



OPEN
REGISTERED
REPORT

The effect of individual visual sensitivity on time perception

Alexandra Ružičková^{1✉}, Lenka Jurkovičová^{2,3}, Julie Páleníková³, Keith A. Hutchison⁴, Jiří Chmelík⁵, Kristína Mitterová^{2,6} & Vojtěch Juřík^{1,7}

The human mind, trying to perceive events coherently, creates the illusion of continuous time passage. Empirical evidence suggests distortions in subjectively perceived time flow associated with well-studied neural responses to sensory stimuli. This study aimed to investigate whether visually uncomfortable patterns, causing exceptionally strong brain activation, affect short time estimates and whether these estimates vary based on the overall reported sensory sensitivity and cortical excitability of individuals. Two experiments in virtual reality testing our assumptions at different levels of complexity of timed stimuli provided initial insight into the studied processes in highly controlled and realistic conditions. Data analysis results did not support our hypotheses, but showed that subjectively most visually uncomfortable simple patterns, i.e., achromatic gratings, cause more variable temporal judgments. Supposedly, this inaccuracy depends on the currently perceived visual comfort and thus the current visual system sensitivity, which cannot be satisfactorily derived from trait-based measures. The exploration of the effect of complex stimuli, i.e., virtual exteriors, suggested that their visual comfort does not affect time perception at all. Biological sex was an important variable across experiments, as males experienced temporal compression of stimuli compared to females. Neuroimaging research is needed for a deeper investigation of the origin of these results.

Protocol registration: The Stage 1 manuscript associated with this Registered Report was in-principle accepted on 4 March 2024 prior to data collection for hypothesis testing. The accepted version of the manuscript can be found in the publicly available OSF repository at <https://doi.org/https://doi.org/10.17605/OSF.IO/K3YZE>.

Psychological time is distorted by various factors, including physical properties of perceived stimuli. Strong and salient stimuli (e.g., loud, bright, fast in movement) promote information extraction that is positively correlated with subjective stimulus duration (see¹, for a review). In terms of neuroscience, Eagleman and Pariyadath^{2,3} point out that perceived duration depends on efficiency of neural coding. Stimuli activating larger neural networks, such as those that are strong, salient, or novel, expand their apparent time duration^{4–8}. Some evidence even suggests that the relative strength of sensory cortex responses, reflecting low-level sensory processing, may be directly responsible for time perception and independent of arousal levels, as another subjective time distorting factor^{5,9}. In this work, we therefore build on the assumption that the magnitude of neural response per se may determine stimulus subjective duration.

Crucially, the magnitude of neural response to external stimulation (e.g., blood-oxygen-level-dependent signal in fMRI or increased event-related potential amplitude in EEG) varies between individuals¹⁰. In interaction with the surrounding world, individuals differ in the intensity of sensory stimuli processing, which in turn shapes their behavioral reactions to them^{11,12}. Sensory hypersensitivity, the feeling of sensory overload when exposed to specific stimuli (e.g., bright lights, loud noises, intense odors) and sensory hyposensitivity, with the opposite effect, define two poles of the scale used to measure sensory sensitivity. Both hypersensitivities and hyposensitivities tend to be reported simultaneously in the same individuals and across multiple senses¹². Further, manifestations of sensory sensitivity are strongly associated with differences in the magnitude of physiological response to perceived stimuli^{10,13,14}. Within the visual domain, these mechanisms are studied by

¹Department of Psychology, Faculty of Arts, Masaryk University, Brno, Czech Republic. ²Centre for Neuroscience, CEITEC – Central European Institute of Technology, Masaryk University, Brno, Czech Republic. ³Department of Neurology, St. Anne's University Hospital and Medical Faculty of Masaryk University, Brno, Czech Republic. ⁴Department of Psychology, Montana State University, Bozeman, MT, USA. ⁵Department of Visual Computing, Faculty of Informatics, Masaryk University, Brno, Czech Republic. ⁶Applied Neuroscience Research Group, Central European Institute of Technology, Masaryk University, Brno, Czech Republic. ⁷Institute of Computer Aided Engineering and Computer Science, Faculty of Civil Engineering, Brno University of Technology, Brno, Czech Republic. ✉email: alexandra.ruzickova@mail.muni.cz

exposing participants to certain patterns inducing an increased neural response, amplified according to the level of visual system sensory sensitivity and the level of visual cortex excitability^{15–20}.

Images containing patterns whose structure deviates from the natural $1/f$ amplitude spectrum involve a less sparse coding and stronger neural response, because the visual system is not optimized for encoding them efficiently^{21,22}. The spatial frequency (f) of these deviations from natural $1/f$ image structure peaks between 1 and 4 cycles per degree (cpd) and is consistently judged as the most uncomfortable to look at (e.g.,^{23–26}). Examples of such visually uncomfortable stimuli in real life conditions include the repeated striped patterns that typically pervade urban landscapes^{22,27}. Relatedly, a considerable number of studies confirms that it is visually more comfortable to observe natural environments compared to urban, non-natural ones (e.g.,^{27–31}). A neuroimaging study of Le and colleagues²⁷ demonstrates the inefficient processing of stimuli of modern architecture at the neural level. Several sub-studies conducted within authors' study show that (i) photographs of buildings possessing visually uncomfortable patterns are consistently rated as more uncomfortable to look at compared to photographs of shrubbery, (ii) observation of photographs of unnatural urban scenes elicits a larger hemodynamic response, meaning rapid delivery of blood to active neuronal tissue, (iii) photographs of urban scenes are a surrogate for the real-life scenes themselves as the ratings of subjective visual discomfort correlate.

In laboratory conditions, the effect of unnatural spatial frequencies on sensory sensitivity is studied using the *Pattern Glare Test*^{15,16,19,32} consisting of achromatic gratings of three spatial frequencies. A midrange spatial frequency close to 2–3 cpd is considered as being the most visually unpleasant due to producing exceptionally strong neural responses^{18–20}. Besides, the observation of aversive spatial frequencies is associated with aberrant visual experiences that also appear in everyday life (e.g., visual distortions, loss of visual information, or visual irritation) and are referring to the individuals' cortical excitability^{33,34}. Researchers studying time perception using aversive achromatic gratings as an infrequent, unexpected or novel 'oddball' stimuli suggest that the perceptual property of spatial frequency influences timing³⁵. In their study, it did not matter whether the midrange spatial frequency was presented as a standard or 'oddball' stimulus or in a series of other higher and lower spatial frequencies, its presentation always stretched the subjective time. The most recent finding demonstrated that subjectively experienced visual discomfort on these aversive patterns correlates negatively with resting state primary visual cortex (V1) GABA concentration¹⁷. In line with this, perceived time duration contractions are associated with elevated V1 GABA concentrations³⁶, suggesting the role of V1 excitability in time perception while observing uncomfortable patterns.

Experiencing uncomfortable or even painful situations tends to expand subjective time³⁷. The present study strove to investigate this effect in visually uncomfortable patterns together with interindividual differences in how sensitively they are perceived, because the current scientific inquiry is insufficient. More precisely, although previous research suggested differences in individual timing based on emotionality³⁸, or cognitive abilities³⁹, the role of stimulus processing intensity has not yet been addressed. The results contribute to a number of areas in which sensory sensitivity and visual comfort have a tremendous impact on subjective well-being. For instance, clinical samples of migraines and people with autistic spectrum disorder exhibit increased sensory sensitivity^{14,40–43}, show a greater neural response to the sensory stimuli^{40,44} and also have abnormally large visual cortex activation in response to the Pattern Glare Test stimuli^{23,45–48}. Importantly, existing tools for quantifying sensory sensitivity tend to be based on subjective statements, whereas this study may expand the possibilities of how to detect it behaviorally. To begin this promising endeavor, we conducted two parallel experiments on a single experimental sample of healthy individuals using immersive and highly controlled virtual reality environments^{49,50}. The perception of short time intervals (within 2 s) was tested by the temporal bisection paradigm^{51–54}. Various spatial frequencies of achromatic gratings were used as timed stimuli in Experiment A (EA). In Experiment B (EB), we utilized more ecologically valid scenes of urban and natural environments to simulate time perception in real-life conditions. We formulated the hypotheses separately for each experiment:

(EAH1) The most visually uncomfortable midrange spatial frequency (3 cpd) will cause the greatest expansion of subjective time compared to high (8 cpd) and low (0.5 cpd) spatial frequencies.

(EAH2) Individuals scoring higher in sensory sensitivity will experience greater subjective dilatation of time while observing aversive achromatic gratings compared to less sensory sensitive people.

(EAH3) Because sensory sensitivity is at the neuronal level reflected by cortical hyperexcitability, we propose that increased subjectively reported cortical excitability will predict prolonged time when observing aversive achromatic gratings.

(EBH1) Observing unnatural urban scenes will most significantly extend the subjectively perceived time compared to exposure to natural environments. The greatest expansion of subjective time we expect to appear in the most visually uncomfortable urban environments.

(EBH2) Increased subjective sensory sensitivity will predict a longer perceived duration of presented visually uncomfortable urban scenes.

(EBH3) The perceived duration of the most visually uncomfortable urban scenes will be positively predicted by the level of cortical hyperexcitability reported by participants.

Methods

Ethics information

The study was approved by the Research Ethics Committee of Masaryk University under the project code EKV-2023-013-E1. All experimental procedures and methods were in accordance with the ethical principles outlined in the Declaration of Helsinki. Providing informed consent from each participant was essential to take part in this study. Participation was completely voluntary, with a financial reward of 300 CZK (~ 13 USD). Participants were informed that they could leave the experiment whenever they want without any negative consequences or loss of financial reward, no explanation requested. The study received funding after the in-principle acceptance of the Stage 1 manuscript of this registered report, so the participants' remuneration was not pre-registered.

Preparatory study

For the purposes of Experiment B, a preparatory study was conducted. To raise the objectivity of the selection of scenes that served as stimuli in Experiment B, we recruited several observers ($N = 26$, $\bar{x}_{\text{age}} = 23$ years, $SD = 2.33$) to rate a set of urban ($N = 25$) and natural ($N = 25$) scenes according to their visual comfort, similar to the study of Le and colleagues²⁷. Images were obtained from the freely available Google Maps application and presented on a computer screen in the research laboratory. Ratings were assigned using a seven-point Likert scale ranging from 1 ('Very comfortable') to 7 ('Very uncomfortable').

Based on the ratings, we selected thirteen scenes. From twelve of them, we created clusters of three stimuli that received the most extreme average visual comfort ratings (comfortable/uncomfortable) in each (natural/urban) category. More precisely, we formed clusters of (i) the most visually comfortable natural scenes ($\bar{x}_{\text{cluster}} = 1.60$, $SD = 0.79$), (ii) the least visually comfortable natural scenes ($\bar{x}_{\text{cluster}} = 3.09$, $SD = 1.27$), (iii) the most visually comfortable urban scenes ($\bar{x}_{\text{cluster}} = 2.59$, $SD = 1.16$), and (iv) the least visually comfortable urban scenes ($\bar{x}_{\text{cluster}} = 4.45$, $SD = 1.58$), each consisting of three stimuli. In this study, our main focus was on clusters of the most visually comfortable natural scenes and the least visually comfortable urban scenes. Clusters of the most visually comfortable urban scenes and the least visually comfortable natural scenes served as controls. The thirteenth selected (natural) scene, which received a neutral average rating, served as a training stimulus. The full description of the preparatory study is reported in the Supplementary Information, and spherical photographs of all selected scenes are available at the OSF repository, which can be accessed through the link included in the Data availability statement.

Questionnaires

To determine the overall level of subjective sensory sensitivity and visual cortical excitability of the participants, we used validated self-report questionnaires. We furthermore took into account reported autistic traits⁴¹, biological sex and menstrual cycle^{17,55–57}, sleep deprivation⁵⁸ and cybersickness^{32,59}, because all these factors are known to significantly affect studied variables. The amount of autistic traits and the level of cybersickness was tested by questionnaires, the remaining aspects were asked directly. Given that the research was conducted on the Czech-speaking population, the questionnaires were translated into Czech language by two independent researchers, and both researchers agreed on the final version.

Sensory sensitivity

Glasgow Sensory Questionnaire (GSQ)¹² contains 42 items assessing sensory sensitivity across visual, auditory, tactile, gustatory, olfactory, proprioceptive and vestibular sensory modalities. Each sensory modality is examined by six items, half ($n = 3$) measuring hypersensitivity, while the other half examines hyposensitivity. Thus, the questionnaire provides three types of scores. The sum of all item scores (ranging from 0 to 168) can be calculated to determine overall sensory sensitivity. Further, by dividing the total score according to the focus on hyper- or hyposensitivity, we obtained two separate scores (ranging from 0 to 84) that measure two possible directions of increased sensory sensitivity. Finally, the questionnaire also provides one separate score (ranging from 0 to 24) for each sensory modality. Participants are prompted to respond using a 5-point Likert scale of 0 ('Never'), 1 ('Rarely'), 2 ('Sometimes'), 3 ('Often'), and 4 ('Always').

Autistic traits

Autism-Spectrum Quotient Short (AQ-Short)⁶⁰ is a shortened version of the 50-item Autism-Spectrum Quotient questionnaire (AQ)⁶¹ that is not biased towards the male autism phenotype⁶². It is a non-diagnostic instrument for identifying the extent of autistic traits exhibited by adults of normal intelligence with sufficient communication and reasoning skills. It comprises 28 items that evaluate social skills, attention switching, a preference for routines, imagination and a fascination with numbers and patterns. The questionnaire has a clear factor structure consisting of two higher-order factors—social behavior factor (23 items) and a numbers and patterns factor (5 items). Participants assign 4-point Likert ratings on a scale of 'Definitely agree', 'Slightly agree', 'Slightly disagree', and 'Definitely disagree'. The maximum achievable score is therefore 112 points, the minimum 28. Higher scores indicate greater endorsement of autistic traits. A score of 70+ is considered as being the threshold for suspecting clinically significant levels of autistic traits.

Cortical hyperexcitability

Cortical Hyperexcitability index — II (Chi-II)³⁴ is a revised version of the original Cortical Hyperexcitability index (Chi)³³. The questionnaire is considered an indirect proxy measure for signs of visual cortical hyperexcitability. It is composed of 30 items, with each item containing a question about a specific aberrant visual experience, followed by two 7-point unipolar Likert scales measuring participants' corresponding 'frequency' (0 'Never' and 6 'All the time') and 'intensity' (0 'Not at all' and 6 'Extremely intense') of such experiences. The measure comprises three factors: Heightened Visual Sensitivity and Discomfort, Aura-like Hallucinatory Experiences, and Distorted Visual Perception. Higher scores on the Aura-like Hallucinatory Experiences factor correlate with significantly elevated pattern-glare scores in healthy individuals³⁴. The sum of the frequency and intensity ratings for each question provides a single score of a maximum of 12 points. Cortical Hyperexcitability index — II is the sum of scores for all 30 items (max. = 360).

Simulator sickness/cybersickness

Simulator Sickness Questionnaire (SSQ)⁶³ is the most widely used method to measure simulator sickness and cybersickness^{64,65}. The questionnaire assesses 16 symptoms of discomfort caused by the simulator or virtual reality simulations divided into three subcategories: Nausea, Oculomotor, and Disorientation. Examples of investigated symptoms are blurred vision, nausea or eye strain. Each symptom is evaluated on a scale of 0 ('No

symptom'), 1 ('Mild'), 2 ('Moderate'), and 3 ('Severe'). The increased overall number and intensity (score 0–48) of symptoms indicates more severe cybersickness.

Temporal bisection task

In this study, we used the bisection method^{51–54} as a tool for grasping individually perceived time in virtual reality (VR). Within the *training phase*, participants first learned to discriminate two anchor durations of the presented stimulus: 'Short' (400 ms) and 'Long' (1600 ms). Training stimuli resembled test phase stimuli in both experiments (EA: black ellipse; EB: training outdoor environment), i.e., they were similar in type, but neutral compared to the test stimuli. Stimulus presentation was pseudo-random. There were 10 training trials for each duration (20 presentations in total) with an inter stimulus interval (ISI) of one second. Participants answered using VR controllers in their right and left hands. To ensure that participants clearly understood the task, they received feedback ('Correct' or 'Incorrect') after each stimulus categorization.

During the *test phase*, participants were presented with the standard 'Short' (400 ms) and 'Long' (1600 ms) durations, as well as novel, intermediate durations, that varied between the anchors (600, 800, 1000, 1200, 1400 ms). Participants were instructed to press the intended key on the left or right handheld VR controller to decide whether the duration of the novel stimulus was closer to the 'Short' or 'Long' anchor duration. Timed stimuli were again specific to both experiments (EA: ellipses of achromatic gratings; EB: experimental outdoor environments). Each stimulus was presented for each duration eight times in pseudo-random order. Responses were followed by a blank screen between trials (ISI = 1000 ms). Participants fixated their gaze on a white fixation square in front of them during the entire *Temporal Bisection Task* (TBT).

Virtual reality

The Meta Quest 2 head-mounted display device (Meta Platforms, Inc., Menlo Park, CA, USA) was used to render the TBT in a virtual environment. Hardware-wise, the stimuli were presented on two 3.43-inch fast-switch LCD displays with a resolution of 1832 × 1920 pixels per eye and a refresh rate up to 90 Hz. The Meta Quest 2 is all-in-one VR system that does not require any external sensors or cameras. The wireless headset tracks the movement of both head and body, then translates them into VR with realistic precision and thereby enables unrestricted movement of the participant in the virtual environment. However, participants in this study were intentionally constrained to a stationary sitting position. We used a chin rest to fix the head position of the participants to prevent undesirable head movements which could potentially increase cybersickness³².

Stimuli for Experiment A were created using the latest MATLAB version (The MathWorks Inc., Natick, MA, USA) and saved as PNG images. Experiment B involved downloaded textures from the Google Maps application, projected around the user in VR for a given time interval. Both the virtual distance from the test stimuli objects and the luminance of the stimuli were normalized. An object in the shape of a white square was always placed in the textures and participants were asked to fix their gaze on it. To provide responses in TBT tasks, there was an implementation of self-tracked Meta Quest 2 controllers and their derived functionality. The Unity engine and SteamVR platform served to display stimuli in both experiments. The nondeterminism in the Unity engine's real-time rendering frequency could be a cause of slight delays in the accuracy of stimulus onset (at a stable 90 Hz framerate, the maximum input/output delay window [two frames] is 22 ms). However, this variation is acceptable, given that it was equal for all conditions, and we were only interested in the categorizations of stimuli whose durations were sufficiently different from each other (400, 600, 800, 1000, 1200, 1400, 1600 ms).

The use of VR in this study enabled the creation of a highly controlled and at the same time realistic experimental environment for testing our hypotheses. More specifically, in Experiment A, VR ensured stable lighting conditions and stimulus contrast, as well as a standardized uniform background that did not provide any cues to improve time estimates. In Experiment B, the greatest advantage of VR was in presenting the stimuli exactly as they appear in the real world^{166,67}, while the exposure was strictly controlled in terms of duration and primarily stimulating the visual domain, which was theoretically most important to us. Some studies have also demonstrated more distracted attention in sensory sensitive individuals in the general population^{68,69}. Thus, isolation in a VR environment could also increase the level of concentration on an attention-demanding task.

Design and procedure

Upon arrival at the laboratory, the experimental procedure, as seen in Fig. 1, was summarized to the participants and subsequently an informed consent was signed. Participants were aware that we were studying time duration judgments when observing various types of images or scenes. Furthermore, they were informed of the risk of potential visual discomfort and cybersickness when using head-mounted displays³². Emphasis was placed on voluntary participation, i.e., the possibility of withdrawing from the experiment without providing a reason and without loss of reward, as well as on anonymized data collection. Brief information about the study, aspects of participation, possible risks (especially cybersickness), exclusion criteria and restrictions on drinking caffeinated beverages at least 4 h prior to the participation were emailed to the participants in advance. They also received a contract regarding the reward payment, which they could fill out in advance.

Because the present study had a within-subject design, all participants underwent the same experimental procedure. Nonetheless, the order in which the experiments were administered was randomized so that roughly half of the participants started with Experiment A and continued with Experiment B, while the other half had the reverse order. Questions on biological sex, menstrual cycle day, sleep, initial cybersickness (SSQ1) were answered prior to the VR exposures. To prevent participants from postural sway caused by visually uncomfortable flashing stimuli exacerbating possible cybersickness^{32,70}, they were seated on a chair throughout both experiments and their head was positioned into the chin rest. A VR headset was put on and VR controllers were placed in the hands of participants. Control instructions were provided.

Session run scheme

Action	Introduction	Q1	Experiment A/B	Q2	Experiment B/A	Q3	Debriefing	Total
Duration	10:00	5:00	16:00	20:00	19:00	25:00	5:00	1:40:00
Material	Informed consent	Biological factors SSQ 1	VR	SSQ 2 GSQ SSQ 3	VR	SSQ 4 AQ-Short Chi-II		
Location	Preparation area		Test area	Preparation area	Test area	Preparation area		

Q (1–3) – Questionnaires

SSQ (1–4) – Simulator Sickness Questionnaire

VR – Virtual reality

AQ-Short – Autism-Spectrum Quotient Short

GSQ – Glasgow Sensory Questionnaire

Chi – II – Cortical Hyperexcitability index – II

Experimental run scheme

Experiment	Experiment A			Experiment B		
Phase	Assimilation phase	Training phase	Test phase	Assimilation phase	Training phase	Test phase
Duration	3:00	3:00	10:00	3:00	3:00	13:00
Material	Living room virtual environment	Black ellipse	Achromatic gratings	Outdoor virtual environments		

Fig. 1. Schematic representation of the experimental procedure. The table above shows the procedural sequence of the entire session. The table below specifies the run of the experiments that were administered in random order.

In *Experiment A*, participants were initially allowed to adapt to the VR environment in a room with furniture set to appear as a living space. By moving the head, it was possible to look around the room. Afterwards, we transferred participants to the experimental environment. The simulated experimental environment comprised a dark box-shaped room with gray walls, black floor and ceiling, similar to that used by O’Hare and colleagues³². At the beginning, the instructions for Experiment A appeared on the virtual wall in front of the participant. After reading them, TBT training and testing phases followed. We used a black ellipse with blurred edges as a timed training stimulus. In the test phase, the stimuli were black and white gratings that are widely used for stimulation in the Pattern Glare Test^{19,20,32–34}. Sine-wave gratings were elliptical in shape with blurred edges and corresponded to approximately (i) 0.5 cpd (low frequency grating), (ii) 3 cpd (the crucial midrange frequency grating), (iii) and 6 cpd (high frequency grating)^{32,34,35}. Contrary to the pre-registered research plan where the high spatial frequency grating was supposed to have 8 cpd, we were forced to enlarge the strips to 6 cpd. The resolution of the used VR headset technically enabled the rendering of a grating with a frequency of 8 cpd, however, pilot testing showed that slightly incorrect headset fitting and occasional head movements lead to flickering of the stimulus, thus potentially inducing discomfort not related to spatial frequency. The viewing distance was set to 2.5 m from the front, experimental wall, which provided a visual angle of 8.53×11.0 degrees. The dimensions of the stimuli were approximately 48×38 cm. All gratings had a Michelson contrast of 0.70 (cd/m^2) and were presented in the center of the gray virtual wall with a white fixation square in the middle (see Fig. 2 for an illustration of one experimental trial). Answers were provided using VR controllers—left/right trigger button. After completing TBT task, which included 168 trials in total (7 durations \times 3 stimuli \times 8 presentations), the participants assessed the general subjectively perceived visual comfort of each stimulus on a scale: – 5 (‘Very uncomfortable’), 0 (‘Neither comfortable nor uncomfortable’), 5 (‘Very comfortable’). Answers were marked by VR controllers’ trigger buttons.

There was a break separating the two experiments when the head-mounted displays were removed, and participants had the opportunity to rest and refresh themselves. Meanwhile, participants also completed the second questionnaire on cybersickness (SSQ2) and the questionnaire regarding sensory sensitivity (GSQ). Before Experiment B, participants filled out the third questionnaire on cybersickness (SSQ3), so that we could control for changes in their physiological state.

Within *Experiment B*, participants were allowed to adapt to the VR environment, nonetheless this time they were teleported to a static outdoor environment. This environment subsequently served as a stimulus for the TBT training phase. Participants were able to sit and look around 360 degrees by turning their heads, without the possibility to interact with the environment. After the participants had adapted to the virtual environment, they were teleported to an experimental box-shaped room. Their position in virtual space was adjusted, so that they sit 2.5 m in front of a virtual wall. Then instructions were presented to participants and TBT training phase started. During the test phase of TBT, participants were transported from the box-shaped room, where ISIs

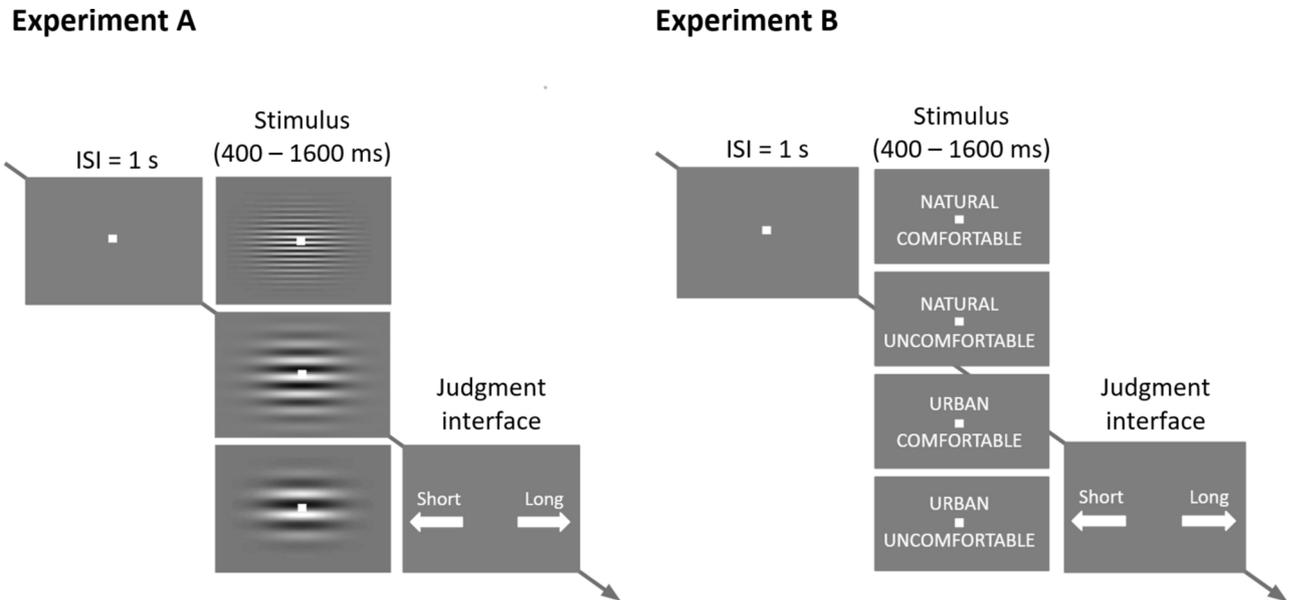


Fig. 2. One TBT trial of the test phase in Experiment A (left) and in Experiment B (right). Participants first observed the fixation square for one second. Subsequently, they were presented with a stimulus for a certain duration, which they then categorized as closer to ‘Short’ or closer to ‘Long’ anchor duration learned during the training phase.

and evaluations of stimuli durations took place, to outdoor environments selected in the preparatory study (see Supplementary Information). Each participant was randomly assigned one environment from each of the four clusters (urban/natural, comfortable/uncomfortable) of stimuli. The scenes differed between participants, but within participants were always the same. By increasing the stimulus sample between participants, we aimed to control for other potential factors affecting time perception than the visual discomfort from outdoor scenes. Spatial frequency referred here to the spatial repetition of contours on the retina²⁷. To fix the participants’ gaze, we placed an object in the shape of a white fixation square in the center of the virtual scene. The total number of TBT trials in Experiment B was 224 (7 durations \times 4 stimuli \times 8 presentations) for each participant and responses were indicated using VR controllers. Consistent with Experiment A, we asked participants for subjective reports of the general visual comfort associated with each of the four environments presented to them during the TBT test phase.

After finishing the second experiment, participants completed the remaining questionnaires on cybersickness (SSQ4), autistic traits (AQ-Short), and cortical hyperexcitability (Chi-II). Finally, they were debriefed and thanked for their participation. In total, the participation took approximately 1 h and 40 min. Participants received the financial reward within a few weeks by transfer to the indicated bank account.

Sampling

We recruited 99 self-reported neurotypical young adults (19–35 years, 64% were females) living in the Czech Republic, with normal or corrected-to-normal vision, allowing them to undertake tasks in virtual reality. Abstinence from drinking caffeinated beverages at least four hours⁷¹ prior to the participation was required. Exclusion criteria precluded participation with a history of migraine symptoms, photosensitive epileptic seizures, recent eye surgery, and optic neuropathies (e.g., glaucoma, binocular vision disorders) as these might interfere with the study. Participants were recruited primarily via social media, university pool of participants, and by snowball method.

To determine a sufficient sample size, we searched for studies with a similar design, using differently processed images as timed stimuli (e.g.,^{72–77}). These studies most often deal with the effect of arousal on time perception. In our case, we considered the discovery of hypothesized relationships with effect sizes equal to or greater than those in the reviewed studies to be meaningful. With the lowest estimated effect size $f^2 = 0.28$, required statistical power of 0.95, alpha level 0.05 and four predictors, we needed approximately 72 participants to test all of our hypotheses. The calculation was performed using G*power.

Participants whose autism quotient exceeded the clinical threshold (score 70+; $N = 23$) were excluded from the dataset. These quotients were checked continuously to ensure that we collected a large enough sample according to the power analysis. We also excluded those whose performance indicated deliberate non-cooperation or misunderstanding of instructions ($N = 1$). A few participants produced missing values in TBT of both experiments by not categorizing durations immediately (within 5 s) in 3 trials. Missingness seemed to be random and in small numbers, so we used data from these participants, except for the missing trials. No participant was excluded or withdrawn from the experiment due to cybersickness or any other reason. The resulting sample used in analyses consisted of 75 participants (67% were females), aged between 20 and

35 years. Participants were of different nationalities, Czech (72%), Slovak (19%), Russian (5%), Ukrainian (3%), Belarusian (1%), but all of them were fluent in the Czech language.

Analysis

All analyses were performed using R statistical software, version 4.4.1⁷⁸. In order to examine the direct representation of subjective time, we localized a bisection point or *temporal indifference point* (TIP) for each participant and experimental stimulus (EA) and cluster (EB). TIP establishes a duration that subjects classify as ‘Long’ or ‘Short’ with equal probability. Raw responses were converted into proportions of ‘Long’ time interval responses and plotted against actual stimulus durations using a 7-point psychometric function from the ‘quickpsy’ R package⁷⁹. A shift in the bisection point (TIP) of the psychometric function that tracks participants’ responses indicates a bias in perceived time. In general, times’ subjective expansion (longer perceived duration) produces leftward displacements of the psychophysical functions and thus a smaller TIP. While TIP represents the mathematical mean of a psychometric function, *Weber fraction* (WF) is the standard deviation divided by TIP. WF was calculated to measure temporal sensitivity. Smaller values indicate more sensitive and less variable timing.

TIP and WF were then modeled with linear mixed models (LMMs), with type of stimulus, biological sex and scores on the sensory sensitivity, cortical hyperexcitability and cybersickness questionnaire treated as predictors. The effect of the order of administration of the experiments was tested initially and kept in the model whenever significant. LMMs are robust to violations of sphericity and do not inflate Type I errors⁸⁰. R packages intended to perform LMMs are ‘lme4’⁸¹ and ‘lmerTest’⁸². Because we expected the measures of sensory sensitivity and cortical hyperexcitability to be correlated, we used only one of them at a time. The best model fit was primarily selected based on Akaike Information Criterion (AIC)⁸³. Model assumptions were checked by plotting the model residuals with *check_model()* function from the ‘performance’ R package⁸⁴. We obtained confidence intervals using the ‘lme4’ R package⁸¹ for bootstrapping, 10,000 iterations for LMM. Final proposed model structures for each experiment separately were as follows:

(EAH1)

Outcome variable ~ stimulus type1 + stimulus type2 + cybersickness + biological sex + (1 | participant)

(EAH2, EAH3)

Outcome variable ~ stimulus type1*sensitivity measure + stimulus type2 + cybersickness + biological sex + (1 | participant)

(EBH1)

Outcome variable ~ stimulus type1 + stimulus type2 + stimulus type3 + cybersickness + biological sex + (1 | participant)

(EBH2, EBH3)

Outcome variable ~ stimulus type1*sensitivity measure + stimulus type2 + stimulus type3 + cybersickness + biological sex+ (1 | participant).

‘Outcome variable’ here denotes TIP and WF, and ‘sensitivity measure’ is a unified designation for measures of sensory sensitivity and cortical hyperexcitability. The most visually uncomfortable stimuli are marked as ‘stimulus type1’ (EA: midrange frequency grating; EB: scenes from the cluster of least visually comfortable urban stimuli). The remaining stimuli were coded as ‘stimulus type2-3’ (EA: high frequency grating; EB: scenes from the cluster of most visually comfortable urban stimuli, scenes from the cluster of least visually comfortable natural stimuli). Low frequency grating (EA) and scenes from the cluster of most visually comfortable natural stimuli (EB) served as reference levels and are therefore redundant in this notation. Importantly, when analyzing the data for Experiment B, we were not interested in the specific stimulus, only in the cluster from which it came. We did not distinguish between the stimuli from the respective cluster and considered them equivalent for the purposes of the analysis.

Cybersickness scores calculated as the difference between the participant’s final and initial state for each experiment were added as a control variable together with biological sex. The categorical variable ‘biological sex’ was coded binary, while the variable ‘stimulus type’ was dummy coded as described above. Scores of continuous variables ‘sensitivity measure’ and ‘cybersickness’ were converted to a standardized scale. To test the second and third hypotheses of each experiment, an interaction with the sensitivity measure was added to the most visually uncomfortable stimuli. Separate intercept was added for each participant to account for repeated measures. Among the analyses we conducted but did not pre-register were planned contrasts for testing all hypothesized differences in perception of stimulus type durations and equivalence testing for non-significant statistical results. Because these analyses complement the pre-registered ones, we report their results together with the results of pre-registered analyses.

Results

Pre-registered analysis for EA

Contrary to expectations, perceived durations of midrange spatial frequency gratings were not distorted (i.e., TIP was not shifted) compared to the perception of control low spatial frequency gratings (EAH1; $B = 0.021$, $p = 0.301$, CI 95% [− 0.019, 0.059]). Likewise, the main effect of high spatial frequency was not present ($B = -0.001$, $p = 0.970$, CI 95% [− 0.041, 0.038]). The observed effect size for the stimulus variable was Cohen’s $f^2 = 0.002$ (negligible). In order to examine EAH1 completely, we performed a planned contrast t-test between the midrange frequency

grating and the high frequency grating, but did not detect a significant difference (diff. = 0.021, $p = 0.447$, CI 95% [- 0.026, 0.068], Cohen's $d = 0.176$). Equivalence testing with a 90% confidence interval and the established effect size of interest Cohen's f^2 of 0.28 (converted to Cohen's $d = 0.56$ to set equivalence bounds), yielded non-significant results, indicating that the midrange spatial frequency effect compared to the effect of low ($d = 0.170$, CI 90% [- 0.168, 0.507]) and high ($d = 0.176$, CI 90% [- 0.162, 0.514]) spatial frequencies is equivalent to zero. Psychometric functions illustrating similarities between the perception of low, midrange, and high spatial frequencies are shown in Fig. 3.

Interactions of aversive midrange frequency with overall subjectively reported sensory sensitivity (EAH2; $B = 0.012$, $p = 0.472$, CI 95% [- 0.022, 0.046], $f^2_{\text{GSO}^*_{\text{mid}}} = 0.001$) or cortical hyperexcitability (EAH3; $B = 0.007$, $p = 0.674$, CI 95% [- 0.026, 0.041], $f^2_{\text{CHI-II}^*_{\text{mid}}} < 0.001$) were not significant. These interaction effects were established to be equivalent to zero, as both confidence intervals fell within the critical region of effect-size-of-interest bounds: sensory sensitivity \times midrange frequency $d = 0.102$, CI 90% [- 0.131, 0.335]; cortical hyperexcitability \times midrange frequency $d = 0.060$, CI 90% [- 0.173, 0.293]. Overall, the results suggest that if hypothesized relationships actually exist, their effects are much smaller than we considered interesting.

Among the rest of primarily hypothesized relationships, only participants' biological sex had a significant influence on TIP position. Male participants evaluated stimuli in general as lasting a shorter time than females ($B = 0.122$, $p = 0.012$, CI 95% [0.030, 0.213], $f^2 = 0.070$). The order of administration of the experiment had a significant effect on overall perception of stimulus duration as well. Whenever Experiment A was administered second, the stimuli caused an expansion of subjective time ($B = - 0.146$, $p = 0.002$, CI 95% [- 0.232, - 0.058], $f^2 = 0.113$). We therefore kept this predictor in the model as a control while testing the effect of all other above-mentioned predictors.

In all analyses for Experiment A with WF as an outcome, we used its logarithm because the variable's raw scores and residuals were non-normally distributed. Reported results are thus exponentiated. Of note, the logarithmic transformation was not originally pre-registered. The analyses showed that the participants judged high spatial frequency duration significantly less accurately than low spatial frequency (i.e., produced greater WF; $B = 1.186$, $p = 0.016$, CI 95% [1.036, 1.361], $d = 0.400$), although there was again non-significant effect of midrange spatial frequency on WF when compared to low spatial frequency ($B = 1.087$, $p = 0.236$, CI 95% [0.949, 1.245], $d = 0.194$ with CI 90% [- 0.143, 0.532]). Furthermore, there was a non-significant difference between WFs of midrange and high spatial frequencies indicated by planned contrast t-test (diff. = 0.916, $p = 0.376$, CI 95% [0.777, 1.081], $d = - 0.205$ with CI 90% [- 0.543, 0.133]). The overall observed stimulus effect size was $f^2 = 0.017$ (small).

As for TIP analysis, the accuracy with which the midrange frequency was judged did not significantly depend on the sensory sensitivity ($B = 1.018$, $p = 0.771$, CI 95% [0.901, 1.147], $f^2_{\text{GSO}^*_{\text{mid}}} < 0.001$) or cortical excitability ($B = 1.019$, $p = 0.751$, CI 95% [0.907, 1.147], $f^2_{\text{CHI-II}^*_{\text{mid}}} < 0.001$) of participants. Both interactions, with sensory sensitivity ($d = 0.041$, CI 90% [- 0.192, 0.274]) and cortical hyperexcitability ($d = 0.045$, CI 90% [- 0.188, 0.278]), were established to be statistically equivalent. Apart from the above, no other proposed predictors had a significant influence on timing accuracy.

Exploratory analysis for EA

Because the main hypothesized predictors of time perception were mostly non-significant, we performed several exploratory analyses in an attempt to inspect other possible explanations of the investigated processes. These analyses were not pre-registered, but we deliberately pre-registered the collection of additional data in case the results turned out this way.

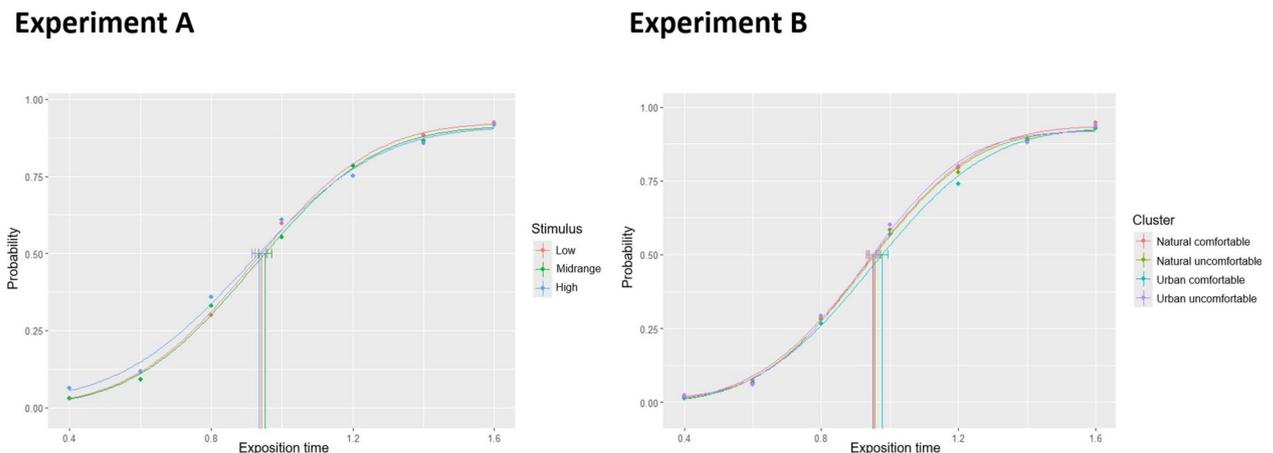


Fig. 3. Psychometric functions for stimuli of Experiment A (left) and Experiment B (right). The plotted stimuli of EA are (1) low spatial frequency, (2) midrange spatial frequency, and (3) high spatial frequency. For EB, these are clusters of (1) natural, visually comfortable scenes, (2) natural, visually uncomfortable scenes, (3) urban, visually comfortable scenes, and (4) urban, visually uncomfortable scenes. There are 95% confidence intervals at the points where subjects categorized a given stimulus as lasting 'Long' in half of the exposures.

First, we examined the influence of the stimulus variable on temporal judgments (TIP and WF as outcomes) in interaction with the participants' sensory sensitivity measures (GSQ and CHI-II) and then gradually with all their subscales individually. Second, we performed detailed analysis using standardized ratings of subjective visual comfort from stimuli as a predictor, because they were found to correlate with trait-based measures of sensitivity (GSQ, CHI-II and all their dimensions) only weakly to negligible ($r \leq 0.3$). All subjective ratings were significantly different among their levels ($p < 0.001$, pairwise t-test with Bonferroni correction) with means and standard deviations on the original scale: $\bar{x} = 0.99$, $SD = 2.23$ (low spatial frequency); $\bar{x} = -0.19$, $SD = 1.87$ (midrange spatial frequency); $\bar{x} = -1.68$, $SD = 2.34$ (high spatial frequency). Third, we examined the effect of the menstrual cycle, amount of sleep for the previous night, and the average amount of sleep on time perception. Final, best model structures extending the findings from the pre-registered analyses are presented in Table 1.

The exploratory analyses showed that the accuracy of time perception (WF) can be even better explained by the type of stimulus depending on how visually comfortable participants found it to be than when only taking into account the stimulus type (see Table 1). In this model, WF was significantly predicted, in addition to the original effect of high spatial frequency, by positive interactions of midrange spatial frequency ($B = 1.293$, $p = 0.005$, $CI\ 95\% [1.158, 2.218]$, $f^2_{SC^{mid}} = 0.036$) and high spatial frequency ($B = 1.35$, $p < 0.001$, $CI\ 95\% [1.294, 2.364]$, $f^2_{SC^{high}} = 0.053$) with subjective comfort ratings. More precise timing was related to lower subjective comfort from the given stimulus.

Analyses on female participants who reported which day of their menstrual cycle they were in (counting from the first day of menstruation; $N = 42$) revealed a significant negative interaction between high spatial frequency and the first day of their menstrual cycle ($B = 0.974$, $p = 0.011$, $CI\ 95\% [0.910, 0.987]$, $f^2_{MC^{stimulus}} = 0.028$, $f^2_{MC} = 0.060$) and a positive main effect of midrange spatial frequency ($B = 1.485$, $p = 0.023$, $CI\ 95\% [1.150, 4.346]$) on WF. However, the check of the model with the menstrual cycle indicated a high collinearity between its predictors ($VIF \geq 10$), which does not allow us to reliably interpret the influence of these predictors.

Pre-registered analysis for EB

Analyses for Experiment B did not confirm our hypotheses either. TIP position differed significantly only in the effect of visually-comfortable-urban-scenes cluster exposure compared to exposure to natural, visually comfortable environments ($B = 0.030$, $p = 0.010$, $CI\ 95\% [0.046, 0.331]$, Cohen's $d = 0.427$). Participants perceived durations of urban scenes as lasting shorter than in reality. There was non-significant, zero-equivalent (Cohen's d of interest of 0.56) result for the uncomfortable-urban-scenes cluster (EBH1; $B = 0.005$, $p = 0.644$, $CI\ 95\% [-0.109, 0.173]$, $d = 0.076$ with $CI\ 90\% [-0.301, 0.452]$). Planned contrast also failed to reveal significant differences between visually uncomfortable urban scenes and uncomfortable natural scenes ($diff. = -0.010$, $p = 0.529$, $CI\ 95\% [-0.020, 0.040]$, $d = 0.146$ with $CI\ 90\% [-0.522, 0.231]$) as well as between visually comfortable urban scenes and visually uncomfortable natural scenes ($diff. = 0.015$, $p = 0.375$, $CI\ 95\% [-0.044, 0.015]$). Although the latter was not established to be statistically equivalent ($d = 0.205$, $CI\ 90\% [-0.171, 0.582]$). An observed effect size for the cluster variable was Cohen's $f^2 = 0.005$ (negligible). Psychometric functions are shown in Fig. 3.

Besides the cluster effect, the only other significant predictor of TIP was biological sex. As in Experiment A, males perceived all stimuli types as overall shorter in duration than females ($B = 0.008$, $p = 0.031$, $CI\ 95\% [0.047, 0.928]$, $f^2 = 0.054$). The effect of sensitivity measures in interaction with visually uncomfortable urban environments was not statistically significant—for sensory sensitivity (EBH2) it was $B = 0.005$, $p = 0.602$, $CI\ 95\% [-0.014, 0.023]$, $f^2_{GSQ^{UU}} < 0.001$, and for cortical hyperexcitability (EBH3) $B = -0.009$, $p = 0.319$, $CI\ 95\% [-0.028, 0.010]^*$, $f^2_{CHI-II^{UU}} = 0.001$. Equivalence was established in both cases: sensory sensitivity \times urban uncomfortable scenes $d = 0.70$, $CI\ 90\% [-0.150, 0.289]$; cortical hyperexcitability \times urban uncomfortable scenes $d = -0.134$, $CI\ 90\% [-0.353, 0.086]$. The final model structure is presented in Table 2.

When we tested the effect of hypothesized predictors in the model with WF, no model was better than the model containing intercept only. There was non-significant main effect of urban-uncomfortable-scenes cluster ($B = 0.008$, $p = 0.569$, $CI\ 95\% [-0.020, 0.038]^*$, $f^2 = 0.001$, Cohen's $d = 0.093$ with $CI\ 90\% [-0.283, 0.470]$) or its interaction with sensory sensitivity ($B < 0.001$, $p = 0.977$, $CI\ 95\% [-0.022, 0.022]$, $f^2 < 0.001$, $d = -0.004$ with $CI\ 90\% [-0.224, 0.216]$) or cortical hyperexcitability ($B = 0.002$, $p = 0.854$, $CI\ 95\% [-0.020, 0.024]^*$, $f^2 < 0.001$, $d = 0.025$

Experiment A	TIP				WF					
	Predictor	B	SE	CI 95%		Predictor	B	SE	CI 95%	
				Lower	Upper				Lower	Upper
Intercept	1.022***	0.035	0.956	1.089	Intercept	1.363***	1.025	0.770	1.255	
Biological sex (males)	0.122**	0.047	0.030	0.213	Midrange	0.972	1.028	0.763	1.312	
Order (2nd)	-0.146**	0.045	-0.232	-0.058	High	1.097**	1.030	1.057	1.911	
					Comfort	0.959*	1.022	0.621	0.959	
					Midrange*comfort	1.080*	1.034	1.158	2.218	
					High*comfort	1.135***	1.031	1.294	2.364	
R ² (cond.) = 0.731, R ² (marg.) = 0.142, AIC = -138.925					R ² (cond.) = 0.419, R ² (marg.) = 0.100, AIC = -89.015					

Table 1. Final model structures for Experiment A. According to the AIC criterion, these model structures were the best fit when considering the main predictors and auxiliary variables, such as subjective ratings of visual comfort and the number of hours of sleep, with the data available for the entire sample. All estimates for the model with WF as an outcome are exponentiated. $p \leq 0.05$ (*), $p \leq 0.01$ (**), $p \leq 0.001$ (***)

Experiment B	TIP				
	Predictor	B	SE	CI 95%	
				Lower	Upper
Intercept	0.959***	0.022	0.917	1.001	
Natural uncomfortable	0.016	0.012	-0.007	0.038	
Urban comfortable	0.030**	0.012	0.008	0.053	
Urban uncomfortable	0.005	0.012	-0.017	0.028	
Biological sex (males)	0.077*	0.035	0.008	0.145	
R ² (cond.) = 0.807, R ² (marg.) = 0.057, AIC = -485.839					

Table 2. Final model structures for Experiment B. We present the model structure that we selected as the best based on AIC value only for the model with TIP as an outcome. After modeling WF, no model was retained. $p \leq 0.05$ (*), $p \leq 0.01$ (**), $p \leq 0.001$ (***)

with CI 90% [-0.195, 0.244]). There were also non-significant differences between visually uncomfortable urban scenes and uncomfortable natural scenes (diff. = 0.004, $p = 0.843$, CI 95% [-0.039, 0.031], $d = 0.046$ with CI 90% [-0.331, 0.422]) and between visually comfortable urban scenes and visually uncomfortable natural scenes (diff. = 0.004, $p = 0.830$, CI 95% [-0.039, 0.031], $d = 0.050$ with CI 90% [-0.327, 0.426]) detected by planned contrasts t-tests. Of note, some bootstrap analyses for the confidence intervals failed to converge with 10,000 iterations, so we reduced the number of iterations to 1000 and marked affected statistics with asterisks (*).

Exploratory analysis for EB

We conducted exploratory analyses in the same manner as for Experiment A. These analyses did not yield any improvements to the original models except for the analysis of the effect of the menstrual cycle on WF of the female participants ($N = 42$). Specifically, the further women were from the first day of menstruation, the more accurately they were able to discriminate durations of all stimuli ($B = -0.003$, $p = 0.030$, CI 95% [-0.006, -0.000], $f^2 = 0.057$). Combined with the results from EA, this suggests that variables such as biological sex or menstrual cycle may play an important role when investigating time perception in the context of visual sensitivity.

As with EA, subjective ratings of the visual comfort of the stimuli were weakly to negligibly correlated ($r \leq 0.3$) with measures of sensitivity (GSQ, CHi-II and all their dimensions). Mean ratings and their standard deviations for each stimulus were: $\bar{x} = 3.00$, $SD = 2.00$ (natural comfortable scenes), $\bar{x} = 1.20$, $SD = 2.03$ (natural uncomfortable scenes), $\bar{x} = 0.92$, $SD = 1.78$ (urban comfortable scenes), $\bar{x} = -1.00$, $SD = 2.50$ (urban uncomfortable scenes). The ratings are in line with the rating of participants in the preparatory study. All stimuli ratings differed significantly from each other ($p < 0.001$, pairwise t-test with Bonferroni correction).

Discussion

This registered report sheds light on distortions in time perception caused by visual stimuli, namely by the intensity of their neural coding and the interindividual sensitivity of their perception. We tested whether visually uncomfortable stimuli, the processing of which accompanies a larger neural response (e.g.,^{23–26}) magnified by the individual's visual system sensitivity¹⁰, prolong their subjectively perceived duration in accordance with the *neural coding efficiency theory*^{2,3}. Conducting two parallel experiments, we tested our hypotheses with use of simple stimuli (achromatic gratings), ensuring internal validity, and complex, ecologically valid stimuli (virtual exteriors). All stimuli varied in their presumed visual comfort and were installed in the temporal bisection paradigm^{51–54}. It turned out that evidence for none of the main hypothesized effects was detectable in our data, although several valuable and novel insights are present.

The current investigation did not capture the effect of achromatic gratings on time perception as was observed previously in Aeon's et al.³⁵ small sample ($N = 6$) study. Considering that small samples are more prone to produce extreme results, this effect may actually be negligible, as evidenced by our sufficiently large sample of naive participants. We do not rule out that another reason could be that the present study is only a conceptual replication. More precisely, the authors used a different type of task, an oddball task, presented on a computer screen, to investigate time perception. This task does not rely on memory storage to the same extent as the temporal bisection task we used. Second, the highest spatial frequency grating was up to 8 cpd compared to our 6 cpd. Third, the gratings were vertical, circular in shape, and smaller in size than in this study. Listed factors vary across the literature, and yet the stimuli tend to yield comparable effects (see for instance^{15,16,21,32,34,85,86}). Lastly, the authors did not control for the level of the autistic quotient of the participants.

However, spatial frequency and visual comfort of achromatic gratings had a significant impact on the accuracy of temporal judgments. High spatial frequency (6 cpd) grating, rated here as the least visually comfortable stimulus in EA, significantly decreased time perception accuracy. Exploratory analyses further showed that the influence of midrange and high spatial frequency on temporal sensitivity is moderated by ratings of their visual comfort. This suggests that not the sole effect of spatial frequency, but the subjectively perceived comfort has a significant impact on participants' temporal judgments. The fact that we discovered a significant pure effect of high but not midrange spatial frequency on WF together with exploratory results, raises the possibility that neural processing is not as important a factor here as subjective visual comfort. If this were true, it would be more consistent with explanations of time perception distortions addressing emotions and discomfort³⁷ rather than the *neural coding efficiency theory*^{2,3,5}. Notably, as suggested in the literature, excessive neural activation

occurs only after a few seconds of presenting uncomfortable stimuli and so was possibly not fully present in such short stimuli durations⁸⁷. Another possibility is that state-based subjective ratings are a sufficient proxy of cortical response and it is necessary to take them into account for detecting the effect. Definitive evidence to disentangle this issue requires a neuroimaging study.

Experiment B, unlike Experiment A, implies that the visual comfort of complex real-life stimuli does not relate to changes in the perception of short time intervals at all. We found a significant difference between the perception of visually comfortable urban scenes and visually comfortable natural scenes, but not visually uncomfortable urban scenes and visually comfortable natural scenes. As per previous studies, urban patterns should cause greater neural response and visual discomfort^{22,27}. Accordingly, all urban scenes in this study were rated as significantly less visually comfortable than natural scenes. Nevertheless, we did not observe an expansion of subjective time as *neural coding efficiency theory* would suggest, in fact, visually comfortable urban scenes led to its contraction. Such results possibly illustrate that the processing of complex stimuli is more intricate. Time perception in EB may have been greatly influenced by multiple factors like, for instance, arousal and emotions^{88,89} associated with varying restorativeness of outdoor environments (e.g.,^{90–93}). Out of concern is not even the presentation time, which could be too short to cause an excessive neural response as in the case of achromatic gratings⁸⁷. Alternatively, the effect of visually comfortable urban scenes could have been a false positive, given the large number of statistical tests performed.

Crucially, the effects of the stimuli in both experiments were not moderated by trait-based levels of sensory sensitivity or cortical hyperexcitability. Moreover, these trait-based scales were only weakly correlated with subjective ratings of visual comfort, which is contrary to our expectations based on previous findings^{13–16}. It may be that state-based sensitivity of the visual system varies over time and due to stimulation so much that it reduced its relationship with trait-based measurements in the current design^{10,94}. This again suggests that future studies should rather take into account the current level of sensitivity of the visual system. However, one reliably replicated result of both experiments was that males perceived stimuli in general as lasting shorter than females, contributing to previous findings of sex differences in timing (e.g.,^{95–97}). These results must be interpreted with caution, though, as we had twice as many females (67%) than males in our study. Exploratory analyses further suggested a role of the menstrual cycle phase on timing accuracy, perhaps due to fluctuations of excitatory and inhibitory neurotransmitters in the brain^{55–57}, hormones affecting timing along with the day time⁹⁸, or the relation of menstrual cycle phase with subjective visual comfort from aversive patterns⁸⁶. Considering the above speculation about the reason for the discrepancy between state-based and trait-based measures of visual system sensitivity, this result points to the rapidly changing sensitivity of the visual system as well.

In light of the results, the biggest limitation of the current investigation is that neuroimaging methods were not used to clarify the underlying neural mechanisms of our assumptions about cortical excitability. As we have mentioned above, future neuroimaging research is necessary before establishing a deficiency in *neural coding efficiency theory* or in the hypothesized effect of discomfort stimuli. This study only hints at such a deficiency. It could be that the problem lies in presenting pattern glare stimuli in EA for a shorter time than recommended (i.e., 5 seconds⁸⁷), but, if the theory is correct, this does not explain why we detected any effects of aversive stimuli or their interaction with self-report ratings of visual comfort. In addition, a study by O'Hare and colleagues⁹⁹ demonstrates a distorting effect of midrange spatial frequency grating during visual search tasks with an average length of exposure to the stimulus of 2 s. Of note, in our research design, the high spatial frequency grating had only 6 cpd due to technical limitations, i.e., half of what is usually used, but still outside the range of greatest discomfort (1–4 cpd; e.g.,^{15,16,23–26,34,87}). This partly explains and partly challenges its self-report ratings as the most visually uncomfortable. Importantly, it did not affect the hypothesis testing as the critical comparison of low and midrange spatial frequency ensuring validity (see¹⁰⁰) was preserved. The potential limit of EB was that the spatial frequencies of urban and natural outdoor scenes were not given also mathematically—this would be possible with 2D presentation using existing algorithms²². Algorithm-labeled visual discomfort, however, should be interchangeable to subjective discomfort ratings in this context²⁷.

In a nutshell, this work did not demonstrate a clear association between visual comfort linked to the extent of visuocortical activation and alterations in the perception of short time intervals. On the other hand, it provides several clues that can be used for further investigation. It suggests that the accuracy of perceiving the duration of simple stimuli (achromatic gratings) could depend on their currently perceived visual comfort, but it is up to future research whether also on the current excitability of the visual system. Furthermore, the specific stimuli we used in both experiments appear to affect male and female participants differently, possibly due to factors such as the phase of the menstrual cycle which is in line with our previous research on a different sample⁸⁶. Careful attention deserves an examination of other possible aspects by which outdoor scenes affect time perception than visual discomfort, i.e., emotional response. Likewise, the timing of stimulus presentation and other time perception tasks may be put under researchers' scrutiny. Overall, future research should consider the implications of our findings to more accurately map and explain interindividual differences in time perception through the visual domain, best while engaging neuroimaging methods in its study design.

Data availability

All materials and data aggregated within this study, including preparatory study data, are publicly available in the OSF repository at <https://osf.io/bf3rc/>.

Code availability

We share all the codes created within this study, i.e., R-code for data analysis, VR applications and their source codes, in the publicly available OSF repository at <https://osf.io/bf3rc/>.

Received: 5 July 2023; Accepted: 30 January 2025

Published online: 24 February 2025

References

1. Matthews, W. J. & Meck, W. H. Temporal cognition: Connecting subjective time to perception, attention, and memory. *Psychol. Bull.* **142**, 865–907 (2016).
2. Eagleman, D. M. & Pariyadath, V. Is subjective duration a signature of coding efficiency? *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1841–1851 (2009).
3. Pariyadath, V. & Eagleman, D. The effect of predictability on subjective duration. *PLoS ONE* **2**, e1264 (2007).
4. Kinzuka, Y., Sato, F., Minami, T. & Nakauchi, S. Effect of glare illusion-induced perceptual brightness on temporal perception. *Psychophysiology* **58**, e13851 (2021).
5. Kruijine, W., Olivers, C. N. L. & van Rijn, H. Neural repetition suppression modulates time perception: Evidence from electrophysiology and pupillometry. *J. Cogn. Neurosci.* **33**, 1230–1252 (2021).
6. Matthews, W. J. & Gheorghiu, A. I. Repetition, expectation, and the perception of time. *Curr. Opin. Behav. Sci.* **8**, 110–116 (2016).
7. Roseboom, W. et al. Activity in perceptual classification networks as a basis for human subjective time perception. *Nat. Commun.* **10**, 267 (2019).
8. Sadeghi, N. G., Pariyadath, V., Apte, S., Eagleman, D. M. & Cook, E. P. Neural correlates of subsecond time distortion in the middle temporal area of visual cortex. *J. Cogn. Neurosci.* **23**, 3829–3840 (2011).
9. Cai, M. B., Eagleman, D. M. & Ma, W. J. Perceived duration is reduced by repetition but not by high-level expectation. *J. Vis.* **15**, 19 (2015).
10. Ward, J. Individual differences in sensory sensitivity: A synthesizing framework and evidence from normal variation and developmental conditions. *Cogn. Neurosci.* **10**, 139–157 (2018).
11. Aron, E. N. & Aron, A. Sensory-processing sensitivity and its relation to introversion and emotionality. *J. Pers. Soc. Psychol.* **73**, 345–368 (1997).
12. Robertson, A. E. & Simmons, D. R. The relationship between sensory sensitivity and autistic traits in the general population. *J. Autism Dev. Disord.* **43**, 775–784 (2013).
13. Green, S. A. et al. Overreactive brain responses to sensory stimuli in youth with autism spectrum disorders. *J. Am. Acad. Child Adolesc. Psychiatry* **52**, 1158–1172 (2013).
14. Green, S. A. et al. Neurobiology of sensory overresponsivity in youth with autism spectrum disorders. *JAMA Psychiatry* **72**, 778–786 (2015).
15. Braithwaite, J. J., Brogna, E., Bagshaw, A. P. & Wilkins, A. J. Evidence for elevated cortical hyperexcitability and its association with out-of-body experiences in the non-clinical population: New findings from a pattern-glare task. *Cortex* **49**, 793–805 (2013).
16. Braithwaite, J. J. et al. Signs of increased cortical hyperexcitability selectively associated with spontaneous anomalous bodily experiences in a nonclinical population. *Cognit. Neuropsychiatry* **18**, 549–573 (2013).
17. Jurkovičová, L. et al. Resting GABA and glutamate concentrations in primary visual cortex and right anterior insula predict subjective visual sensitivity [Unpublished manuscript]. Department of Neurology, Masaryk University (2023).
18. Wilkins, A. What is visual discomfort? *Trends Neurosci.* **9**, 343–346 (1986).
19. Wilkins, A. et al. A neurological basis for visual discomfort. *Brain* **107**, 989–1017 (1984).
20. Wilkins, A. J. *Visual stress*. (OUP Oxford, 1995).
21. Hibbard, P. B. & O'Hare, L. Uncomfortable images produce non-sparse responses in a model of primary visual cortex. *R. Soc. Open Sci.* **2**, 140535 (2014).
22. Penacchio, O. & Wilkins, A. J. Visual discomfort and the spatial distribution of Fourier energy. *Vision Res.* **108**, 1–7 (2015).
23. Huang, J. et al. fMRI evidence that precision ophthalmic tints reduce cortical hyperactivation in migraine. *Cephalalgia* **31**, 925–936 (2011).
24. Juricevic, I., Land, L., Wilkins, A. & Webster, M. A. Visual discomfort and natural image statistics. *Perception* **39**, 884–899 (2010).
25. O'Hare, L. & Hibbard, P. B. Spatial frequency and visual discomfort. *Vision Res.* **51**, 1767–1777 (2011).
26. Wilkins, A. J., Binnie, C. D. & Darby, C. E. Visually-induced seizures. *Prog. Neurobiol.* **15**, 85–117 (1980).
27. Le, A. T. D. et al. Discomfort from urban scenes: Metabolic consequences. *Landsc. Urban Plan.* **160**, 61–68 (2017).
28. Briellmann, A. A., Buras, N. H., Salingaros, N. A. & Taylor, R. P. What happens in your brain when you walk down the street? Implications of architectural proportions, biophilia, and fractal geometry for urban science. *Urban Sci.* **6**, 3 (2022).
29. Burtan, D. et al. The nature effect in motion: visual exposure to environmental scenes impacts cognitive load and human gait kinematics. *R. Soc. Open Sci.* **8**, 201100 (2021).
30. Menzel, C. & Reese, G. Implicit associations with nature and urban environments: Effects of lower-level processed image properties. *Front. Psychol.* **12**, 591403 (2021).
31. Penacchio, O., Haigh, S. M., Ross, X., Ferguson, R. & Wilkins, A. J. Visual discomfort and variations in chromaticity in art and nature. *Front. Neurosci.* **15**, 711064 (2021).
32. O'Hare, L., Sharp, A., Dickinson, P., Richardson, G. & Shearer, J. Investigating head movements induced by 'riloid' patterns in migraine and control groups using a virtual reality display. *Multisensory Res.* **31**, 753–777 (2018).
33. Braithwaite, J. J., Marchant, R., Takahashi, C., Dewe, H. & Watson, D. G. The Cortical Hyperexcitability Index (CHI): A new measure for quantifying correlates of visually driven cortical hyperexcitability. *Cognit. Neuropsychiatry* **20**, 330–348 (2015).
34. Fong, C. Y., Takahashi, C. & Braithwaite, J. J. Evidence for distinct clusters of diverse anomalous experiences and their selective association with signs of elevated cortical hyperexcitability. *Conscious. Cogn.* **71**, 1–17 (2019).
35. Aaen-Stockdale, C., Hotchkiss, J., Heron, J. & Whitaker, D. Perceived time is spatial frequency dependent. *Vision Res.* **51**, 1232–1238 (2011).
36. Terhune, D. B., Russo, S., Near, J., Stagg, C. J. & Kadosh, R. C. GABA predicts time perception. *J. Neurosci.* **34**, 4364–4370 (2014).
37. Rey, A. E. et al. Pain dilates time perception. *Sci. Rep.* **7**, 1–6 (2017).
38. Tipples, J. Negative emotionality influences the effects of emotion on time perception. *Emotion* **8**, 127–131 (2008).
39. Bartholomew, A. J., Meck, W. H. & Cirulli, E. T. Analysis of genetic and non-genetic factors influencing timing and time perception. *PLoS ONE* **10**, e0143873 (2015).
40. Coutts, L. V., Cooper, C. E., Elwell, C. E. & Wilkins, A. J. Time course of the haemodynamic response to visual stimulation in migraine, measured using near-infrared spectroscopy. *Cephalalgia* **32**, 621–629 (2012).
41. Haigh, S. M. Variable sensory perception in autism. *Eur. J. Neurosci.* **47**, 602–609 (2018).
42. Schwedt, T. J. Multisensory integration in migraine. *Curr. Opin. Neurol.* **26**, 248–253 (2013).
43. Song, C., Schwarzkopf, D. S., Kanai, R. & Rees, G. Neural population tuning links visual cortical anatomy to human visual perception. *Neuron* **85**, 641–656 (2015).
44. Schwarzkopf, D. S., Anderson, E. J., de Haas, B., White, S. J. & Rees, G. Larger extrastriate population receptive fields in autism spectrum disorders. *J. Neurosci.* **34**, 2713–2724 (2014).
45. Bargary, G., Furlan, M., Raynham, P. J., Barbur, J. L. & Smith, A. T. Cortical hyperexcitability and sensitivity to discomfort glare. *Neuropsychologia* **69**, 194–200 (2015).
46. Huang, J., Cooper, T. G., Satana, B., Kaufman, D. I. & Cao, Y. Visual distortion provoked by a stimulus in migraine associated with hyperneuronal activity. *Headache J. Head Face Pain* **43**, 664–671 (2003).

47. Milne, E., Dickinson, A. & Smith, R. Adults with autism spectrum conditions experience increased levels of anomalous perception. *PLoS ONE* **12**, e0177804 (2017).
48. Takarae, Y. & Sweeney, J. Neural hyperexcitability in autism spectrum disorders. *Brain Sci.* **7**, 129 (2017).
49. Kaplan, A. D. et al. The effects of virtual reality, augmented reality, and mixed reality as training enhancement methods: A meta-analysis. *Hum. Factors* **63**, 706–726 (2021).
50. Ugwitz, P., Šašinková, A., Šašinka, Č., Stachoň, Z. & Juřík, V. Toggle toolkit: A tool for conducting experiments in unity virtual environments. *Behav. Res. Methods* **53**, 1581–1591 (2021).
51. Allan, L. G. & Gibbon, J. Human bisection at the geometric mean. *Learn. Motiv.* **22**, 39–58 (1991).
52. Church, R. M. & Deluty, M. Z. Bisection of temporal intervals. *J. Exp. Psychol. Anim. Behav. Process.* **3**, 216–228 (1977).
53. Wearden, J. H. Human performance on an analogue of an interval bisection task. *Q. J. Exp. Psychol. Sect. B* **43**, 59–81 (1991).
54. Wearden, J. H. & Ferrara, A. Stimulus spacing effects in temporal bisection by humans. *Q. J. Exp. Psychol. Sect. B* **48**, 289–310 (1995).
55. Rudroff, T., Workman, C. D., Fietsam, A. C. & Kamholz, J. Response variability in transcranial direct current stimulation: Why sex matters. *Front. Psychiatry* **11**, 585 (2020).
56. Smith, M. J. et al. Menstrual cycle effects on cortical excitability. *Neurology* **53**, 2069–2069 (1999).
57. Smith, M. J., Adams, L. F., Schmidt, P. J., Rubinow, D. R. & Wassermann, E. M. Effects of ovarian hormones on human cortical excitability. *Ann. Neurol.* **51**, 599–603 (2002).
58. Meisel, C. et al. Intrinsic excitability measures track antiepileptic drug action and uncover increasing/decreasing excitability over the wake/sleep cycle. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 14694–14699 (2015).
59. Kemeny, A., Chardonnet, J.-R. & Colombet, F. Self-motion perception and cybersickness. *Get. Rid Cybersickness* https://doi.org/10.1007/978-3-030-59342-1_2 (2020).
60. Hoekstra, R. A. et al. The construction and validation of an abridged version of the autism-spectrum quotient (AQ-Short). *J. Autism Dev. Disord.* **41**, 589–596 (2011).
61. Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J. & Clubley, E. The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *J. Autism Dev. Disord.* **31**, 5–17 (2001).
62. Grove, R., Hoekstra, R. A., Wierda, M. & Begeer, S. Exploring sex differences in autistic traits: A factor analytic study of adults with autism. *Autism* **21**, 760–768 (2017).
63. Kennedy, R. S., Lane, N. E., Berbaum, K. S. & Lilienthal, M. G. Simulator sickness questionnaire: An enhanced method for quantifying simulator sickness. *Int. J. Aviat. Psychol.* **3**, 203–220 (2009).
64. Davis, S., Nesbitt, K. & Nalivaiko, E. Systematic review of cybersickness. In *Proceedings of the 2014 conference on interactive entertainment* (2014). https://doi.org/10.1145/2677758.2677780?casa_token=GgMabV9LzzkAAAAA%3AnMY1V7OB-6FeZWuWc1E675SChrrUwBvLBCz95kzv0sCp2tMAPIZlB-3YS_-LcG_76_CfkgwCUpN. (Accessed 28th June 2023)
65. Lim, H. K. et al. Test-retest reliability of the virtual reality sickness evaluation using electroencephalography (EEG). *Neurosci. Lett.* **743**, 135589 (2021).
66. Makransky, G. & Mayer, R. E. Benefits of taking a virtual field trip in immersive virtual reality: Evidence for the immersion principle in multimedia learning. *Educ. Psychol. Rev.* **34**, 1771–1798 (2022).
67. Radianti, J., Majchrzak, T. A., Fromm, J. & Wohlgenannt, I. A systematic review of immersive virtual reality applications for higher education: Design elements, lessons learned, and research agenda. *Comput. Educ.* **147**, 103778 (2020).
68. Panagiotidi, M., Overton, P. G. & Stafford, T. The relationship between ADHD traits and sensory sensitivity in the general population. *Compr. Psychiatry* **80**, 179–185 (2018).
69. Panagiotidi, M., Overton, P. G. & Stafford, T. The relationship between sensory processing sensitivity and attention deficit hyperactivity disorder traits: A spectrum approach. *Psychiatry Res.* **293**, 113477 (2020).
70. Pöhlmann, K. M. T., Föcker, J., Dickinson, P., Parke, A. & O'Hare, L. The relationship between vection, cybersickness and head movements elicited by illusory motion in virtual reality. *Displays* **71**, 102111 (2022).
71. Wolde, T. Effects of caffeine on health and nutrition: A Review. *Food Sci. Qual. Manag.* **30**, 59–65 (2014).
72. Droit-Volet, S., Lamotte, M. & Izaute, M. The conscious awareness of time distortions regulates the effect of emotion on the perception of time. *Conscious. Cogn.* **38**, 155–164 (2015).
73. Droit-Volet, S., Fayolle, S. & Gil, S. Emotion and time perception in children and adults: The effect of task difficulty. *Timing Time Percept.* **4**, 7–29 (2016).
74. Droit-Volet, S. & Gil, S. The emotional body and time perception. *Cogn. Emot.* **30**, 687–699 (2016).
75. Grommet, E. K., Hemmes, N. S. & Brown, B. L. The role of clock and memory processes in the timing of fear cues by humans in the temporal bisection task. *Behav. Processes* **164**, 217–229 (2019).
76. Kliegl, K. M., Watrin, L. & Huckauf, A. Duration perception of emotional stimuli: Using evaluative conditioning to avoid sensory confounds. *Cogn. Emot.* **29**, 1350–1367 (2015).
77. Tipples, J. When time stands still: Fear-specific modulation of temporal bias due to threat. *Emotion* **11**, 74–80 (2011).
78. R Core Team. A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria* (2023). <http://www.R-project.org/>
79. Linares, D. & López-Moliner, J. quickpsy: An R package to fit psychometric functions for multiple groups. *R J.* **8**, 122–131 (2016).
80. Kellen, H. S., David. An introduction to mixed models for experimental psychology. In *New Methods in Cognitive Psychology* (Routledge, 2019).
81. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. (2014). <https://arxiv.org/abs/1406.5823>
82. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest Package: Tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).
83. Akaike, H. Information theory and an extension of the maximum likelihood principle. In *Selected Papers of Hirotugu Akaike* (eds Parzen, E. et al.) 199–213 (Springer, 1998).
84. Lüdtke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**, 3139 (2021).
85. O'Hare, L. Visual discomfort from flash afterimages of riloid patterns. *Perception* **46**, 709–727 (2017).
86. Jurkovičová, L. et al. Subjective visual sensitivity in neurotypical adults: Insights from a magnetic resonance spectroscopy study. *Front. Neurosci.* **18**, 1417996 (2024).
87. Evans, B. J. W. & Stevenson, S. J. The pattern glare test: A review and determination of normative values. *Ophthalmic Physiol. Opt.* **28**, 295–309 (2008).
88. Lake, J. I., LaBar, K. S. & Meck, W. H. Emotional modulation of interval timing and time perception. *Neurosci. Biobehav. Rev.* **64**, 403–420 (2016).
89. Schirmer, A. How emotions change time. *Front. Integr. Neurosci.* **5**, 58 (2011).
90. Bratman, G. N., Daily, G. C., Levy, B. J. & Gross, J. J. The benefits of nature experience: Improved affect and cognition. *Landsc. Urban Plan.* **138**, 41–50 (2015).
91. González-Espinar, J., Ortells, J. J., Sánchez-García, L., Montoro, P. R. & Hutchison, K. Exposure to natural environments consistently improves visuospatial working memory performance. *J. Environ. Psychol.* **91**, 102138 (2023).

92. Ojala, A., Korpela, K., Tyrväinen, L., Tiittanen, P. & Lanki, T. Restorative effects of urban green environments and the role of urban-nature orientedness and noise sensitivity: A field experiment. *Health Place* **55**, 59–70 (2019).
93. Van den Berg, A. E., Joye, Y. & Koole, S. L. Why viewing nature is more fascinating and restorative than viewing buildings: A closer look at perceived complexity. *Urban For. Urban Green.* **20**, 397–401 (2016).
94. Romei, V. et al. Spontaneous fluctuations in posterior α -band EEG activity reflect variability in excitability of human visual areas. *Cereb. Cortex* **18**, 2010–2018 (2008).
95. Hancock, P. A. & Rausch, R. The effects of sex, age, and interval duration on the perception of time. *Acta Psychol. (Amst.)* **133**, 170–179 (2010).
96. Williams, C. L. Sex differences in counting and timing. *Front. Integr. Neurosci.* **5**, 88 (2012).
97. Wittmann, M. & Szelag, E. Sex differences in perception of temporal order. *Percept. Mot. Skills* **96**, 105–112 (2003).
98. Morofushi, M., Shinohara, K. & Kimura, F. Menstrual and circadian variations in time perception in healthy women and women with premenstrual syndrome. *Neurosci. Res.* **41**, 339–344 (2001).
99. O'Hare, L., Clarke, A. D. & Hibbard, P. B. Visual search and visual discomfort. *Perception* **42**, 1–15 (2013).
100. Wilkins, A., Allen, P. M., Monger, L. J. & Gilchrist, J. M. Visual stress and dyslexia for the practicing optometrist. *Optom. Pract.* **17**, (2016).

Acknowledgements

We acknowledge the technical support of Grey Lab at the Department of Psychology, Faculty of Arts, Masaryk University and HCI Lab, Faculty of Informatics, Masaryk university. Hereby, we would also like to thank Edita Chvojka, Pavel Ugwitz and Peter Kravár for valuable comments during the preparation of the manuscript, and Karolína Bezemková, Klára Voršilková, and Kristýna Prošková for their help with data collection. The study was funded by the Grant Agency of Masaryk University within the Student Research Support Programme—Excellent Diploma Thesis, MUNI/C/0013/2024.

Author contributions

Authors contributed according to their competences and interests as follows, A.R. and L.J. built the concept; V.J., L.J., and J.C. consulted the experiments; K.M., J.P. and V.J. consulted the analysis; A.R. collected the data; A.R. and J.P. analyzed the data; A.R. drafted the manuscript; L.J., V.J., J.P., J.C. and K.A.H. edited and revised the manuscript; V.J. and K.A.H. supervised the project.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-88778-8>.

Correspondence and requests for materials should be addressed to A.R.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025