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Novelty exposure induces stronger sensorimotor representations during a manual adaptation task

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Active exploration of novel spatial environments enhances memory for subsequently presented explicit, declarative information in humans. These effects have been attributed to novelty promoting dopamine release via mesolimbic dopaminergic pathways in the brain. As procedural motor learning has been linked to dopamine as well, we predict that novelty effects extend to this domain. To test this hypothesis, the present study examined whether spatial novelty exploration benefits subsequent sensorimotor adaptation. Participants explored either two different virtual environments (i.e., novelty condition; $n = 210$) or two identical environments (i.e., familiar condition; $n = 253$). They then performed a manual adaptation task in which they had to adapt joystick movements to a visual perturbation. We assessed the rate of adaptation following the introduction of this perturbation, and the rate of deadaptation following its removal. While results showed reliable adaptation patterns and similar adaptation rates across both conditions, individuals in the novelty condition showed slower deadaptation. This suggests that exposure to spatial novelty induced stronger sensorimotor representations during adaptation, potentially through novelty-induced dopaminergic effects in mesocortical and/or nigrostriatal pathways. Novelty exposure may be employed to promote motor learning on tasks that require precision movements in altered sensory contexts, for example, in astronauts moving in microgravity or patients with impaired motor processing.

Keywords: exploration; motor learning; procedural memory; sensorimotor adaptation; spatial novelty

Introduction

Prior work in both animals and humans has shown generalizable beneficial effects of novelty exposure on memory (for a review, see Ref. 1). For example, exposure to a series of pictures of novel rather than familiar scenes before learning a list of unrelated words has been shown to promote recollection for these words.[2] Using virtual reality, Schomaker and colleagues demonstrated that individuals who explored novel virtual environments (VEs) showed better recollection on an unrelated word learning task administered immediately following VE exploration than those who explored familiar VEs.[3] More recent studies have suggested that, in particular, active exploration of spatially novel environments has beneficial effects on memory,[4,5] whereas passive exposure seems less effective.[6,7] Regarding the mechanisms underlying the beneficial effects of the exploration of novel environments, rodent studies suggest that novelty exploration causes signaling from the hippocampus to the substantia nigra/ventral tegmental area, triggering dopamine release, and promoting plasticity in the hippocampus by lowering the threshold for long-term potentiation via a backprojection (a mechanism that is

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covered in several theoretical frameworks: see Refs. 1, 8–10). The locus coeruleus has been identified as another potential source of such dopaminergic signaling.[11,12]

So far, beneficial effects of novelty exploration in humans have mostly been shown for explicit, declarative learning and memory performance known to be associated with hippocampal engagement. It remains an open question whether these effects generalize to other functions that rely on dopaminergic contribution but do not specifically require hippocampal involvement. In the present study, we, therefore, aimed to determine whether, in addition to declarative memory, procedural memory is similarly benefitted by novelty. Specifically, we investigated whether exploring a novel VE benefits subsequent sensorimotor adaptation, which is also thought to involve dopaminergic mechanisms (at least partially; see below). Sensorimotor adaptation refers to our ability to make behavioral adjustments in response to changing environmental or internal demands in order to maintain appropriate, goal-directed motor performance. For example, imagine adjusting to the driving characteristics of a rental car on holiday and then having to readjust when driving in your own car again. While our discrete distinction between explicit, declarative memory versus procedural memory may give the impression that we envisage these types of memory as relating to fully distinct and independent mechanisms, we acknowledge that sensorimotor adaptation is known to involve both implicit and more explicit, declarative processes.[13,14] In the present study, we, therefore, set out to evaluate whether novelty effects extend beyond the nonmotor performance benefits that have been reported thus far, but do not mean to suggest that we differentiate between effects on explicit and implicit contributions to adaptation.

In the laboratory, adaptation has been widely studied using paradigms in which participants adapt their movements to mechanical perturbations (e.g., robotic or treadmill manipulations)[15–17] or to visual perturbations (e.g., prism lenses or rotated feedback).[18–23] In these paradigms, participants first show impairment in their ability to achieve the goal of their movement following initial perturbation. With practice, they learn to adapt their movements to the changed requirements and performance gradually improves. Upon removal of the perturbation, the adapted movement typically persists for a certain period of time, resulting in difficulty with goal-directed movement before a gradual return to regular performance is observed (i.e., deadaptation). Such after-effects are generally observed in the opposite direction of the performance-errors introduced by the perturbation, reflecting that participants learned to compensate for it. Moreover, the after-effects are assumed to be indicative of changes in motor commands that are required to effectively cope with the perturbation, thus showing that a change in sensorimotor representation occurred.

Sensorimotor adaptation has been linked to the involvement of dopaminergic processes. For example, prior neuroimaging work demonstrated that the basal ganglia are involved in adaptation, with the putamen, globus pallidus, and caudate nucleus being engaged during adaptation[23,24] and the putamen being engaged during deadaptation.[23] More indirect indications for dopaminergic involvement come from several studies documenting that patients with Parkinson's disease exhibit impairments in sensorimotor adaptation,[25–28] although some studies have reported normal adaptation.[29–31] Other indications come from genetic studies showing that the rate of sensorimotor adaptation is associated with the number of alleles that an individual carries for genes involved in efficient dopaminergic transmission.[32] Given this dopaminergic link, it seems reasonable that, through the effects of novelty on dopamine, sensorimotor adaptation may benefit from novelty exposure.

Here, we investigated for the first time whether novelty exploration can enhance subsequent sensorimotor adaptation. As part of a public science experiment, we had participants spanning a wide age range complete a manual adaptation task after exploring either two different or two identical VEs, and compared their adaptation performance. The prospect of enhancing adaptation through novelty exploration could have important implications for rehabilitation programs aimed at improving motor performance in stroke patients or those with Parkinson's disease, as well as for training programs that facilitate astronauts to adapt to the microgravity environment during spaceflight and to the 1-*g* environment upon return to Earth. We hypothesized that exploration of a novel rather than familiar environment would improve sensorimotor adaptability. As individuals differ in their tendency to seek and appreciate novelty,[33] and because this

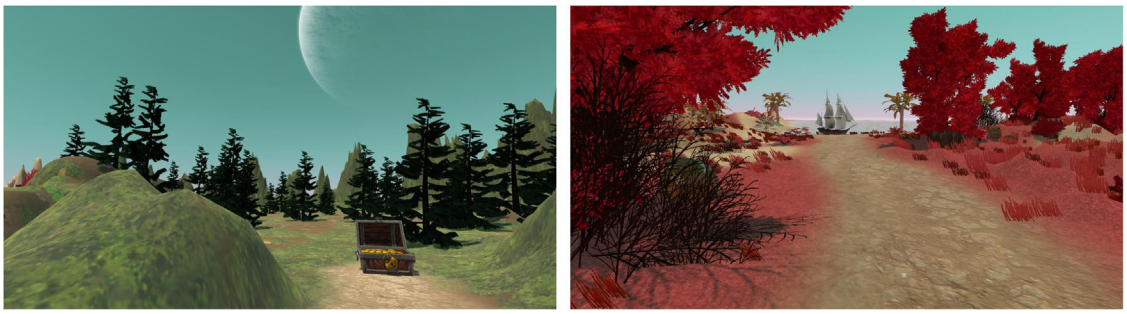

Figure 1. **Screenshots illustrating the two virtual environments that participants freely explored. Both were matched in terms of size, path length, number of intersections, and number of landmarks participants could encounter.**

personality trait has been linked to individual differences in dopaminergic binding potential,[34,35] we also explored the role of novelty seeking in the effect of novelty exploration on adaptation.

Methods

Participants

A total of 483 participants, with a minimum of 8 years of age, enrolled in the study. Several participants had to be excluded due to technical problems ($n = 7$), color blindness ($n = 1$), or failure to follow the sensorimotor adaptation task instructions ($n = 12$). Consequently, our final sample comprised 463 participants, aged 8–73 years old (mean age = 24 ± 16 years; 51% male). According to self-reported data, 412 participants were right-handed, 21 were left-handed, and 10 were ambidextrous. The number of participants assigned to the familiar and novel exploration conditions was 253 and 210, respectively. The study was part of *Science Live*, an innovative research program of the NEMO Science Museum in Amsterdam aimed at allowing visitors to the museum to participate in actual scientific research on a voluntary basis. Written informed consent was obtained from all participants (or their parents in the case of underaged children). The study was approved by the Psychology Research Ethics Committee of Leiden University, the Netherlands.

Novelty manipulation

Two different VEs were created using Unity software (version 2017.2.21f1; see Fig. 1). Both consisted of fantasy islands with unusual landmarks (such as a slot machine; 20 unique landmarks per VE), included land and a body of water, and were matched in terms of size (square of 200 × 200 Unity meters), path length, and number of intersections (nine). In line with indications that active exploration as opposed to passive exposure of spatially novel environments is more effective in eliciting novelty effects, we used a spatial navigation task in which participants explored the VEs themselves. They received scripted verbal instructions regarding how to navigate through the VEs using the keyboard and mouse. More specifically, participants had to press the "w" key (for "walk") to move forward and could use the mouse to rotate and determine heading direction. They were instructed that they could navigate freely but should try to stay on the paths where possible. During the first exploration phase, participants explored one of the two VEs (counterbalanced between participants). In the second exploration phase, those in the familiar condition ($n = 253$) explored the same environment again, whereas those in the novelty condition ($n = 210$) explored another environment. Each exploration phase lasted 3 min; after each phase, participants were asked to indicate their mood and arousal on a 9-point visual analog scale with self-assessment manikins.[36]

Sensorimotor adaptation task

The manual visuomotor adaptation task used in this study has been used extensively to study adaptation.[18,19,22–24,37–40] Participants used a dual-axis joystick (Logitech G Extreme 3D Pro) with their preferred hand to hit targets presented on the laptop screen. The joystick controlled a red circle (i.e., the cursor; diameter = 0.3 cm) that was presented at the central position on the screen when the joystick was centered. At the start of each

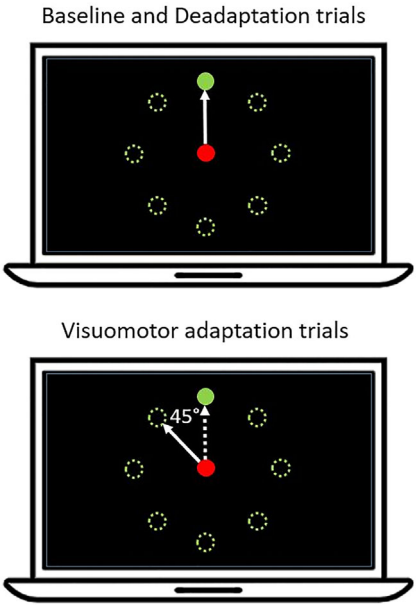

Figure 2. **The task consisted of eight baseline trials, 40 adaptation trials, and 16 deadaptation trials. During baseline and deadaptation trials, the movements of the red cursor followed the exact path of the joystick movement. During visuomotor adaptation trials, the movement of the cursor was rotated by 45° counterclockwise relative to the joystick movement.**

trial, a green target circle (diameter = 0.3 cm) was presented for 1000 ms at one of eight locations 4.6 cm from the center of the screen (Fig. 2). Participants were instructed to move the red circle into the green circle as quickly as possible by moving the joystick, and to relax their force on the joystick handle after target disappearance to allow the cursor to recenter for the next trial. Each movement was initiated from the central position on the screen and the order of the target locations was pseudorandomized such that each target appeared once in every eight trials. Participants could practice the task during eight trials and then completed another eight trials under normal visual feedback (i.e., baseline trials). The next 40 trials were performed under 45° counterclockwise-rotated feedback (i.e., adaptation trials). Finally, participants completed another 16 trials under normal visual feedback, which allowed us to measure the after-effects of adaptation (i.e., deadaptation trials). Stimulus presentation, timing, and data recording were controlled by PsychoPy software (version 1.84.1).

Novelty-seeking questionnaire

To assess individual differences in novelty-seeking personality traits, we used a computerized version of the novelty-seeking scale of the Tridimensional Personality Questionnaire.[33,41] Participants aged 18 years or older completed the original 34-item version; children completed a simplified, abbreviated 20-item version of the questionnaire. The outcome measure was the total novelty-seeking score, with higher scores representing greater novelty seeking. As the 20-item version for children was merely designed to obtain a novelty-seeking estimate that could be communicated as a fun fact following their participation and has not been validated, only the trait scores of adults were included in the analyses reported here.

Procedure

Upon entering the testing room, participants were asked to read an information letter and provide written informed consent; in case the participant was a minor, their parent was asked to complete the consent form. The experimental procedure began by presenting participants with instructions about the first task. They then explored the first VE for 3 min, after which they rated their mood and arousal using the visual analog scales. Next, participants explored either a new or the same VE as before for another 3 min and again completed the visual analog scales. Participants subsequently performed a word learning task, the sensorimotor adaptation task, and a landmark memory task (details and results regarding the word learning and landmark tasks will be reported elsewhere[4]). Finally, participants provided their demographic details and completed the novelty-seeking questionnaire. Following completion of the tasks, participants received a debriefing form and a certificate as a souvenir of their participation. The entire experimental procedure took about 20–25 minutes.

Data processing and analysis

Motor performance was assessed by measuring direction error (DE), defined as the angle between the straight line from the start position to the target and the line from the start position to the cursor's position at the time of peak movement velocity.[18,19,23,37,39,40] Trials in which the DE deviated more than 2.5 standard deviations from the mean were replaced by the mean DE to minimize the influence of such trials.[22,24] This was done per

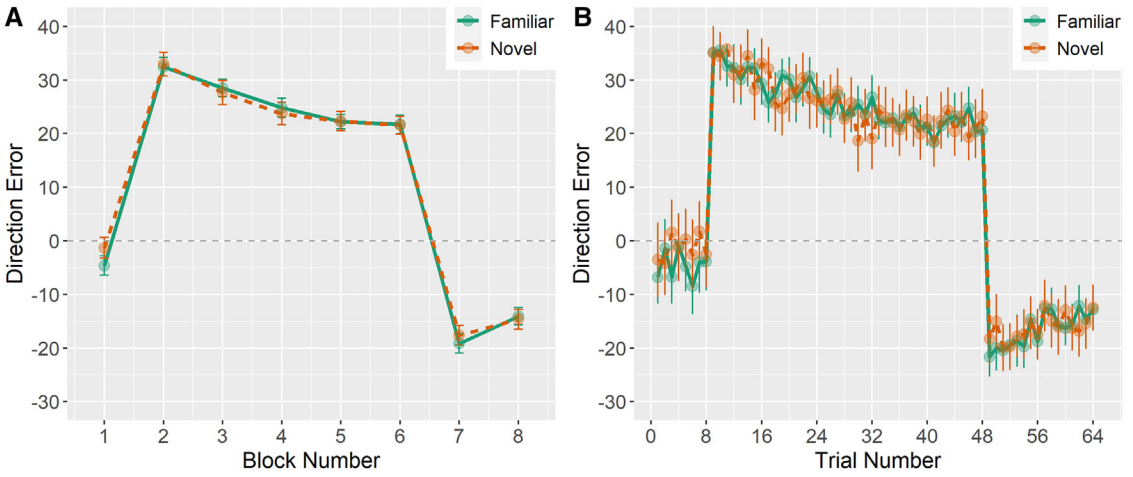

Figure 3. Mean direction error during the various blocks (A; 1 = baseline, 2–6 = adaptation, and 7–8 = deadaptation) and across all trials (B) in the manual adaptation task as a function of familiar versus novel exploration condition. Error bars represent standard errors.

participant and separately for the baseline, adaptation, and deadaptation phases, resulting in the replacement of 2.2% of the trials overall. Furthermore, we determined the rate of adaptation by calculating the decay constant across adaptation trials (fit using an exponential decay function)[20,24,42] and used this score as the primary outcome measure for studying adaptation. We separately determined the adaptation rates across all adaptation trials and across all deadaptation trials.

We used both the traditional null-hypothesis significance testing approach and a Bayesian approach for the adaptation analyses; below, we, therefore, report both *P* values and Bayes factors (BFs). Note that in all adaptation analyses presented here, we included age as a covariate since previous studies have consistently shown age differences in adaptation performance.[40,43–46]

Results

Mood and arousal ratings

To evaluate whether mood and arousal changes could underlie potential effects of novelty exploration, we ran two mixed analyses of covariance (ANCOVA) on the visual analog scale ratings with time (two levels; pre versus post exploration) as a within-subject variable, exploration condition (two levels; novel versus familiar) as a between-subject variable, and age as a covariate. The ratings were available for 446 participants. Results showed that older age was associated with lower arousal ratings ($F(1,443) = 25.23$, $P < 0.001$, $\eta^2_p = 0.05$). There were no significant main or interaction effects of time and exploration condition on either the mood (all Ps > 0.36) or arousal ratings (all Ps > 0.23).

General adaptation patterns

To verify that our data were in line with the general pattern observed in sensorimotor adaptation studies, we performed a mixed ANCOVA on DE with exploration condition (two levels; novel versus familiar) as a between-subjects variable, block (eight repetitions) as a within-subjects variable, and age as a covariate. Results showed an effect of block ($F(7,3220) = 369.15$, $P < 0.001$, $\eta_p{}^2 = 0.44$, BF $>$ 100). Figure 3A shows that, in line with the typical adaptation pattern, participants' performance dropped when the rotated feedback was introduced in the first adaptation block but gradually improved during the subsequent adaptation blocks. When the rotation was removed in the deadaptation blocks, participants had to readapt to the veridical feedback, leading to initial overshooting of the target in the opposite direction of that induced by the perturbation. In line with previous observations, results further showed an effect of age ($F(1,460) = 4.64$, $P = 0.032$, $\eta_p{}^2 = 0.01$, BF $= 0.61$). There was no significant main or interaction effect of exploration condition (Ps > 0.13, BFs $= 0.0008$–0.05), suggesting that novelty exposure did not affect the overall

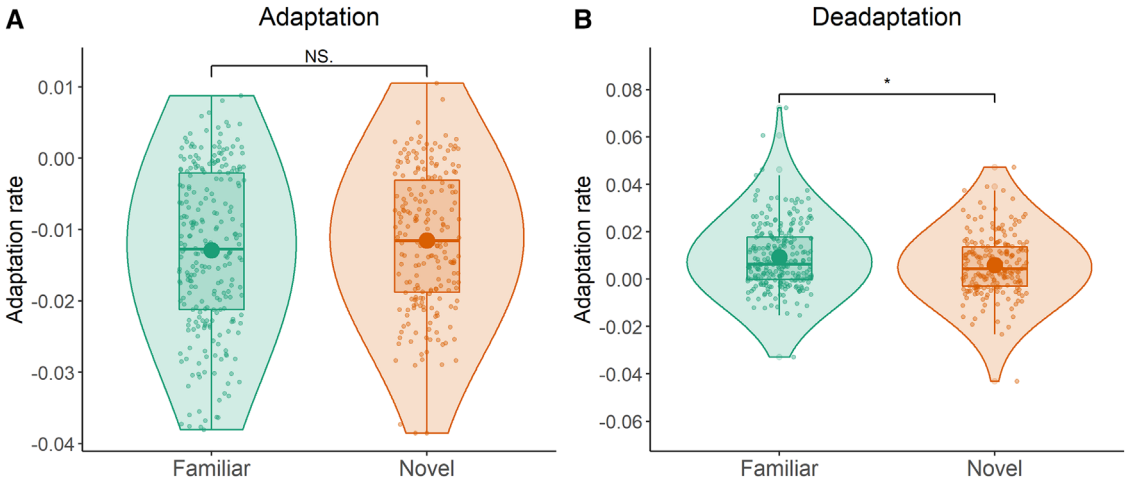

Figure 4. **Adaptation rates across all adaptation trials (A) and deadaptation trials (B) as a function of exploration condition. More negative adaptation rates and more positive deadaptation rates indicate a steeper decay over the trials, that is, faster improvement. Note that the y-axes have different scales.**

pattern of performance. For illustration purposes, we also present the trial-by-trial performance data for the familiar and novel exploration conditions in Figure 3B.

Adaptation rates

Next, we performed a mixed ANCOVA on adaptation rates across all adaptation trials, with exploration condition as a between-subject variable and age as a covariate, in order to examine the effect of novelty exposure on adaptability. Results showed that adaptation rates did not significantly differ between participants in the familiar and novelty conditions (0.013 ± 0.011 versus -0.012 ± 0.010; $P = 0.21$, BF $= 0.22$; Fig. 4A).[a] In line with prior observations, we also found an effect of age on adaptation rate ($F(1,460) = 18.17$, $P < 0.001$, $\eta_p{}^2 = 0.04$, BF > 100). When further examining this effect via a post-hoc quadratic regression analysis, we found that both younger and older age were associated with slower adaptation (see Fig. S1A, online only; $F(2,462) = 41.14$, $P < 0.001$, $r^2 = 0.15$).

We also ran a mixed ANCOVA on adaptation rates across deadaptation trials. Results showed a significant effect of exploration condition ($F(1,460) = 7.27$, $P = 0.007$, $\eta_p{}^2 = 0.02$, BF $= 3.53$). As illustrated in Figure 4B, participants were faster at readapting to the normal feedback after they had explored a familiar environment than a novel environment (0.009 ± 0.013 versus 0.006 ± 0.012), suggesting that a stronger change in sensorimotor representation occurred in the latter group. Again, we found a significant effect of age ($F(1,460) = 9.29$, $P = 0.002$, $\eta_p{}^2 = 0.02$, BF $= 9.47$). Results of a post-hoc quadratic regression analysis showed that both younger and older age were associated with slower deadaptation (see Fig. S1B, online only; $F(2,462) = 13.55$, $P < 0.001$ ($r^2 = 0.06$)).

Finally, we checked whether this pattern of results holds when adjusting for individual differences in initial bias to the rotated feedback. To that end, we reran our ANCOVAs on adaptation rates while including the mean DE from the first adaptation block as an additional covariate. Results confirmed that even when correcting for initial biases, adaptation rates did not significantly differ between participants in the familiar and novelty conditions ($P = 0.32$, BF $= 0.17$). Similarly, results confirmed that participants were significantly faster at readapting to the normal feedback after they had explored a familiar environment than a novel envi-

[a]To test potential differences early on in adaptation, right after the introduction of the rotated feedback, we also ran this analysis on adaptation rates across the eight trials within the first adaptation block. Results showed no effects of exploration condition ($P = 0.30$, BF $= 0.17$) nor age ($P = 0.65$, BF $= 0.11$), suggesting that initial adaptation was similar across participants.

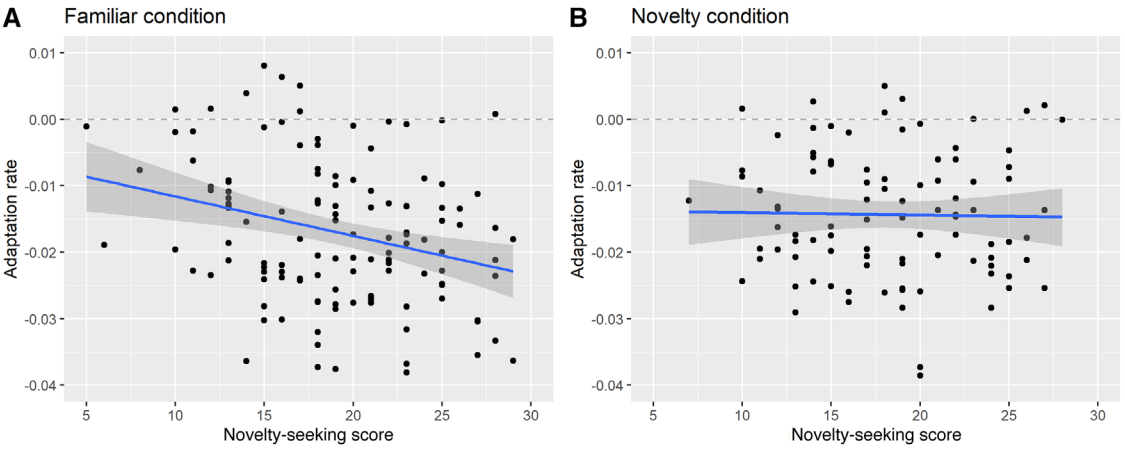

Figure 5. **Scatter plots showing the association between novelty-seeking scores and adaptation rates across all adaptation trials for individuals in the familiar (A) and the novel (B) exploration conditions.**

ronment, even when correcting for initial biases ($F(1,459) = 7.12, P = 0.008, \eta_p{}^2 = 0.015$, BF = 3.48).

Role of novelty-seeking personality

As mentioned above, analyses on novelty-seeking scores were based on data from adults only ($n = 220$; mean age = 38 ± 12 years; 50% male). Results of an independent *t*-test showed that scores did not differ significantly between participants in the novel and familiar exploration conditions (18.3 versus 18.9, respectively; $P = 0.37$). We ran regression analyses to evaluate whether individual differences in the novelty-seeking personality trait were predictive of adaptation rates for participants in the novel and familiar conditions. Results showed that steeper adaptation rates across all adaptation trials were associated with higher novelty-seeking scores for participants in the familiar condition (Fig. 5A; $\beta = -0.287, t(125) = -3.34, P = 0.001, r^2 = 0.08$), but not the novelty condition ($P = 0.85$; Fig. 5B). An additional regression that included the exploration condition × novelty-seeking score interaction term confirmed that the regression coefficients for the familiar and novelty conditions were significantly different ($t(219) = -2.04, P = 0.042$). There were no significant associations between novelty-seeking scores and adaptation rates in the deadaptation phase (familiar $P = 0.93$; novel $P = 0.53$).

Discussion

In the present study, we investigated whether the beneficial effects of novelty exposure on memory in humans extend beyond the declarative domain and also apply to the procedural, motor domain. Our findings support that the exploration of a spatially novel VE improves sensorimotor adaptation in humans. Interestingly, although novelty did not affect the rate of adaptation, we observed that subsequent deadaptation (when participants were performing under veridical feedback again) was slower when participants had previously explored a novel versus a familiar environment. Importantly, this effect of novelty was not confounded by changes in mood/arousal following exploration. In line with prior observations, we further found that age had a quadratic relationship with adaptation rates, such that adaptability was poorer in both younger[43,45] and older ages.[40,44,46] Our findings demonstrate that novelty exploration strengthened the sensorimotor representation that was created when feedback was rotated during performance, as became evident *after* removal of the perturbation. We thus observed beneficial effects of novelty during deadaptation and not during adaptation itself. This suggests that novelty influenced the strength of the updated visuomotor representation, rather than the rate at which it developed—similar to studies finding beneficial effects of novelty on the persistence of declarative memory.[1,47]

Prior work revealed that novelty exploration promotes the consolidation of declarative memories through dopaminergic pathways.[1,12,48] Specifically, these studies have identified mesolimbic dopaminergic pathways in the brain to underlie beneficial

effects on semantic and episodic memory. However, the link between novelty exposure and procedural learning in humans has not previously been investigated. Sensorimotor functioning, including adaptation as assessed in the current task, is more strongly associated with mesocortical and nigrostriatal dopamine.[49–51] Although the role of these latter dopaminergic pathways in novelty processing has been investigated less extensively compared with mesolimbic pathways, there are studies hinting at their involvement as well. For example, mesocortical pathways have been linked to novelty-induced locomotor activity in rodents,[52] suggesting that novelty can influence motor behavior through this pathway. In addition, other rodent work suggests that exposure to environmental novelty increases dopaminergic functioning in nigrostriatal pathways.[53] The beneficial effect of novelty on sensorimotor adaptation in the current study could thus potentially be explained by novelty-induced dopamine increases in these mesocortical and/or nigrostriatal pathways. This seems reasonable, as prior work on the neural correlates of sensorimotor adaptation has demonstrated the involvement of frontal cortical and basal ganglia areas during both adaptation and deadaptation, which, respectively, would be linked to the mesocortical and nigrostriatal pathways.

While our findings on the beneficial effect of novelty exposure on deadaptation extend beyond previous (nonmotor) studies in this area, an open question remains to what extent novelty affected strategy use and explicit versus implicit processes of adaptation. Future experimental designs and paradigms should, therefore, aim at elucidating the mechanistic nature of novelty effects on motor adaptation by disentangling effects on implicit and explicit processes contributing to adaptation. A challenge in this endeavor may be that while there is broad agreement on the existence of these two distinct processes, their exact relationship and how they jointly contribute to adaptation remains unclear.[54] Replication of the present work with different degrees of rotation or other adaptation paradigms (e.g., gradual rotation and clamped feedback) that can dissociate explicit and implicit processes will contribute to a more comprehensive understanding of beneficial effects of novelty exposure on motor performance.

When examining the role of individual differences in novelty-seeking personality traits—which positron emission tomography studies have previously linked to dopaminergic binding potential[34,35]—we found that participants in the familiar condition who scored higher on novelty seeking showed faster adaptation. The association between trait scores and adaptation rates was not significant for participants in the novelty condition. We propose that this may be linked to the differential involvement of exploration strategies and trial-and-error processes in adaptation between the two groups. Learning in a reaching task can be characterized by a trade-off between exploration and exploitation,[13,14] where individuals initially use strategic processes to discover which actions may yield task success (i.e., exploration). Once they have identified a solution, it is reinforced over time through intrinsic reward associated with the successful outcome of the movement (i.e., exploitation). We suggest that for individuals in the familiar condition, those who scored higher on novelty seeking were inclined to use more exploration strategies during the adaptation task, contributing to faster adaptation. For individuals in the novelty condition, preferences for seeking out novelty were already satisfied via the novelty manipulation, where they actively explored two different VEs and, therefore, did not further drive adaptation strategies during the subsequent sensorimotor adaptation task.

A notable strength of the present study is its sample size, which greatly exceeds those reported in prior investigations on novelty effects, as well as sensorimotor adaptation. Furthermore, the fact that we observed the typical adaptation pattern supports the notion that the experimental paradigm translates to settings outside of a controlled laboratory. It may, therefore, be considered a more realistic reflection of the effect of novelty exposure on sensorimotor adaptation in the real world. At the same time, it could be argued that the participants' visit to the interactive museum automatically resulted in a certain degree of exposure to novelty and mood/arousal stimulation prior to participating in this study. As this would have affected participants in both the familiar and novelty conditions, the fact that we found beneficial effects of novelty exploration suggests that there was

still sufficient room for this manipulation to impact performance. Furthermore, results of the visual analog scale ratings ruled out potential confounding effects of mood and arousal.

Future studies should test whether the observed effects of novelty on sensorimotor adaptation generalize to other types of motor performance (e.g., sequence learning). Another question remains whether spatial novelty exploration could also benefit retention and savings of learning. Participants in the present study performed the visuomotor adaptation task only once, but previous studies have shown that participants adapt faster when they are exposed to the same perturbation in a later session. This suggests that changes in sensorimotor representations after adaptation and/or memories of adaptation strategies can outlast the initial training session. Indeed, savings of adaptation have been observed 1 day after initial performance,[55,56] several months later,[15,24,57] and even as much as 1 year after initial adaptation.[58] Future studies could investigate whether novelty exploration can positively impact the amount of savings and/or prolong the period during which the obtained motor representations can be retrieved.

In conclusion, we demonstrated for the first time that the beneficial effects of novelty exploration, which have been observed for declarative memory performance, also extend to the procedural domain. These results could have implications for the design of neuropsychological rehabilitation or other training programs targeted at sensorimotor adaptation and motor learning. Specifically, such programs may be optimized by including novelty exposure to accelerate the creation of strong sensorimotor representations, for example, in clinical populations (e.g., split-belt adaptation in stroke patients or prism adaptation in neglect patients)[59] or specific professions (e.g., astronauts). In addition, our results may allow for the development of novelty-exposure interventions that can potentially counteract and/or slow age-related declines in motor learning. Future studies should further examine the long-term beneficial effects of novelty and examine savings of adaptation.

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Author contributions

M.R. and J.S. conceived, designed, and coordinated the study, and were involved in data collection. V.K. and R.S. contributed to study design and data interpretations. M.R., V.K., and J.S. contributed to data processing. M.R. performed statistical analyses, wrote the first draft, and takes responsibility for the integrity of information presented. All authors reviewed the manuscript and approved the final version.

Supporting information

Additional supporting information may be found in the online version of this article.

Figure S1. Scatter plots showing the association between age and adaptation rates across all adaptation trials (A) and deadaptation trials (B). More negative adaptation rates and more positive deadaptation rates indicate a steeper decay over the trials, that is, faster improvement. Note that the y-axes have different scales.

Competing interests

The authors declare no competing interests.

References

1. Schomaker, J. 2019. Unexplored territory: beneficial effects of novelty on memory. *Neurobiol. Learn. Mem.* **161:** 46–50.
2. Fenker, D.B., J.U. Frey, H. Schuetze, *et al.* 2008. Novel scenes improve recollection and recall of words. *J. Cogn. Neurosci.* **20:** 1250–1265.
3. Schomaker, J., M.L.V. van Bronkhorst & M. Meeter. 2014. Exploring a novel environment improves motivation and promotes recall of words. *Front. Psychol.* **5:** 918.
4. Schomaker, J., V. Baumann & M.F.L. Ruitenberg. 2021. Effects of exploring a novel environment on memory across the lifespan. PsyArXiv preprint. https://doi.org/10.31234/osf.io/r2tdn.
5. Schomaker, J. & B.C. Wittmann. 2021. Effects of active exploration on novelty-related declarative memory enhancement. *Neurobiol. Learn. Mem.* **179:** 107403.
6. Biel, D. & N. Bunzeck. 2019. Novelty before or after word learning does not affect subsequent memory performance. *Front. Psychol.* **10:** 1379.

7. Biel, D., T.K. Steiger, T. Volkmann, *et al.* 2020. The gains of a 4-week cognitive training are not modulated by novelty. *Hum. Brain Mapp.* **41:** 2596–2610.
8. Düzel, E., N. Bunzeck, M. Guitart-Masip, *et al.* 2010. NOvelty-related motivation of anticipation and exploration by dopamine (NOMAD): implications for healthy aging. *Neurosci. Biobehav. Rev.* **34:** 660–669.
9. Gruber, M.J. & C. Ranganath. 2019. How curiosity enhances hippocampus-dependent memory: the prediction, appraisal, curiosity, and exploration (PACE) framework. *Trends Cogn. Sci.* **23:** 1014–1025.
10. Schomaker, J. & M. Meeter. 2015. Short- and long-lasting consequences of novelty, deviance and surprise on brain and cognition. *Neurosci. Biobehav. Rev.* **55:** 268–279.
11. Kempadoo, K.A., E.V. Mosharov, S.J. Choi, *et al.* 2016. Dopamine release from the locus coeruleus to the dorsal hippocampus promotes spatial learning and memory. *Proc. Natl. Acad. Sci. USA* **113:** 14835–14840.
12. McNamara, C.G. & D. Dupret. 2017. Two sources of dopamine for the hippocampus. *Trends Neurosci.* **40:** 383–384.
13. McDougle, S.D., R.B. Ivry & J.A. Taylor. 2016. Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends Cogn. Sci.* **20:** 535–544.
14. Taylor, J.A., J.W. Krakauer & R.B. Ivry. 2014. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J. Neurosci.* **34:** 3023–3032.
15. Shadmehr, R. & T. Brashers-Krug. 1997. Functional stages in the formation of human long-term motor memory. *J. Neurosci.* **17:** 409–419.
16. Malone, L.A., E.V.L. Vasudevan & A.J. Bastian. 2011. Motor adaptation training for faster relearning. *J. Neurosci.* **31:** 15136–15143.
17. Morton, S.M. & A.J. Bastian. 2006. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J. Neurosci.* **26:** 9107–9116.
18. Anguera, J.A., P.A. Reuter-Lorenz, D.T. Willingham, *et al.* 2010. Contributions of spatial working memory to visuomotor learning. *J. Cogn. Neurosci.* **22:** 1917–1930.
19. Anguera, J.A., P.A. Reuter-Lorenz, D.T. Willingham, *et al.* 2011. Failure to engage spatial working memory contributes to age-related declines in visuomotor learning. *J. Cogn. Neurosci.* **23:** 11–25.
20. Morehead, J.R., S.E. Qasim, M.J. Crossley, *et al.* 2015. Savings upon re-aiming in visuomotor adaptation. *J. Neurosci.* **35:** 14386–14396.
21. Morton, S.M. & A.J. Bastian. 2004. Prism adaptation during walking generalizes to reaching and requires the cerebellum. *J. Neurophysiol.* **92:** 2497–2509.
22. Ruitenberg, M.F.L., Y.E. De Dios, N.E. Gadd, *et al.* 2018. Multi-day adaptation and savings in manual and locomotor tasks. *J. Motor Behav.* **50:** 517–527.
23. Seidler, R.D., D.C. Noll & P. Chintalapati. 2006. Bilateral basal ganglia activation associated with sensorimotor adaptation. *Exp. Brain Res.* **175:** 544–555.
24. Ruitenberg, M.F.L., V. Koppelmans, Y.E. De Dios, *et al.* 2018. Neural correlates of multi-day learning and savings in sensorimotor adaptation. *Sci. Rep.* **8:** 14286.
25. Contreras-Vidal, J.L. & E.R. Buch. 2003. Effects of Parkinson's disease on visuomotor adaptation. *Exp. Brain Res.* **150:** 25–32.
26. Mollaei, F., D.M. Shiller & V.L. Gracco. 2013. Sensorimotor adaptation of speech in Parkinson's disease. *Mov. Disord.* **28:** 1668–1674.
27. Mongeon, D., P. Blanchet & J. Messier. 2013. Impact of Parkinson's disease and dopaminergic medication on adaptation to explicit and implicit visuomotor perturbations. *Brain Cogn.* **81:** 271–282.
28. Paquet, F., M.A. Bedard, M. Levesque, *et al.* 2008. Sensorimotor adaptation in Parkinson's disease: evidence for a dopamine dependent remapping disturbance. *Exp. Brain Res.* **185:** 227–236.
29. Cressman, E.K., D. Salomonczyk, A. Constantin, *et al.* 2021. Proprioceptive recalibration following implicit visuomotor adaptation is preserved in Parkinson's disease. *Exp. Brain Res.* **239:** 1551–1565.
30. Leow, L.A., A. De Rugy, A.M. Loftus, *et al.* 2013. Different mechanisms contributing to savings and anterograde interference are impaired in Parkinson's disease. *Front. Hum. Neurosci.* **7:** 55.
31. Leow, L.A., A.M. Loftus & G.R. Hammond. 2012. Impaired savings despite intact initial learning of motor adaptation in Parkinson's disease. *Exp. Brain Res.* **218:** 295–304.
32. Noohi, F., N.B. Boyden, Y. Kwak, *et al.* 2014. Association of COMT val158met and DRD2 G>T genetic polymorphisms with individual differences in motor learning and performance in female young adults. *J. Neurophysiol.* **111:** 628–640.
33. Cloninger, C.R. 1987. A systematic method for clinical description and classification of personality variants: a proposal. *Arch. Gen. Psychiatry* **44:** 573–588.
34. Suhara, T., F. Yasuno, Y.Y. Sudo, *et al.* 2001. Dopamine D2 receptors in the insular cortex and the personality trait of novelty seeking. *Neuroimage* **13:** 891–895.
35. Zald, D.H., R.L. Cowan, P. Riccardi, *et al.* 2008. Midbrain dopamine receptor availability is inversely associated with novelty-seeking traits in humans. *J. Neurosci.* **28:** 14372–14378.
36. Bradley, M.M. & P.J. Lang. 1994. Measuring emotion: the self-assessment manikin and the semantic differential. *J. Behav. Ther. Exp. Psychiatry* **25:** 49–59.
37. Lametti, D.R., M.Y. Quek, C.B. Prescott, *et al.* 2020. The perils of learning to move while speaking: one-sided interference between speech and visuomotor adaptation. *Psychon. B Rev.* **27:** 544–552.
38. Mazzoni, P. & J.W. Krakauer. 2006. An implicit plan overrides an explicit strategy during visuomotor adaptation. *J. Neurosci.* **26:** 3642–3645.
39. Seidler, R.D. 2005. Differential transfer processes in incremental visuomotor adaptation. *Motor Control* **9:** 40–58.
40. Seidler, R.D. 2006. Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Res. Bull.* **70:** 337–346.
41. Cloninger, C.R., T.R. Przybeck & D.M. Svrakic. 1991. The Tridimensional Personality Questionnaire: U.S. normative data. *Psychol. Rep.* **69:** 1047–1057.

42. Zarahn, E., G.D. Weston, J. Liang, *et al.* 2008. Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. *J. Neurophysiol.* **100:** 2537–2548.
43. Rossi, C., C.W. Chau, K.A. Leech, *et al.* 2019. The capacity to learn new motor and perceptual calibrations develops concurrently in childhood. *Sci. Rep.* **9:** 9322.
44. Seidler, R.D. 2007. Aging affects motor learning but not savings at transfer of learning. *Learn. Mem.* **14:** 17–21.
45. Vasudevan, E.V.L., G. Torres-Oviedo, S.M. Morton, *et al.* 2011. Younger is not always better: development of locomotor adaptation from childhood to adulthood. *J. Neurosci.* **31:** 3055–3065.
46. Wolpe, N., J.N. Ingram, K.A. Tsvetanov, *et al.* 2020. Age-related reduction in motor adaptation: brain structural correlates and the role of explicit memory. *Neurobiol. Aging* **90:** 13–23.
47. Baumann, V., T. Birnbaum, C. Breitling-Ziegler, *et al.* 2020. Exploration of a novel virtual environment improves memory consolidation in ADHD. *Sci. Rep.* **10:** 21453.
48. Duszkiewicz, A.J., C.G. McNamara, T. Takeuchi, *et al.* 2019. Novelty and dopaminergic modulation of memory persistence: a tale of two systems. *Trends Neurosci*. **42:** 102–114.
49. Hosp, J.A. & A.R. Luft. 2013. Dopaminergic meso-cortical projections to M1: role in motor learning and motor cortex plasticity. *Front. Neurol.* **4:** 145.
50. Matsumoto, N., T. Hanakawa, S. Maki, *et al.* 1999. Nigrostriatal dopamine system in learning to perform sequential motor tasks in a predictive manner. *J. Neurophysiol.* **82:** 978–998.
51. Sommer, W.H., R.M. Costa & A.C. Hansson. 2014. Dopamine systems adaptation during acquisition and consolidation of a skill. *Front. Integr. Neurosci.* **8:** 87.
52. Hooks, M.S. & P.W. Kalivas. 1995. The role of mesoaccumbens-pallidal circuitry in novelty-induced behavioral activation. *Neuroscience* **64:** 587–597.
53. Bardo, M.T., S.L. Bowling & R.C. Pierce. 1990. Changes in locomotion and dopamine neurotransmission following amphetamine, haloperidol, and exposure to novel environmental stimuli. *Psychopharmacology* **101:** 338–343.
54. Maresch, J., L. Mudrik & O. Donchin. 2021. Measures of explicit and implicit in motor learning: what we know and what we don't. *Neurosci. Biobehav. Rev.* **128:** 558–568.
55. Seidler, R.D., B.S. Gluskin & B. Greeley. 2017. Right prefrontal cortex transcranial direct current stimulation enhances multi-day savings in sensorimotor adaptation. *J. Neurophysiol.* **117:** 429–435.
56. Villalta, J.I., S.M. Landi, A. Fló, *et al.* 2015. Extinction interferes with the retrieval of visuomotor memories through a mechanism involving the sensorimotor cortex. *Cereb. Cortex* **25:** 1535–1543.
57. Bock, O., S. Schneider & J. Bloomberg. 2001. Conditions for interference versus facilitation during sequential sensorimotor adaptation. *Exp. Brain Res.* **138:** 359–365.
58. Landi, S.M., F. Baguear & V. Della-Maggiore. 2011. One week of motor adaptation induces structural changes in primary motor cortex that predict long-term memory one year later. *J. Neurosci.* **31:** 11808–11813.
59. Roemmich, R.T. & A.J. Bastian. 2018. Closing the loop: from motor neuroscience to neurorehabilitation. *Annu. Rev. Neurosci.* **41:** 415–429.