

A common neural mechanism underlies experiences of passage of time

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Abstract

Depending on the situation, the passage of time (PoT) can be experienced as slow or fast, irrespective of the actual duration of the situation. Although commonly used to describe everyday life situations, it is unresolved whether these different experiences of PoT involve a common underlying neural mechanism or situation-dependent processes. To answer this question, we employed electroencephalography (EEG) in controlled Virtual Reality (VR) environments which systematically manipulated PoT experience, based on the *velocity* and *density* of a moving visual array of colored stars (or starfield). Using multivariate analysis, we show that neural oscillatory patterns while viewing the starfield predict the experience of PoT. This prediction is situation-independent and stable across different velocities and densities of the presented starfields. Our findings support the claim that PoT experiences, despite being highly situation-sensitive, rely on a common neural mechanism.

Introduction

Time passing by differently or the variety of experiences of passage of time (PoT) is a phenomenon of daily human life. Expressions like ‘time flies’, e.g. in stimulating debates, or ‘time stands still’ as in boring waiting situations seem to clearly describe different situations ¹. PoT judgments (PoTJ) are used as descriptions of a wide variety of situations that differ substantially from each other, sensorially ², cognitively ^{3–5} or emotionally ^{6,7}. Notably, the PoT (i.e., time passing by slow or fast) is distinct from the perceived physical duration of time (i.e., how much time has passed in seconds/minutes/hours) ^{8–10}. Although the duration of a particular time interval (e.g., 10 s) might be accurately judged in two different situations, this same interval might be judged to pass slowly in one situation and quickly in the other ^{2,11–13}.

The independence of PoT from physical time raises the question of which dimension of subjective experience PoT refers to ^{13,14}. Given the range of situations in which PoT is experienced differently, it is unclear whether all these different situational characteristics are processed by a single neural mechanism. Instead, PoTJs might serve merely as a general vocabulary to retrospectively describe different situational experiences. Previous M/EEG studies of duration estimations have identified key roles for oscillatory processes in all canonical frequency bands including alpha band ^{15,16}, beta band ^{17–22}, delta band ^{17,23,24} and theta band ^{21,25,26}. However, the relevance of these time-related neural processes for the PoT experience is unclear.

In the current study, we sought to address the question whether a common process underlies the experience of PoT by studying the related *brain states*. According to account 1, the PoT experience in different situations (e.g., inspiring debate vs. boring waiting room) originate from the same neurobiologically grounded process similar to perception (in the following: ‘PER account’). A perception-like process would predict a consistent relationship between situational brain state and PoT experience across different situations. In contrast, according to the alternative account 2, PoTJs are the result of

retrospective reflections (in the following: ‘REF account’) that reconcile various dimensions of situations and only rely on a common vocabulary. In this latter case, the relationship between the brain state in the situation and subsequently reported PoT experience could differ between situations.

Our approach to distinguish between these competing accounts of the PoT experience involved the following two steps. First, we sought to identify brain states evoked by different standardized situations that are capable of predicting how a person would judge the PoT in that situation. Second, if such predictive states were indeed identifiable, we sought to evaluate whether the brain-to-PoTJ prediction rules in one situation were the same across different situations (as expected by PER but not REF account).

For this purpose, we employed the *starfield color tracking task*² which allows for systematic and repeated manipulation of PoT. In brief (Fig. 1A, see Methods), on each trial, participants view an array of colored moving stars (i.e., a starfield) over a duration of 19-21s. Following this display, participants reported the dominant color followed by a PoTJ (analog scale ranging from 0 - very slow to 100 - very fast). Two visual features of the starfield, namely, the *velocity* of the stars and their *density*, have been found to reliably influence PoT experience². Therefore, different PoT-relevant situations were generated by systematically varying the combination of the *velocity* (‘zero’, ‘slow’, ‘fast’) and *density* (‘few’, ‘many’) of starfield features. To ensure an optimal stimulation of PoT experience, the starfield stimulus was presented in fully immersive virtual reality (VR) via a head-mounted display (HMD)^{27,28}, but also see²⁹. While participants were performing the task, their ongoing neural activity was recorded using 64 channel electroencephalography (EEG) (see Methods). The acquired EEG was analyzed with a machine learning approach to assess whether a person’s neural state in one variant of starfield (i.e., a specific *velocity* and *density* combination) can predict the experienced PoT in that given situation and whether this prediction would be generalizable across other starfield variants (with different *velocity* and/or *density*). We used a general strategy previously employed to analyze dynamic oscillatory activity during *rest*³⁰ (see Methods). We considered the rest state (e.g., a 5–10 minute period of task-free wakeful rest) to be particularly relevant due to the suggestive similarity to each trial in our study, namely, a long period of 19–21 s without any overt behavior.

The neural state during starfield presentation was defined by the oscillatory power in five canonical frequency bands (delta, theta, alpha, β_{low} , β_{high}) at 64 channels across the scalp. To obtain robust predictors, this oscillatory state was sampled at 2-s snapshots (epochs) over each trial, where each snapshot was defined by 320 values (5 x 64).

To study the activity snapshots from each trial, we used a Support Vector Regression (SVR) algorithm³¹ to estimate a *situation-specific* predictor (Fig. 1A., see Methods). This predictor would take as input a single neural activity snapshot and output the predicted PoTJ as a value between 0–100 (analogous to the participant’s judgments). The predictor’s performance was determined by the strength of the correlation between the actual and the predicted PoTJs (Fig. 1B).

In a second step we tested whether the relationship between brain states and corresponding PoT were the same across different situations. Specifically, we asked: is a neural predictor estimated for one situation (e.g., a high *velocity*, low *density* starfield; Fig. 1A) capable of predictions with activity for other situations (e.g., a low *velocity*, high *density* starfield; Fig. 1B). The PER account would predict that the predictive capacity is generalizable across variants of the starfield – in contrast to REF.

Before and after the starfield color tracking task, 5 minutes of resting state (RS) measurements (no instructions other than to keep the eyes open and focus a specific point) were conducted. EEG data from starfield color tracking trials was contrasted against data from RS to ensure that participants continued to focus their attention to stimulus and task. Activity related to tracking colors while observing the starfield should result in decreased alpha band activity compared to the observation of an unchanging environment during the RS task ³².

Results

Passage of time experience varies with starfield visual features

The study's rationale relied on the assumption that the PoT experience can be influenced by modifying *velocity* and *density* ². Here, we used immersive VR to further increase this effect. However, in comparison to Jording et al. (2022), other aspects of the experimental situations changed (e.g., fewer color changes, different laboratory setting, additional technical equipment).

For each participant, we first checked the accuracy score in the color rating task to ensure continued attention to the stimulus and adherence to the instructions. All participants met the criterion of an average color rating accuracy score of at least 0.8 (mean = 0.98, SD = 0.03, min = 0.88, max = 1.0). Furthermore, we validated that different levels of *velocity* and *density* of the starfield presented in VR via a head-mounted display (HMD) while recording EEG would result in different PoTJs (Fig. 2). Likelihood ratio tests showed that including the continuous factors *velocity* ($X^2(1) = 903.33$, $p < 0.001$), *density* ($X^2(1) = 11.15$, $p < 0.001$) as well as their interaction *velocity* * *density* ($X^2(1) = 7.83$, $p = 0.005$) significantly improved model fits. Coefficients of the best fitting model ($PoTJ \sim velocity + density + velocity*density$) suggest that PoTJs per step from 'zero' to 'slow' or 'slow' to 'fast' increased on average by 0.075 (SE = 0.010) but decreased on average by 0.0179 (SE = 0.013) for many stars compared to few stars. However, both factors interacted so that per step in *velocity*, higher *density* led to an increase in PoTJs of 0.01746 (SE = 0.00624) according to the coefficient. Pairwise comparisons (Tukey corrected) revealed significant differences in all comparisons between different steps of *velocity*, irrespective of *density*. Conversely, higher *density* increased PoTJs significantly in 'slow' ($t(3103) = 3.0$, $p = 0.03$; $M = 0.072$, $SE = 0.088$) and 'fast' starfields ($t(3103) = 3.300$, $p = 0.010$; $M = 0.29$, $SE = 0.0088$), but no significant difference could be observed in 'zero' *velocity* variants between few and many star starfields ($t(3103) = 0.6$, $p = 0.990$; $M = 0.005$, $SE = 0.0088$). In summary, these results confirm that the different

starfield variants elicited different experiences of PoT. A general decrease of PoT with increasing *density* as suggested by the coefficient for *density* was not expected². However, as evident in the interaction *velocity*density*, this effect was stronger in lower *velocity* levels; and visual inspection as well as pairwise comparisons suggest that only when *velocity* was 'zero', *density* had no effect on PoTJs but that with moving starfields, PoTJs increased with *density*.

Starfield variants induce distinctive oscillation states

Behavioral results (color rating scores, PoTJs; see above) only attested for the participants attention to stimuli and the stimulus' effect on time experience. However, our experiment and analysis approach was based on two critical assumptions First, the starfield color tracking task induces a PoT-relevant state over the entire trial of 19-21s. Second, neural oscillations are markers of this state.

Several lines of evidence confirmed the face validity of our operationalization of these states as the oscillatory power in different frequency bands and the comparability of 2 s snapshots of these states across a trial.

Contrary to the assumed PoT-relevant state, the long behavior-free duration of each trial (19–21 s) could have induced a rest-like state following the stimulus onset irrespective of the starfield variant.

Accordingly, we checked for a classical signature of RS, namely elevated power in oscillatory power in occipital channels. Visual inspection of the power spectrum over occipital channels (Fig. 3A) in RS had a RS-typical form with a prominent peak in the alpha frequency band. The power spectrum in the task-states also showed a similar peak, aligned to the peak frequency from RS. However, as expected for tasks with higher visual stimulation (see Methods), we found a significant decrease in occipital alpha-band activation for the color tracking task compared to RS ($X^2(1) = 3410$, $p < 0.001$, coefficient task: $M = -1.07616$, $SE = 0.01799$; Fig. 3B). The reduced alpha power in the task-state was consistent with a task involving visual stimuli requiring attention. These results additionally confirmed the general viability of the EEG data and the absence of substantial distortions due to the HMD placement over EEG electrodes.

Passage of time experience can be predicted from oscillations states

The main research question was whether it would be possible to predict the experienced PoT, from 2 s snapshots of EEG activity recorded during the stimulus presentation. Therefore, we used a machine learning algorithm (see Methods) to estimate (or learn) PoTJ predictors from snapshot features in a portion of the data (i.e. training set). Prediction accuracy was then assessed as the z-standardized correlation between predicted and real PoTJ for the previously unseen data (test-set) in a 5-fold cross-validation.

We first tested whether epoch features and subsequent PoTJs were generally associated, irrespective of the specific starfield variant. For each participant, snapshots from all six possible starfield variants (*velocity*: 'zero', 'slow', 'fast' * *density*: low, high) were combined to training and test sets in a 5-fold cross-validation. The average correlation coefficients across the group was $r = 0.474$ ($SD = 0.151$) with a one-sample students t-test showing that participant-wise z-transformed correlation coefficients significantly exceeded zero ($t(40) = 5.228$, $p < 0.001$). This demonstrates that oscillation states during starfield color tracking task predicted subsequent PoTJs above guessing rate (Fig. 5, pink bars).

To ensure that the cross-validation procedure worked correctly, we conducted a permutation test. Prediction accuracy was assessed for randomly shuffled input data in 5000 runs per participant. Results for randomly shuffled input data grouped around zero (Fig. 5, blue bars) and did not indicate any substantial distortions due to problems with training and testing of predictors in the cross-validation procedure-.

Oscillation-based prediction of PoT are independent of velocity and density

After confirming that the trained predictors are able to detect associations between snapshot features and PoTJs, we tested whether these associations were specific to one variant of starfield or whether these patterns generalized to other starfield variants by assessing the generalization of predictors between *velocity* levels and between *density* levels. First, we confirmed an association between snapshot features and PoTJs within specific starfield variants (specific level of *velocity* or *density*) in a 5-fold cross-validation of predictors trained and tested on data from these variants. Second, we tested whether these same predictors would also be able to predict correctly PoTJs in other starfield variants (other levels of *velocity* and *density*). If the predictors accuracy scores did exceed zero significantly, we additionally tested whether accuracy scores differed between levels of *velocity* or *density*.

Accuracy scores of predictors trained and tested in a 5-fold cross-validation on snapshots from the same *velocity* (Fig. 6A & 6B) significantly exceeded zero ($t(40) = 14.674$, $p < 0.001$), i.e., guessing rate. This was also true of the accuracy scores for snapshots from the same *density* (Fig. 6C & 6D; $t(40) = 15.014$, $p < 0.001$). These findings confirmed the association between the snapshot features and PoTJs.

This association can exceed individual *velocity* or *density* variants, as evident in the performance of predictors trained on snapshots from one *velocity* variant on data from one of the other two *velocity* variants ($t(40) = 4.944$, $p < 0.001$) or from Predictors trained on one *density* variant on data from the other *density* variant ($t(40) = 9.424$, $p < 0.001$). Comparing the prediction accuracy between generalizations, a likelihood-ratio test revealed a suggestive difference depending on the *velocity* variant ($X(2) = 6.020$, $p = 0.049$). Subsequent pairwise comparisons (Tukey corrected) showed a significantly increased generalizability of predictors trained on data from the slow variant compared to predictors trained on the zero variant. ($t(78.1) = 2.463$ $p = 0.042$; $M = 0.064$, $SE = 0.026$). Accuracy scores did not differ significantly depending on the *density* variant ($X(1) = 0.070$, $p = 0.796$). Thus, except for small differences between

zero and slow *velocity*, we have no indication to believe that generalizability was limited to predictors trained on specific velocity or density levels.

Predictor generalization was tested across either *velocity* or *density* variants, but not both, i.e. datasets contained data from one specific *velocity* variant but both *density* variants or from one *density* variant but all *velocity* variants. Accordingly, we can infer that PoT related brain states are stable independent of *velocity* or of *density*.

Oscillation-based prediction of PoT are independent of moment-to-moment change rate

In order to test whether PoT related brain states are also independent of the general moment-to-moment change rate (as the product of *velocity* and *density*), we tested the generalization of predictors across *velocity* – *density* combinations (Fig. 7A). Again, we first ensured the existence of a general association between snapshot features and PoTJs within each combination of *velocity* and *density* in a 5-fold cross-validation ($t(40) = 17.395$, $p < 0.001$, Fig. 7B). The subsequent generalization test revealed that predictors generalized from one specific *velocity-density* variant to other *velocity-density* variants ($t(40) = 5.105$, $p < 0.001$), showing that PoT related brain states were also not mere correlates of moment-to-moment change rate. Testing for differences in prediction accuracy between variants, we did not find any significant effects neither for *velocity* ($X(2) = 1.44$, $p = 0.486$) nor for *density* ($X(1) = 2.39$, $p = 0.122$), but for the interaction *velocity * density* ($X(2) = 9.19$, $p = 0.010$). This suggests that certain combinations of *velocity* and *density* might potentially result in especially universal PoT states. However, pairwise comparisons only suggested that generalizations from ‘slow/few’ to other combinations were significantly more accurate than generalizations from ‘zero/few’ to other combinations ($t(196) = 2.996$, $p = 0.036$; $M = 0.084$, $SE = 0.028$).

Discussion

We investigated the status of passage of time as a unifying experience of phenomenologically distinct situations. We show evidence of stable neural patterns that predict the participants’ experience of passage of time over different situations. The stability of patterns suggests a shared neural mechanism. This substantiates the significance of the experience of PoT in relating otherwise incommensurable experiences.

Previous studies have identified the experience of PoT as distinct from other forms of time-related experiences like the perception of durations^{8–10}. Duration judgments provide information about how much time has passed between two given events and are more or less accurate approximations of a true value of physical clock time. In contrast, PoTJs are not assumed to be an objective measure but are considered an expression of subjective experiences. Applying the concept of accuracy, as a measure of adequate approximation of a true value, to PoTJs is pointless.

We have shown before that PoT experience responds to stimulus features in a dynamic situation, e.g. a reduced starfield environment with maximally simple elements like light points during an interval of interest (Jording et al. 2022). PoT might serve to complement judgments about the duration of time as it does no longer require the capacity to adapt with a physical clock but is grounded in subjective experience (Wearden, 2015). Since situational dynamics vary within a situation with a given duration, PoT experience might be useful to adequately interpret both physical aspects of the experienced situation (e.g. duration) and subjective aspects of it (e.g. meaning, value). In addition, PoT could also serve in accounting for subtle distortions in duration judgments. This could potentially explain why in a previous study visual change of a starfield affected perceived duration in participants that also had to rate their experience of PoT but not in participants who only had to assess duration but not PoT (Jording et al., 2022). However, patients with psychiatric conditions who report reduced or extended PoT in the sense of “slowing of time” in different contexts, do not necessarily differ in their accuracy of duration estimations³³. Key to assessing the relevance of PoT experience in everyday life would be the identification of its neurobiological foundations.

The search for a neural mechanism that conveys the experience of PoT requires to integrate the different sources that inform about the dynamics of a given situation. The starfield stimulus was designed based on the assumption that the intensity of visual stimulus changes influences PoTJs². Specifically, a higher intensity of visual stimulus changes (determined by *velocity* and *density*) was associated with a faster progression of time, hence higher PoTJs. We now further increased the salience and immersiveness of visual changes by using VR and replicated the results. Interestingly, even when there were no visual changes (zero *velocity*, zero *density*), the PoT was not rated as zero. This suggests that the visual stimuli only modify but do not generate a baseline PoT, which is constituted also by other sources of dynamic information. Here, the indicator of change purely relied on visual perception. Other situations might be fused with other sensory sources of change-related information, e.g., auditory¹⁵, olfactory³⁴, or interoceptive^{35,36}.

Given the diverse indicators of situational change, the challenge has been to explain what, if anything, is common across situations and specific to PoT. Specifically, is there a dedicated time-related mechanism by which sensory evidence of situational dynamics is converted into a PoT experience as suggested by PER account? Or does the experience of PoT refer to reflections that somehow reconstruct the experience in retrospect (REF account)? This fundamental distinction between PER and REF account thus reminds of early debates of emotions as either being directly elicited by bodily signals³⁷ vs. emotions being based on (additional) cognitive appraisal³⁸. Similarly, it can also be related to the discussion about intentions-to-act as preceding and causing actions or as being reconstructed by the brain after the action was initiated³⁹.

With regard to the two alternative accounts of PoT, our findings are consistent with PoT experience having its origin in a perception-like state based on a common neural mechanism across situations.. Although we cannot rule out that retrospective reflections also play a role in generating subsequent

PoTJs (as suggested by the REF account), our empirical findings support the PER account as the main basis for PoT experience. This claim is essentially based on two arguments.

First, if PoTJs were generated in a reflective process, triggered by the prompt at the end of each 20s trial, we should not be able to identify PoT-related brain signatures during the stimulus presentation of 20 s. However, the 2s EEG snapshot extracted throughout the 20s trial contained sufficient information to predict the PoTJ before this judgment was made at the end of the trial (see Fig. 5).

Second, even though potentially relevant reflective processes might be similar across situations, the contents of the reflection would be different. Referring back to the debate about the basis for emotions, the central argument against emotions being elicited by bodily signals was the observation that particular bodily signals (e.g. sweating) could be associated with different emotions (e.g. fear or excitement) and were held unspecific³⁸, i.e. it is not possible to predict emotions from bodily signals in one situation, based on knowledge about the relationship between bodily signals and emotions in another situation. Similarly, it could have been the case that knowledge about the relationship between brain states and PoTJs in one situation (i.e., low *velocity*, low *density* starfield) was not generalizable, i.e. would not help in predicting PoTJs from brain states in another situation (i.e., high *velocity*, high *density* starfield). Contrary, however, our critical findings are that there was a generalization across velocities and densities (see Fig. 6B&D, 7B).

In conclusion, for the first time we provide evidence for a brain signature of the experience of PoT: From this signature during the stimulus perception, we can predict subsequent PoTJs with a high accuracy. Furthermore, trained predictors transcend and are informative for all different starfield variants presented by manipulating two fundamentally different starfield features, namely *velocity* and *density*. This evidence of a consistent and continuous neural process underlying the experience of PoT encourages further experimental neuroscientific investigations aiming at a deeper understanding the mechanisms behind PoT experience. The origin of PoT experience will likely not be determined in one study but in a continued process of collecting evidence in favor of different alternative explanations. Further, this also emphasizes the question of the functional role of PoT and what it means to experience time differently in different situations.

Methods

Participants

42 healthy volunteers participated in the experiment and were compensated monetarily. After exclusion of one participant (see below), 41 participants (27 identifying as female, 14 as male; 34 right-handed, 7 left-handed) remained for analysis. Participants had normal or corrected to normal vision with no impairments in color vision, no history of psychiatric or neurological disease and were under no psychoactive medication. Prior to participation participants gave their informed written consent. The

study complied with the Declaration of Helsinki and was approved by the ethics committee of the Faculty of Medicine of the University of Cologne (reference number 21-1548).

Stimuli

The stimulus was a 3D environment presented via a head-mounted display (HMD) VR system (HTC Vive pro eye), with a resolution of 1440 x 1600 pixels per eye, a refresh rate of 90Hz and a horizontal x vertical field of view of 98° x 98°. The 3D environment (Fig. 8A) was custom-created and showed the interior of a spaceship cockpit with one chair in the middle of the room facing the cockpits forward window (distance: 6.5m; screen width: 11.9m, height: 7.4m). The chair in the 3D environment was spatially aligned with the 'real-world' chair participants were seated on physically during the experiment. From the participants perspective, the wind screen in front of them filled approximately 84.94° of the horizontal and 54.11° of the vertical field of view.

During the experiment (with exception of the RS periods, see Methods) a starfield stimulus was displayed outside the windscreen (Fig. 8B). A starfield is characterized by colored spheres ('stars') appearing in the far distance in front of the spaceship (close to the center of the screen from the participants perspective). Stars then move towards the spaceship, continuously increasing in size and brightness, eliciting the impression of flying through the starfield. When stars reach the level of the spaceship, they disappear at the edge of the screen and new stars are created at the horizon. Each star was assigned one of three colors (red, green, blue) based on a color ratio specified for the entire stimulus. The ratio between colors was always 80% for one color versus 10% for each of the other two colors, i.e. one color always predominated the starfield. In 80% of the trials, the color ratio stayed constant over the duration of the trial. In 20% of trials, the starfield changed its color abruptly between one and three times per trial (color-change trials). *velocity* (speed with which stars move towards the edge) varied between the levels 'zero' (0 m/s), 'slow' (20000 m/s) and 'fast' (80000 m/s) and *density* (number of stars displayed at any given moment) varied between 'few' (250 stars) and 'many' (1000 stars). Custom VR environment implemented in Unreal Engine 4 (UE4)® as well as custom script (Python 3.13) controlling the VR environment (start and end of starfield, starfield parameters, display of rating scales (see below) and inter trial pauses) available at:

https://github.com/MathisJording/SFCT_EEG_Analysis

Procedure

After arrival, participants were shown the laboratory including the EEG and the HMD setup and were seated in the laboratory chair which was then adjusted to their body height. The general procedure as well as the experimental task was then explained to participants and participants performed four practice trials with the above described VR environment shown on a 2D computer screen positioned on the table in front of them.

Participants task in the starfield color tracking paradigm in every trial was to observe a starfield stimulus and constantly observe, which star color was predominating. Participants were made aware of the fact,

that the predominant color could change at any moment during the trial. After the trial, participants were first asked to report the dominant color (prompt: 'Which color dominates in this moment?'; German: 'Welche Farbe dominiert im Moment?'); response options: 'red', 'green', 'blue'). After their response, participants were asked to report PoTJs (prompt: 'How fast has time passed?'; German: 'Wie schnell ist die Zeit vergangen?'; Response option: analog scale ranging from 0 - very slow to 100 - very fast). Participants were asked to think of situations in their everyday life when they experienced time as passing either very slowly or very quickly, and to use these examples as reference points for the extremes of the PoTJ scale. They were then asked to rate their current experience of the PoT in relation to these two examples.

For the practice trials, an experimenter checked the participants responses and gave feedback about the correctness of the color response. Afterwards the EEG cap was positioned and electrode gel was applied. Skin-electrode impedance was brought below 15 k Ω before starting the recording. In addition, ECG electrodes were attached to the participants chest as well as their left leg. After attaching the EEG and ECG electrodes and before putting on the HMD, participants were asked to fill out a cyber-sickness questionnaire before the proper experiment. The HMD was then carefully positioned on top of the EEG cap, ensuring a tight but comfortable fit while also constantly visually checking data quality of the EEG channels.

The experiment itself was split into three parts, commencing with a five-minute period in which participants were instructed to focus their gaze on a specific point in front of them but with no other specific task (RS measurement). Afterwards, five blocks (15 trials each) of starfield color tracking paradigm followed. In each trial, the starfield was presented for 19–21 s, followed by prompts asking for the predominant color and the current PoT judgement (see above). In total each trial took approximately 25–30 s, including an inter-trial-interval of 2 ± 1 s. Between blocks, participants were given the opportunity to take a short break. The five blocks were then followed by another five-minute RS measurement. The overall duration of the 5 blocks including breaks was approximately 40–45 min.

The five blocks of starfield color tracking paradigm were then followed by another RS measurement with the same instructions as before (open eyed). Afterwards, participants were asked to fill out post-experimental questionnaires.

Data acquisition

During the experiment, participants rated the dominant color as well as PoTJs in each trial via the HTC Vive Pro Eye controller (see above). The color ratings were used to ensure continuous attention towards the stimulus and adherence to instructions. Raw, untransformed PoTJs (ranging from 0–100) were the main focus of the behavioral analysis and used for classifier training and the investigation of classifier generalizability.

Scalp-EEG was acquired with a 64-channel active Ag/AgCl electrode system (actiCap, Brain Products, Germany) with a standard 10–20 spherical array layout (ground electrode at forehead, reference

electrode was the Cz channel). Measured voltages (0.04883 $\mu\text{V/bit}$ resolution) were amplified, filtered (low cut-off: DC, high cutoff: 280 Hz) and digitized at a sampling rate of 1 kHz (ActiCHamp, BrainProducts GmbH, Germany).

In addition to data acquired during the experiment, participants filled out the following questionnaires: a demographic questionnaire (including items about e.g. age, gender, years of education, handedness), a questionnaire about experiences with computer games and VR; Becks Depression Inventory, BDI ⁴⁰ assessing depressive symptoms; Autism-Spectrum-Quotient, AQ ⁴¹ assessing autistic symptoms; and Virtual Reality Sickness Questionnaire, VRSQ ⁴² assessing symptoms of cybersickness. Data from the BDI were used to ensure that no participants had any clinically relevant depressive symptomatology. AQ data were used in an exploratory fashion to investigate potential relationships between autistic symptoms and changes in time experience. The difference between the pre- and the post-experimental VRSQ was used to assess the severity of cyber sickness symptoms elicited by the HMD during the experiment.

EEG Preprocessing

The EEG data were preprocessed with custom scripts using MNE Python ⁴³. EEG data were first down-sampled to 250 Hz and then low-pass filtered to 40 Hz before being visually analyzed, bad channels were marked manually. A copy of the data filtered with 1 Hz high-pass filter was used to identify artefacts due to oculomotor activity (based on activity in channels FP1 and F8) with an independent component analysis ⁴⁴. These artefacts were then corrected in the main data which in the meanwhile had been high-pass filtered to 0.1 Hz. Afterwards, bad channels were interpolated before data from all channels were re-referenced to a common average reference. Subsequently, time periods containing artefacts due to paroxysmal amplitude changes, electromyographic contamination, electrical noise or signal loss were visually identified and rejected.

Snapshot definition and feature extraction

Continuous EEG trial data (approx. 20 s) were split into ten snapshots of 2 s duration each. Periods rejected due to artefacts as well as the 2 s periods following color changes were treated as interrupting continuous trial data and any overlapping snapshots were excluded from analysis. For each snapshot, each channels power spectrum over the range of 1–30 Hz (0.5 Hz resolution) was then computed with a fast Fourier transformation. The average power in five canonical frequency bands (δ : 1–3.5 Hz; θ : 4–7.5 Hz; α : 8–13.5 Hz; β_1 [low β]: 14–22.5; β_2 [high β]: 23–30 Hz) was then calculated per channel and logarithmically transformed so that the resulting distribution across snapshots approximates the normal distribution. Average power values in the five frequency bands were subsequently used to describe each channels activity during one snapshot. Accordingly, each snapshots activity was described by a vector of 320 features resulting from concatenating the 5 features from each of the 64 channels. These feature vectors (in combination with PoTJs from the corresponding trials) were the basis for all classification analyses.

Data quality assessment

All participants met the criterium of an average color rating accuracy score of at least 0.8 and thus the requirement for inclusion in further analysis.

We furthermore required each participants dataset to contain less than six ineffective channels and more than 75% available data from starfield color tracking task trials. Since total durations of trials were jittered (20 +- 1 s) and some trials contained color changes that would result in the automatic exclusion of any overlapping snapshot, computing the maximally possible number of snapshots per participant was not feasible. Therefore, data availability for each participant was assessed as the data available solely from trials not containing any color changes, counting a maximum of nine snapshots per trial. The maximally possible snapshot count per participant was thus 540 (60 trials without color changes with nine snapshots each).

One participant (371 available snapshots, corresponding to 68.7% of 540) did not meet the data availability criterium. For the remaining 41 participants a mean of 499.41 (SD = 36.29, min = 409, max = 539) starfield color tracking snapshots were available, corresponding to 92.48% of 540 maximally possible snapshots. In total, 20,476 snapshots were available for the analysis.

From the RS snapshots, a mean of 282.34 snapshots (SD = 19.03, min = 219, max = 300), corresponding to 94.11% of 300 maximally possible RS snapshots, was available for these participants. For the whole sample, in total 11,576 RS snapshots were available for the analysis.

Analysis of PoTJs

We used R ⁴⁵ and RStudio ⁴⁶ to analyze the effect of starfield *velocity* and *density* on PoTJs. We fitted mixed effects models with the `lmer()` function from the `lme4` package ⁴⁷ to predict PoTJs. Where possible, models included the maximal random effects structure with random intercepts for participants and random slopes of *velocity* and *density* for participants. In the case of non-converging models, we first removed the random slope for *density* then the random slope for *velocity*. We compared the fit of models including the factors *velocity* or *density* with Null-models, not including the factor in likelihood ratio tests with the `anova()` function. All statistical tests were performed against an alpha level of $p < 0.05$. For the analysis of individual model coefficients we used the `lmerTest()` function ⁴⁸ which corrects for multiple comparisons using the Satterthwaite's degree of freedom approximation.

EEG face validity check: Comparisons of alpha-activity and neural representation similarity between starfield variants

The participants adherence to the color tracking task was assessed based on the correctness of their reports of the dominant color and the decrease of alpha band activity while observing the starfield compared to the observation of an unchanging environment during the RS ³². We compared the mean occipital alpha-band activation between RS and starfield color tracking tasks snapshots in the occipital region as the average of the alpha feature of eight occipito-parietal channels ('O1', 'Oz', 'O2', 'PO7', 'PO3', 'POz', 'PO4', 'PO8').

We assessed the similarity of neural patterns within starfield variants in relation to between starfield variants based on correlations of feature vectors from the snapshots from different variants. For each participant, we first computed the full correlation matrix between the feature vectors of all snapshots (max 750), resulting in a 750 x 750 (max) correlation matrix. We then collapsed the matrix, averaging all correlations per starfield variant ('RS', 'zero/few', 'slow/few', 'fast/few', 'zero/many', 'slow/many', 'fast/many'; e.g. we averaged all correlations between 'slow/few' and 'fast/many' or all correlations between 'zero/many' and 'zero/few' snapshots). This step resulted in one 7x7 matrix of average correlations for each participant.

Mean occipital alpha-band activation as well as participant-wise correlation coefficients were analyzed in mixed effects models with random intercepts for participants using the same tools and following the same likelihood ratio test approach as described for PoTJs (see above).

Machine Learning algorithm

Predictors were learned using a soft-margin linear support vector regression (SVR) algorithm, implemented in the LinearSVC package of the scikitlearn library ⁴⁹ in Python 3.13. The SVM algorithm was pragmatically selected for being a robust and well-documented standard algorithm that is commonly used. SVM learning was initialized with standard parameters (epsilon = 0.0, tolerance = 0.0001, max iterations = 1000, loss = 'epsilon_insensitive'). The hyper-parameter C had a value of 1, which has been shown to be a reasonable default for M/EEG classification ⁵⁰.

The predictors accuracies were determined as the ratio between the PoTJs predicted based on snapshot features and the real PoTJs. To this end, the correlation between real and predicted PoTJs was computed for each combination of training and test-set and for each participant. Correlation coefficients were then z-transformed using the inverse hyperbolic tangent ⁵¹ to more closely resemble a normal distribution and to allow averaging over different test sets or different participants. Significant positive deviation from zero would thus mean that predicted and real PoTJs correlated significantly (on average) and thus that the predictor's prediction accuracy exceeded guessing rate.

Predictor training and testing was conducted in a 5-fold cross-validation ⁵²: For each participant, all data snapshots were split into five folds with each fold containing the same amount of snapshots per starfield variant. Four of the five folds were then used to train a classifier (training-set) and the last fold was used to test the classifier (test-set). This was conducted for each participant separately and for each of the five possible combinations of folds into training and test-set. The five resulting correlation coefficients were then z-transformed and averaged for each participant.

For the permutation test predictors were trained on randomly associated snapshot features and PoTJs. In each of the 5000 permutation runs, first the mapping between snapshot features and the corresponding PoTJ was randomly shuffled for each participant. Afterwards, a participant-wise five-fold cross-validation (see above) was performed for the randomly re-shuffled data.

Evaluating robustness of associations between EEG signal and PoT experience

Next, we tested whether predictors would be able to generalize from feature-PoTJs associations from a specific situation A, i.e., a specific starfield variant, to feature-PoTJs associations from situation B, i.e. a different starfield variant.

To this end, we first always tested in a five-fold cross-validation whether predictors were able to predict PoTJs within a given specific situation of a *velocity-density* variant. Therefore, participant wise, all snapshots from the specific starfield variant(s) were split equally into five folds. Folds were then combined into five different training and test sets so that each possible combination of four folds was used once as training-set with the remaining fold constituting the corresponding test-set. The predictors predictions for each of the five test-sets was then correlated against the respective true PoTJs. The resulting five correlation coefficients were then z-transformed and averaged per participant. Averaged, z-transformed correlation coefficients from the whole group were then again tested against a mean of zero one-sample students t-test.

In order to test the generalizability between different situations A and B, we then trained a classifier on all snapshots from situation A and tested the accuracy of the predictors' predictions for situation B. As in the cross-validation tests, we again computed the correlation between predicted and true PoTJs per participant, before testing z-transformed correlation coefficients from the whole group against zero in a test.

Preregistration

All hypotheses and general procedures related to data acquisition, preprocessing, quality and analysis were preregistered at: <https://osf.io/y4vbn> (date of registration: May 26th, 2023).

Declarations

Competing Interests

The authors declare no competing interests. For disclosure: S.V. is currently employed at Brain Products GmbH.

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Author Contribution

M.J., D.H.V.V., S.V., and K.V. designed the study protocol. M.J. and S.V. developed the analysis strategy, M.J. implemented the paradigm code, M.J., M.W, and M.M. conducted the experiments, M.J. analyzed the data, and drafted the manuscript. All authors critically revised the manuscript.

Data Availability

Raw data (BIDS format) are available at:[doi:10.18112/openneuro.ds007454.v1.0.0](https://doi.org/10.18112/openneuro.ds007454.v1.0.0) Code and group level data for replication of results and generation of figures, including Jupyter Notebooks (based on MNE Python) for preprocessing of data and training of machine learning algorithms and R scripts for statistical analysis are available at:https://github.com/MathisJording/SFCT_EEG_Analysis.git

Code availability

Code and group level data for replication of results and generation of figures, including Jupyter Notebooks (based on MNE Python) for preprocessing of data and training of machine learning algorithms and R scripts for statistical analysis are available at:

https://github.com/MathisJording/SFCT_EEG_Analysis.git

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Figures

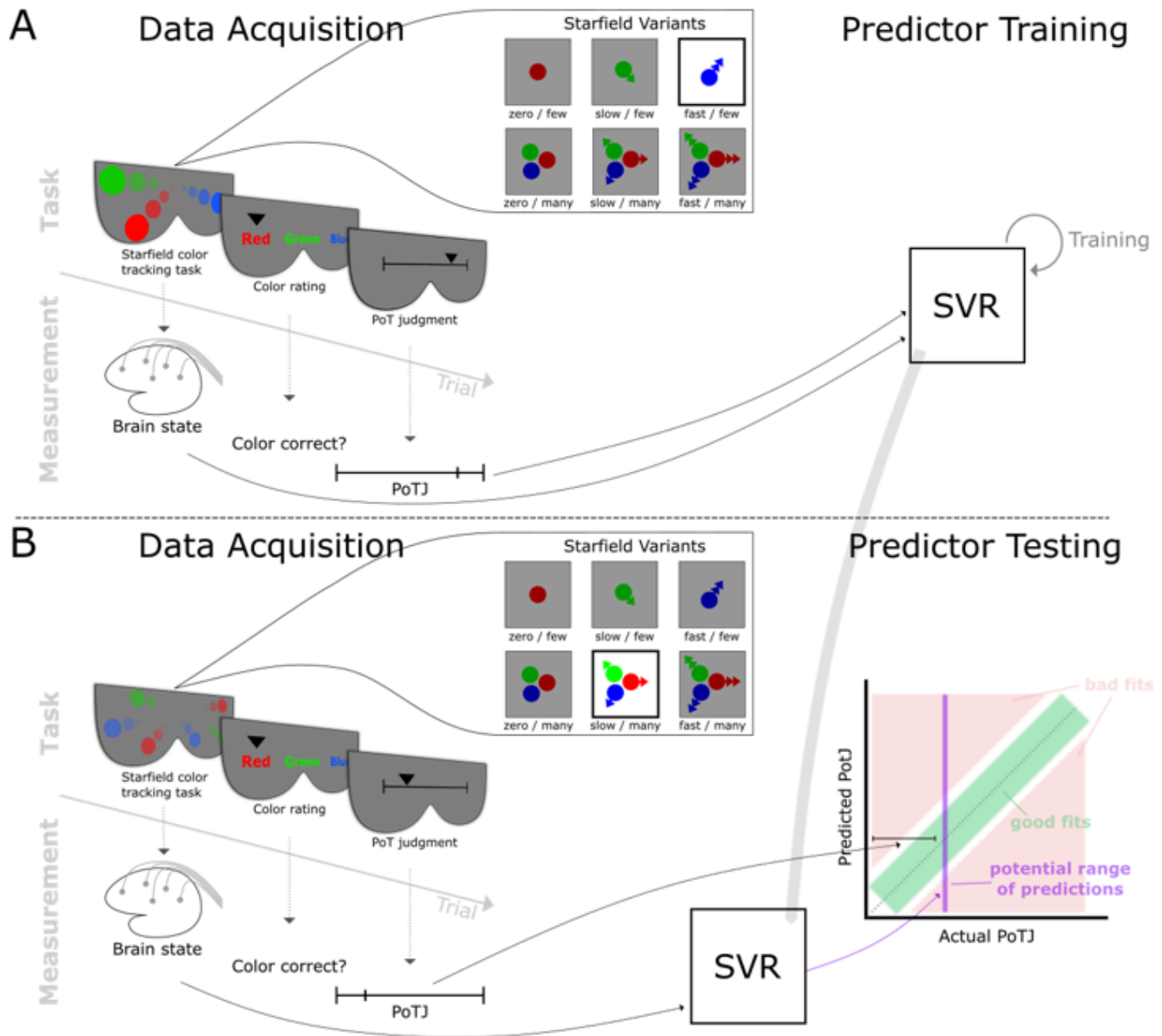


Figure 1

Figure 1. Illustration of the comparison of brain states associated with passage of time experience across different starfield variants. The participant's task is to track the colors of stars in a starfield presented in VR (schematic head-mounted display, far left; starfield stimuli exemplified as 2D perspective projection with stars moving radially while increasing in size and illumination). Starfields vary in velocity (zero, slow and fast movement) and density (few and many stars). Subsequently participants in VR are prompted to report the predominant color ('color rating') and to report their experience of PoT on a visual analog scale ('PoT Judgment'). While participants perform the starfield color tracking task, a 64 channel EEG is recorded. A: Using machine learning (SVR) we trained on associations between the brain state in one out of 6 different types of starfield environments (e.g., here: 'fast/few') and PoT. B: The resulting predictor was then used to predict PoT from brain states in all other of the 5 remaining combinations of starfield environments (e.g. here: 'slow/many'). The range

of potentially predicted PoTs is depicted as purple bar. As a metric for prediction success and thus stability of brain states across situations we computed the correlation between actual and predicted PoT.

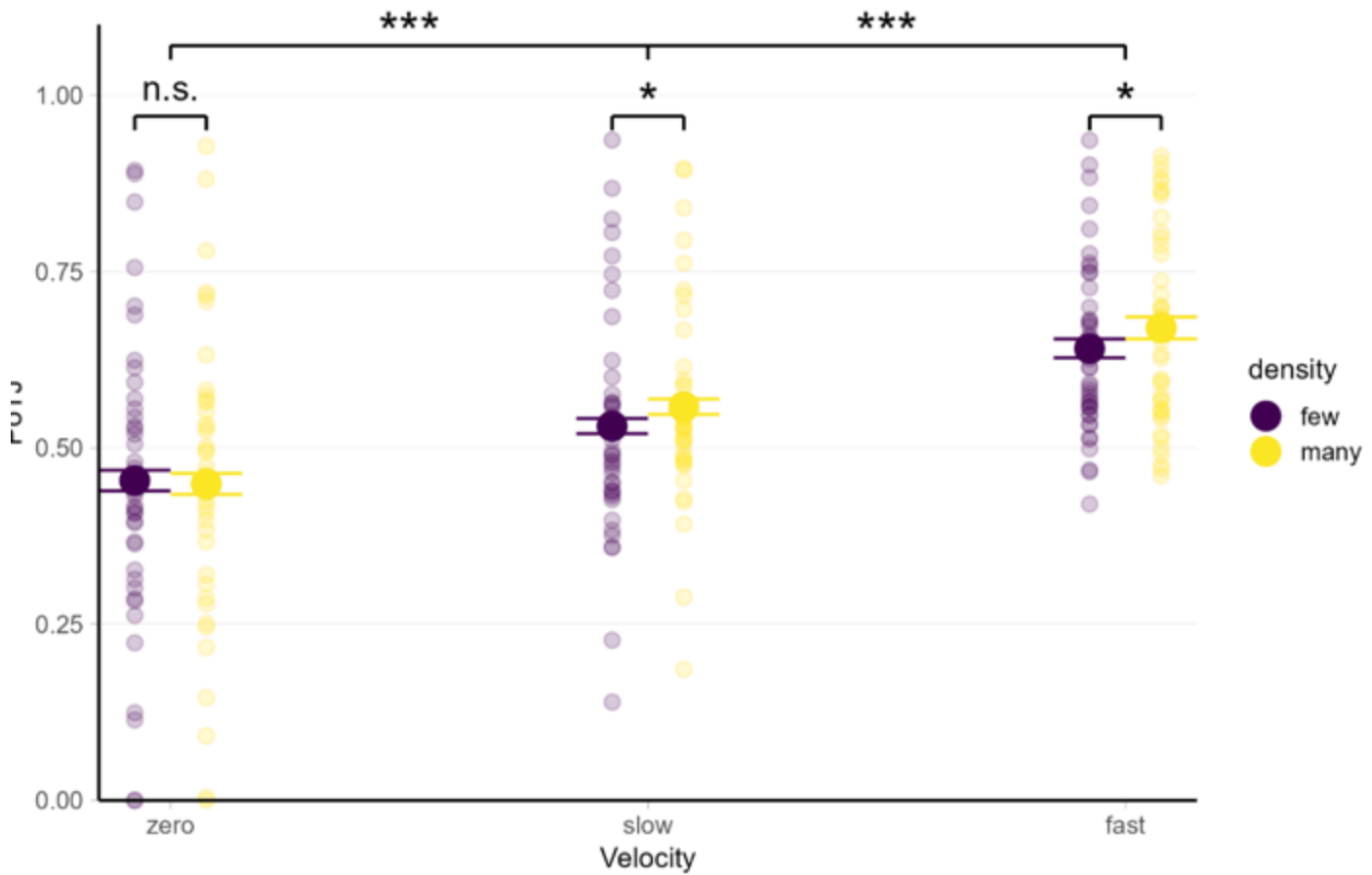


Figure 2

Figure 2. Participant-wise PoTJs (y-axis) averaged for each variant of Velocity (x-axis) and Density (colors). Participants averages are depicted as small, transparent circles, group averages per level are depicted as bigger opaque circles, 95% within-participant confidence intervals are shown as error bars. Pairwise comparisons revealed significant differences between all variants with different Velocity levels and between low and high Density when Velocity was slow or fast but not zero (* < 0.05; ** < 0.01, *** < 0.001, n.s.: not significant).

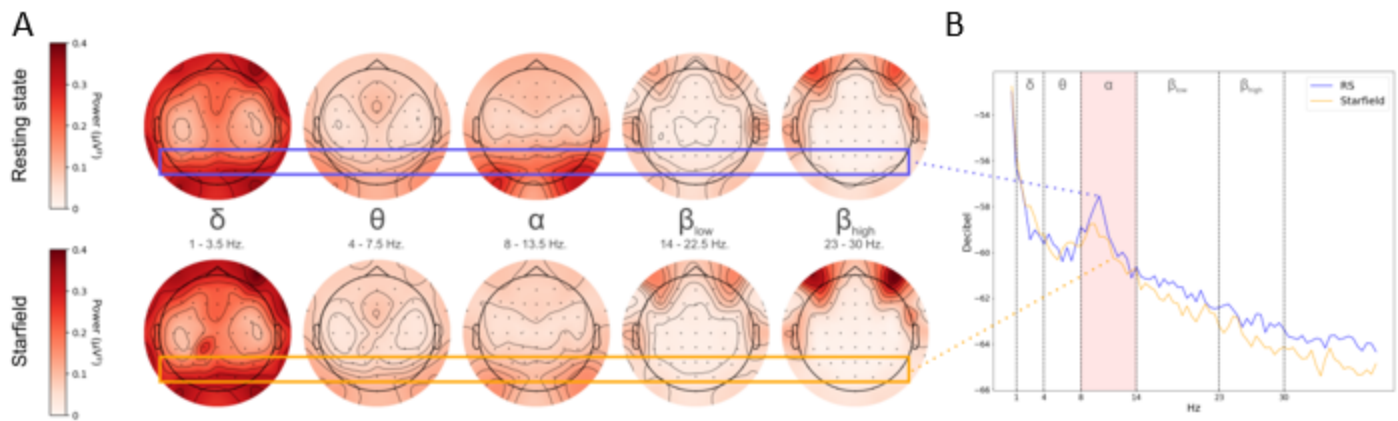


Figure 3

Figure 3. A: Topological plots of distribution of mean power in each frequency band for RS (top) and starfield (bottom) epochs (averaged over all epochs within each participant and over all participants). B: Power spectrum density plot showing average powers in occipital channels (marked by blue and yellow rectangles in A) in RS (blue) and starfield (yellow) epochs. Marked in light pink is the alpha band, showing increased average power for RS compared to starfield epochs.

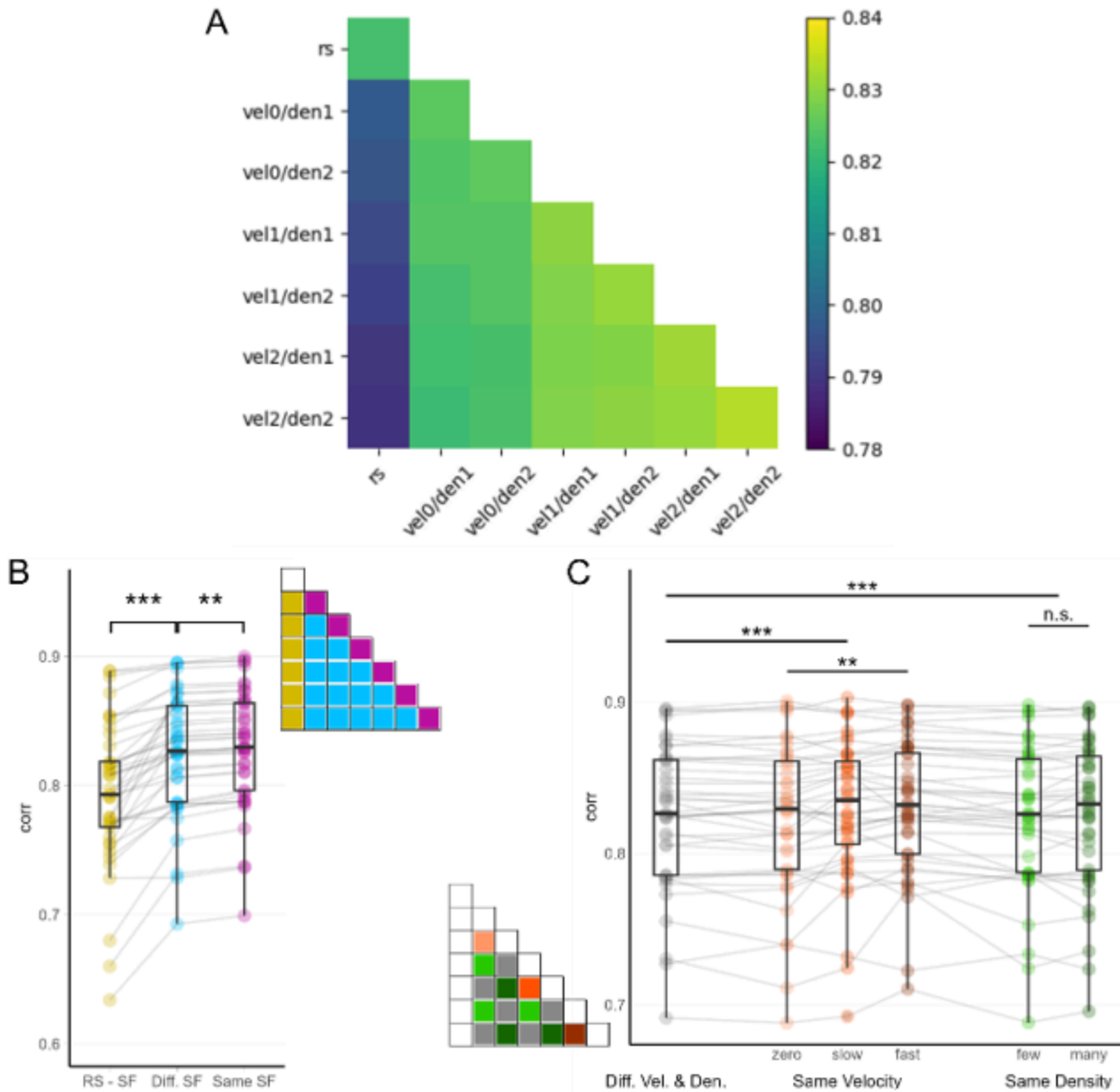


Figure 4

Figure 4. A: Matrix of epoch feature correlations, averaged over all participants and for each combination of resting state (RS) and starfield (SF) variants ('vel' = Velocity; '0' = zero, '1' = slow, '2' = fast / 'den' = Density; '1' = few, '2' = many). B: Boxplots of epoch feature correlations showing the significantly increasing similarity from RS - SF pairs (yellow) to SF pairs of different variants (blue) to SF pairs of the same variant (purple). Triangle of differently colored fields (right) illustrates mapping to correlation matrix of group averages (A). C: Boxplots of epoch feature correlations showing a significant increase of similarity for same velocity SF pairs (orange) and same density SF pairs (green) compared to different velocity and density pairs (grey) as well as a significantly increased similarity for higher velocities pairs compared to lower velocity pairs (light to dark orange). Triangle of differently colored fields (left) illustrates mapping to correlation matrix of group averages (A). Circles: Participant-wise averaged epoch feature correlation. Boxplots: middle line: median; hinges: 25% - 75%-quantile;

whiskers: smallest value below 25%-quantile and largest values above 75%-quantile within 1.5 x inter-quartile-range. Significance levels of t-tests: * < 0.05; ** < 0.01, *** < 0.001, n.s.: not significant.

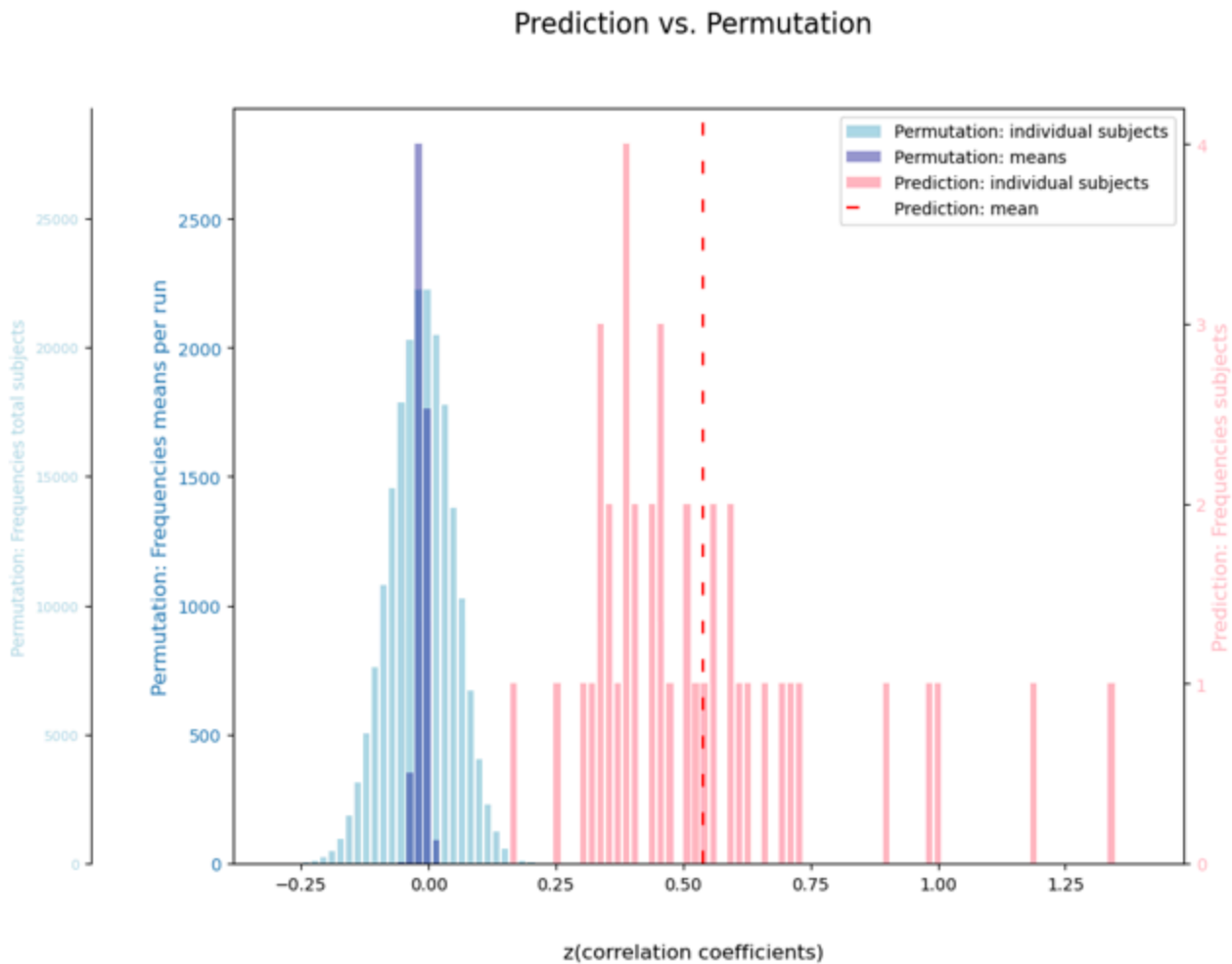


Figure 5

Figure 5. Histogram of accuracy scores (z-standardised correlation coefficients between predicted and true PoTJ) from cross-validation in all individual participants (light pink; mean: red dotted line) and from 5000 runs of permutation tests (light blue: accuracy scores from all participants in each permutation run; dark blue: mean accuracy scores per run). In each permutation run, a 5-fold cross-validation was performed following the same procedure as bevor (see above) but with randomly shuffled PoTJs.

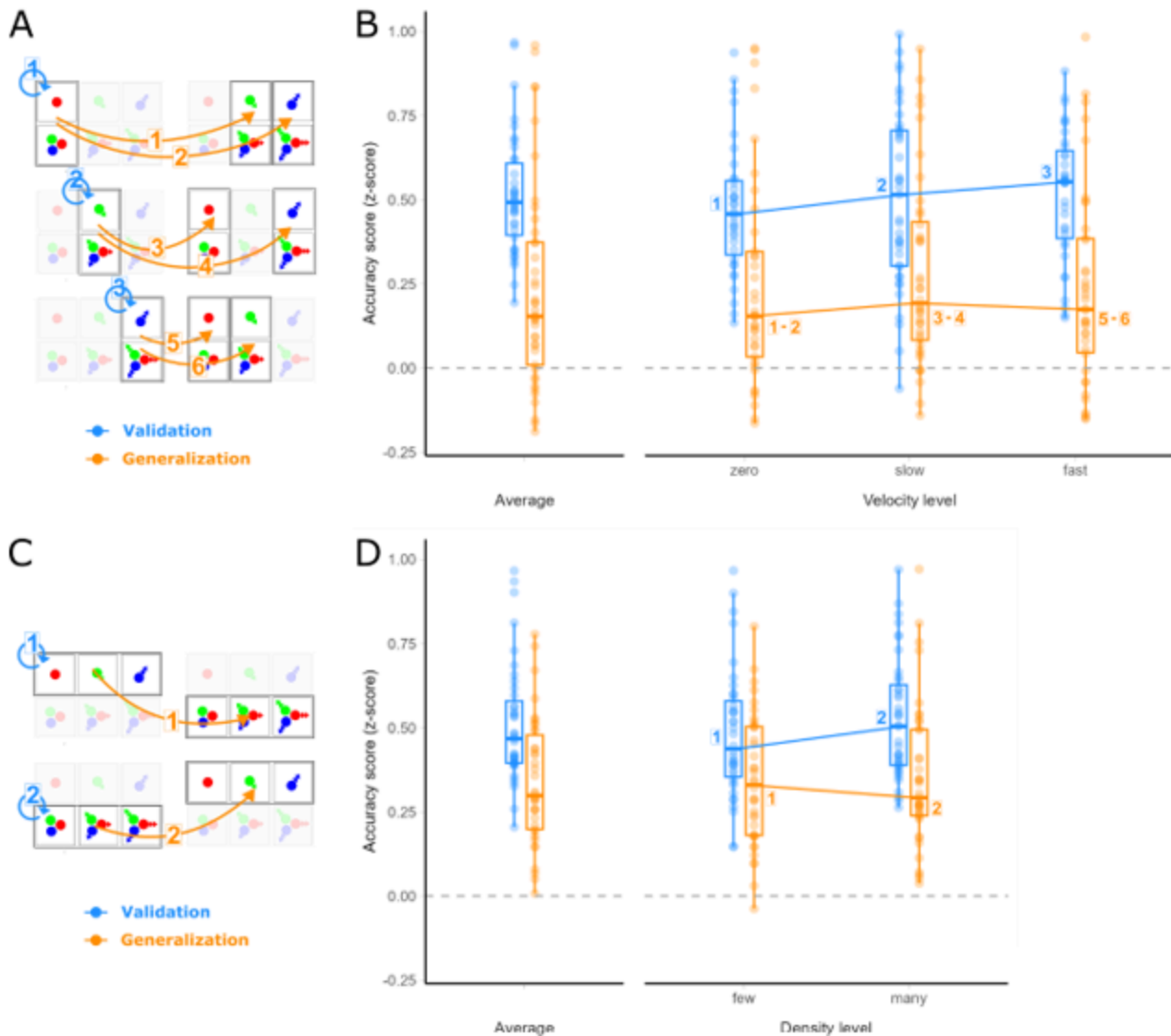


Figure 6

Figure 6. Starfield variants (combination of Velocity and Density) in training and test sets and accuracy scores from 5-fold cross-validation and generalization between variants of different Velocity (A+B) or different Density (C+D). A+C: Schematic illustration of trainings-set (highlighted in left column; blue numbers) and test-sets (right column). For cross-validation, test-sets were composed of snapshots from the same Velocity or the same Density variants (blue arrows). For generalization, we tested whether predictors trained on one variant of Velocity could predict PoTJs in the other Velocity variants and predictors trained on one variant of Density could predict PoTJs in the other Density variants (orange arrows and figures). B+D: Participant-wise averaged accuracy scores (z-standardized correlation coefficients between predicted and true PoTJs) for cross-validation (blue) and generalization (orange). Left most column (B+D): averaged for all cross-validations and generalizations; Right columns in B: separate results for cross-validations within individual Velocity variants (blue numbers, corresponding to A) and averages for generalizations from 'zero' to 'slow'/'fast' (orange 1-2), from 'slow' to 'zero'/'fast' (orange 3-4) and from 'fast' to 'zero'/'slow' (orange 5-6; all

numbers corresponding to A); Right columns in D: separate results for cross-validations within individual Density variants (blue numbers, corresponding to C) and for generalizations from few to many (orange 1) and from many to few (orange 2, corresponding to C). Each participants averages are depicted as small, transparent circles. Boxplot showing group median (middle line), 25% - 75% quantile (hinges) and the smallest value below 25% (lower whisker) and the largest value above the 75% quantile (upper whiskers) that are within 1.5 of the inter quartile range (distance between quantile 25% and 75%).

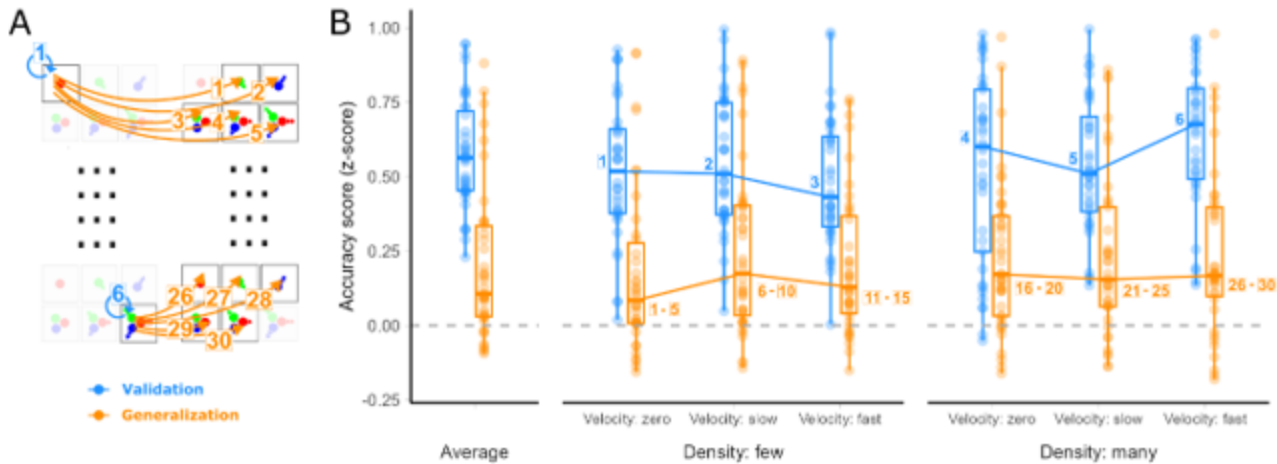


Figure 7

Figure 7. Starfield variants (combination of Velocity and Density) in trainings- and test-sets and accuracy scores from 5-fold cross-validation and generalization between variants of different Velocity and Density. A: Schematic illustration of trainings-set (highlighted in left column; blue numbers 1-3) and test-sets. For cross-validation, test-sets were composed of the same starfield variant (marked by blue arrows). For generalization, we tested whether predictors trained with one variant could also predict PoTJs in the other variants (orange arrows and numbers). B: Participant-wise averaged accuracy scores (z-standardized correlation coefficients between predicted and true PoTJs) for cross-validation (blue) and generalization (orange). Left most column: averaged for all cross-validations and generalizations; Right columns: separate results for cross-validations within variants (blue numbers, corresponding to A) and averages for generalizations from each specific variant to all other variants (orange numbers, corresponding to A). Each participants averages are depicted as small, transparent circles. Boxplot showing group median (middle line), 25% - 75% quantile (hinges) and the smallest value below 25% (lower whisker) and the largest value above the 75% quantile (upper whiskers) that are within 1.5 of the inter quartile range (distance between quantile 25% and 75%).

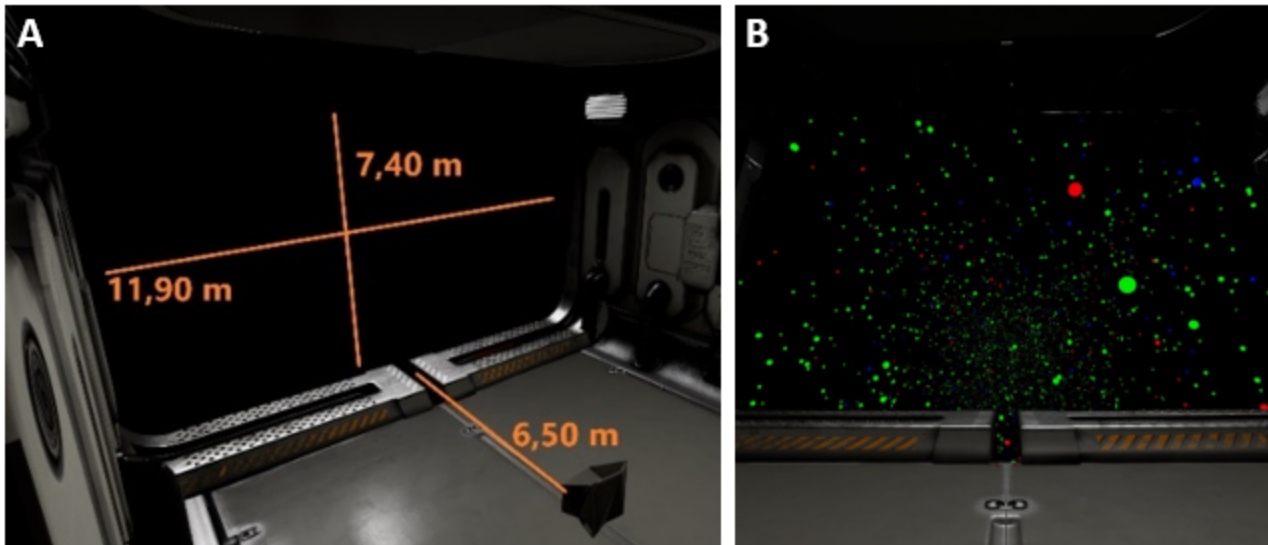


Figure 8

Figure 8. A: Illustration of the 3D environment showing the inside of the spaceship with the central chair for participants facing the windscreen. Width and height of the cockpit's windscreen and distance between the participants chair and the windscreen are marked in orange. B: Screenshot of the starfield from the participants perspective (for illustration purposes rendered for a standard 2D display; depicted here is a starfield variant with high Density and green as predominating color).