ years; Age range = 20–33 years; $SD = 3.4$ years). Participants were assigned to the active, and the passive exploration condition in a counterbalanced fashion (17 in the active: 13 female; $M_{Age} = 24.5$ years; Age range = 20–33 years; $SD = 3.4$ years; 19 passive: 12 female; $M_{Age} = 25.6$ years; Age range = 20–31 years; $SD = 3.0$ years). Participants either received course credit or financial compensation of 8 Euros/hour. All participants were informed about possible adverse effects, including dizziness or nausea induced by VR and gave informed consent. The study received a positive vote of the ethics committee of the Department of Psychology and Sports Science at Justus Liebig University, Giessen, Germany.

5. Stimuli and apparatus

The VEs were created using Unity Version 5.3.4f1 (Unity Technologies, 2017). See Fig. 1 for a top view of an example VE. Both VEs were plausible real-life environments, and both included indoor and outdoor areas that could be explored. One represented a city apartment, while the other was a more industrial location similar to a distribution center. They were matched in terms of indoor and outdoor area size, and both included audio effects (e.g., cars driving by, crackling of fire, chirping of birds). Some objects (like small trash cans) would move when the participant collided with them, but more complex or meaningful interaction with objects was not possible. The VEs were presented on a PC running on Windows 7 (Microsoft, 2009) and an NVIDIA Geforce GTX 970 graphics card. Participants in both the active and passive condition viewed the VEs in a seated position through Oculus Rift DK2 3D augmented reality glasses (Oculus VR Inc., 2014), using Runtime App Version 0.8.00 (Oculus VR Inc., 2014). In the active condition, participants navigated using an Xbox One controller, and the screen was recorded using Open Broadcaster Software (OBS 0.16.6, 2012). In the active condition, head movements were tracked, leading to strong

immersion within the VE. The recordings were presented to participants in the passive condition using AutoPlayVR V085 (VRLINES, 2017), such that both groups received the same visual stimulation, but would either be exploring actively (high agency) or be passively exposed to the exploration behavior of another participant (no agency). Questionnaires were created using SoSci Survey (SoSci Survey GmbH, 2013). The distractor and word learning tasks were programmed and presented using Open Sesame 3.1.8 (Mathôt, Schreij, & Theeuwes, 2012).

5.1. Procedure

Participants were tested on three separate testing days that were scheduled on days of the same week, with one day between sessions (i.e., Monday, Wednesday and Friday; referred to as day 1, day 2 and day 3 respectively). On day 1 participants were familiarized with one of two VEs. On day 2 and 3 they were exposed (actively or passively) to the same or a novel VE, for which order was counterbalanced between participants. Which VE served as familiar and which as novel was also counterbalanced between participants.

Table 1 shows the sequence of tasks for each of the testing days. On day 1, all participants gave informed consent and received written instructions with regard to the experimental procedure. Participants in the active condition received additional written instructions about how to use a controller to navigate the VEs. All participants were instructed to immediately report symptoms of motion sickness (nausea, dizziness or flushing) to the experimenter. No instructions for the trajectory of navigation were given, nor were participants instructed to remember particular aspects of the environment. At the beginning of each VR session, the VR system was adjusted to the participants' head and eye

Table 1

Sequence of tasks. The sequence of task on testing days 1, 2 and 3. See the text for descriptions of the tasks.

Day 1	Day 2	Day 3
Informed consent	VR session: Novel/familiar	VR session: Novel/familiar
Instructions	IPQ	IPQ
VR session: Familiarization	Rating scales 1: Motivation; Boredom; Attention	Rating scales 1: Motivation; Boredom; Attention
IPQ	Distractor task 1	Distractor task 1
TPQ	Rating scales 2: Arousal; Tiredness; Happiness; Sadness	Rating scales 2: Arousal; Tiredness; Happiness; Sadness
	Word learning: List 1 or 2	Word learning: List 1 or 2
	Distractor task 2	Distractor task 2
	Memory test: Free recall	Memory test: Free recall



Fig. 1. Virtual environment. Top view of the outside area of one of the VEs as shown in Unity. Participants could hear environmental noises, such as birds, and cars driving by. Participants in the active condition could navigate the VEs from a first-person perspective.

distance. All participants wore over-ear headphones during exposure to VR, and those in the active exploration condition also held the controller. On day 1, participants started with a familiarization phase, during which they could explore or were passively exposed to a VE for 5 min. After this they filled out the IPQ and Tridimensional Personality Questionnaire (TPQ) via online surveys.

Day 2 and 3 also started with a 5-minute VR session (novel or familiar; counterbalanced between subjects). On all three testing days, participants completed a German translation of the IPQ after the VR session. Filling in the IPQ took approximately 5–10 min. On day 2 and 3, participants indicated their subjective experience of motivation (from very demotivated to very motivated), boredom (from very bored to not bored at all), and attention (from very inattentive to very attentive) during the VR session on five-point Likert scales after finishing the IPQ, after which they performed a 1-back task, to overwrite working memory. During this first distractor task (distractor task 1) two-digit numbers were presented in a sequence. Participants had to indicate whether the present number was smaller or larger than the previous one (1-back task). They had to press the left arrow when the number was smaller, and the right arrow if the number was larger. Distractor task 1 consisted of 66 trials, with numbers from 31 to 95, and was completed in approximately 3 min. After completing distractor task 1, participants were asked to rate their arousal (from calm and relaxed to excited), tiredness (from extremely tired to fully awake), happiness (from not happy at all to very happy) and sadness (from not sad at all to very sad) levels on five-point Likert scales.

On day 2 and 3 participants performed a word learning task after filling out the second ratings (arousal, tiredness, happiness and sadness). For this task, 44 concrete neutral German nouns were used from Lahl, Göritz, Pietrowsky & Rosenberg (2009). The selected words were divided into two word lists, each containing 22 words. Word lists were additionally matched concerning valence, arousal, concreteness, word length and frequency of appearance in German everyday language. Each participant learned both lists, one after exposure to the previously familiarized VE and the other after exposure to the novel VE (order – day 2 or day 3 - counterbalanced). For the learning phase, they were instructed to memorize as many words as possible. The words were presented in the middle of the screen in a random order for 2000 ms each. Between words a fixation cross was presented for 500 ms. Each of the 22 words was presented once. The word learning phase was finished in approximately 1–2 min.

After the learning phase, participants performed distractor task 2, a short version of the 1-back distractor task, to reduce serial-position and recency effects (Gavett & Horwitz, 2012). Numbers were randomly chosen from a list of numbers from 31 to 43. They performed 13 trials in approximately 30 s. Finally, they were asked to type in all words that they remembered from the words presented before. The instructions and tasks on day 1 were completed in approximately 35 min. All tasks on day 2 and 3 were finished in approximately 30 min.

6. Statistical analyses

Memory performance was operationalized as the proportion of correctly recalled words. Typed in words were identified as correct if they had been presented during the learning phase. Incorrectly typed words were identified as correct if not more than two letters were wrong or mixed up. When it was unclear whether an error was due to a typo or false memory, the answer was labeled as incorrect (e.g., if “well” had been presented, and “wall” was entered, it would have been labeled incorrect, despite only one letter being wrong). The effects of novelty and exposure type on memory performance were investigated using 3*2 mixed ANCOVA with Novelty of the VE (novel; familiar) as a within-subjects, Exposure (passive; active), Session (novel day 2; novel day 3) as between-subjects factors and NS as a covariate. To further investigate the interaction between novelty and exposure type we conducted Bayesian statistics using the statistical package JASP version 0.13.1.0

(JASP Team, 2020), comparing the evidence for a model with the interaction between exposure type and novelty, and a model with just the main effects of novelty and exposure type. The Bayes factor (BF10) is reported, indicating the likelihood of the data given the interaction model, divided by the posterior probability of the model with just the main effects.

Ratings on arousal, motivation, attention, boredom, arousal, tiredness, happiness, and sadness and IPQ presence ratings were investigated with the same mixed ANOVA as memory performance, but without the NS covariate. To explore differences to the familiarization session, IPQ presence ratings for the different sessions (familiarization; novel; familiar) were compared with paired-sample *t*-tests. Additionally, the effect of session was investigated with a repeated-measures ANOVA with Session day (1; 2; 3) as a within-subjects factor. We used Bonferroni-correction to correct for multiple comparisons.

To further investigate whether the NS trait, IPQ scores and other constructs measured by the ratings influenced memory performance, we ran general linear regression models in R version 4.0.0 using the *glm* function. We ran two models to predict memory performance as measured by recall in the novel and familiar condition separately. Predictors were motivation, boredom, arousal, happiness, sadness, tiredness, attention, IPQ, NS, and exposure type (active, passive) as a dummy variable. All data was first centered and multicollinearity was investigated by calculating variance inflation (VIF) factors. All VIF values were <2.1 for the novel and <4.0 for the familiar condition, suggesting the predictors were not highly correlated.

7. Results

7.1. Memory scores

Fig. 2 shows mean memory performance as measured by the proportion of correctly recalled words for the two exposure (passive and active) and novelty conditions (novel and familiar). Fig. 3 shows recall performance further divided by whether participants were subjected to the novel condition in session 2 or 3. There were no main effects of exposure type, novelty or NS ($p = .749$, $p = .247$ and $p = .582$ respectively), but there was a main effect of session. Overall memory performance was higher when participants explored a novel environment on day 2 rather than on day 3, $F(1,31) = 5.85$, $p = .022$, $\eta^2 = .159$. Novelty and exposure type exhibited an interaction pattern, $F(1,31) = 4.59$, $p = .040$, $\eta^2 = .13$, with higher memory performance after active exploration of a novel versus a familiar environment, and the reverse effect for passive exposure, with higher memory performance for the familiar versus novel conditions. No other interactions were found ($ps > .249$).

The interaction effect between novelty and exposure type was further investigated with a Bayesian repeated-measures ANOVA. Specifically, we investigated the interaction between novelty and exposure type by comparing the model that included the interaction to the model that only included the main effects of novelty and exposure type. The Bayes Factor (BF10) was 1.401, indicating that the data were 1.401 times more likely under the model including the novelty and exposure type interaction, compared to the model including just main effects. This is commonly categorized as weak evidence, which is in line with the *p*-value of .040 in the main analyses.

8. Ratings and novelty seeking trait

Participants reported subjective states on several scales after exploring the environments and filling out the IPQ (motivation, boredom, and attention) and after distractor task 1 (arousal, tiredness, happiness, and sadness). Fig. 4 shows the mean motivation, attention, tiredness, happiness, and sadness ratings after exploring novel and familiar VEs. Fig. 5 shows the mean arousal (Fig. 5A) and boredom (Fig. 5B) ratings, further differentiated by the novelty, exposure and session conditions. Scores on the NS TPQ subscale ranged from 10 to 25

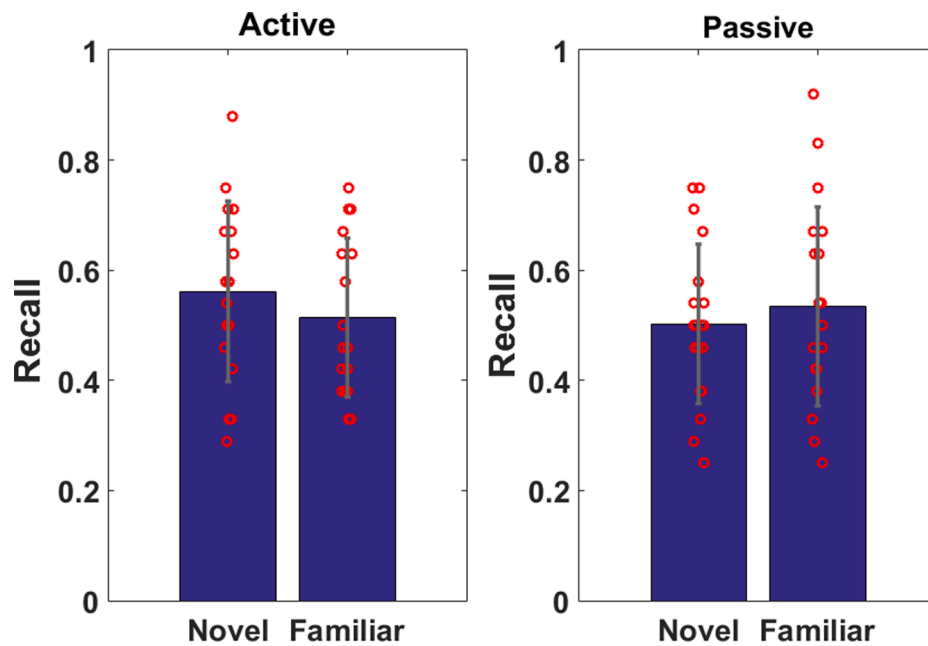


Fig. 2. Mean memory performance for the different exposure and novelty conditions. Memory performance is shown as proportion recalled words for the novel and familiar conditions after active exploration and passive exposure to VEs. Bars show the mean, red dots individual data points, and error bars reflect standard errors of the mean.

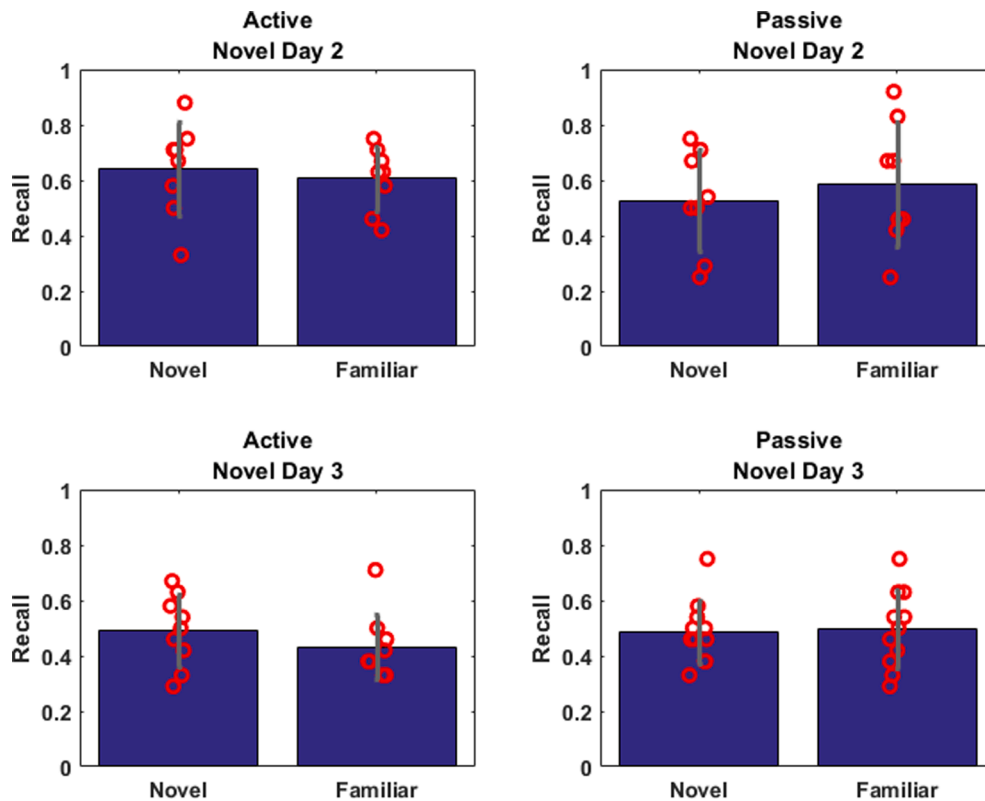


Fig. 3. Mean memory performance for the different exposure and novelty conditions for the participants who explored a novel environment on day 2 or 3. Memory performance is shown as proportion recalled words for the novel and familiar conditions after active exploration and passive exposure to VEs. Bars show the mean, red dots individual data points, and error bars reflect standard errors of the mean.

points on a 35-point scale (mean = 17.07, SE = .64).

Motivation ratings were higher after participants explored or were exposed to a novel compared to a familiar environment, $F(1,32) = 7.88$, $p = .008$, $\eta^2 = .198$. Exposure type ($p = .121$) or session ($p = .514$) did

not affect the motivation ratings, nor were any interactions observed (all $ps > .121$).

Arousal ratings were higher when participants explored the novel environment on day 2 rather than day 3, $F(1,32) = 4.82$, $p = .036$, $\eta^2 =$

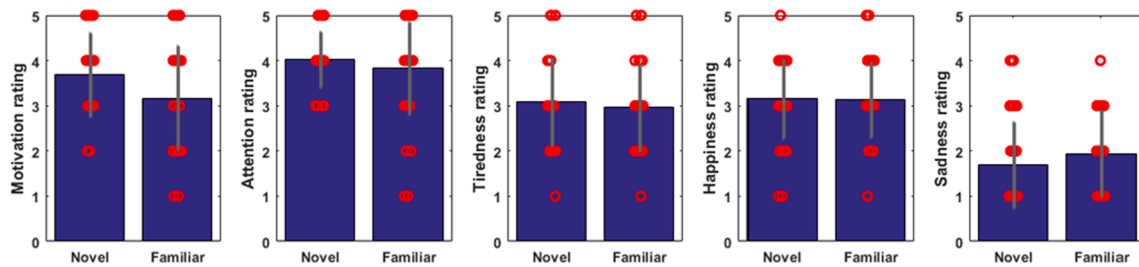


Fig. 4. Mean subjective ratings. Mean motivation, and attention ratings were reported by participants after being exposed (actively or passively) to familiar and novel environments on day 2 and 3. Tiredness, happiness, and sadness were reported after the first distractor task. All ratings were given on a five-point Likert scale. Mean ratings for A) motivation, attention, tiredness, happiness, and sadness for familiar and novel conditions. Error bars reflect standard errors of the mean.

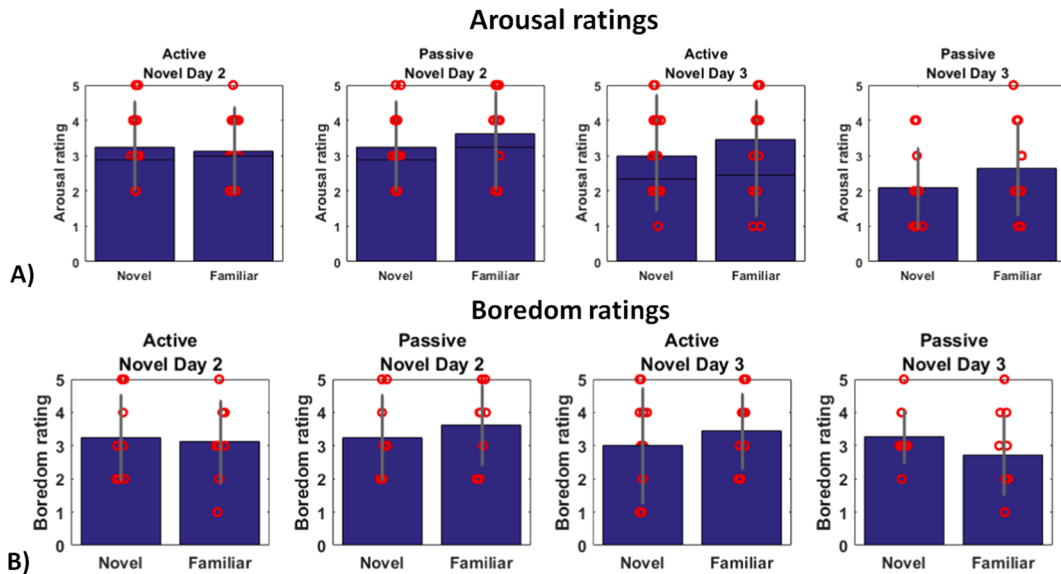


Fig. 5. Mean subjective ratings. Participants reported arousal after the first distractor task. Boredom ratings were reported after being exposed (actively or passively) to familiar and novel environments on day 2 and 3. All ratings were given on a five-point Likert scale. Mean ratings for A) arousal B) boredom for both passive and active conditions for participants who experienced the novel condition on day 2 and 3 separately. Error bars reflect standard errors of the mean.

.131. Neither novelty ($p = .196$) nor exposure type ($p = .862$) affected the arousal ratings, nor did any of these interact (all $ps > .441$). There were no main effects (all $ps > .143$) or interactions (all $ps > .120$) for attention, boredom, tiredness, happiness, or sadness.

To test a post-hoc hypothesis that repeated exposure to the environments increased boredom and had a negative effect on motivation and attention, we also compared the second- and third-day measures of these scales. Indeed, boredom increased, $t(33) = 5.34, p < .001$, but motivation remained unaffected ($p = .112$) from day 2 to day 3. No differences in attention ($p = .324$), nor tiredness, arousal, sadness, or happiness ratings were observed between sessions ($ps > .201$).

9. Virtual presence

See Fig. 6 for the mean IPQ scores for all sessions (day 1, 2 and 3), and Fig. 7 for all the ratings per novelty and exposure type condition for participants who had the novel condition on day 2 and 3. For testing day, a comparison of the first versus the second and third day ratings showed that presence was highest after the familiarization phase, and decreased on further testing days (deviation contrast: day 1 versus mean day 2 and 3), $F(34) = 18.95, p < .001, \eta^2 = .351$. Virtual presence ratings were also higher after the familiarization session (mean = 13.74, SD = 2.62) than after exploring or being exposed to a novel (mean = 11.62, SD = 2.70; $t(34) = 3.82, p = .001$), or familiar (mean = 11.87, SD = 2.71; $t(34) = 3.81, p = .001$) environment.

We also analyzed the effects of exposure type, session (novel day 2 or

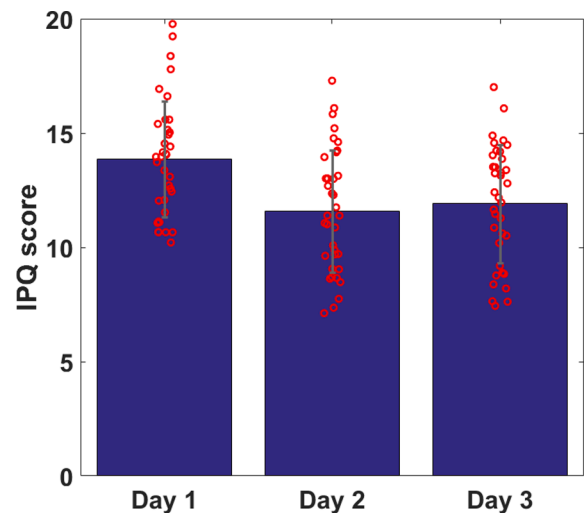


Fig. 6. Mean IPQ virtual presence ratings. Mean IPQ ratings are shown for testing day 1 (the familiarization session), day 2 and day 3. Error bars reflect standard errors of the mean.

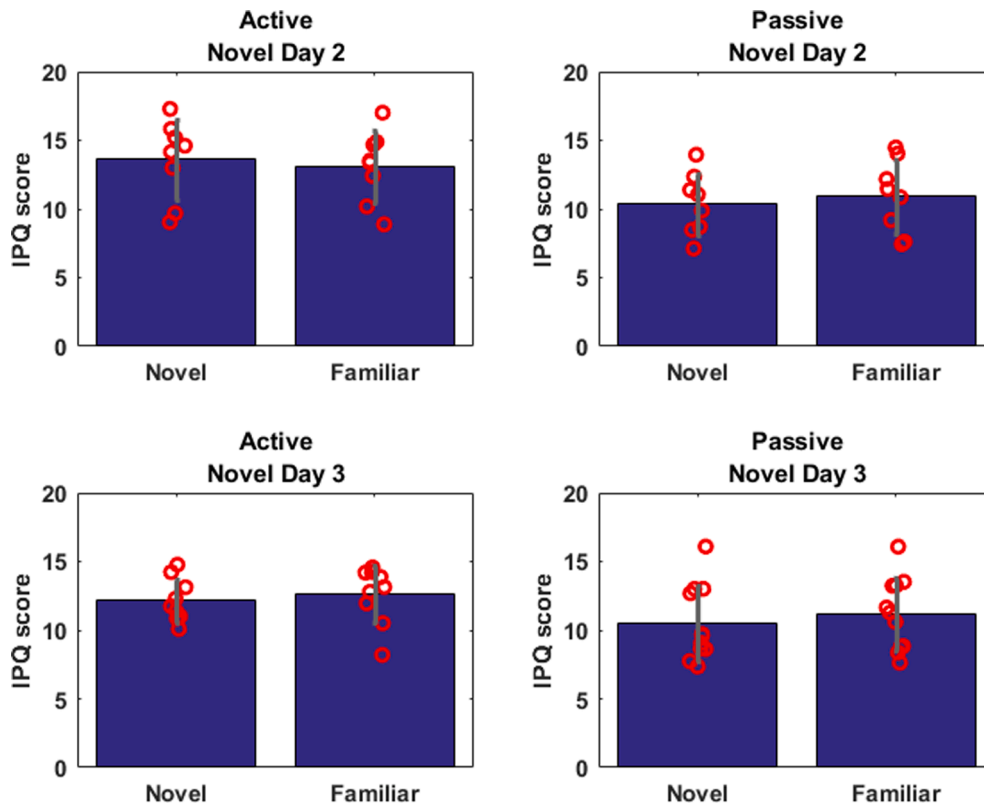


Fig. 7. Mean IPQ virtual presence ratings. Mean IPQ ratings are shown for novel and familiar conditions after both active exploration (left panels) and passive exposure (right panels) for participants who experienced the novel condition on day 2 (top panels) and day 3 (bottom panels) separately. Error bars reflect standard errors of the mean.

3), and novelty. Presence ratings were higher after participants actively explored a VE rather than were passively exposed to the exploration behavior of another participant, $F(1,32) = 7.46, p = .010, \eta^2 = .19$. There was no effect of session ($p = .632$) or novelty ($p = .327$), nor were any interaction effects observed ($ps > .327$).

10. Factors that could influence memory success

We further investigated whether any of the constructs measured by the subjective ratings and the NS questionnaire predicted memory success. The general linear model for both the novel condition (all $ps > .235$) and familiar condition (all $ps > .135$) suggested that none of the predictors contributed to memory success significantly (see Table 2).

11. Discussion

Findings from the current study suggest that memory enhancement by exposure to a novel environment may depend on active exploration behavior. An interaction effect between novelty and exposure type in a mixed model suggested that memory performance for an unrelated word list was higher following active versus passive experience of a novel environment, whereas these effects were reversed for a familiar environment. Bayesian statistics further confirmed that there was weak evidence for an interaction between exposure type and novelty. This suggests that agency may contribute to a temporally extended memory enhancement by novelty. In a recent large cross-sectional study ($n > 400$; manuscript in preparation) we confirmed the beneficial effects of novelty on recall using a similar design, but in that study we only had an active condition. Therefore, future studies will be required to confirm the role of volition observed in the current study

Subjective ratings showed that motivation was higher after exposure to a novel rather than familiar environment. Since motivation ratings

Table 2

General linear model results for the model predicting recall in the novel and familiar conditions. The b-value reflects the regressors' slope.

	Recall: b-value//t-value/p-value
Observations	36 subjects
Novel condition	
Exposure type (dummy)	-.05 / -.81 / .428
Motivation	.04 / .89 / .385
Boredom	-.02 / -.70 / .489
Arousal	-.01 / -.37 / .713
Happiness	-.04 / -.96 / .345
Sadness	-.02 / -.46 / .653
Tiredness	.02 / .45 / .655
Attention	-.06 / -1.22 / .235
Igroup Presence Questionnaire	.01 / .39 / .700
NS	-.02 / -.71 / .487
Familiar condition	
Exposure type (dummy)	.02 / .36 / .723
Motivation	-.04 / -.99 / .330
Boredom	.01 / .34 / .739
Arousal	<.01 / .13 / .897
Happiness	.06 / 1.55 / .135
Sadness	.03 / .88 / .389
Tiredness	.02 / .44 / .662
Attention	-.04 / -1.24 / .226
Igroup Presence Questionnaire	.01 / 1.06 / .300
NS	.01 / .36 / .723

were unaffected by exposure type, it is unlikely that motivation contributed to the effect of active novelty exploration on memory directly. In contrast, as expected, virtual presence ratings were higher after participants actively explored the environment, rather than were passively exposed to it, with no effect of novelty on these ratings. As the IPQ scale measuring virtual presence includes questions regarding agency these findings are expected (Schubert, Friedmann, &

Regenbrecht, 2001), and generally suggest that agency heightened the sense of being in the VE. The reported experience of presence in the VR and ratings of internal states showed no interaction of exploration type and novelty, suggesting that these factors could not have mediated the memory effect. General linear models including the subjective ratings and the NS trait did not reveal any factors contributing to recall performance. This further confirms that the effect of active novelty exploration on memory was not influenced by any of these measures.

An interaction between novelty and exposure type (agency) is in line with a previous study that showed recall benefits after active exploration of a novel compared to a familiar environment (Schomaker, van Bronkhorst, & Meeter, 2014), and two recent studies that failed to find positive effects of novelty on long-term memory and working memory in passive exposure paradigms (Biel & Bunzeck, 2019; Biel et al., 2020). In the Biel & Bunzeck (2019) study, participants were passively exposed to nature videos that were either novel or repeated, but no differences in memory performance on a subsequent word learning task were found. They suggested that a sense of agency is required for novel environments to influence memory performance. Agency, however, was not experimentally manipulated in their study, and the null effect could also have been due to another aspect of their stimulus material or experimental design. The current study now provides weak evidence that active exploration may indeed be a prerequisite for the beneficial effects of novelty on memory for subsequently presented material. A potential mechanism underlying the role of agency could be that active exploration of novel environments induces a theta state, associated with learning rather than recall (Lisman and Otmakhova, 2001; Kaplan et al., 2012), thereby improving learning in the active novel compared to the familiar condition in the present study. Agency has also been shown to be necessary for both immediate and delayed memory effects of reward (Koster, Guitart-Masip, Dolan, Duzel, 2015), which are partly based on similar neuromodulatory processes as the effects of novelty (for reviews, see Lisman, Grace, & Duzel, 2011; Duzel et al., 2010).

Overall memory performance nor the memory effect of active novelty exploration were influenced by individual differences in NS, and NS was not found to be a predictor of memory success in our general linear model. A lack of an effect of NS may be due to our relatively small sample or to the narrow and upwards-shifted range of NS scores in the present study: No participants had a NS score of > 1 SD below the mean normative data (Cloninger, Przybeck, & Svrakic, 1991). This limited variability in the sample could potentially explain why no link between NS and memory performance was observed. Future studies with larger samples and a broader range of NS scores would be required to further elucidate the link between NS, exposure to novelty, and memory.

Overall memory performance was higher for participants who explored or were exposed to a novel environment on day 2 rather than day 3. This could potentially hint towards differences between the two participant groups but could also indicate that the effects of exposure to VR on memory also depend on previous exposure. In line with this hypothesis is the finding that presence and arousal ratings were also higher during the earlier rather than later sessions, while boredom increased over sessions. The effects of repeated exposure on presence, arousal and boredom, however, did not directly influence memory as shown by the regression analyses.

Presence ratings were highest after the familiarization session. In a previous study, we found that higher presence ratings were associated with stronger experimental effects (Schomaker et al., 2014; Schomaker, Tesch, Bülthoff, & Bresciani, 2011), potentially due to higher involvement of participants. In the current study, participants' boredom increased over sessions, possibly reducing involvement and the subjective experience of spatial presence. Another, possibly related, reason for strong spatial presence for the first session may be that there was an additional novelty effect. During the first session, all participants were exposed to the VEs (and VR in general) for the first time, which may have increased the perceived immersion. In line with both interpretations, we found a negative effect for presence ratings from

testing day 1 to the subsequent testing days 2 and 3: When the novelty of exploring a VE was wearing off, boredom increased, and arousal decreased.

A limitation of the current study is that participants in the passive exposure condition were exposed to the exploration behavior of another participant. This other participant may have explored parts of the environment not explored by the participant in the familiarization session, therefore making the familiar passive exposure condition potentially more novel than the active condition (in which people might have explored the same regions again). Possibly, this could explain the finding that memory performance in the familiar condition was better after passive exposure compared to active exploration. However, the environments were small and rather limited, making it unlikely that substantial areas were unexplored after five minutes of familiarization.

A related limitation is that we did not quantify differences in exploration behavior, for example the area covered, walking speed, or overlap between first and second explorations. An estimate of exploration in the active familiar condition could have given us some insight into the exposure to novel parts of the familiar environment and would have allowed us to compare this aspect between the passive and active familiar conditions. It would also be interesting to investigate whether high novelty seekers explore more, and whether this influences the effects of novelty. Future studies could include exploration measures to further elucidate which aspect of exploring a novel environment induces memory benefits (also see: Schomaker, 2019). Future work is also required to identify the specific mechanism (e.g., motivation, attention or arousal) underlying the observed weak effect of active novelty exploration on memory.

To conclude, active exploration of novel environments may promote subsequent encoding of unrelated material more than passive exposure. Our findings are potentially relevant for developing novelty exposure applications to combat age- and disease-related memory decline in the future (Düzel et al., 2010; Schomaker & Meeter, 2015). Active experience may induce beneficial effects, while passive exposure may not. However, future studies are required to confirm this finding as the Bayesian analyses suggested that the effects were not very strong.

CRediT authorship contribution statement

J. Schomaker: Conceptualization, Methodology, Software, Formal analysis, Visualization, Project administration, Funding acquisition. **B. C. Wittmann:** Conceptualization, Methodology, Project administration, Funding acquisition.

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References

- Aly, M., & Turk-Browne, N. B. (2016). Attention promotes episodic encoding by stabilizing hippocampal representations. *Proc Natl Acad Sci USA*, 113(4), E420–E429.
- Ballarini, F., Martínez, M. C., Perez, M. D., Moncada, D., & Viola, H. (2013). Memory in elementary school children is improved by an unrelated novel experience. *PloS one*, 8(6), e66875.
- Ballarini, F., Moncada, D., Martínez, M. C., Alen, N., & Viola, H. (2009). Behavioral tagging is a general mechanism of long-term memory formation. *Proceedings of the National Academy of Sciences*, 106(34), 14599–14604.
- Biel, D., & Bunzeck, N. (2019). Novelty Before or After Word Learning Does Not Affect Subsequent Memory Performance. *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2019.01379>.
- Biel, D., Steiger, T. K., Volkman, T., Jochems, N., & Bunzeck, N. (2020). The gains of a 4-week cognitive training are not modulated by novelty. *Human Brain Mapping*.

- Cloninger, C. R. (1987). A systematic method for clinical description and classification of personality variants: A proposal. *Archives of general psychiatry*, 44(6), 573-588.
- Cloninger, C. R., Przybeck, T. R., & Svrakic, D. M. (1991). *The Tridimensional Personality Questionnaire*. U.S. normative data. Psychological Reports.
- Cloninger, C. R., Svrakic, D. M., & Przybeck, T. R. (1993). A Psychobiological Model of Temperament and Character. *Archives of General Psychiatry*. <https://doi.org/10.1001/archpsyc.1993.01820240059008>.
- Cloninger, C. R. (1986). A unified biosocial theory of personality and its role in the development of anxiety states. *Psychiatric Developments*.
- Davis, C. D. (2004). Novel Environments Enhance the Induction and Maintenance of Long-Term Potentiation in the Dentate Gyrus. *Journal of Neuroscience*, 24(29), 6497-6506. <https://doi.org/10.1523/JNEUROSCI.4970-03.2004>.
- Duszkiewicz, A. J., McNamara, C. G., Takeuchi, T., & Genzel, L. (2019). Novelty and Dopaminergic Modulation of Memory Persistence: A Tale of Two Systems. *Trends in Neurosciences*, 42(2), 102-114.
- Düzel, E., Bunzeck, N., Guitart-Masip, M., & Düzel, S. (2010). NOvelty-related Motivation of Anticipation and exploration by Dopamine (NOMAD): Implications for healthy aging. *Neuroscience & Biobehavioral Reviews*, 34(5), 660-669.
- Fenker, D. B., Frey, J. U., Schuetze, H., Heipertz, D., Heinze, H.-J., & Düzel, E. (2008). Novel Scenes Improve Recollection and Recall of Words. *Journal of Cognitive Neuroscience*, 20(7), 1250-1265.
- Frey, S., & Frey, J. U. (2008). 'Synaptic tagging' and 'cross-tagging' and related associative reinforcement processes of functional plasticity as the cellular basis for memory formation. *Progress in brain research*, 169, 117-143.
- Frey, U., & Morris, R. G. M. (1997). Synaptic tagging and long-term potentiation. *Nature*, 385(6616), 533-536.
- Gavett, B. E., & Horwitz, J. E. (2012). Immediate List Recall as a Measure of Short-Term Episodic Memory: Insights from the Serial Position Effect and Item Response Theory. *Archives of Clinical Neuropsychology*, 27(2), 125-135.
- Kaplan, R., Doeller, C. F., Barnes, G. R., Litvak, V., Düzel, E., Bandettini, P. A., & Burgess, N. (2012). Movement-related theta rhythm in humans: coordinating self-directed hippocampal learning. *PLoS biology*, 10(2), e1001267.
- Kemp, A., & Manahan-Vaughan, D. (2004). Hippocampal long-term depression and long-term potentiation encode different aspects of novelty acquisition. *Proceedings of the National Academy of Sciences*, 101(21), 8192-8197.
- Kempadoo, K. A., Mosharov, E. V., Choi, S. J., Sulzer, D., & Kandel, E. R. (2016). Dopamine release from the locus coeruleus to the dorsal hippocampus promotes spatial learning and memory. *Proc Natl Acad Sci USA*, 113(51), 14835-14840.
- Koster, R., Guitart-Masip, M., Dolan, R. J., & Düzel, E. (2015). Basal Ganglia Activity Mirrors a Benefit of Action and Reward on Long-Lasting Event Memory. *Cereb. Cortex*, 25(12), 4908-4917.
- Koster, R., Seow, T. X., Dolan, R. J., & Düzel, E. (2016). Stimulus novelty energizes actions in the absence of explicit reward. *PLoS One*, 11(7), e0159120.
- Krebs, R. M., Schott, B. H., & Düzel, E. (2009). Personality Traits Are Differentially Associated with Patterns of Reward and Novelty Processing in the Human Substantia Nigra/Ventral Tegmental Area. *Biological Psychiatry*, 65(2), 103-110.
- Lahl, O., Göritz, A. S., Pietrowsky, R., & Rosenberg, J. (2009). Using the World-Wide Web to obtain large-scale word norms: 190,212 ratings on a set of 2,654 German nouns. *Behavior Research Methods*, 41(1), 13-19.
- Li, S., Cullen, W. K., Anwyl, R., & Rowan, M. J. (2003). Dopamine-dependent facilitation of LTP induction in hippocampal CA1 by exposure to spatial novelty. *Nat Neurosci*, 6(5), 526-531.
- Lisman, J. E., & Grace, A. A. (2005). The Hippocampal-VTA Loop: Controlling the Entry of Information into Long-Term Memory. *Neuron*, 46(5), 703-713.
- Lisman, J., Grace, A. A., & Düzel, E. (2011). A neoHebbian framework for episodic memory; role of dopamine-dependent late LTP. *Trends in Neurosciences*, 34(10), 536-547.
- Lisman, J. E., & Otmakhova, N. A. (2001). Storage, recall, and novelty detection of sequences by the hippocampus: Elaborating on the SOCRATIC model to account for normal and aberrant effects of dopamine. *Hippocampus*, 11(5), 551-568.
- Mather, M., & Sutherland, M. R. (2011). Arousal-Biased Competition in Perception and Memory. *Perspect Psychol Sci*, 6(2), 114-133.
- Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behav Res*, 44(2), 314-324.
- McNamara, C. G., & Dupret, D. (2017). Two sources of dopamine for the hippocampus. *Trends in Neurosciences*, 40(7), 383-384.
- Meade, M. E., Meade, J. G., Sauzeon, H., & Fernandes, M. A. (2019). Active navigation in virtual environments benefits spatial memory in older adults. *Brain Sciences*. <https://doi.org/10.3390/brainsci9030047>.
- Misslin, R., & Ropartz, P. (1981). Effects of methamphetamine on novelty-seeking behaviour by mice. *Psychopharmacology*, 75(1), 39-43.
- Moncada, D., Ballarini, F., & Viola, H. (2015). Behavioral Tagging: A Translation of the Synaptic Tagging and Capture Hypothesis. *Neural Plasticity*, 2015, 1-21.
- Moncada, D., & Viola, H. (2007). Induction of Long-Term Memory by Exposure to Novelty Requires Protein Synthesis: Evidence for a Behavioral Tagging. *Journal of Neuroscience*, 27(28), 7476-7481.
- Olson, A. K., Eadie, B. D., Ernst, C., & Christie, B. R. (2006). Environmental enrichment and voluntary exercise massively increase neurogenesis in the adult hippocampus via dissociable pathways. *Hippocampus*, 16(3), 250-260.
- Otmakhova, N., Düzel, E., Deutch, A. Y., & Lisman, J. (2013). The hippocampal-VTA loop: The role of novelty and motivation in controlling the entry of information into long-term memory. In *Intrinsically Motivated Learning in Natural and Artificial Systems*. https://doi.org/10.1007/978-3-642-32375-1_10.
- Plancher, G., Barra, J., Orriols, E., & Piolino, P. (2013). The influence of action on episodic memory: A virtual reality study. *Quarterly Journal of Experimental Psychology*, 66(5), 895-909.
- Robbins, T., & Iversen, S. D. (1973). A dissociation of the effects of d-amphetamine on locomotor activity and exploration in rats. *Psychopharmacologia*, 28(2), 155-164.
- Sajikumar, S., & Frey, J. U. (2004). Late-associativity, synaptic tagging, and the role of dopamine during LTP and LTD. *Neurobiology of Learning and Memory*, 82(1), 12-25. <https://doi.org/10.1016/j.nlm.2004.03.003>.
- Schomaker, J. (2019). Unexplored territory: Beneficial effects of novelty on memory. *Neurobiology of Learning and Memory*, 161, 46-50.
- Schomaker, J., & Meeter, M. (2014). Facilitation of responses by task-irrelevant complex deviant stimuli. *Acta Psychologica*, 148, 74-80.
- Schomaker, J., van Bronkhorst, M. L. V., & Meeter, M. (2014). Exploring a novel environment improves motivation and promotes recall of words. *Frontiers in Psychology*, 5. <https://doi.org/10.3389/fpsyg.2014.00918>.
- Schomaker, J., & Meeter, M. (2012). Novelty Enhances Visual Perception. *PLoS ONE*, 7(12). <https://doi.org/10.1371/journal.pone.0050599>.
- Schomaker, J., Tesch, J., Bühlhoff, H. H., & Bresciani, J.-P. (2011). It is all me: The effect of viewpoint on visual-vestibular recalibration. *Exp Brain Res*, 213(2-3), 245-256.
- Schomaker, J., & Meeter, M. (2015). Short- and long-lasting consequences of novelty, deviance and surprise on brain and cognition. *Neuroscience & Biobehavioral Reviews*, 55, 268-279.
- Schubert, T., Friedmann, F., & Regenbrecht, H. (2001). The Experience of Presence: Factor Analytic Insights. *Presence: Teleoperators & Virtual Environments*, 10(3), 266-281.
- Sierra-Mercado, D., Dieguez, D., Jr., & Barea-Rodriguez, E. J. (2008). Brief novelty exposure facilitates dentate gyrus LTP in aged rats. *Hippocampus*, 18(8), 835-843.
- Straube, T., Korf, V., & Frey, J. U. (2003). Bidirectional modulation of long-term potentiation by novelty-exploration in rat dentate gyrus. *Neuroscience Letters*, 344(1), 5-8.
- Takeuchi, T., Duszkiewicz, A. J., Sonneborn, A., Spooner, P. A., Yamasaki, M., Watanabe, M., Smith, C. C., Fernández, G., Deisseroth, K., Greene, R. W., & Morris, R. G. M. (2016). Locus coeruleus and dopaminergic consolidation of everyday memory. *Nature*, 537(7620), 357-362.
- Wang, S.-H., Redondo, R. L., & Morris, R. G. M. (2010). Relevance of synaptic tagging and capture to the persistence of long-term potentiation and everyday spatial memory. *Proceedings of the National Academy of Sciences*, 107(45), 19537-19542.
- Yamasaki, M., & Takeuchi, T. (2017). Locus Coeruleus and Dopamine-Dependent Memory Consolidation. *Neural Plasticity*, 2017, 1-15.