

A novel virtual plus-maze for studying electrophysiological correlates of spatial reorientation

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Abstract

Quick reorientation is an essential part of successful navigation. Despite growing attention to this ability, little is known about how reorientation happens in humans. To this aim, we recorded EEG from 34 participants. Participants were navigating a simple virtual reality plus-maze where at the beginning of each trial they were randomly teleported to either the North or the South alley. Results show that the teleportation event caused a quick reorientation effect over occipito-parietal areas as early as 100 msec; meaning that despite the known stochastic nature of the teleportation, participants built up expectations for their place of arrival. This result has important consequences for the optimal design of virtual reality locomotion.

Keywords: reorientation, cross-maze, teleportation

1. Introduction

Regaining our spatial orientation in an environment is essential for every-day navigation. Usually, spatial orientation is maintained during locomotion through the integration of multisensory (in humans, these are mostly proprio-
5 ceptive, vestibular and visual) signals of the body and environment [1]. While

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this is mostly a seamless process, from time to time, we need to make further efforts to regain our spatial orientation. This often happens when exploring an unknown environment [2, 3], wandering inside buildings [4], or walking distracted by our cell phone [5]. A large body of research explored how certain environmental cues affect reorientation both in animals [6, 7] and in humans [8, 9]. While the neural mechanisms underlying spatial orientation are well described in animal models, compelling evidence linking neural activity with reorientation in humans remains elusive. In order to examine the effect of reorientation in humans, we recorded the encephalogram (EEG) while teleporting human subjects to different starting locations in a virtual plus-maze, the gold standard to assess reorientation behavior in rodents [10].

The introduction of teleportation (or wormholes) means a violation to the Euclidean laws of geometry. Since the real world obeys Euclidean principles, one would easily assume that the human cognitive system does so, as well. Interestingly though, not only people are able to learn environments with non-Euclidean geometries (e.g., wormholes [11, 12]) but they are often unaware of such violation. Moreover, a recent study by Vass et al. [13] showed that when participants knew the start and end points of such wormholes, they navigated them just like real routes as was apparent from the unattenuated theta oscillation in their hippocampi. These results suggest that the human brain maintains a flexible, graph like cognitive map [14, 15] of the environment.

Another experiment [16], involving an unexpected teleportation from one known environment to another, showed that the brain of the rodents responded to this induced disorientation with an interesting pattern of activity. In the first few seconds, CA3 neurons showed short bistable flickering between the place map specific to the new and that of the old environment and later settled down on the earlier. The first switch to the place cell map specific to the new environment (i.e., reorientation) happened in the first second in the majority of the cases (see Supplementary Fig 11 of [16]). This activity is likely related to the temporally unexpected nature of the teleportation and shows that in the case of mismatch between expectation based on past and present experiences

the neural system is making efforts to regain spatial orientation.

In the experiment of Jezek et al. [16] the teleportation was unexpected. Since no such flickering or any sign of disorientation was observed in experiments involving expected teleportation events [13, 11], we can conclude that predictability is an important feature of spatial representations. We expect that what we imagine to be behind a closed door [17] or on the other end of a wormhole, once traversed, would be reinforced by the new sensory inputs. The question arises though what happens if an expected teleportation after being fully predictable becomes probabilistic.

In the present study, we explored such a situation. In this experiment, participants' start position was first consistent across trials (always starting from the South alley) and then in a test phase became inconsistent across trials (random teleportation events to North or South starting alleys). Given that the navigation system of rodents is highly sensitive to such reorientation effects in the plus-maze, we expected that the reorientation in the virtual plus-maze may have similar effects and may therefore be visible in the EEG. Given the novelty of this approach, we refrain from making any specific prediction. Nevertheless, these results here provide insights into human navigation processes related to reorientation during navigation and illustrate an approach for future research on combining EEG with virtual navigation as a means to parallel animal and computational models of spatial navigation.

2. Materials and methods

2.1. Participants

Thirty-four participants (16 males; 34 right-handed; aged 19–29, $M = 22$, $SD = 2.6$) with normal or corrected-to-normal vision participated in the experiment. Participants were undergraduate students recruited from the Budapest University of Technology and Economics and the Eötvös Loránd University and each received course credit or a monetary compensation for their participation. All participants gave informed consent. The study was approved by the local

research ethics committee and was conducted in accordance with the ethical standards prescribed in the 1964 Declaration of Helsinki.

2.2. Apparatus and stimuli

The experiments were run in a CAVE-like virtual reality environment [18] of
70 the 3DICC Laboratory, MTA SZTAKI. Participants were seated in a comfortable chair in the centre. Three back-projected screens (3(width) by 2(height) m each) surrounded them providing an immersive experience. They wore passive stereo glasses (Infitec). Motion was controlled by the Left and Right arrow keys on a keyboard placed in the lap of the participant. The virtual reality environment was a cross-shaped maze (see Fig 1). The maze consisted of 4 alleys, each
75 of which had different textures on the walls. The maze’s diameter was 7 m, and alleys were 3 m wide. The maze was rotated between participants so we were able to counterbalance the effect of the physical difference between textures. There was a platform with a 1 m diameter in each alley, and reward objects
80 were presented floating over it. A 0.5 m tall and 0.5 m wide yellow (golden) apple and a similar sized blue (magic) plum were used as feedback objects. The scenario was created in NeuroCogSpace, a custom XML interface built in the VIRCA environment [19, 20].

During the task, EEG was recorded from 62 sites placed according to the
85 10/20 system. The recording was done with BrainAmp amplifiers and MOVE system (Brain Products GmbH) with 1000 Hz sampling rate. An online 0.1-70 Hz bandpass filter was applied during acquisition. During recording all impedances were kept below 30 k Ω .

2.3. Procedure

90 Participants were placed in a cross-maze where they were instructed to collect as many points as they could by finding reward fruits in the maze. They were told that the appearance of reward and non-reward objects followed a complex rule (in reality, they occurred randomly and $P(\text{reward}) = 0.5$). In the instructions, we explained that the number of trials is fixed (400) and there is

95 no time limit on their choice during the experiment. They started each trial in
 either α or β (see Fig 1). First, they saw the intersection for 800 msec; then, a
 double arrow sign appeared at the centre of the maze. They were told to choose
 one horizontal alley when the sign appeared. After they made their decision,
 they were translated and rotated to face the chosen alley in 550 msec (see Fig
 100 1). 500 msec after they arrived at the alley, the reward stimulus was presented
 for 800 msec. For half of the participants, the golden apple valued 5 points; for
 the other half, the magic plum was the reward. The non-reward object valued 0
 points. Critically, after the feedback stimulus disappeared, they were teleported
 (white screen for 300 msec) to either of the vertical alleys to start the next trial.
 105 Participants were told that the teleportation follows a random order. Through-
 out the instructions, we took extra care of not using the words left, right, East,
 West, etc., which could have indicated the experimenters' preference for one
 strategy.

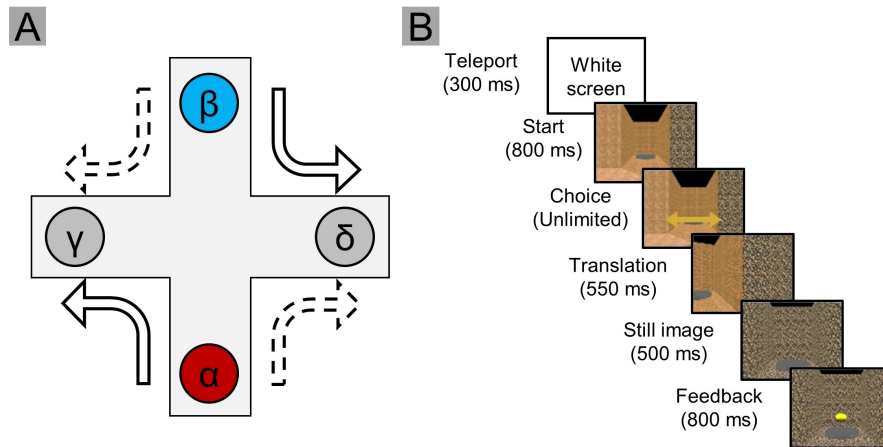


Figure 1: The layout of the plus-maze and the trial timeline. (A.) Participants started each trial randomly in either the α or β alley. (B.) Then they chose between the other two alleys, translated there, and received a feedback (positive or neutral).

In order to establish a stable allocentric frame before the experiment [21],

110 a practice phase of 130 trials was run where participants always started from
the lower alley. After the practice phase, 4 blocks of 100 trials were recorded
(total of 400 trials). The experiment lasted approximately 90 minutes with the
electrode cap setup and debriefing.

2.4. Data preprocessing

115 Preanalysis of the electrophysiological data was done using Matlab and
EEGLAB [22]. First, data were re-referenced to average reference [23], and
the original reference was retained (FCz). Then, we filtered the data with a 0.2-
30 Hz band-pass FIR filter, epoched using a -100 msec and +500 msec window
relative to the appearance of trial starts. Independent component analysis [22]
120 and amplitude thresholding were used to reduce eye blinks and muscle artifacts.
Detailed description of these steps can be found in [21].

2.5. Modeling and statistical analysis

2.5.1. Behavioral data analysis

We calculated the median decision times in the task in the two possible
125 starting positions and compared them in a Bayesian paired-samples t -test using
JASP [24]. Median decision times were used since distribution was very much
left skewed (Fig S1). The null hypothesis (H_0) was that there is no difference in
the decision times from the two starting positions, whereas the alternative hy-
pothesis (H_+) was that decisions take more time from the non-default starting
130 alley. If we found evidence for the null, it would suggest smaller cognitive effort
of reorientation, whereas if we found evidence for the alternative hypothesis, it
would suggest larger cognitive effort. Following the objective Bayesian analy-
sis routine [25], we specified 0.707 as the width of the half-Cauchy distribution
prior. According to Wagenmakers et al. [26], $BF_{Alternative-Null}$ values between
135 1 and 3 indicate anecdotal evidence for $H_{Alternative}$, while values between 3 and
10 indicate substantial evidence for $H_{Alternative}$.

2.5.2. *Electrophysiological data analysis*

Because each trial started with the participant randomly placed in either the South or North alley (see Fig. 1), they had to reorient themselves every time. Therefore, we looked at whether the event-related potentials (ERPs) time-locked to the start events differ for the two starting positions. As a data-driven approach, we calculated (1) global field power (GFP) and (2) topographic dissimilarity (TD) [27, 28, 29] using RAGU (Randomization Graphical User interface; <http://www.thomaskoenig.ch/Ragu.htm>). Before the TD analysis, scalp topographies were normalized by the intensity of the signals at each time point; thus, significant results reflect pure topographic differences, probably driven by the involvement of new generators or change in the existing generators. The threshold for all randomization based statistical testing was set to $p < .05$ based on 5000 iterations [30]. The analysis was only performed for timepoints where the assumption of topographic consistency was not violated between subject according to topographic consistency test [31]. Furthermore, only differences meeting the Global Duration Statistics Criteria are reported.

After the topographic analysis, differences in topography were further explored on the electrodes where the scalp topography difference was greatest. Here, the results of the analyses are reported with False Discovery Rate (FDR) and Cluster method corrections applied [32].

3. Results

3.1. *Behavioral results*

First, we investigated if the reorientation process had any behavioral correlates. Earlier analysis showed that participants were engaged in the task and were not choosing alleys randomly [21]. Further, because during the practice phase participants were always starting in the South alley, they built up a strong a priori expectation for the starting alley [21]. Consequently, they developed an intrinsic start facing preference in their internal map. We tested whether

165 starting in the non-default (North) vs. in the default (South) alley would lead
to longer decision times as a behavioral correlate of the reorientation process.

The analysis revealed moderate evidence for no difference being present in
decision times ($BF_{+0} = 0.302$, $\text{error}\% < 0.001$, $M_{North} = 753.0$ msec, SE_{North}
 $= 52.32$ msec, $M_{South} = 745.5$ msec, $SE_{South} = 52.40$ msec). The effect means
170 that the hypothesis of no difference is approximately 3 times more likely based
on the data than the alternative hypothesis of existing difference. As Figure 2
shows, evidence was favoring the null hypothesis all along the experiment.

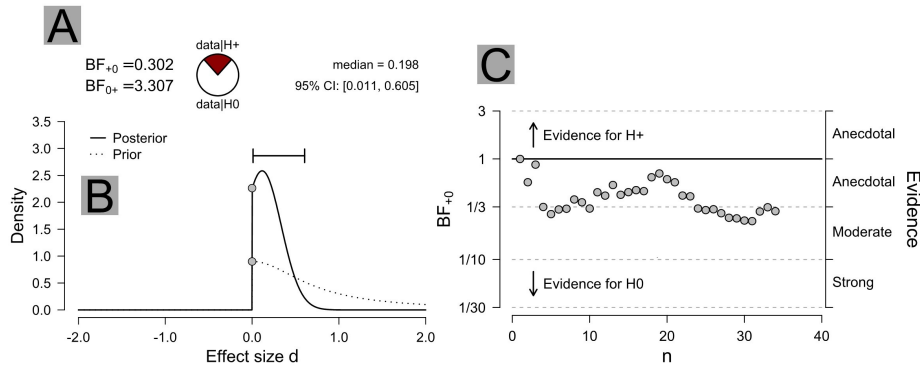


Figure 2: Results of the Bayesian t-test. A) The modeling found moderately strong evidence ($BF \sim 3$) for the hypothesis that there is no decision times difference after starting in the unexpected vs expected alley. B) As can be seen, the posterior distribution largely overlaps with the prior distribution. C) Sequential testing also shows that the results are more likely to support the null hypothesis with the addition of each participant.

Based on the behavioral data, we expected to find neural correlates of the reorientation process in earlier stages of processing that would not lead to in-
175 creased decision time during the task.

3.2. Results of the topographic EEG analysis

3.2.1. Results of the topographic dissimilarity analysis

Here, ERPs were compared between the expected vs. unexpected starting alley to find evidence for a reorientation process in the unexpected but not in the

180 expected alley. First, differences in topographic dissimilarities were examined. The topographic dissimilarity analysis (TANOVA [28]) revealed differences in scalp topographies between the two conditions. First, scalp topographies were significantly different between 103 and 134 msec ($p < .05$, see Fig. 3). The difference of the scalp topographies showed a large negativity over the parieto-
 185 occipital midline in the unexpected starting location (Fig. 3). As the difference was maximal over the POz electrode, we analyzed waveforms here using both parametric testing (with FDR correction) and non-parametric testing (with Cluster method correction). Differences were found between 114 and 163 msec, where a negative deflection is visible on the waveforms when participants started
 190 in the North alley (see Fig. S2). Additional differences were found between 179 and 197 msec.

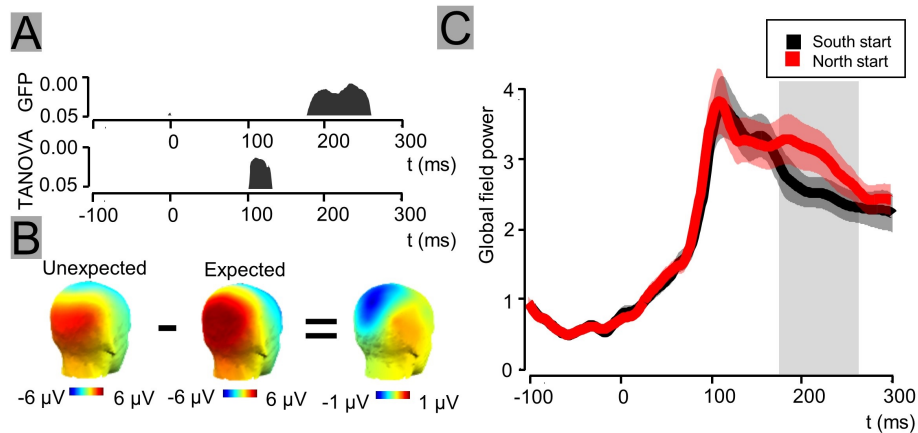


Figure 3: Reorientation at trial starts. A) Analysis revealed significant difference between scalp topographies from 103 to 134 msec and a global field power difference from 182 to 262 msec. These differences were significant after the application of Global Duration Statistics Criteria. B) The topographic difference is attributable to a negative deflection over parieto-occipital sites in the unexpected starting alley. C) The global field power difference means that there the same topographies are more pronounced in the time window of 182-262 msec

3.2.2. Results of the global field power analysis

Next, we conducted analysis on the global field power values. Since topographic dissimilarity revealed an activity around 100 msec, we expected difference in the global field power in this or later time windows showing a cognitive effort to accommodate the unexpected North starting position. In line with our expectation, the analysis revealed difference in global field power from 181 to 264 msec ($p < .05$, see Fig. 3), where the scalp field power was stronger for North starting position.

In general, the difference in global field power means a stronger presence of the same scalp topography in one condition. Here it showed stronger activation in the right lateralized parieto-occipital processing with a peak over the O2 electrode (see Fig. S3). The difference was also the greatest over this electrode. Analysis of the waveforms was done using parametric testing (with FDR correction) and non-parametric testing (with Cluster method correction) on this electrode and showed significant differences between 123 msec and 152 msec and between 175 and 300 msec.

A more simplistic explanation to the found effects would have been that the differences are attributable solely to bottom-up visual processing of texture information without top-down spatial processing. A control analysis (see Supplementary Material S4) ruled out this alternative hypothesis. Furthermore, the effect was not attenuating over the course of the experiment meaning it was robust to habituation (see Supplementary Material S5).

4. Discussion

We presented electrophysiological evidence for early, reorientation-related processes in an experiment involving virtual teleportation to random starting position in the beginning of trials. We found that starting in the unexpected alley did not result in longer decision times but was correlated with an early (~100 msec) medial parieto-occipital negativity and a later increased bilateral occipital activity in the EEG waveforms. The present results are the first scalp

EEG evidence for spatial reorientation processes in human.

The difference in expected vs. unexpected starting alleys suggests that participants practiced expectation for a default starting alley. Importantly, the timing of the teleportation events was fully predictable and the participants were
225 aware of the fact that the destination of the teleportation is random. Therefore, in theory, they could have (consciously or unconsciously) inhibited the processes that led to expectations regarding the destination of the teleportation. EEG evidence tells, however, that they nonetheless established prior expectations for the destination. Further, the found topographic differences are not bottom-up
230 correlates of alley texture processing (see Supplementary Fig. S4) but results of top-down spatial orientation processes based on the visual information conveyed by the alley textures. The presence of the expectation of a default starting alley implies that learning the spatial layout of an environment is not only automatic [33] but a consistency constraint is applied on the memory. Further
235 studies are required to see whether such a default expectation develops also if the teleportation works in a random fashion from the beginning, and to see whether this expectation wanes over time (we did not find such effect in the current experiment, see Supplementary Material S5).

A further interesting question deriving from the current study is whether
240 reorientation would be faster based on geometry than on textural cues. Ample evidence suggests that geometry serves as the most important cue for reorientation both in animals [34] and in children [35]. Non-geometrical cues – such as texture – are also important, especially if geometrical cues are unreliable [7] or if language is available to the actor [36]. In the current experiment, the geome-
245 try served no reliable cue for reorientation; however, the environment could be easily modified in a way where not textural but geometrical cues would help the reorientation. Interestingly, the latency of the found effects assumes that the complex visual information was evaluated rapidly, arguably in the same time scale as simpler visual features. This is in line with results from another study
250 [37] showing that complex natural scenes are identified as rapidly as simple line directions.

We did not find difference in decision times in the current experiment, which is likely attributable to our experimental design and not to reorientation in general. The environment was very simple: since teleportation destinations were
255 always either the North or South alleys, the unexpected alley meant only one alley and not three that the environment would have otherwise made possible. Therefore, the unexpected location was only “moderately unexpected”. Further studies may explore how increased uncertainty regarding the unexpected position would affect decision times. Also, note that participants were not in-
260 structed to make quick choices but to try to find an underlying rule for the placement of the feedback object. Future studies may include more stringent reaction time tasks.

Although EEG provides a valuable window to the temporal dynamics of cortical processes, it lacks spatial resolution. Further studies using fMRI and EEG
265 co-registration could explore the neural underpinnings of this reorientation process. Earlier findings showed that the retrosplenial cortex plays an important role in maintaining an allocentric frame of reference in an egocentric viewpoint-based task [38, 39]. These results are further supported by single cell evidence that revealed cells in the retrosplenial complex process information in both ego-
270 centric and allocentric reference frames [40]. Furthermore, retrosplenial activity is often detected over the parieto-occipital sites of the scalp EEG [39], where the current activity was concentrated as well.

Teleportation of the physical body of a living organism is a favorite topic of science fiction. However, virtual teleportation is not science fiction but an
275 efficient way of locomotion in VR environments. Previous results showed that environments with wormhole-like teleports are readily learned [11, 12] and naturally traversed [13]. Our current findings extend these results by showing EEG evidence for processing the mismatch between expected and unexpected destinations of such teleportation events as early as 100 msec. Importantly, our results
280 are valid for a known environment. Participants knew both starting positions well, enabling quick reorientation. It would be interesting to see what happens when the teleportation brings them to a new environment or a previously unseen

position in the current environment.

Considering these results, we can provide important practical directions for
285 teleportation-based locomotion methods in virtual reality. It seems that not
only temporal but temporal-spatial predictability is an important prerequisite of
effective teleportation. Otherwise, if teleportation is either spatially (see current
results) or temporally unpredictable, a reorientation process has to occur [16].
If used effectively though, teleportation could open up new ways of environment
290 design, such where the layout does not obey the Euclidean principles yet is easily
learned and memorized by people.

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420 Supplementary Material

Distribution of decision times

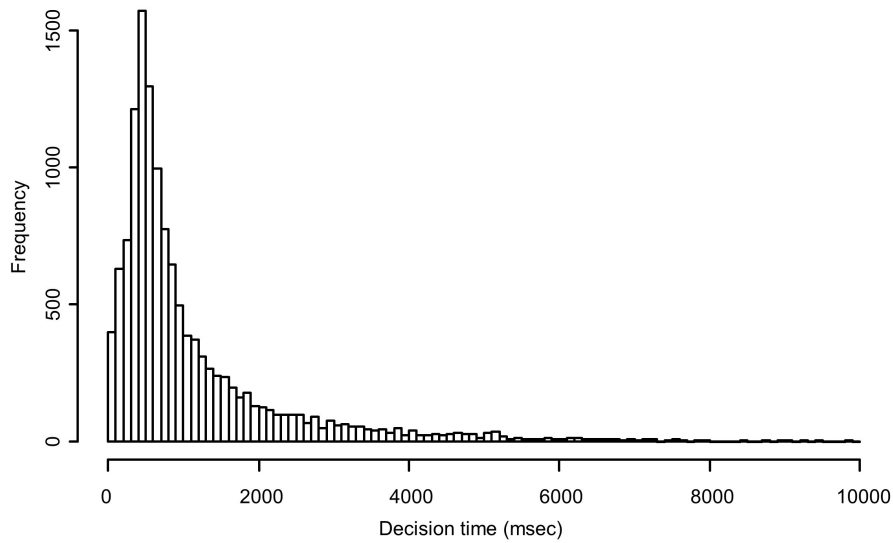


Figure S1: Distribution of decision times. As can be seen in the figure, the distribution of the decision times in the experiment showed a strongly left skewed distribution both when examined collapsed on all subjects (2.766) and when examined on the single subject level ($M_{skewness} = 2.801$, $Min_{skewness} = 1.018$, $Max_{skewness} = 9.923$). Therefore, we calculate the median instead of the mean of the distributions. Nonetheless, the pattern of results remains when mean is calculated ($t(33)=0.910$, $p = .815$).

Analysis of the TANOVA maxima

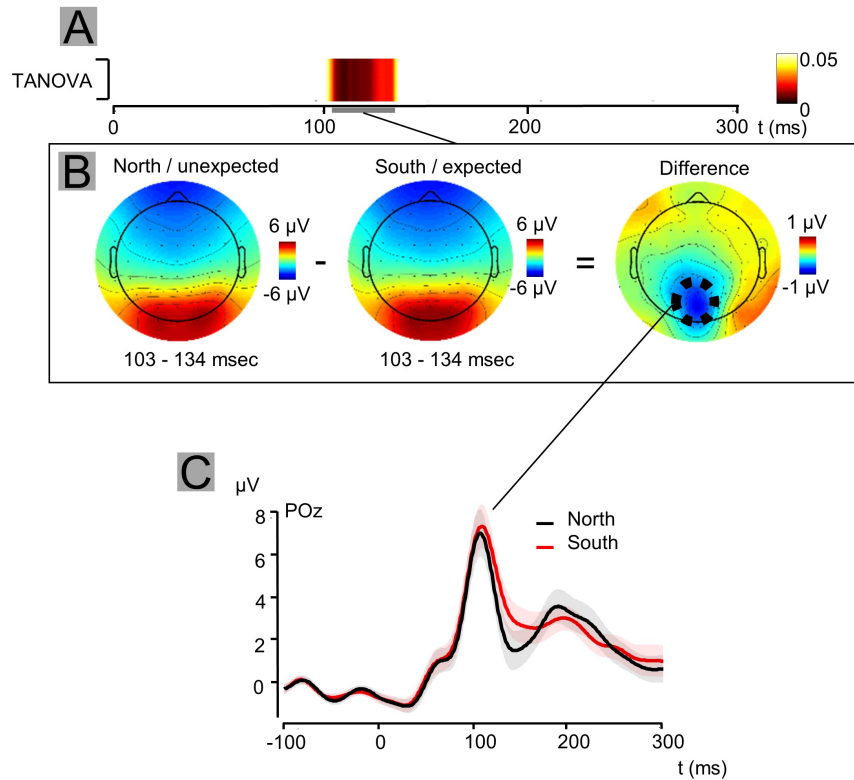


Figure S2: Analysis of the TANOVA maxima. A) TANOVA analysis revealed significant differences in topography between the unexpected and expected starting location at time points from 103 to 134 msec. B) The difference between topographies was a negative deflection over parieto-occipital sites, with a maximum on POz. C) Analysis on this electrode revealed significant difference between 114 and 163 msec and between 179 and 197 msec. These differences were significant both after FDR and cluster correction.

Analysis of the GFP maxima

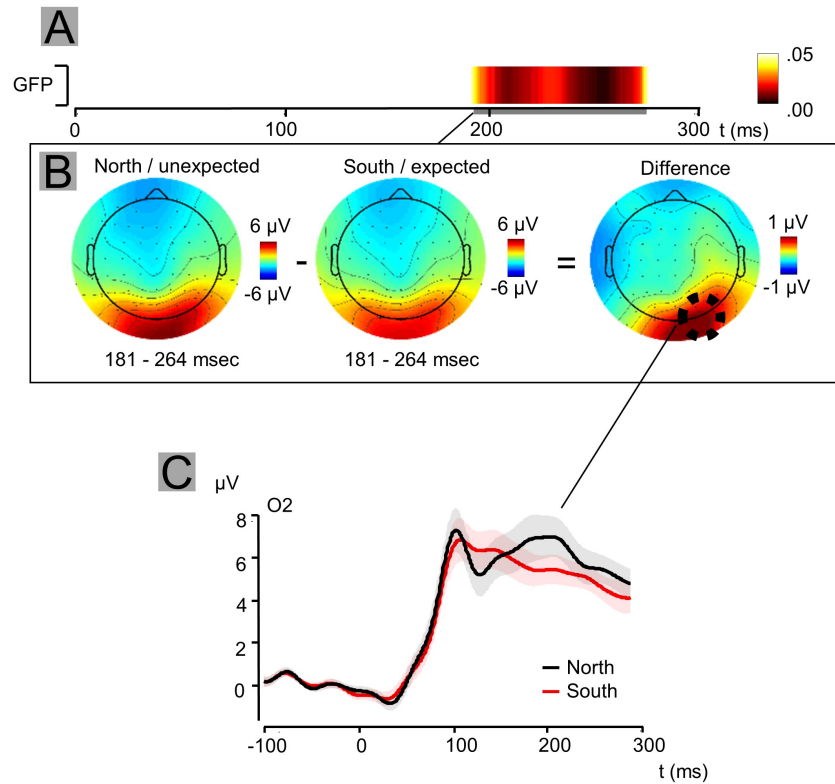


Figure S3: Analysis of the GFP maxima. A) GFP analysis revealed significant differences in topography between the unexpected and expected starting location at time points from 181 to 264 msec. B) The difference between topographies was a positive deflection slightly right from the occipital midline, with a maxima on O2. C) Analysis on this electrode revealed significant difference between 123 msec and 152 msec and between 175 and 300 msec. These differences were significant both after FDR and cluster correction.

Analysis of the texture related effects

425 A more parsimonious explanation for the found effect could be that partic-
ipants did not reorient themselves during the task because the known random
nature of teleportation events did not reinforce such seemingly invalid expecta-
tions for a default starting alley. In this case, we would expect the processing
differences based on the texture (and not the spatial position) of the starting
430 alleys.

Therefore, we did a control analysis by comparing the EEG to different
textures in the starting alleys. Since we randomly rotated the order of the
wall textures for each participant and four textures were used, we were able
to create two groups. In the first group, Texture 1 or Texture 3 were seen at
435 the beginning of each trial (as South or North alleys, for one half of the group
Texture 1 was South, for the other half it was Texture 2), in the second group,
Texture 2 and 4 were seen. We also quantified the visual complexity of the
different textures by calculating their Feature Congestion [41]; based on this,
the matched textures were similarly different in complexity for both groups. We
440 ran a separate analysis of topographic dissimilarity and global field power on
both groups using the same parameters that we used during the main analysis.

This analysis did not yield significant results in either groups (see Fig. S4).
Thus, we found no evidence for reorientation process that would have been
driven by visual differences alone.

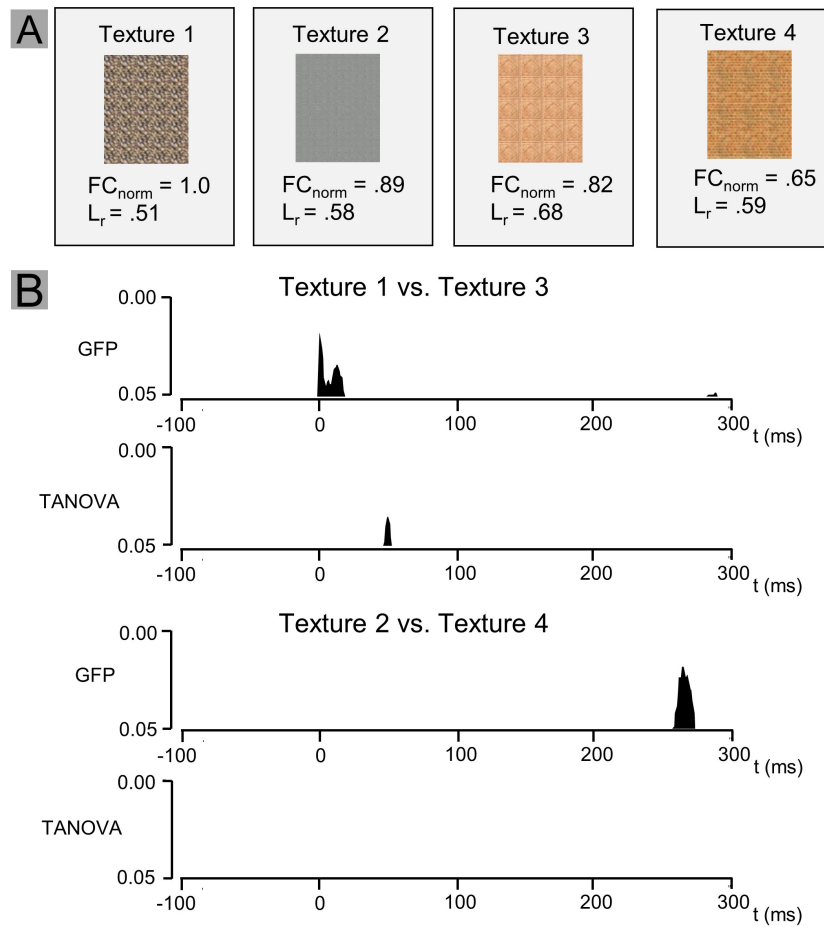


Figure S4: Control analysis of comparing the EEG to different textures in the starting alleys. The results show no evidence supporting the alternative hypothesis of pure visual differences underlying the effect without spatial processing. Raw results are shown without Global Duration Statistics thresholding.

445 Comparison between the first and second half of the experiment

The teleportation was deterministic first but then become probabilistic. Although our results showed that despite this change participants practiced an expectation for a default starting, one would assume that due to habituation, this expectation becomes less pronounced over time. Therefore, we compared

450 the first and second half of the experiment with the same topographic EEG anal-
ysis method. If habituation exists, there should be an interaction between Part
(first vs. second half) and Starting alley (default vs. non-default). The GFP
analysis showed the same effect that was found in the main analysis (between
173 and 262 ms) and no interaction between Part and Starting alley. Similarly,
455 the TANOVA analysis showed difference between starting alleys between 93 and
162 ms and no interaction between Part and Starting alley. The main effect of
Part was significant between 165 and 220 ms, indicating some general processing
difference between the first and second half but, critically, not between the two
starting alleys. This result suggests that no habituation happens during the
460 task, which could be because either the length of the experiment was too short
or that the cognitive map of the environment is resistant to habituation.

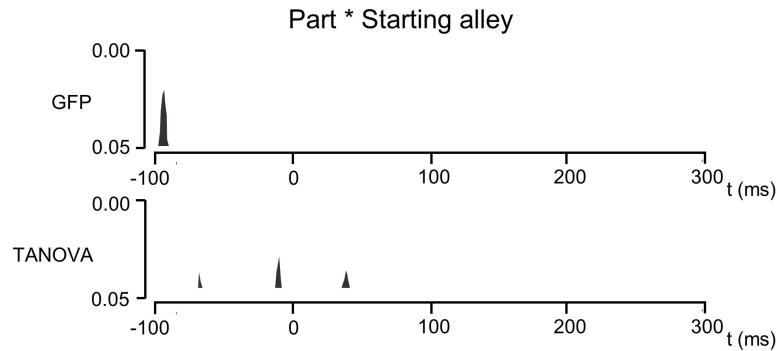


Figure S5: Control analysis for testing habituation effect in reorientation. The results show no evidence supporting the hypothesis of habituation during the task. Raw results are shown without Global Duration Statistics thresholding.