

1 Title: Temporal dynamics of object location processing
2 in allocentric reference frame

3 Authors: Ágoston Török^{1,2,3}, Andrea Kóbor¹, György Persa^{4,5}, Péter Galambos^{4,6}, Péter
4 Baranyi^{4,5}, Valéria Csépe¹, Ferenc Honbolygó^{1,3}

5 1: Brain Imaging Centre, Research Centre for Natural Sciences, Hungarian Academy
6 of Sciences, Budapest, Hungary

7 2: Systems and Control Laboratory, Institute for Computer Science and Control,
8 Hungarian Academy of Sciences, Budapest, Hungary

9 3: Department of Cognitive Psychology, Faculty of Pedagogy and Psychology, Eötvös
10 Loránd University, Budapest, Hungary

11 4: 3D Internet-based Control and Communications Laboratory, Institute for Computer
12 Science and Control, Hungarian Academy of Sciences, Budapest, Hungary

13 5: Széchenyi István University, Győr, Hungary

14 6: Óbuda University, Antal Bejczy Center for Intelligent Robotics, Budapest, Hungary

15 Manuscript of the article that appeared in:
16 *Psychophysiology* 2017; Vol. 54(9):1346–1358
17 DOI: 10.1111/psyp.12886

18 Corresponding author: Ágoston Török

19 E-mail: torok.agoston@ttk.mta.hu

20 Phone: 0036-1354-2290

21 Address: Brain Imaging Centre,

22 Research Centre of Natural Sciences,

23 Hungarian Academy of Sciences,

24 H-1117, Budapest, Magyar tudósok körútja 2. HUNGARY

25

26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41

Abstract

The spatial location of objects is processed in egocentric and allocentric reference frames, the early temporal dynamics of which has remained relatively unexplored. Previous experiments focused on event-related brain potential (ERP) components related only to egocentric navigation. Therefore, we designed a virtual reality experiment to see whether allocentric reference frame related ERP modulations can also be registered. Participants collected reward objects at the end of the West and East alleys of a cross maze and their ERPs to the feedback objects were measured. Participants made turn choices from either the South or the North alley randomly in each trial. This way, we were able to discern place and response coding of object location. Behavioral results indicated a strong preference for using the allocentric reference frame, and a preference for choosing the rewarded place in the consecutive trial, suggesting that participants developed probabilistic expectations between places and rewards. We also found that the amplitude of the P1 was sensitive to the allocentric place of the reward object, independent of its value. We did not find evidence for egocentric response learning. These results show that early event-related potentials are sensitive to the location of objects during navigation in allocentric reference frame.

Keywords: navigation, P1, place learning, spatial location, cross maze

42

Introduction

43 Environmental objects are essential components of spatial representations. They serve as
44 orientation aids (Chadwick, Jolly, Amos, Hassabis, & Spiers, 2015; Mou, Fan, McNamara, & Owen,
45 2008; Pecchia & Vallortigara, 2012), they are associated with specific actions (Janzen & van
46 Turennout, 2004), they can be the borders of the environment (Doeller, King, & Burgess, 2008), or
47 they may be the very goal of our navigation (Howard et al., 2014; Niediek et al., 2014). We learn their
48 position quickly and without effort (Janzen & van Turennout, 2004; Simon-Thomas, Brodsky,
49 Willing, Sinha, & Knight, 2003). Previous studies showed that early ERPs, such as the P1 and the
50 NT170, are sensitive to object location encoding (Baker & Holroyd, 2009, 2013; Simon-Thomas et al.,
51 2003). In the present study, we investigated what exactly humans learn as the spatial location of
52 objects in a cross maze; more specifically, we were interested in the ERP correlates of object location
53 processing in an allocentric reference frame (Klatzky, 1998).

54 This question has been of interest to numerous studies since the 1950s. Two contrasting
55 theories have been proposed. One suggested that animals use egocentric reference frame, and they
56 learn the position of objects referenced to the egocentric response that leads to it (Lashley &
57 McCarthy, 1926). The other stated that animals use an allocentric reference frame, and learn the
58 allocentric position of objects (Tolman, 1948). Tolman introduced the cross maze, a simple paradigm
59 that can be used to decide whether place or response learning happens in a task (Tolman, Ritchie, &
60 Kalish, 1946). In the simplest version of the cross maze, the animal is trained from one starting point
61 to choose a side alley (see figure 1). Then, on the probe trial, the animal is placed to the opposite
62 starting point, from where response learning results in the same egocentric turn and place learning
63 results in the same allocentric place. Studies revealed that strategy depends on the relevant information
64 in the task (Restle, 1957), and animals predominantly use place learning in heterogeneous
65 environments, when short inter-trial intervals are used and when they are not stressed. They only
66 switch to response learning after several days of training. Animals show response learning by default
67 in homogeneous environments, if long inter-trial intervals are used and when the animals are stressed
68 (M G Packard & McGaugh, 1996; Mark G. Packard & Goodman, 2013). Our study was based on this

69 classic paradigm exploiting the modern 3D virtual technology in order to study the temporal dynamics
70 of object location processing in humans.

71 Place and response learning has been studied in humans, as well. Some experiments found
72 evidence for place learning (Schmitzer-Torbert, 2007) while others found predominantly response
73 learning (Baker & Holroyd, 2013; de Condappa & Wiener, 2016). Interestingly, in some studies, one
74 half of the participants showed place learning, the other half showed response learning (Iaria, Petrides,
75 Dagher, Pike, & Bohbot, 2003; Marchette, Bakker, & Shelton, 2011) in response to the same
76 environment. Due to their higher cognitive abilities, humans are capable of developing more complex
77 strategies and can even dynamically switch between place- and response learning (Iglói, Zaoui,
78 Berthoz, & Rondi-Reig, 2009). Unfortunately, neither behavioural nor brain imaging evidence helps
79 us to disentangle what and when people *learned* in these tasks from what and when people *used* in
80 these tasks. This question can only be answered with methods that give a good temporal resolution of
81 neural processing, such as EEG (Simon-Thomas et al., 2003; van Hoogmoed, van den Brink, &
82 Janzen, 2012; Weidemann, Mollison, & Kahana, 2009). Baker and Holroyd (Baker & Holroyd, 2009,
83 2013) investigated ERPs for objects appearing in simple and complex T- and tuning-fork-mazes. They
84 identified an ERP component, the topographical N170 (referred to as NT170), which was found to be
85 sensitive to the *egocentric location* of an object. Their main finding was that the latency of the NT170
86 was shorter (and sometimes the amplitude higher) when the object was in the right alley as compared
87 to the left alley. They verified that this effect was related to the spatial location of the object and not to
88 its reward value (Baker & Holroyd, 2009). Interestingly, this effect could only be recorded if the task
89 was done in a navigation context (Baker & Holroyd, 2013).

90 Although the NT170 is interpreted as a correlate of egocentric reference frame use, the
91 experimental design of Baker and Holroyd (2009, 2013) did not enable differentiation between
92 egocentric and allocentric coding since the alleys were only approached from one direction (either left
93 or right). Nevertheless, the design of Baker and Holroyd was possibly more conducive to response
94 learning, because participants started each trial from the same alley and thus egocentric path
95 integration was easy. Favoring this explanation, Waller and Hodgson (2006) found in their task that

96 while after small rotations, participants made pointing errors consistent with the use of an egocentric
97 reference frame; after more severe disorientation, they showed a switch to an allocentric strategy.
98 Based on this result, in the current cross maze paradigm, we introduced disorientation, and participants
99 were randomly teleported to either the South or North alley of a cross maze at the beginning of each
100 trial and were able to approach each alley from both left and right directions. With this manipulation,
101 we aimed to extend the paradigm of Baker and Holroyd (2009), to differentiate between egocentric
102 and allocentric coding of location. We hypothesized that this manipulation will favor the use of an
103 allocentric reference frame, the ERP correlates of which have not been investigated yet. There is one
104 possible ERP candidate of allocentric place coding, the P1, the amplitude of which is modulated by the
105 number of locations seen (Simon-Thomas et al., 2003).

106 For this purpose, we designed a virtual reality paradigm where participants searched rewards
107 in the side alleys of a cross maze (Tolman et al., 1946). Based on the literature, we hypothesized that
108 (1) at the behavioral level, participants would primarily use allocentric strategies in the task, and (2)
109 their ERPs time-locked to the appearance of the feedback objects would differ for objects appearing in
110 the East vs. West alleys but not between the left and right alleys. We will use the terms left, right,
111 East, and West here for convenience, and this does not necessarily mean that participants used exactly
112 these labels during task solving.

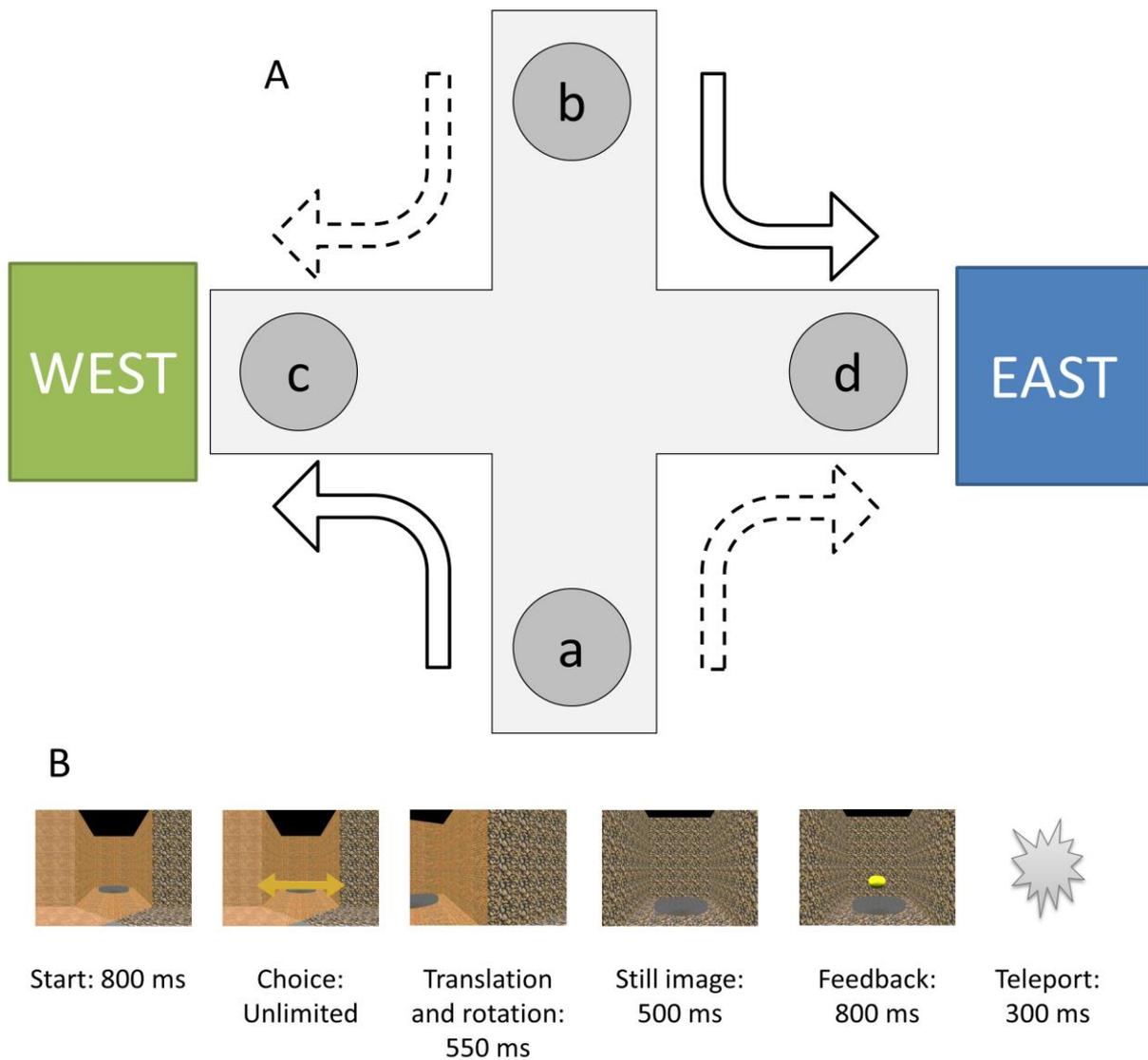


Figure 1. The layout of the cross maze and the trial timeline. A. Participants started either in point a or b and were told to choose between the two horizontal alleys. After they chose, they were translated and rotated to look into the chosen alley where the reward object appeared (point c and d). In the turn choice analysis we considered only trials where after a rewarded trial the next trial started in the opposite alley. For example, if the first trial started in alley a and the participant chose alley d the next trial was considered only if it started in alley b, where egocentric reference frame predicts alley c and allocentric predicts alley d. For an easier interpretation of the consecutive figures, hereafter left turns are marked with continuous and right turns with dashed

lines, whereas turns that led to the West alley are with green color and turns that led to East alley are with blue color. B. Illustration of a trial's timeline. First, participants saw the opposite starting alley with the intersection; after 800 msec, a green arrow sign appeared in the intersection. After participants made their choice they were virtually translated and rotated (550 msec) to face the chosen alley. After they arrived to the chosen alley, they watched the alley for 500 msec and then the feedback stimulus was presented. The feedback was visible for 800 msec, and then the screen turned white, and they were teleported into one of the possible starting alley, and the next trial started.

113

Method

114

Participants

115

EEG data was collected from 38 participants. Four participants' data was later excluded

116

because of recording error or of not meeting the inclusion criteria (see below). Of the remaining 34

117

participants, 18 were females. Participants were naïve to the aims of the study and all of them were

118

right-handed. Their mean age was 22 years ($SD = 2.26$, $Min = 19$, $Max = 29$). They had normal

119

hearing and normal or corrected-to-normal vision. Participants were neither color nor stereoblind.

120

They were university students from either the Budapest University of Technology and Economics or

121

the Eötvös Loránd University and received payment or course credits for their participation. They gave

122

informed consent prior to the experimental session. The study was approved by the Ethical Review

123

Committee for Research in Psychology (EPKEB).

124

Apparatus and stimuli

125

The experiment was run at the CAVE-like virtual reality arena (Cruz-Neira, Sandin, &

126

DeFanti, 1993) of the 3DICC Laboratory, MTA SZTAKI (Fig S1-S2). Participants sat in a

127

comfortable chair in the center of the virtual environment; they were surrounded by three screens

128

(3(w) by 2(h) m each) from the front and the two sides. They wore stereoglasses (Infitec) and 3D

129 stereopsis was generated by two projectors on each screen (passive stereo projection). Motion was
130 controlled by the left and right arrow keys on a keyboard placed in the lap of the participant.

131 The virtual reality environment was a cross-shaped maze (see Figure 1). The maze consisted
132 of 4 alleys, each of which had different textures on the walls. The maze's diameter was 7 m and alleys
133 were 3 m wide. The maze rotated between participants, thus we were able to counterbalance the effect
134 of the physical difference between textures. There was a platform with a 1 m diameter in each alley
135 and reward objects were presented floating over it. A 0.5 m tall and 0.5 m wide yellow (golden) apple
136 and a similar sized blue (magic) plum were used as feedback objects. The scenario was programmed in
137 NeuroCogSpace, a custom xml interface built in the VIRCA environment (Persa et al., 2014).

138 EEG was recorded from 62 sites placed according to the 10/20 system, reference was at the
139 FCz and ground was AFz. Recording was done with BrainAmp amplifiers and MOVE system (Brain
140 Products GmbH) with 1000 Hz sampling rate. An online 0.1 – 70 Hz bandpass filter was applied
141 during acquisition.

142 **Procedure**

143 Before the start, the experimenter explained the task to the participants with a video
144 presentation. According to the instructions, they were placed in a cross maze where they had to collect
145 as many points as they could. They were told that the appearance of rewarding and nonrewarding
146 objects follow a complex rule. We deliberately did not specify to them what the complex rule was, we
147 only told them that it was not simple. Throughout the instructions, we took extra care of not using the
148 words left, right, East, West, etc., which could have indicated the experimenters' preference for one
149 strategy. They started each trial in either the upper or lower alley (see Figure 1). There, they saw the
150 intersection for 800 msec, and then a double arrow sign appeared at the center of the maze. They were
151 told to choose one horizontal alley when the sign appeared. We did not limit the time for the choice.
152 After they made their decision, they were translated and rotated to face the chosen alley in 550 msec.
153 In pilot experiments we made sure that the speed of the translation and rotation was not too fast and/or
154 caused nausea. The reward stimulus was presented 500 msec after they arrived at the alley for 800

155 msec. For half of the participants the golden apple valued 5 points, for the other half the magic plum
156 was the reward. The nonreward object valued 0 points. After the feedback stimulus disappeared, they
157 were teleported (white screen for 300 msec) to either of the vertical alleys to start the next trial.
158 Participants were told that the teleportation follows a random order.

159 The experiment started with a practice phase of 130 trials where participants always started
160 from the lower alley. After the practice phase, 4 blocks of 100 trials were recorded. Trials were
161 presented in pseudorandom order in each block, where no more than three of the same starting alleys
162 followed each other, but reward and nonreward trials followed each other in random order. That is, in
163 contrast to previous rodent studies, but in line with the studies of Baker and Holroyd (Baker &
164 Holroyd, 2009, 2013), we did not reinforce one specific alley, and each alley was rewarded with equal
165 probability (50%). The experiment lasted cca. 90 minutes with the electrode cap setup and debriefing.

166 **Statistical analyses**

167 **Behavioral data**

168 We analyzed the behavioral data to test whether the cross maze design activates allocentric or
169 egocentric strategies. The test consisted of two parts. First, we tested whether participants prefer any
170 of the actions (egocentric turns) or places (allocentric alleys) by identifying the most frequent
171 responses in both. This method cannot effectively characterize feedback related strategies. Therefore,
172 in the second analysis, we calculated whether participants show a preference for the same rewarded
173 place/action in the next trial (win-stay strategy). For this, we only used the subset of trials where there
174 was no teleportation. Then, we investigated if this preference was specific to the rewarded place or to
175 the rewarded action. To quantify this, we selected only trials with teleportation (i.e., where the
176 preceding trial started in the opposite alley). In contrast to the behavioral analyses, the EEG analysis
177 was run on the whole dataset. The calculation of these scores and the analysis was run in R (R. C.
178 Team, 2014) and in JASP (J. Team, 2016).

179 **EEG data**

180 Preanalysis of the electrophysiological data was done using Matlab and EEGLAB (Delorme &
181 Makeig, 2004). First, data was re-referenced to average reference (Bertrand, Perrin, & Pernier, 1985),

182 and the original reference was retained (FCz). Then, we filtered the data with a 0.2-30 Hz band-pass
183 FIR filter according to the directions of Rousselet (2012). Continuous EEG was epoched using a - 100
184 msec and + 500 msec window relative to the appearance of feedback objects in the side alleys. Data
185 were then decomposed by independent component analysis to help artifact removal (Delorme &
186 Makeig, 2004). For each participant, the ICA returned 63 components. We rejected components
187 carrying eye blinks and muscle artifacts, then, recomposed the channel based data. Moreover, we
188 rejected every epoch where the EEG signal exceeds a +/- 100 μ V limit within the -100 to 500 msec
189 time window. Baseline potential was calculated using the -100 – 0 msec window.

190 The analysis of feedback object processing consisted of two parts. First, we analyzed if no-
191 reward objects compared to reward objects elicited feedback-related activity. Studies of spatial
192 processing often use rewards to motivate their subjects to explore (Baker & Holroyd, 2009; Niediek et
193 al., 2014; M G Packard & McGaugh, 1996; Tolman, 1948). Unlike with spatial processing, extensive
194 literature is available on how reward value of feedback stimuli modulates ERPs. Among the most
195 studied ERP correlates of feedback processing, the feedback-related negativity (FRN) is a fronto-
196 central or medial frontal negative deflection occurring 250-270 msec after the onset of a negative
197 (unfavorable) outcome (Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997; Nieuwenhuis, Yeung,
198 Holroyd, Schurger, & Cohen, 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). The
199 FRN is thought to mirror the rapid evaluation of external feedback and phasic dopaminergic changes
200 in activity between the basal ganglia and the anterior cingulate cortex, as proposed by the
201 reinforcement learning theory (Holroyd & Coles, 2002).

202 Second, in two separate tests, we analyzed whether ERPs differed when an object (regardless
203 of its value) appeared in the left vs. right alley (i.e., coding in an egocentric reference frame) and in the
204 East vs. West alley (i.e., coding in an allocentric reference frame). Due to the cross maze design and
205 the different starting points, the current paradigm made it possible to differentiate between these two
206 reference frames. Since there exists previous ERP literature on the topic (Baker & Holroyd, 2009,
207 2013; Simon-Thomas et al., 2003; van Hoogmoed et al., 2012), we were able to make specific
208 hypotheses of when we expect the earliest spatial location dependent ERP differences. These time

209 windows were those in which the P1 (Simon-Thomas et al., 2003) and the NT170 (Baker & Holroyd,
210 2013) ERP components usually appear. We identified the time window for the topographic analysis
211 for the P1 between 90 and 110 and for the NT170 between 180 and 200 msec. The FRN was identified
212 between 200-300 msec.

213 Statistical analysis of scalp topographies was done in Ragu (Koenig, Kottlow, Stein, Melie-
214 García, & Melie-garc, 2011), where randomization tests were done on the averaged data in the above
215 specified time intervals. We performed 1000 randomization runs and applied a 5% significance
216 threshold (Koenig et al., 2011). Before the statistical hypothesis testing, we checked topographic
217 consistency, and if inconsistent scalp topographies were found, further analysis was not performed
218 (Koenig & Melie-García, 2010). Randomization statistics were calculated for global field power
219 (GFP) and for topographic dissimilarity (TD) (Koenig & Melie-Garcia, 2009; Wirth et al., 2008). GFP
220 equals to the root mean square of potentials across the electrode montage, and it shows how ‘strong’ a
221 given scalp map is. On the other hand, TD is orthogonal to GFP: it equals to the root mean square of
222 the difference of the two GFP vectors. Because TD is a single measure of the distance between two
223 electric field topographies, parametric tests are not adequate; therefore we used topographic ANOVA
224 (TANOVA, Murray et al., 2008) a randomization based nonparametric statistical analysis to assess TD
225 differences. These two measures provide a reference free measure of change in the strength (GFP) and
226 distribution/topography (TD) of event-related EEG scalp dynamics (Lehmann & Skrandies, 1980;
227 Murray et al., 2008). After the topographic analysis, differences in topography were further explored
228 on the electrodes where the difference scalp topography was the greatest using point-by-point analysis
229 strategy. Here, the results are reported with False Discovery Rate (FDR) and Cluster method
230 corrections applied (Maris & Oostenveld, 2007). This strategy was used to minimize the chance of
231 reporting false positive results because of multiple comparisons.

232

233

Results

234

Behavioral results

235

236

237

238

239

240

241

242

243

244

245

246

We analyzed the participants' choices to see whether they show preference to an allocentric reference frame in the task. First, we calculated the simple place (allocentric) and action (egocentric) preference scores. These were quantified by counting choices of the West and East alley and the left and right turn, respectively, and taking the more frequent for both. Participants reported more complex, feedback dependent strategies during the debriefing, thus we hypothesized that a simple preference would not describe adequately their performance in the task. Therefore we tested whether the collected data favored the null hypothesis (H_0 , i.e. the simple preference scores did not reveal any systematic preference for one alley or turn), or the alternative hypothesis (H_1) using a Bayesian paired-sample t -test. Following the objective Bayes analysis routine (Berger, 2006); we specified 0.707 as the width of the half-Cauchy distribution prior. According to Wagenmakers et al. (Wagenmakers, Wetzels, Borsboom, & van der Maas, 2011), BF_{01} values between 1 and 3 indicate anecdotal evidence for H_0 , while values between 3 and 10 indicate substantial evidence for H_0 .

247

248

249

250

251

252

253

254

255

256

257

Participants showed 53.88 (3.29) % simple preference for one egocentric choice and 55.03 (5.83) % for one allocentric alley. The analysis showed moderately strong evidence that the simple preference scores were the same in both egocentric and allocentric reference frames ($M_{diff} = 8.824$, $t(33) = 0.869$, $p = .391$, $BF_{01} = 3.840$, error % < 0.001). This pattern shows that simple preference scores were not describing adequately the response strategies in the task. We also inspected if there were any participants showing an extreme preference for one specific alley/choice, which would have biased the ERP calculation due to the low number (< 50) of trials in the condition. Only 6 participants showed preference for one alley or choice in at least 62.5 % (250/400) of the cases. Importantly, none of them had less than 120 trials in any condition, which enabled us the reliable calculation of ERP averages in the latter analysis. In the next step, we examined whether participants' choices depended on the rewards.

258 In order to test the effect of feedback on their choices, we first investigated if participants
259 preferred the rewarded place/response in the next trial (win-stay) or to switch (win-shift). We took the
260 subsample of trials where after a reward the participant started in the same alley (i.e., no teleportation).
261 We used a binomial regression to test our hypothesis. Here only the intercept was estimated, and, if it
262 was different for the two conditions, that indicated either win-shift or win-stay behavior. The results
263 indicated a clear preference for win-stay behaviour ($\beta = .64$, $z(33) = 16$, $p < .001$, $M_{prop\ win\ stay} = .66$
264 (.19) see Fig. 2).

265 Because the same place and same action choices are not distinguishable when the next trial
266 started from the same alley, next, we took only the subset of trials where after a reward the next trial
267 started in the opposite alley. Analysis of these trials could show if the win-stay strategy found was
268 specific to the rewarded place or to the rewarded action. According to the results, participants
269 preferred the choice of an allocentric place over an egocentric response ($\beta = .45$, $z(33) = 13.95$, $p <$
270 $.001$, $M_{prop\ same\ place} = .61$ (.20) see Fig. 2) in the task. Based on these scores, we were able to classify
271 participants to allocentric (22/34), unknown (7/34), and egocentric (5/34) groups (see Suppl. section
272 4); this grouping also shows that the task was predominantly allocentric. Interestingly, a comparison
273 between the first and second half of the experiment showed that allocentric win-stay preference
274 became stronger during the experiment ($t(33) = -2.23$, $p = 0.03$, $M_{1st} = .58(.22)$, $M_{2nd} = .64(.20)$). This
275 result may indicate a stabilization of strategy.

276 Lastly, we tested the participants' behavior after no-reward events. For this, like with the test
277 of win-shift or win-stay strategies, we selected the trials without teleportation. Because according to
278 the task, these events were not actual loss events but simple no reward events, we did not expect large
279 no-reward dependent strategy. Indeed, we only found a small preference for lose-shift behavior (β
280 $= .09$, $z(33) = 2.3$, $p = .02$, $M_{prop\ lose\ shift} = .52$ (.17) see Fig. 2). Analysis of the trials with teleportation
281 did not enable us to specify if the lose-shift strategy was specific to place or action ($p = .44$).

282 Summarizing the analysis of the behavioral data, we found that (1) participants did not show
283 simple preference for one place or action, but (2) they did follow a win-stay and (3) lose-shift

284 strategies, and (4) chose often the same place after a rewarded trial. This strategy required them to
 285 encode and use the allocentric spatial coordinates of the object during the task. Importantly, because
 286 there was no association between the objects and alleys, they had to encode their ad-hoc spatial
 287 coordinates in each trial. Therefore, in the analysis of the EEG data, we aimed to identify the
 288 electrophysiological correlates of this process.

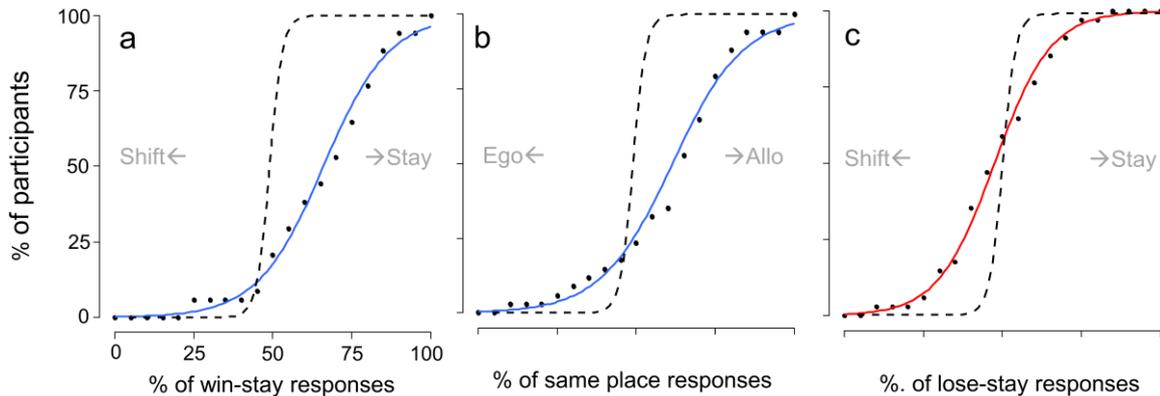


Figure 2. Reward dependent strategies in the experiment. We found (a) that most of the participants showed win-stay preference in more than 50% of the cases in the next trial, which behaviour (b) was specific to the rewarded alley. (c) Also, we found a smaller lose-shift preference. Black dots indicate the five percent bins of the cumulative distributions, solid lines indicate the fitted binomial distributions, blue is used for the reward related analyses and red for the nonreward related analysis. The dashed line is for presentation purposes. It is generated based on Bernoulli trials of the same length as the participants' choice sequences. It shows what shape of cumulative distribution would have been expected if choices sequences were random.

289

290 EEG analysis

291 We started with analyzing whether reward and nonreward objects elicit FRN. According to
 292 our analysis method, we explored differences in global field power and topographic dissimilarity using
 293 randomization statistics. Significant differences were found between 200-300 msec in the global field
 294 powers and in the topographies. These long-lasting differences signaled the processing of reward

295 information. Consistent with our expectations, the elicited negativity in the nonreward condition was
296 maximal over the FCz electrode. Here the difference was significant between 153 and 266 msec
297 (results are significant after cluster-threshold and FDR correction). This result shows that participants
298 were involved in the task and evaluated the rewards, in line with the behavioral results.

299 We, then, turned to the spatial processing related analysis to explore whether the feedback
300 objects were processed in an allocentric and possibly even in an egocentric reference frame. Because
301 the feedback related activity appeared to strongly affect ERPs, we included feedback value as an
302 additional factor in the analysis. According to the behavioral results, participants followed mostly
303 allocentric strategies during the task. Both GFP analysis and TANOVA were run in the predefined
304 window for the P1 (90-110 msec) and for the NT170 (180-200 msec). The analysis showed a
305 significant difference in scalp topographies in the P1 time window (TANOVA, $p = .003$, GFP, n.s.)
306 but not in the NT170 time window (TANOVA, n.s., GFP, n.s.). The difference was greatest over
307 parieto-occipital sites, consistent with earlier studies (Baker & Holroyd, 2009, 2013; Simon-Thomas et
308 al., 2003). Analysis on the PO8 electrode found difference of ERPs between 74 and 115 msec after
309 FDR and cluster-threshold correction (see Figure 3). The P1 was more positive when the object
310 appeared in the West alley than when it appeared in the East alley. The interaction with the feedback
311 value was not significant in any of the two time windows ($ps > .5$). Furthermore, the P1 modulation
312 did not differ in trials preceded by reward and trials which were not preceded by reward (see Suppl.
313 section 5). Also, we did not find evidence for a change in this pattern between the first and second half
314 of the experiment (see Suppl. section 2).

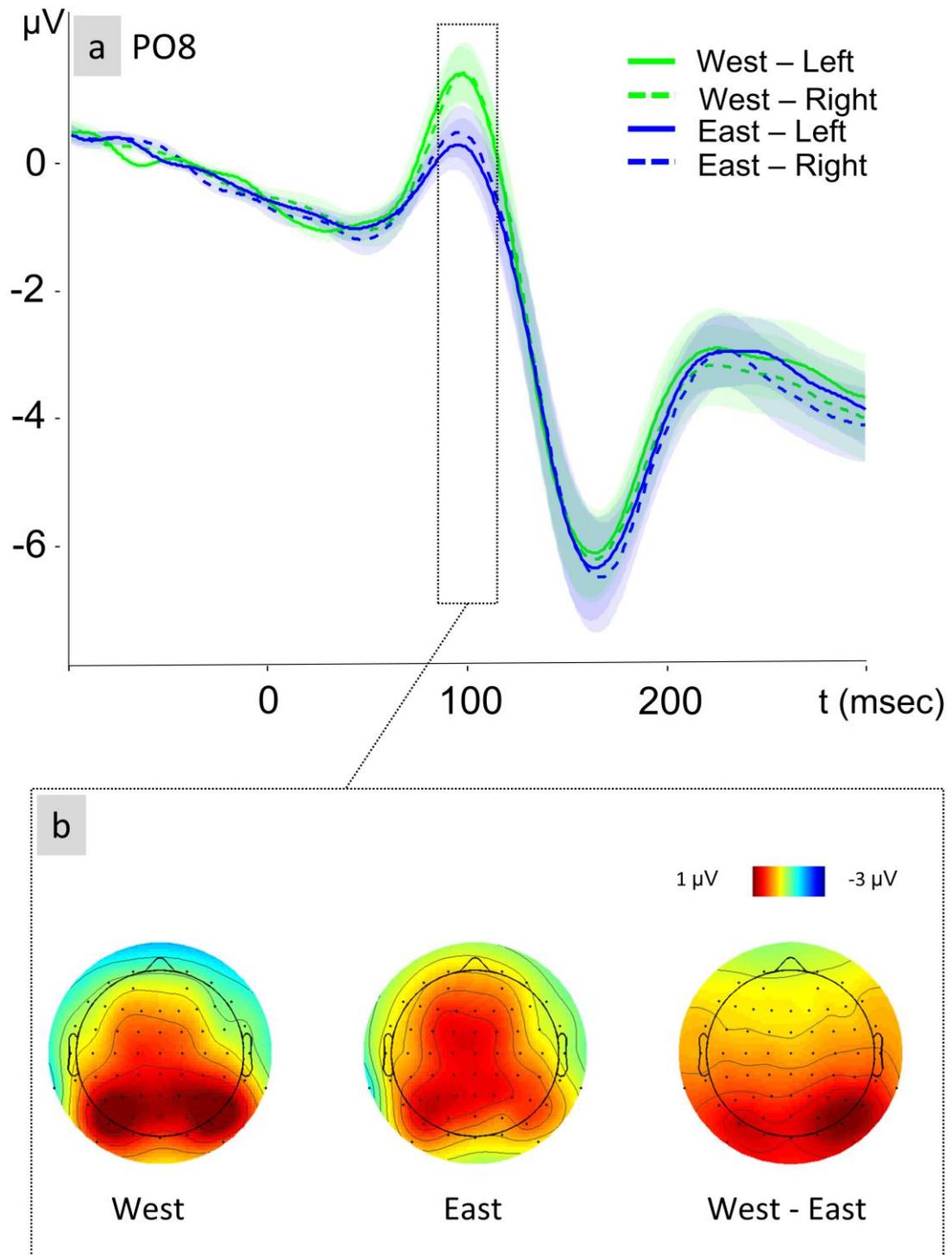


Figure3. Processing of the location of feedback objects in allocentric reference frame.(a) The topographic dissimilarity analysis showed difference between West and East object locations but not between Left and Right in the P1 time window (between 90-110 msec). We show the difference

in waveforms on the PO8 electrode. (b) Scalp maps show topographic difference between West and East locations in the P1, difference scalp map indicate that the topographic difference was caused by an activity with right lateralized parieto-occipital maxima.

315

316 Next, although the behavioral analysis reflected a dominant allocentric strategy, we tested
317 whether any ERP difference related to egocentric processing would also occur in the task. Neither the
318 global field power nor the topographic dissimilarity analysis yielded significant result exceeding the
319 duration threshold (see Figure 3). Also, we tested whether there is NT170 difference in the egocentric
320 strategy follower group of participants and we did not find evidence for that either (Suppl. section 3).

321 Lastly, we further analyzed the difference on PO8 electrode. For the purpose of comparison
322 with the related findings, we followed the peak analysis method of Baker and Holroyd (Baker &
323 Holroyd, 2009). That is, first, we identified the latency and amplitude of the P1 by finding the most
324 positive value between 50 and 150 msec (see Table 1). Then, using this latency as the onset of the
325 NT170, we identified the peak of the NT170 from here to 200 msec as the most negative point (see
326 Table 1). Peak amplitudes and latencies were compared in the 2 by 2 repeated measures ANOVA
327 separately for the P1 and for the NT170. We found a significant amplitude difference on the P1
328 between the two allocentric places ($F(1,33) = 4.46, p = .042, \eta^2_p = .12$), consistent with the results
329 above. None of the other effects were significant, importantly, neither the amplitude ($F(1,33) = 0.06, p$
330 $= .806, \eta^2_p < .01$) nor the latency of the NT170 ($F(1,33) = 0.02, p = .891, \eta^2_p < .01$) differed between
331 left and right turns. Because the effect seemed to affect the P1 bilaterally, we tested the effect on the
332 PO7 electrode, too. We found difference on tendency level ($F(1,33) = 3.93, p = .056, \eta^2_p = .11$).
333 Similarly to PO8, we did not find significant egocentric NT170 effect on the PO7. These results
334 suggest that robust egocentric processing did not occur in the first 300 ms after the feedback object
335 appeared.

336

337

338 >> INSERT TABLE 1 HERE <<

339 **Discussion**

340 In the present study, we sought deeper understanding of the temporal dynamics of object
341 location processing. We designed a virtual cross maze task where participants started either in the
342 South or North alley and searched for rewards in the side alleys. Using this paradigm, we were able to
343 observe psychophysiological correlates of object location in allocentric reference frame.

344 Analysis of turn choices showed a strong behavioral preference for using allocentric reference
345 frame in the task. This finding is in line with previous results of rodent studies that also showed
346 allocentric preference first, and a shift to egocentric strategy use only after prolonged training (Botreau
347 & Gisquet-Verrier, 2010; Chang & Gold, 2003; Iaria et al., 2003; Iglói, Doeller, Berthoz, Rondi-Reig,
348 & Burgess, 2010; Schmitzer-Torbert, 2007). We found that participants did not show simple
349 preference for one alley over the other, but rather they were more likely to choose the rewarded place
350 in the next trial. This means participants developed probabilistic expectations on a trial-by-trial basis
351 between places and rewards. Because objects and places were not associated with one another
352 throughout the task, this process required a successful evaluation of reward value *and* the coding of
353 feedback object in an allocentric reference frame.

354 In the analysis of EEG data, we found that nonrewarding objects elicited an FRN after 150
355 msec, a fronto-central negativity previously found to be related to feedback value processing (Baker &
356 Holroyd, 2009, 2013). This effect indicated that participants were engaged in the reward finding task.
357 This is in line with previous studies using similar designs (Baker & Holroyd, 2009, 2013). However,
358 while in the studies of Baker and Holroyd (2009, 2013) object location was processed in egocentric
359 reference frame, signaled by the latency modulation of the NT170, we did not find such effect in the
360 cross maze. In contrast, we found that the amplitude and topography of the P1 component were
361 sensitive to coding the object location in *allocentric* reference frame. Similarly to earlier results (Baker
362 & Holroyd, 2013; Simon-Thomas et al., 2003), the P1 was maximal over the right parieto-occipital
363 electrode sites. It is important to note that we did not find difference in global field power but in

364 topographies. This means the larger P1 amplitude should not be interpreted as stronger processing of
365 objects in the West alley, but as a different topographic distribution for the P1 in the West alley, which
366 resulted in larger amplitude over parieto-occipital sites but smaller elsewhere. Importantly, we found
367 that the spatial location related activity in the P1 window was not affected by the reward value of the
368 object. This indicates a very early modulation of visual processing related ERPs by allocentric spatial
369 information. P1 has been shown to be affected by spatial attention (Luck, Heinze, Mangun, &
370 Hillyard, 1990; Martínez et al., 1999). Moreover, this component has been shown to be modulated by
371 complex information, like the spatial location of a graspable object (Handy, Grafton, Shroff, Ketay, &
372 Gazzaniga, 2003).

373 Our results extend the interpretation of Baker and Holroyd (2009) stating that the egocentric
374 encoding of object location is conveyed in the latency effect of the NT170 component. Here we
375 provide evidence that the allocentric encoding of an object is reflected in the topography of the P1
376 component. Presumably, the allocentric coding, instead of egocentric, in the current task is partly due
377 to the introduction of the teleportation and hence the disruption of continuous (or at least predictable)
378 egocentric path integration. Path integration is an important part of the formation of egocentric spatial
379 memory (Buzsáki, 2005; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006). More broadly, the
380 spatio-temporal congruity of successive events has been shown to be important for episodic memory
381 formation in general (Buzsáki & Moser, 2013). These processes are strongly related to theta
382 oscillations in the brain (Baker & Holroyd, 2013; Caplan et al., 2003; O'Keefe & Recce, 1993) and to
383 the hippocampal-parahippocampal system (Baker, Umemoto, Krawitz, & Holroyd, 2015; Cornwell,
384 Johnson, Holroyd, Carver, & Grillon, 2008). Normally, repeated experiences in an environment lead
385 to the formation of semantic memory (Buzsáki, 2005), which is thought to be more of allocentric in
386 nature (Buzsáki & Moser, 2013). Semantic memory is more related to alpha activity (Brötzner,
387 Klimesch, Doppelmayr, Zauner, & Kerschbaum, 2014) and less dependent on hippocampal areas
388 (Corkin, 2002; Vargha-Khadem et al., 1997; Winson, 1978). While the relationship between semantic
389 vs. episodic memory and de facto spatial navigation is still an active research area (Buzsáki & Moser,
390 2013), this duality helps the interpretation of current results. Alpha activity has been shown to play

391 important role in allocentric navigation in previous studies too (Chiu et al., 2012; Lin, Chiu, &
392 Gramann, 2015; Plank, Müller, Onton, Makeig, & Gramann, 2010). The importance of these
393 frequencies from the perspective of ERPs is that phase-locking of alpha and theta oscillations are
394 generating the P1-N1 complex (Klimesch et al., 2004), and the mean latency of the P1 lies in the alpha
395 frequency range. Therefore, we hypothesize that while the NT170 is related to partial resetting of theta
396 oscillatory activity (Baker & Holroyd, 2013), the P1 modulation found in the current study is more
397 likely related to alpha activity changes. Further studies should explore the event-related spectral
398 perturbations related to the P1-NT170 complex.

399 Also, future studies should use EEG-fMRI co-registration to identify the brain areas
400 responsible for the allocentric processing in the current study and integrate them with the results
401 regarding the egocentric NT170 difference (Baker & Holroyd, 2013; Baker et al., 2015). While the
402 NT170 was related to a partial resetting of the ongoing theta rhythm in the parahippocampal cortex
403 (Baker & Holroyd, 2013), we hypothesize that the allocentric P1 effect is more related to activity
404 differences in the retrosplenial cortex. We form this assumption on the basis of previous results:
405 Sulpizio and colleagues (Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013) showed that
406 although both the retrosplenial cortex and the parahippocampal cortex code object locations in a stable
407 environmental reference frame, only the retrosplenial cortex activation is modulated by the amount of
408 viewpoint change relative to that reference frame. EEG evidence from a recent study (Lin et al., 2015)
409 also found that the retrosplenial cortex plays important role in translating egocentric experience into
410 spatial representation in allocentric reference frame.

411 While the stochastic relocation due to teleportation is the most probable cause of the activity
412 difference between the results of Baker and Holroyd (2009, 2013) and the recent study, there are other
413 possible factors to consider (Mark G. Packard & Goodman, 2013). An important difference in the
414 studies is that in the instructions Baker and Holroyd used the words ‘left’ and ‘right’, in contrast, we
415 used neither these nor the words referring to the cardinal directions. The use of spatial references in
416 language also modulates cognitive processing (Lee, 2002; Taylor & Tversky, 1996). Importantly, the
417 fact that we found the same pattern of activity in the learning phase, where no teleportation happened,

418 as in the experimental phase suggests that the instructions played an important role. Nevertheless, we
419 cannot decide which part of our instruction facilitated the use of an allocentric reference frame in the
420 cross maze: the lack of linguistic reference to egocentric coordinates or the mentioning of
421 teleportation. This requires further explorations. Another potential factor that might influenced the
422 pattern of results in the current study is that while Baker and Holroyd (Baker & Holroyd, 2009)
423 motivated their participants by a more-reward-more-money received instruction, in the current
424 experiment, participants were told to receive a fixed amount of compensation and only their score was
425 affected by the choices. A study of Xu et al. (2016) showed behavioural and ERP evidence that real
426 monetary losses are more aversive than hypothetical ones. Thus, one could argue that the earlier
427 instruction was not only motivating but also more stressing since participants believed that their
428 performance affected the reward they would earn by the end of the experiment. Stress, increased
429 arousal, and anxiety are also factors that favor response learning (McGaugh, 2004; Wingard &
430 Packard, 2008). Future studies should investigate what factors contribute to place and response
431 learning in these tasks in humans.

432 Importantly, none of the ERP differences found in the current study can be attributed to a
433 simple association between textures and reward objects because reward objects were present in both
434 alleys with equal probability. Furthermore, because the orientation of the cross maze also varied
435 randomly between participants and we summed ERPs according to left/right and East/West alley turns,
436 ERPs cannot reflect any texture related cognitive process. Note that earlier studies (Baker & Holroyd,
437 2013) did not reveal a topographical modulation of the egocentric NT170 component when the task
438 was presented in a nonspatial context. This suggests that the presented effects are indeed related to
439 spatial processing. We also analyzed whether there were reward-related changes coinciding with the
440 spatial differences and found that (1) reward based processing started only later in time and (2) with
441 fronto-central topography.

442 We did not find difference in the presence of P1 modulation and lack of NT170 modulation
443 between the allocentric, egocentric and unknown strategy groups (Fig S8-S9). One would have
444 expected P1 amplitude modulation for the participants following allocentric and NT170 latency

445 modulation for the participants following egocentric strategy. Here only a small fraction of
446 participants showed egocentric win-stay responses more often (5/34) and they showed the same P1
447 modulation pattern than the allocentric strategy followers. This could be due to several reasons, for
448 example, it is possible that different neural correlates feature an egocentric strategy when that is the
449 default based on the task specificities (like in the T-maze) versus when the task is predominantly
450 allocentric and the strategy choice is motivated by the participant's aspiration to find out the aim of the
451 experiment. Because the current data did not allow more in-depth analysis of EEG and strategy
452 relationship, further studies are required to investigate any related hypothesis. Importantly, while in
453 the current task reward was found with 50 % probability, future studies should manipulate the reward
454 probability in ways that facilitate the use of different strategies, even with switches between different
455 rewarding fashions during the experiment. This would help enlighten the relationship between strategy
456 and ERP correlates.

457 A limitation of the current study is the use of only limited immersiveness in virtual reality.
458 The current state-of-art enables not only button press interaction and sitting position, but also more
459 direct interaction and even locomotion in virtual spaces while recording EEG (e.g., Snider, Plank,
460 Lynch, Halgren, & Poizner, 2013). Real locomotion would have possibly increased participants' use
461 of egocentric reference frames, as well. Exploring how humans reorient after teleportation in a space
462 where direct locomotion is also enabled would be essential for the development of virtual and
463 augmented reality interfaces (Török, 2016).

464 As an outlook, we think that the simplicity and intuitiveness make this paradigm a promising
465 candidate for neuropsychological testing with elderly individuals. For instance, impaired navigation
466 ability is one of the first signs of Alzheimer's disease (Kunz et al., 2015; Lithfous, Dufour, Blanc, &
467 Després, 2014; Lithfous, Dufour, & Després, 2013). ERP could be a powerful tool to recognize signs
468 of Alzheimer's disease and other dementia even before the appearance of behavioral symptoms.
469 Furthermore, the availability of consumer virtual reality displays (e.g., Oculus Rift) and EEG headsets
470 (e.g., Emotiv EPOC) make it even easier to use paradigms like the cross maze in clinical research in the
471 near future.

472 In sum, we conducted a virtual reality cross maze experiment with humans. We found that
473 participants maximized their reward following an allocentric strategy during navigation in the cross
474 maze. Consistent with their behavioral strategies, we found that the amplitude of the early parieto-
475 occipital P1 reflected the allocentric location of reward objects.

476

477

References

- 478 Baker, T. E., & Holroyd, C. B. (2009). Which way do I go? Neural activation in response to feedback
479 and spatial processing in a virtual T-maze. *Cerebral Cortex (New York, N.Y. : 1991)*, *19*(8),
480 1708–22. doi: 10.1093/cercor/bhn223
- 481 Baker, T. E., & Holroyd, C. B. (2013). The topographical N170: electrophysiological evidence of a
482 neural mechanism for human spatial navigation. *Biological Psychology*, *94*(1), 90–105. doi:
483 10.1016/j.biopsycho.2013.05.004
- 484 Baker, T. E., Umemoto, A., Krawitz, A., & Holroyd, C. B. (2015). Rightward-biased hemodynamic
485 response of the parahippocampal system during virtual navigation. *Scientific Reports*, *5*, 9063.
486 doi: 10.1038/srep09063
- 487 Berger, J. (2006). The case for objective Bayesian analysis. *Bayesian Analysis*, *1*(3), 385–402. doi:
488 10.1214/06-BA115
- 489 Bertrand, O., Perrin, F., & Pernier, J. (1985). A theoretical justification of the average reference in
490 topographic evoked potential studies. *Electroencephalography and Clinical Neurophysiology/
491 Evoked Potentials*, *62*(6), 462–464. doi: 10.1016/0168-5597(85)90058-9
- 492 Botreau, F., & Gisquet-Verrier, P. (2010). Re-thinking the role of the dorsal striatum in
493 egocentric/response strategy. *Frontiers in Behavioral Neuroscience*, *4*, 7. doi:
494 10.3389/neuro.08.007.2010
- 495 Brötzner, C. P., Klimesch, W., Doppelmayr, M., Zauner, A., & Kerschbaum, H. H. (2014). Resting
496 state alpha frequency is associated with menstrual cycle phase, estradiol and use of oral
497 contraceptives. *Brain Research*, *1577*, 36–44. doi: 10.1016/j.brainres.2014.06.034
- 498 Buzsáki, G. (2005). Theta rhythm of navigation: Link between path integration and landmark
499 navigation, episodic and semantic memory. *Hippocampus*, *15*(7), 827–840. doi:
500 10.1002/hipo.20113
- 501 Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-
502 entorhinal system. *Nature Neuroscience*, *16*(2), 130–138. doi: 10.1038/nn.3304
- 503 Caplan, J. B., Madsen, J. R., Schulze-Bonhage, A., Aschenbrenner-Scheibe, R., Newman, E. L., &
504 Kahana, M. J. (2003). Human theta oscillations related to sensorimotor integration and spatial
505 learning. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*,
506 *23*(11), 4726–36.
- 507 Chadwick, M. J., Jolly, A. E. J., Amos, D. P., Hassabis, D., & Spiers, H. J. (2015). A goal direction
508 signal in the human entorhinal/subicular region. *Current Biology*, *25*(1), 87–92. doi:
509 10.1016/j.cub.2014.11.001
- 510 Chang, Q., & Gold, P. E. (2003). Switching Memory Systems during Learning: Changes in Patterns of
511 Brain Acetylcholine Release in the Hippocampus and Striatum in Rats. *J. Neurosci.*, *23*(7),
512 3001–3005.
- 513 Chiu, T. C., Gramann, K., Ko, L. W., Duann, J. R., Jung, T. P., & Lin, C. T. (2012). Alpha modulation
514 in parietal and retrosplenial cortex correlates with navigation performance. *Psychophysiology*,
515 *49*(1), 43–55. doi: 10.1111/j.1469-8986.2011.01270.x
- 516 Corkin, S. (2002). What's new with the amnesic patient H. M.? *Nature Rev. Neurosci.*, *3*(February),
517 153–160. doi: 10.1038/nrn726.
- 518 Cornwell, B. R., Johnson, L. L., Holroyd, T., Carver, F. W., & Grillon, C. (2008). Human
519 hippocampal and parahippocampal theta during goal-directed spatial navigation predicts
520 performance on a virtual Morris water maze. *Journal of Neuroscience*, *28*(23), 5983–90. doi:
521 10.1523/JNEUROSCI.5001-07.2008
- 522 Cruz-Neira, C., Sandin, D. J., & DeFanti, T. A. (1993). Surround-screen projection-based virtual
523 reality. In *Proceedings of the 20th annual conference on Computer graphics and interactive*

- 524 *techniques - SIGGRAPH '93* (pp. 135–142). New York, New York, USA: ACM Press. doi:
525 10.1145/166117.166134
- 526 de Condappa, O., & Wiener, J. M. (2016). Human place and response learning: navigation strategy
527 selection, pupil size and gaze behavior. *Psychological Research*, *80*(1), 82–93. doi:
528 10.1007/s00426-014-0642-9
- 529 Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG
530 dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1),
531 9–21. doi: 10.1016/j.jneumeth.2003.10.009
- 532 Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for
533 landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences*
534 *of the United States of America*, *105*(15), 5915–20. doi: 10.1073/pnas.0801489105
- 535 Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects
536 grab attention when the potential for action is recognized. *Nature Neuroscience*, *6*(4), 421–427.
537 doi: 10.1038/nm1031
- 538 Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: reinforcement
539 learning, dopamine, and the error-related negativity. *Psychological Review*, *109*(4), 679. doi:
540 10.1037/0033-295X.109.4.679
- 541 Howard, L. R., Javadi, A. H., Yu, Y., Mill, R. D., Morrison, L. C., Knight, R., ... Spiers, H. J. (2014).
542 The hippocampus and entorhinal cortex encode the path and Euclidean distances to goals during
543 navigation. *Current Biology*, *24*(12), 1331–1340. doi: 10.1016/j.cub.2014.05.001
- 544 Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent
545 on the hippocampus and caudate nucleus in human navigation: variability and change with
546 practice. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*,
547 *23*(13), 5945–5952.
- 548 Iglói, K., Doeller, C. F., Berthoz, A., Rondi-Reig, L., & Burgess, N. (2010). Lateralized human
549 hippocampal activity predicts navigation based on sequence or place memory. *Proc. Natl. Acad.*
550 *Sci. U. S. A.*, *107*(32), 14466–14471. doi: 10.1073/pnas.1004243107/
- 551 Iglói, K., Zaoui, M., Berthoz, A., & Rondi-Reig, L. (2009). Sequential egocentric strategy is acquired
552 as early as allocentric strategy: Parallel acquisition of these two navigation strategies.
553 *Hippocampus*, *19*, 1199–1211. doi: 10.1002/hipo.20595
- 554 Janzen, G., & van Turenout, M. (2004). Selective neural representation of objects relevant for
555 navigation. *Nature Neuroscience*, *7*(6), 673–7. doi: 10.1038/nm1257
- 556 Klatzky, R. L. (1998). Allocentric and Egocentric Spatial Representations : Definitions , Distinctions ,
557 and Interconnections. In *Lecture Notes in Computer Science* (Vol. 1404, pp. 1–17). London, UK:
558 Springer-Verlag. doi: 10.1007/3-540-69342-4_1
- 559 Klimesch, W., Schack, B., Schabus, M., Doppelmayr, M., Gruber, W., & Sauseng, P. (2004). Phase-
560 locked alpha and theta oscillations generate the P1-N1 complex and are related to memory
561 performance. *Cognitive Brain Research*, *19*(3), 302–316. doi: 10.1016/j.cogbrainres.2003.11.016
- 562 Koenig, T., Kottlow, M., Stein, M., Melie-García, L., & Melie-garc, L. (2011). Ragu: a free tool for
563 the analysis of EEG and MEG event-related scalp field data using global randomization statistics.
564 *Computational Intelligence and Neuroscience*, *2011*, 938925. doi: 10.1155/2011/938925
- 565 Koenig, T., & Melie-Garcia, L. (2009). Statistical analysis of multichannel scalp field data. *Electrical*
566 *Neuroimaging*, 169–189. doi: 10.1017/CBO9780511596889.009
- 567 Koenig, T., & Melie-García, L. (2010). A method to determine the presence of averaged event-related
568 fields using randomization tests. *Brain Topography*, *23*(3), 233–242. doi: 10.1007/s10548-010-
569 0142-1
- 570 Kunz, L., Schröder, T. N., Lee, H., Montag, C., Lachmann, B., Sariyska, R., ... Messing-Floeter, P. C.
571 (2015). Reduced grid-cell-like representations in adults at genetic risk for Alzheimer's disease.
572 *Science*, *350*(6259), 430–433. doi: 10.1126/science.aac8128

- 573 Lashley, K. S., & McCarthy, D. A. (1926). The survival of the maze habit after cerebellar injuries.
574 *Journal of Comparative Psychology*, 6(6), 423. doi: 10.1037/h0073391
- 575 Lee, P. U.-J. (2002). Costs of switching perspectives in route and survey descriptions. In *Dissertation*
576 *Abstracts International: Section B: The Sciences and Engineering*.
577 <https://doi.org/doi=10.1.1.196.6837>
- 578 Lehmann, D., & Skrandies, W. (1980). Reference-free identification of components of checkerboard-
579 evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology*,
580 48(6), 609–21. doi: 10.1016/0013-4694(80)90419-8
- 581 Lin, C. T., Chiu, T. C., & Gramann, K. (2015). EEG correlates of spatial orientation in the human
582 retrosplenial complex. *NeuroImage*, 120, 123–132. doi: 10.1016/j.neuroimage.2015.07.009
- 583 Lithfous, S., Dufour, A., Blanc, F., & Després, O. (2014). Allocentric but not egocentric orientation is
584 impaired during normal aging: An erp study. *Neuropsychology*, 28(5), 761–771. doi:
585 10.1037/neu0000084
- 586 Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the prodromal
587 stage of Alzheimer’s disease: insights from imaging and behavioral studies. *Ageing Research*
588 *Reviews*, 12(1), 201–13. doi: 10.1016/j.arr.2012.04.007
- 589 Luck, S. J., Heinze, H. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials
590 index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1
591 components. *Electroencephalography and Clinical Neurophysiology*, 75(6), 528–542. doi:
592 10.1016/0013-4694(90)90139-B
- 593 Marchette, S. a., Bakker, a., & Shelton, a. L. (2011). Cognitive Mappers to Creatures of Habit:
594 Differential Engagement of Place and Response Learning Mechanisms Predicts Human
595 Navigational Behavior. *Journal of Neuroscience*, 31(43), 15264–15268. doi:
596 10.1523/JNEUROSCI.3634-11.2011
- 597 Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. *Journal*
598 *of Neuroscience Methods*, 164(1), 177–190. doi: 10.1016/j.jneumeth.2007.03.024
- 599 Martínez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., ...
600 Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial
601 attention. *Nature Neuroscience*, 2(4), 364–9. doi: 10.1038/7274
- 602 McGaugh, J. L. (2004). The amygdala modulates the consolidation of memories of emotionally
603 arousing experiences. *Annu. Rev. Neurosci.*, 27, 1–28. doi:
604 10.1146/annurev.neuro.27.070203.144157
- 605 McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M.-B. (2006). Path integration
606 and the neural basis of the “cognitive map”. *Nature Reviews Neuroscience*, 7(8), 663–678. doi:
607 10.1038/nrn1932
- 608 Miltner, W. H. R., Braun, C. H., & Coles, M. G. H. (1997). Event-related brain potentials following
609 incorrect feedback in a time-estimation task: Evidence for a “generic” neural system for error
610 detection. *Journal of Cognitive Neuroscience*, 9(6), 788–798. doi: 10.1162/jocn.1997.9.6.788
- 611 Mou, W., Fan, Y., McNamara, T. P., & Owen, C. B. (2008). Intrinsic frames of reference and
612 egocentric viewpoints in scene recognition. *Cognition*, 106, 750–769. doi:
613 10.1016/j.cognition.2007.04.009
- 614 Murray, M. M., Brunet, Æ. D., Michel, Æ. C. M., Brunet, D., & Michel, C. M. (2008). Topographic
615 ERP analyses: a step-by-step tutorial review. *Brain Topography*, 20(4), 249–264. doi:
616 10.1007/s10548-008-0054-5
- 617 Niediek, J., Bain, J., Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., ... Fried, I. (2014).
618 Cellular networks underlying human spatial navigation. *Frontiers in Systems Neuroscience*,
619 8(August), 1. doi: 10.1038/nature01955.1.
- 620 Nieuwenhuis, S., Yeung, N., Holroyd, C. B., Schurger, A., & Cohen, J. D. (2004). Sensitivity of
621 electrophysiological activity from medial frontal cortex to utilitarian and performance feedback.

- 622 *Cerebral Cortex*, 14(7), 741–747. doi: 10.1093/cercor/bhh034
- 623 O’Keefe, J., & Recce, M. L. (1993). Phase relationship between hippocampal place units and the EEG
624 theta rhythm. *Hippocampus*, 3(3), 317–330. doi: 10.1002/hipo.450030307
- 625 Packard, M. G., & Goodman, J. (2013). Factors that influence the relative use of multiple memory
626 systems. *Hippocampus*, 23(11), 1044–1052. doi: 10.1002/hipo.22178
- 627 Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with
628 lidocaine differentially affects expression of place and response learning. *Neurobiology of*
629 *Learning and Memory*, 65(1), 65–72. doi: 10.1006/nlme.1996.0007
- 630 Pecchia, T., & Vallortigara, G. (2012). Spatial reorientation by geometry with freestanding objects and
631 extended surfaces: a unifying view. *Proceedings. Biological Sciences / The Royal Society*,
632 279(1736), 2228–36. doi: 10.1098/rspb.2011.2522
- 633 Persa, G., Török, Á., Galambos, P., Sulykos, I., Kecskés-Kovács, K., Czigler, I., ... Csépe, V. (2014).
634 Experimental Framework for Spatial Cognition Research in Immersive Virtual Space. In
635 *Cognitive Infocommunications (CogInfoCom), 2014 IEEE 5th International Conference on* (pp.
636 587–593). IEEE. doi: 10.1109/CogInfoCom.2014.7020412
- 637 Plank, M., Müller, H. J., Onton, J., Makeig, S., & Gramann, K. (2010). Human EEG correlates of
638 spatial navigation within egocentric and allocentric reference frames, *Lecture Notes in Computer*
639 *Science: Spatial Cognition VII* 18/191–206. doi: 10.1007/978-3-642-14749-4_18
- 640 Restle, F. (1957). Discrimination of cues in mazes: a resolution of the place-vs.-response question.
641 *Psychological Review*, 64(4), 217–228. doi: 10.1037/h0040678
- 642 Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial
643 frontal cortex in cognitive control. *Science*, 306(5695), 443–447. doi: 10.1126/science.1100301
- 644 Rousselet, G. A. (2012). Does filtering preclude us from studying ERP time-courses? *Frontiers in*
645 *Psychology*, 3(MAY), 131. doi: 10.3389/fpsyg.2012.00131
- 646 Schmitzer-Torbert, N. (2007). Place and response learning in human virtual navigation: behavioral
647 measures and gender differences. *Behavioral Neuroscience*, 121(2), 277–290. doi: 10.1037/0735-
648 7044.121.2.277
- 649 Simon-Thomas, E. R., Brodsky, K., Willing, C., Sinha, R., & Knight, R. T. (2003). Distributed neural
650 activity during object, spatial and integrated processing in humans. *Cognitive Brain Research*,
651 16(3), 457–467. doi: 10.1016/S0926-6410(03)00060-0
- 652 Snider, J., Plank, M., Lynch, G., Halgren, E., & Poizner, H. (2013). Human cortical θ during free
653 exploration encodes space and predicts subsequent memory. *The Journal of Neuroscience : The*
654 *Official Journal of the Society for Neuroscience*, 33(38), 15056–68. doi:
655 10.1523/JNEUROSCI.0268-13.2013
- 656 Sulpizio, V., Committeri, G., Lambrey, S., Berthoz, A., & Galati, G. (2013). Selective role of
657 lingual/parahippocampal gyrus and retrosplenial complex in spatial memory across viewpoint
658 changes relative to the environmental reference frame. *Behavioural Brain Research*, 242, 62–75.
659 doi: 10.1016/j.bbr.2012.12.031
- 660 Taylor, H. A., & Tversky, B. (1996). Perspective in Spatial Descriptions. *Journal of Memory and*
661 *Language*, 35(3), 371–391. doi: 10.1006/jmla.1996.0021
- 662 Team, J. (2016). JASP (Version 0.7.5.5)[Computer software].
- 663 Team, R. C. (2014). R: A language and environment for statistical computing. R Foundation for
664 Statistical Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0.
- 665 Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55(4), 189–208. doi:
666 10.1037/h0061626
- 667 Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. II. Place learning versus
668 response learning. *Journal of Experimental Psychology*, 36(3), 221. doi: 10.1037/h0060262

- 669 Török, Á. (2016). From human-computer interaction to cognitive infocommunications : a cognitive
670 science perspective. In P. Baranyi (Ed.), *IEEE International Conference on Cognitive*
671 *Infocommunications* (pp. 453–459). Wroclaw, Poland: IEEE Press. doi:
672 10.1109/CogInfoCom.2016.7804588
- 673 van Hoogmoed, A. H., van den Brink, D., & Janzen, G. (2012). Electrophysiological correlates of
674 object location and object identity processing in spatial scenes. *PLoS ONE*, 7(7), e41180. doi:
675 10.1371/journal.pone.0041180
- 676 Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M.
677 (1997). Differential effects of early hippocampal pathology on episodic and semantic memory.
678 *Science*, 277(5324), 376–380. doi: 10.1126/science.277.5324.376
- 679 Wagenmakers, E., Wetzels, R., Borsboom, D., & van der Maas, H. L. J. (2011). Why psychologists
680 must change the way they analyze their data: the case of psi: comment on Bem (2011). *J Pers*
681 *Soc Psychol.*, 100(3), 426–432. doi: 10.1037/a0022790
- 682 Weidemann, C. T., Mollison, M. V., & Kahana, M. J. (2009). Electrophysiological correlates of high-
683 level perception during spatial navigation. *Psychonomic Bulletin & Review*, 16(2), 313–319. doi:
684 10.3758/PBR.16.2.313
- 685 Wingard, J. C., & Packard, M. G. (2008). The amygdala and emotional modulation of competition
686 between cognitive and habit memory. *Behavioural Brain Research*, 193(1), 126–131. doi:
687 10.1016/j.bbr.2008.05.002
- 688 Winson, J. (1978). Loss of hippocampal theta rhythm results in spatial memory deficit in the rat.
689 *Science*, 201(4351), 160–163. doi: 10.1126/science.663646
- 690 Wirth, M., Horn, H., Koenig, T., Razafimandimby, A., Stein, M., Mueller, T., ... Strik, W. (2008).
691 The early context effect reflects activity in the temporo-prefrontal semantic system: evidence
692 from electrical neuroimaging of abstract and concrete word reading. *NeuroImage*, 42(1), 423–
693 436. doi: 10.1016/j.neuroimage.2008.03.045
- 694 Xu, S., Pan, Y., Wang, Y., Spaeth, A. M., Qu, Z., & Rao, H. (2016). Real and hypothetical monetary
695 rewards modulate risk taking in the brain. *Scientific Reports*, 6. doi: 10.1038/srep29520
696
697

698

Author Notes

699

The publication was supported by the KTIA_AIK_12-1-2013-0037 project. The project is

700

supported by Hungarian Government, managed by the National Development Agency, and financed

701

by the Research and Technology Innovation Fund. Á.T. was additionally supported by a Young

702

Researcher Fellowship from the Hungarian Academy of Sciences. A.K. was supported by the

703

Postdoctoral Fellowship of the Hungarian Academy of Sciences. We would like to express our sincere

704

appreciation to Orsolya Kolozsvári, Gabi Baliga and Zsuzsanna Kovács for their assistance during the

705

data acquisition. Finally, we gratefully acknowledge István Czigler, Vera Varga, Joe Snider, and

706

Travis E. Baker for their comments on a previous version of this manuscript. The author declare no

707

conflict of interest.

708

709

Tables

710

Table 1. Measured peak amplitudes and latencies on the PO8 and PO7 electrodes.

		PO8		PO7	
<u>Allocentric</u>	<u>Egocentric</u>	<u>P1</u>	<u>NT170</u>	<u>P1</u>	<u>NT170</u>
Amplitude in μ V: Mean (Standard Error)					
East	Left	1.92 (0.34)	-8.87 (0.92)	2.08 (0.41)	-8.58 (0.89)
	Right	1.97 (0.41)	-8.98 (0.99)	2.28 (0.38)	-8.59 (0.92)
West	Left	2.89 (0.49)	-8.70 (0.82)	2.81 (0.44)	-8.33 (0.9)
	Right	2.67 (0.50)	-8.49 (0.86)	2.75 (0.47)	-8.05 (0.87)
Latency in msec: Mean (Standard Error)					
East	Left	104.35 (4.13)	166.82 (3.59)	102.29 (4.04)	166.91 (3.16)
	Right	102.56 (3.56)	166.09 (3.44)	104.62 (3.42)	168.06 (3.44)
West	Left	103.15 (3.20)	165.35 (3.51)	100.82 (3.79)	161.76 (3.39)
	Right	102.76 (2.59)	166.41 (3.34)	98.21 (3.32)	163.56 (3.46)

711

712

713

714

Figure captions

715

716

717

718

719

720

721

722

723

724

725

726

727

728

729

730

Figure 1. The layout of the cross maze and the trial timeline. A. Participants started either in point *a* or *b* and were told to choose between the two horizontal alleys. After they chose, they were translated and rotated to look into the chosen alley where the reward object appeared (point *c* and *d*). In the turn choice analysis we considered only trials where after a rewarded trial the next trial started in the opposite alley. For example, if the first trial started in alley *a* and the participant chose alley *d* the next trial was considered only if it started in alley *b*, where egocentric reference frame predicts alley *c* and allocentric predicts alley *d*. For an easier interpretation of the consecutive figures, hereafter left turns are marked with continuous and right turns with dashed lines, whereas turns that led to the West alley are with green color and turns that led to East alley are with blue color. B. Illustration of a trial's timeline. First, participants saw the opposite starting alley with the intersection; after 800 msec, a green arrow sign appeared in the intersection. After participants made their choice they were virtually translated and rotated (550 msec) to face the chosen alley. After they arrived to the chosen alley, they watched the alley for 500 msec and then the feedback stimulus was presented. The feedback was visible for 800 msec, and then the screen turned white, and they were teleported into one of the possible starting alley, and the next trial started.

731

732

733

734

735

736

737

738

739

Figure 2. Reward dependent strategies in the experiment. We found (a) that most of the participants showed win-stay preference in more than 50% of the cases in the next trial, which behaviour (b) was specific to the rewarded alley. (c) Also, we found a smaller lose-shift preference. Black dots indicate the five percent bins of the cumulative distributions, solid lines indicate the fitted binomial distributions, blue is used for the reward related analyses and red for the no-reward related analysis. The dashed line is for presentation purposes. It is generated based on Bernoulli trials of the same length as the participants' choice sequences. It shows what shape of cumulative distribution would have been expected if choices sequences were random.

740 Figure3. Processing of the location of feedback objects in allocentric reference frame.(a)
741 The topographic dissimilarity analysis showed difference between West and East object locations
742 but not between Left and Right in the P1 time window (between 90-110 msec). We show the
743 difference in waveforms on the PO8 electrode. (b) Scalp maps show topographic difference
744 between West and East locations in the P1, difference scalp map indicate that the topographic
745 difference was caused by an activity with right lateralized parieto-occipital maxima.