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Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest

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ABSTRACT

In cities, the incidence of mental disorders is higher, while visits to nature have been reported to benefit mental health and brain function. However, there is a lack of knowledge about how exposure to natural and urban environments affects brain structure. To explore the causal relationship between exposure to these environments and the hippocampal formation, 60 participants were sent on a one hour walk in either a natural (forest) or an urban environment (busy street), and high-resolution hippocampal imaging was performed before and after the walks. We found that the participants who walked in the forest had an increase in subiculum volume, a hippocampal subfield involved in stress response inhibition, while no change was observed after the urban walk. However, this result did not withstand Bonferroni correction for multiple comparisons. Furthermore, the increase in subiculum volume after the forest walk was associated with a decrease in self-reported rumination. These results indicate that visits to nature can lead to observable alterations in brain structure, with potential benefits for mental health and implications for public health and urban planning policies.

This work was funded by the Max Planck Society. The study was approved by the Local Psychological Ethical Committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany (LPEK-0054). All methods were performed in accordance with the relevant guidelines and regulations. We obtained written informed consent from all participants, and they received monetary compensation.

1. Introduction

It has been repeatedly shown that mental health problems, such as anxiety disorders, schizophrenia, and depression, are more common in cities than in rural areas (Peen et al., 2007; Ventriglio et al., 2021). Moreover, a growing body of research demonstrates that visiting natural environments enhances mental health (Barnes et al., 2019; Berto, 2014; White, 2019). Even brief exposures to nature have a positive impact on mood by increasing positive affect and decreasing negative affect (McMahan and Estes, 2015). Negative affect, in particular depressivity, is related to rumination (Spasojević and Alloy, 2001; Watkins, 2008), a maladaptive pattern of negative self-referential thinking that can predict the onset of depression (Watkins, 2008). Previous research suggests that a nature walk of 90-min (Bratman et al., 2015) or even 30-min (Lopes et al., 2020) can decrease rumination. However, only few studies have examined the neural mechanisms underlying these beneficial effects of nature on rumination and mental health. In a seminal study, it was demonstrated that a walk in nature reduced both rumination and activity in the subgenual prefrontal cortex, suggesting that nature may be beneficial for this brain region linked to self-referential thoughts (Bratman et al., 2015). We have recently shown that a one hour walk in a forest decreased activity in the amygdala, a brain region associated with stress processing, likewise suggesting that nature has salutogenic effects on brain health (Sudimac et al., 2022). Although these studies provide insights into how exposure to natural and urban environments affects brain function, little is known about the effects on brain structure.

Multiple studies have demonstrated that living close to natural environments is positively associated with brain structural health metrics, such as cortical thickness and grey matter volume, suggesting that nature may have salutogenic effects on brain structure (Besser, 2021; Crous-Bou, 2020; Dadvand, 2018; Kühn, 2023; Xu, 2023). A study involving older adults identified a positive correlation between the extent of residential green spaces and increased grey matter volume in the perigenual/subgenual anterior cingulate cortex (pACC/sACC), a

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brain region associated with depression (Kühn et al., 2021a). Along the same line, a cross-sectional study examining differences in brain structure associated with the environment during ontogenetic upbringing showed that hippocampal and parahippocampal formation was larger in adolescents who were raised exclusively in rural areas than in those who were exclusively raised in cities (Kühn et al., 2020). Conversely, long-term exposure to air pollution, more prevalent in urban settings, has been linked to reduced grey matter volume in the frontal cortex and left amygdala (Xu et al., 2023), as well as the left hippocampus (Hedges et al., 2019) in middle-aged and older adults. While these cross-sectional and correlational studies highlight associations between environmental factors and brain structure, they do not provide information on the causality of these associations. To rigorously investigate the causal effects of exposure to natural and urban environments on brain structure, intervention studies are needed. However, to the best of our knowledge, such studies exploring these causal relationships have not to date been conducted. Therefore, in the current study we aim to examine the casual relationship between the physical environment and brain structure.

Even though it is generally assumed that brain structure is relatively stable, several studies have shown rapid changes in structural magnetic resonance imaging (MRI) markers. Namely, spending more time outdoors 24 hours before MRI scanning seems to have a substantial impact on grey matter volume in dorsolateral prefrontal cortex (Kühn et al., 2021b). Along the same line, microstructural changes in the hippocampus and parahippocampus were detected already after two hours of performing a spatial learning task (Sagi et al., 2012). Furthermore, in a recent study in which participants were viewing pictures while structural images were taken in MRI, structural enlargement was found in the visual cortex after less than 263 seconds (Månsson et al., 2020). Given these findings, which suggest a greater degree of plasticity in brain structure than previously assumed, our objective is to explore the changes in brain structure following a short-term exposure to either a natural or an urban environment. In this study we aim to focus on the hippocampal formation, since the hippocampus has previously been associated with the physical environment during upbringing (Kühn et al., 2020) and is known for its potential to display rapid structural reorganization (Sagi et al., 2012). Therefore, in order to investigate the causal effects of the physical environment on brain structure, we set out to examine how a one hour exposure to a natural vs. an urban environment may impact the hippocampal formation. Furthermore, as a walk in nature decreases rumination (Bratman et al., 2015; Lopes et al., 2020), and ruminative thoughts have been associated with the hippocampus (Figueroa et al., 2017; Harel et al., 2016; Mandell et al., 2014), our research also probes the relationship between these structural changes and shifts in rumination, potentially offering groundbreaking insights into environmental neuroscience.

2. Materials and methods

2.1. Subjects

A sample size calculation conducted with G*Power indicated that 54 participants are necessary to achieve a medium effect size in a two-way mixed ANOVA, with a significance level set at 0.05. We opted to recruit an additional nine participants to ensure that exclusions or incomplete data would not reduce our sample size below the number we initially agreed upon. We recruited 63 participants in total, randomly assigning them to either a forest walk or a city walk, while ensuring an equal distribution of men and women. Two participants were excluded due to missing data after the walk, and one participant was excluded due to an error in image processing, resulting in a total of 60 participants (29 women, total mean age = 27.31 years, *SD* = 6.74, age range = 18–47 years; 30 participants in the nature walk condition; 30 participants in the urban walk condition).

The two groups did not show significant differences in terms of age, occupation, education, income, or the proportion of participants who grew up in a city. Supplementary Table S1 in the Supplementary Information provides an overview of the control variables for both conditions. Participants were informed that they would be part of an MRI study involving walking but were not told the specific research question. All participants were German-speaking, right-handed, and had no known neurological disorders.

The study received approval from the Local Psychological Ethical Committee at the Center for Psychosocial Medicine, University Medical Center Hamburg-Eppendorf, Hamburg, Germany (LPEK-0054). All procedures adhered to the relevant guidelines and regulations.

2.2. Study procedure

The data collection was conducted from late summer to fall of 2019, between 10:00 a.m. and 5:00 p.m. A flowchart illustrating the study's procedure is shown in Fig. 1. When participants arrived, they signed informed consent forms, completed questionnaires, and engaged in a working memory task. Following this, they underwent an fMRI scan, which included a resting state sequence and questions related to rumination (Brose et al., 2011; Kühn et al., 2013, 2014), a high-resolution hippocampal imaging sequence, and the Fearful Faces Task (Mattavelli et al., 2014). After the hippocampal sequence, the session concluded with the Montreal Imaging Stress Task (Dedovic et al., 2005). The fMRI results from the Fearful Faces Task, the Montreal Imaging Stress Task, as well as the behavioural data, were previously reported (Sudimac et al., 2022; Sudimac and Kühn, 2022).

After the initial scanning session, participants were randomly assigned to take a one-hour walk in either a natural or urban environment (Fig. 2). While the definitions of "natural" and "urban" environments can be debated (Karmanov and Hamel, 2008), in this study, the "natural environment" refers to an urban forest, Berlin's largest green space. Covering over 3000 hectares, Grunewald forest predominantly consists of coniferous trees and Betulaceae. The path had no built structures and was free from traffic noise. Grunewald is a recreational forest with numerous paths used for walking, jogging, or cycling. Participants walked along Teltower Weg in Grunewald forest, starting at the intersection of Königsweg and Teltower Weg, heading north through the forest. The "urban environment" in this study refers to a busy street in one of Berlin's city central areas, featuring traffic and numerous shopping malls. Specifically, the urban walk took place on Schloßstraße, a busy street in Berlin-Steglitz. Schloßstraße has two to four traffic lanes and is one of Berlin's major shopping districts, featuring three shopping malls and three subway stations. Participants were dropped off at Schloßstraße 84 and walked northeast toward Rheinstraße. They walked along the sidewalk, observing other people, traffic, buildings, shopping

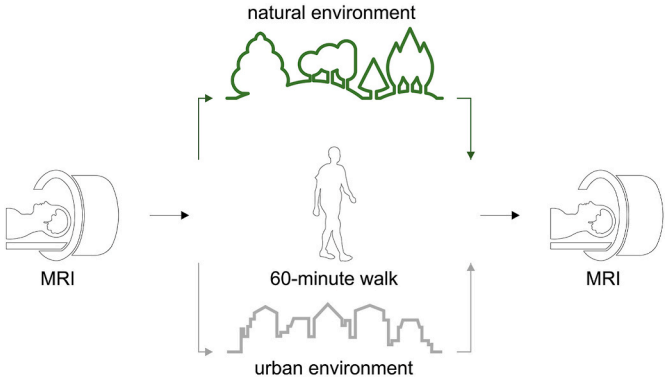

Fig. 1. Flowchart depicting the study procedure. Initially, participants underwent an MRI scanning session. Each participant was then randomly assigned to a one-hour walk in either a natural or urban setting. Following the walk, participants underwent another MRI scanning session. Adapted from "How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature" by Sudimac et al. (2022), *Molecular Psychiatry, 27*, p. 4448.

Fig. 2. Location of the walks. Left: Example image of the walk in the natural environment. **Right:** Example image of the walk in the urban environment. Reprinted from "A one-hour walk in nature reduces amygdala activity in women, but not in men" by Sudimac and Kühn (2022), *Frontiers in Psychology, 13*, pp. 1–13.

malls, and smaller shops. Like most streets in Berlin, Schloßstraße also had trees, primarily along the sidewalks and traffic dividers.

Before leaving the laboratory, participants were given a map displaying the walking route (a straight path). They were then transported by taxi from the laboratory to the beginning of the walk. Participants were instructed to proceed alone and avoid entering shops or using their personal mobile phones to minimise distractions. Instead, they were provided with a study mobile phone that tracked their GPS data to ensure they followed the designated route. Using GPS data we inspected the distance of the walks in both natural and urban environment, as well as participants' velocity. There was no significant difference in the walked distance (natural environment: mean = 4.53 km, SD = 1 km; urban environment: mean = 4.75 km, SD = 0.77 km; $t(56) = -0.98$, $p = 0.329$) or in participants' velocity (natural environment: mean = 4.69 km/h, SD = 0.64 km/h; urban environment: mean = 4.80 km/h, SD = 0.60 km/h; $t(58) = -0.73$, $p = 0.468$) between the natural and the urban environment. While walking, participants wore an Empatica E4 wristband (Empatica S.r.l, Milan, Italy) which measured electrodermal activity and heart rate as physiological indicators of stress, with the results of the physiological data reported elsewhere (Sudimac et al., 2022). After 30 min, an alarm on the phone notified participants to turn around and return to the starting point, wherea taxi then picked them up and brought them back to the laboratory. During the posttest, the identical MRI scanning procedure was performed again. After the high-resolution hippocampal imaging sequence, the session ended with the Social-Evaluative Threat task (Wager et al., 2009). Finally, participants completed questionnaires, were debriefed, and informed about the study's purpose.

2.3. Magnetic resonance imaging

2.3.1. Data acquisition

The structural images were collected using a Siemens Tim Trio 3T scanner (Erlangen, Germany) equipped with a 32-channel head coil. T1 images were acquired with a three-dimensional T1-weighted magnetization-prepared gradient-echo sequence (MPRAGE) following the ADNI protocol (www.adni-info.org) (repetition time (TR) = 2500 ms; echo time (TE) = 4.77 ms; TI = 1100 ms; voxel size = 1 x 1 × 1 mm^3; acquisition matrix = 256 × 256 × 176; flip angle = 7°). For hippocampal subfield measurements, a high-resolution Proton Density (PD) sequence was used (TR = 6500 ms; TE = 16 ms, 0.4 × 0.4 mm in-plane resolution; 2 mm slice thickness; 30 slices).

2.3.2. Hippocampal subfield segmentation

To determine the volumes of the hippocampal subfields, the automated segmentation of hippocampal subfield (ASHS) tool was utilised during post-processing (Yushkevich et al., 2010). This algorithm estimates volumes for the following regions based on the UPenn atlas: CA1-3, dentate gyrus, subiculum, parahippocampal gyrus, entorhinal cortex, BA 35, BA 36, and the sulcus, using similarity-weighted voting, multi-atlas segmentation, and a novel learning-based bias correction technique. The tool has demonstrated excellent agreement with manual segmentation, showing intra-class correlations comparable to those between human evaluators (Giuliano et al., 2017; Wisse, 2016; Yushkevich, 2015). Segmentations were visually inspected for quality assurance. Prior to analysing the environment-by-time interaction, the volumes of the subfields were adjusted for intracranial volume using this linear equation: ROIadj = ROIvol - β (ICV - ICVmean), where ROIadj is the adjusted regional volume, ROIvol is the original volume, β is the slope of the ROI volume regressed on the ICV as assessed by FreeSurfer and provided by ASHS, and ICVmean is the sample mean of the ICV (Raz et al., 2015). Additionally, hippocampal segmentation was performed on T1-weighted images utilising the FreeSurfer tool (Iglesias et al., 2015). However, no significant correlation was observed between the volume estimates obtained from the ASHS and FreeSurfer tools. This discrepancy may be attributed to the lower quality of T1-weighted images used by FreeSurfer for segmentation (Wisse, 2021; Wisse et al., 2014). Given the thin nature of hippocampal subfields, even minor errors by FreeSurfer can substantially affect the measurements of these regions (Wisse et al., 2021). ASHS, specifically designed for the segmentation of hippocampal subfields (Yushkevich et al., 2010), has been shown to provide estimates more consistent with the actual width of these subfields, whereas FreeSrufer may produce a generalised volume estimate that might not accurately reflect the detailed anatomical differences of hippocampal subfields (Wisse et al., 2021). No significant differences in intracranial volume were observed between the pretest and posttest (ICC = 0.97, 95% CI [0.94, 0.98]), indicating a high level of consistency in the measurement of intracranial volume across time points. Hippocampus and amygdala volumes were calculated using FreeSurfer with the aseg command (Fischl et al., 2002). Descriptive statistics of regions of interest before and after the walk, categorised by environment, are presented in Supplementary Table S2 in the Supplementary Information.

2.4. Rumination assessment

Rumination was defined as the recurrence of unwanted or negative thoughts. It was assessed using three items previously employed (Brose et al., 2011; Kühn et al., 2013, 2014), with two items adapted from the Stress Coping Inventory (Janke and Erdmann, 2002). Participants rated how much the statements "*During the past 5 min, I could not get certain thoughts out of my mind.*" and "*During the past 5 min, I kept thinking about something over and over again.*" reflected their recent thoughts and feelings. A third item was created to measure self-related unwanted thoughts, "*During the past 5 min, I had difficulties suppressing thoughts about myself.*". Due to scanner environment constraints, a 4-point

answering scale was used, ranging from 0 (does not apply at all) to 3 (applies very well), whereas these items were previously used with an 8-point scale. Assessments were conducted before and after the walk and immediately following a 5-min resting state MRI session. The average score of the three items was used, indicating the presence of rumination during the resting state measurement.

2.5. Data analysis

Using two-way mixed ANOVA with the factors environment (urban vs. nature) and time (pre vs. post), we computed environment-by-time interactions to detect potential differential changes over time in the subfields of interest defined a priori: the entorhinal cortex, associated with complex representations of the external environment (Nilssen et al., 2019), the parahippocampal gyrus, previously shown to have higher volumes in adolescents raised exclusively in rural environments (Kühn et al., 2020), and the subiculum, involved in the inhibition of hypothalamic-pituitary-adrenal the HPA axis and stress response (O'Mara, 2005), using a Bonferroni corrected p value of $p < 0.017$. Since a walk in nature may reduce rumination (Bratman et al., 2015; Lopes et al., 2020) and rumination in turn has been associated with the hippocampus (Denson et al., 2009; Figueroa et al., 2017; Heller and Bagot, 2020; Mandell et al., 2014), we correlated the volume change in the hippocampal subfield, in which a significant environment-by-time interaction was observed, with the change in self-reported rumination (Brose et al., 2011), (Kühn et al., 2013), (Kühn et al., 2014) within both environments.

3. Results

To examine how exposure to natural vs. urban environments affects the hippocampal formation, we conducted an MRI intervention study (Fig. 1). High-resolution hippocampal imaging was performed before and after a one-hour walk in a natural environment (urban forest Grunewald; Fig. 2 left) vs. an urban environment (busy street in Berlin; Fig. 2 right).

A significant environment-by-time interaction was observed in bilateral subiculum volume ($F(1,58) = 4.717$, $p = 0.034$, $\eta^2_g = 0.01$; Fig. 3), which increased after the walk in nature ($t(29) = -2.758$, $p = 0.010$; see Supplementary Table S2 in the Supplementary Information), but not after the urban walk ($t(29) = -0.133$, $p = 0.895$). However, the significant interaction did not survive conservative Bonferroni multiple comparison correction. Post hoc, we explored potential lateralisation effects and observed that the effect was mostly driven by the right, not the left subiculum (right: $F(1,58) = 5.626$, $p = 0.021$, $\eta^2_g = 0.01$; left: $F(1,58) = 2.259$, $p = 0.138$, $\eta^2_g = 0.01$). No significant interaction was observed in the volumes of the other hippocampal subfields (see Supplementary Table S2). Likewise, the volumes of the amygdala ($F(1, 58) = 0.686$, $p = 0.411$, η^2_g=0.001) and hippocampus ($F(1, 58) = 0.934$, $p = 0.338$, η^2_g=0.0002), corrected for intracranial volume, showed no significant interaction effects. We did not observe a significant interaction in the subiculum volume, adjusted for intracranial volume, using the FreeSurfer tool ($F(1, 58) = 0.45$, $p = 0.507$). However, there was no observed correlation between the subiculum volume measured by ASHS and FreeSurfer tool ($r(118) = -0.061$, $p = 0.510$), which, as previously mentioned, may be due to inconsistencies in measurements by FreeSurfer, such as inaccuracies in measuring the width of the subiculum (Wisse et al., 2021).

We associated the change in subiculum volume, the only hippocampal subfield where an environment-by-time interaction was observed, with the change in rumination score separately for the natural and urban environment. Changes in the bilateral subiculum were negatively associated with changes in rumination in the natural ($r(28) = -0.367$, $p = 0.046$; Fig. 4), but not in the urban environment ($r(28) = 0.102$, $p = 0.592$), with the difference in correlation coefficients being significant (Fisher's $z = 1.79$, $p = 0.037$). There was no environment-by-

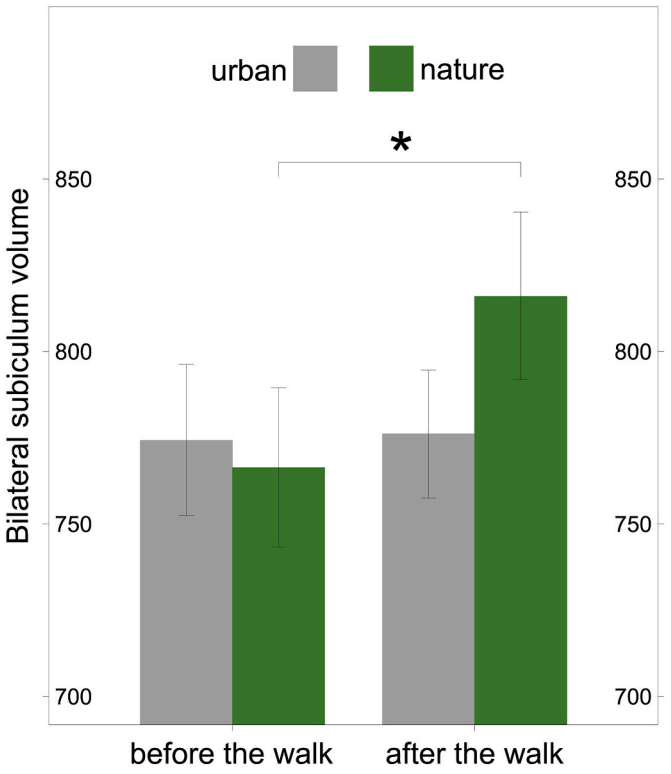

Fig. 3. Bilateral subiculum volume before and after the walk. The volume of the bilateral subiculum increased following the walk in the forest, whereas it remained unchanged after the walk in the urban setting. Note: Significant differences are marked with an asterisk (*p < 0.05); error bars indicate one standard error of the mean.

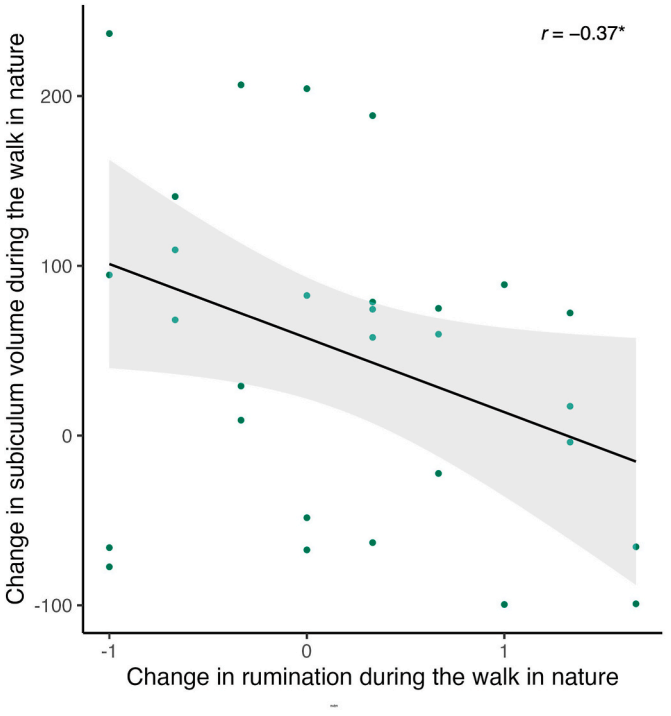

Fig. 4. Negative correlation between the change in bilateral subiculum volume and the change in rumination during the walk in nature. During the walk in nature, the increase in bilateral subiculum volume is associated with decreased rumination. *Note:* Significant differences are indicated with asterisk (*$p < 0.05$).

time interaction effect for self-reported rumination.

4. Discussion

A substantial body of research has indicated that exposure to nature is associated with improved mental health (Barnes et al., 2019; Berto, 2014; McMahan and Estes, 2015). Thus, residential greenery has been linked to brain structural health metrics (Besser, 2021; Crous-Bou, 2020; Dadvand, 2018; Kühn, 2021a, 2023; Xu, 2023), and growing up in a rural environment has been associated with increased size of the hippocampal and parahippocampal formations in adolescents (Kühn et al., 2020). However, the causal relationship between the physical environment and brain structure has not yet been established.

As the hippocampal formation has been related to the environment of upbringing (Kühn et al., 2020) and its structure is highly plastic (Sagi et al., 2012), we examined structural changes in hippocampal subfields after a one-hour walk in a natural vs. urban environment. The results revealed that the walk in a forest caused an increase in subiculum volume in the hippocampal formation, whereas it remained stable after a walk in an urban environment. It should be noted that the environment-by-time interaction did not survive the conservative Bonferroni correction for multiple comparisons, warranting a careful interpretation of the results and underscoring the need for further investigation. The observation of the short-term changes in brain structure, namely in subiculum volume, contradicts the common assumption that brain structure, as measured by MRI, is a relatively stable trait of an individual. Nevertheless, growing evidence suggests that brain structure can undergo alterations within hours or even minutes (Karch, 2019; Kühn, 2021b; Månsson et al., 2020; Sagi et al., 2012; Taubert et al., 2016; Tost, 2010).

The role of the hippocampal subfield subiculum has not been extensively studied, and its exact function remains unclear (Keresztes et al., 2022). In addition to its role in memory and spatial orientation (Keresztes et al., 2022; O'Mara, 2005; O'Mara et al., 2001), the subiculum, more specifically, the ventral subiculum, plays a role in the inhibition of the stress-associated hypothalamic–pituitary–adrenal (HPA) axis (Herman and Mueller, 2006; Lowry, 2002; Mueller et al., 2004; O'Mara, 2005). Additionally, it has been indicated that the subiculum is involved in controling anxiety (Mcnaughton, 2006). This suggests that exposure to nature had a beneficial effect on a brain region which is involved in stress responses inhibition and anxiety control. This finding aligns with previous results from the same study showing that the forest walk decreased stress-related amygdala activity (Sudimac et al., 2022). Therefore, a walk in nature, which reduced stress-related neural activity, may have led to the increase in subiculum volume, which in turn may be related to enhanced inhibition of the HPA axis and inhibition of stress responses. Given the subiculum's role in processing spatial orientation (O'Mara, 2005; O'Mara et al., 2001), it is also plausible to speculate that the observed increase in subiculum volume could be associated with the task of navigating through a novel environment, such as a tranquil forest path. However, these hypotheses warrant further investigation to confirm their validity. Potential biological mechanisms underlying structural plasticity in the subiculum may stem from several proposed mechanisms occurring on a shorter time scale, such as synaptogenesis, supporting glial processes, and dendritic branching, rather than neurogenesis which usually occurs on a longer time scale (Bruel-Jungerman et al., 2007; Butz et al., 2009; Holtmaat and Svoboda, 2009; Keifer et al., 2015; Sagi et al., 2012; Theodosis et al., 2008; Todd et al., 2006; Yang et al., 2009). Nevertheless, it is important to note that the MRI methodology employed in this study, while providing valuable structural data, cannot directly identify the underlying biological mechanisms driving the observed change in subiculum volume after the nature walk (Zatorre et al., 2012). To gain a more comprehensive understanding of these structural changes within biological tissues, future research may benefit from incorporating quantitative MRI or non-invasive in vivo histology techniques, which can offer additional insights into the nuances of such alterations (Weiskopf et al., 2021).

Additionally, the increase in bilateral subiculum volume after the walk in nature was associated with a decrease in self-reported rumination. Even though the study was conducted in healthy participants rather than a clinical population, the results may be seen in line with a previous study showing a reduction in subiculum volume in patients with major depressive disorder characterised by chronic exposure to stress and rumination (Han et al., 2016; Harel et al., 2016). Moreover, a reduction in subiculum volume has been associated with childhood maltreatment and mood disorders (Teicher et al., 2012).

To our knowledge, this is the first intervention study to show evidence of structural brain plasticity after short-term exposure to nature. Even though the environment-by-time interaction in the bilateral subiculum was not maintained following Bonferroni correction, these are seminal findings hinting at a causal relationship between exposure to nature and brain plasticity and therefore we hold them as valuable. Additionally, the results revealed an association between the increase in subiculum volume and a reduction in rumination. These findings extend the results of previous studies showing that rumination decreases after a walk in nature (Bratman et al., 2015; Lopes et al., 2020) and those demonstrating that depression is associated with subiculum volume reduction (Han et al., 2016; Harel et al., 2016). Since both subiculum volume reduction and increased rumination are characteristics of major depressive disorder (Han et al., 2016; Harel et al., 2016), the results of this study, together with previous findings showing that nature decreases rumination (Bratman et al., 2015; Lopes et al., 2020), may hint at the importance of spending time in nature as a potential preventive measure against the development of depression symptoms. Nevertheless, since our sample consisted of healthy participants, further investigation in clinical populations is required to examine the salutogenic effects of nature (a forest in this case) for patients with depression in order to implement exposure to nature in clinical practice, such as green prescription (Van den Berg, 2017).

As this is a seminal study to examine and demonstrate the salutogenic effect of a short-term exposure to nature on brain structure, we cannot infer the long-term effects, namely whether the effect persists over time. Since we observed an increase in grey matter volume in hippocampal subiculum, based on activity-dependent structural plasticity (Butz et al., 2009), it is tempting to speculate that repeated exposure to natural environments may lead to enhanced plasticity benefits in this brain region. An increase in subiculum volume may be mediated by enhanced synaptic connections, dendritic branching, and the swelling of glial cells (Bruel-Jungerman et al., 2007; Butz et al., 2009; Holtmaat and Svoboda, 2009; Keifer et al., 2015; Sagi et al., 2012; Theodosis et al., 2008; Todd et al., 2006; Yang et al., 2009). Repeated stimulation of these brain pathways during nature exposure could strengthen synaptic connections, leading to more stable changes in brain structure. However, according to the expansion-renormalization model (Wenger et al., 2017), grey matter volume might initially increase and then return to baseline with repeated exposures. Therefore, future longitudinal studies are essential to determine whether these short-term changes, as a result of exposure to natural environments, translate into long-term improvements in brain structure and function and how long-lasting these changes are. Such research could provide robust evidence to apply to clinical practice (e.g., green prescription), as well as urban and landscape planning.

Our study has several limitations. First, as already mentioned, the environment-by-time interaction in the bilateral subiculum fails to withstand the Bonferroni correction. However, as these are pioneering findings suggesting a plausible causal link between exposure to forest and brain plasticity, we hold them as valuable contribution to the field. Importantly, we encourage future studies to examine the effects of exposure to natural vs. urban environments on the subiculum volume in a larger sample. Second, the biological mechanisms underlying the subiculum volume increase after walking in a natural environment

remain unclear. Therefore, we encourage future research to incorporate quantitative MRI or non-invasive in vivo histology techniques to gain deeper insights into these alterations. Furthermore, the observed effect may be potentially influenced by factors like increased oxygen intake. Oxygen is more abundant in forests compared to urban areas, and since oxygen consumption during cardiorespiratory fitness has been associated with increased grey matter volume (Liu et al., 2022), it is important to consider this factor. Although our study aimed to examine the holistic effects of natural and urban environments, encompassing different environmental characteristics, we encourage future research to control for oxygen intake in these settings. Third, since different results were observed when using various hippocampus segmentation tools, possible segmentation biases should be also considered. Fourth, it remains unclear what natural features (e.g. the colour green, odours, sounds etc.) are driving the effect of the subiculum volume increase after the walk in nature. Additionally, our study does not clarify the duration of these effects or whether repeated exposure to natural environments might result in long-term changes in brain structure. We recommend that future research explores the long-term effects of exposure to both natural and urban environments on brain structure, as well as try to identify concrete active ingredients driving the effects, with the goal of providing evidence for clinical applications. Fifth, our sample mostly consisted of participants who were born and raised in Germany. Therefore, we encourage future studies to include participants from different geographical and cultural backgrounds to enhance the generalizability of the findings.

Code availability

The code associated with the data analysis within this study is available on a public repository at https://osf.io/xt2wn/

Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

CRediT authorship contribution statement

Sonja Sudimac: Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Simone Kühn:** Writing – review & editing, Validation, Supervision, Software, Resources, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting the findings of this study are available on a public repository at https://osf.io/xt2wn/

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Appendix A. Supplementary data

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