

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

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## 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.

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

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## Introduction

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

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

69 (M G Packard & McGaugh, 1996; Mark G. Packard & Goodman, 2013). Our study was based on this  
70 classic paradigm exploiting the modern 3D virtual technology in order to study the temporal dynamics  
71 of object location processing in humans.

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

91 Although the NT170 is interpreted as a correlate of egocentric reference frame use, the  
92 experimental design of Baker and Holroyd (2009, 2013) did not enable differentiation between  
93 egocentric and allocentric coding since the alleys were only approached from one direction (either left  
94 or right). Nevertheless, the design of Baker and Holroyd was possibly more conducive to response

95 learning, because participants started each trial from the same alley and thus egocentric path  
96 integration was easy. Favoring this explanation, Waller and Hodgson (2006) found in their task that  
97 while after small rotations, participants made pointing errors consistent with the use of an egocentric  
98 reference frame; after more severe disorientation, they showed a switch to an allocentric strategy.  
99 Based on this result, in the current cross maze paradigm, we introduced disorientation, and participants  
100 were randomly teleported to either the South or North alley of a cross maze at the beginning of each  
101 trial and were able to approach each alley from both left and right directions. With this manipulation,  
102 we aimed to extend the paradigm of Baker and Holroyd (2009), to differentiate between egocentric  
103 and allocentric coding of location. We hypothesized that this manipulation will favor the use of an  
104 allocentric reference frame, the ERP correlates of which have not been investigated yet. There is one  
105 possible ERP candidate of allocentric place coding, the P1, the amplitude of which is modulated by the  
106 number of locations seen (Simon-Thomas et al., 2003).

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

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## Method

### Participants

116 EEG data was collected from 38 participants. Four participants' data was later excluded  
117 because of recording error or of not meeting the inclusion criteria (see below). Of the remaining 34  
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119 participants, 18 were females. Participants were naïve to the aims of the study and all of them were  
120 right-handed. Their mean age was 22 years ( $SD = 2.26$ ,  $Min = 19$ ,  $Max = 29$ ). They had normal  
121 hearing and normal or corrected-to-normal vision. Participants were neither color nor stereoblind.  
122 They were university students from either the Budapest University of Technology and Economics or  
123 the Eötvös Loránd University and received payment or course credits for their participation. They gave  
124 informed consent prior to the experimental session. The study was approved by the Ethical Review  
125 Committee for Research in Psychology (EPKEB).

## 126 **Apparatus and stimuli**

127 The experiment was run at the CAVE-like virtual reality arena (Cruz-Neira, Sandin, &  
128 DeFanti, 1993) of the 3DICC Laboratory, MTA SZTAKI (Fig S1-S2). Participants sat in a  
129 comfortable chair in the center of the virtual environment; they were surrounded by three screens  
130 (3(w) by 2(h) m each) from the front and the two sides. They wore stereoglasses (Infitec) and 3D  
131 stereopsis was generated by two projectors on each screen (passive stereo projection). Motion was  
132 controlled by the left and right arrow keys on a keyboard placed in the lap of the participant.

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

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

144        **Procedure**

145            Before the start, the experimenter explained the task to the participants with a video  
146 presentation. According to the instructions, they were placed in a cross maze where they had to collect  
147 as many points as they could. They were told that the appearance of rewarding and nonrewarding  
148 objects follow a complex rule. We deliberately did not specify to them what the complex rule was, we  
149 only told them that it was not simple. Throughout the instructions, we took extra care of not using the  
150 words left, right, East, West, etc., which could have indicated the experimenters' preference for one  
151 strategy. They started each trial in either the upper or lower alley (see Figure 1). There, they saw the  
152 intersection for 800 msec, and then a double arrow sign appeared at the center of the maze. They were  
153 told to choose one horizontal alley when the sign appeared. We did not limit the time for the choice.  
154 After they made their decision, they were translated and rotated to face the chosen alley in 550 msec.  
155 In pilot experiments we made sure that the speed of the translation and rotation was not too fast and/or  
156 caused nausea. The reward stimulus was presented 500 msec after they arrived at the alley for 800  
157 msec. For half of the participants the golden apple valued 5 points, for the other half the magic plum  
158 was the reward. The nonreward object valued 0 points. After the feedback stimulus disappeared, they  
159 were teleported (white screen for 300 msec) to either of the vertical alleys to start the next trial.  
160 Participants were told that the teleportation follows a random order.

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

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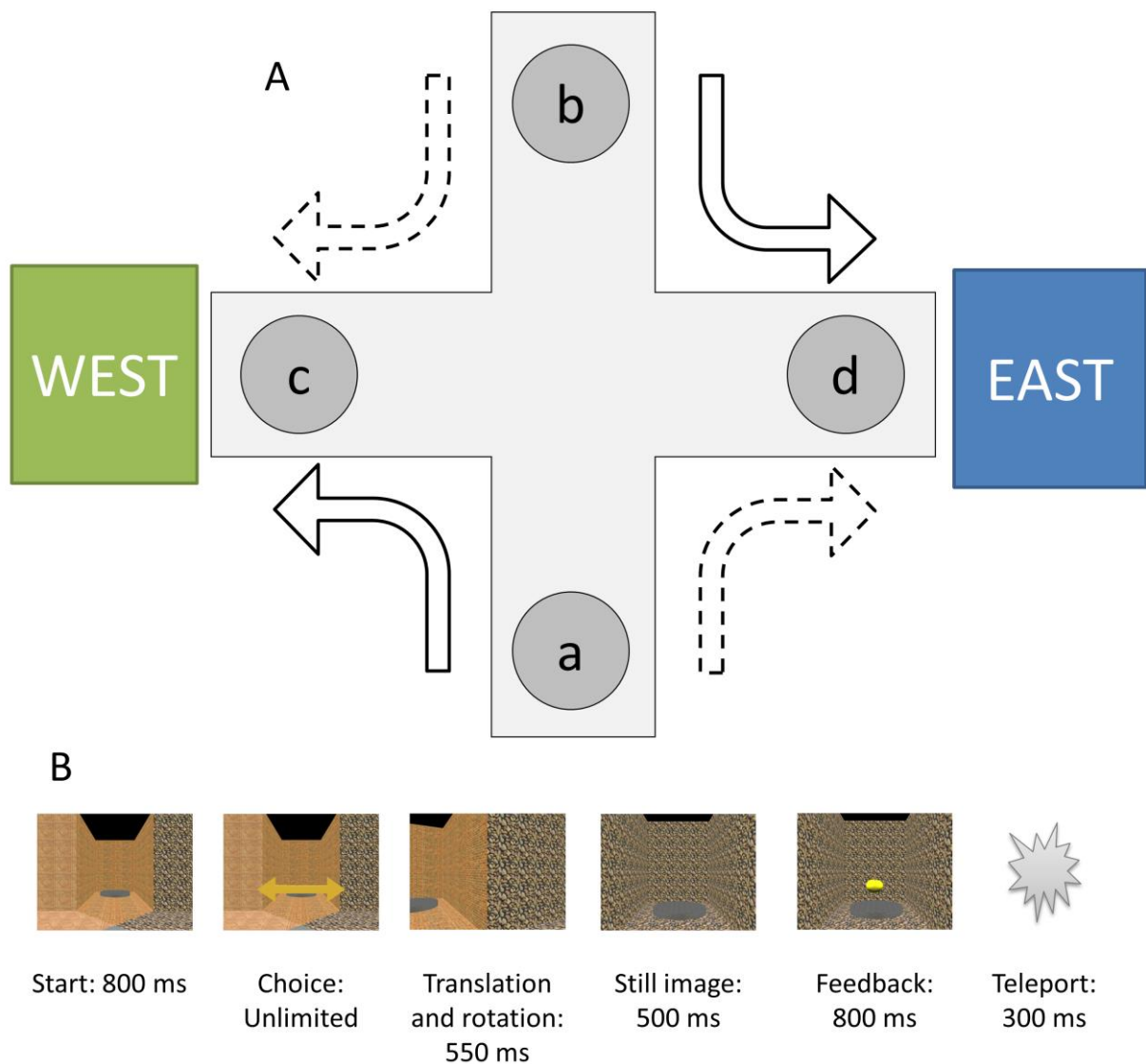


Figure 1. The layout of the cross maze and the trial timeline. A. Participants started either in point a or b and were told to choose between the two horizontal alleys. After they chose, they were translated and rotated to look into the chosen alley where the reward object appeared (point c and d). In 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.



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## 170 **Statistical analyses**

### 171 **Behavioral data**

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

### 183 **EEG data**

184 Preanalysis of the electrophysiological data was done using Matlab and EEGLAB (Delorme &  
185 Makeig, 2004). First, data was re-referenced to average reference (Bertrand, Perrin, & Pernier, 1985),  
186 and the original reference was retained (FCz). Then, we filtered the data with a 0.2-30 Hz band-pass  
187 FIR filter according to the directions of Rousselet (2012). Continuous EEG was epoched using a - 100  
188 msec and + 500 msec window relative to the appearance of feedback objects in the side alleys. Data  
189 were then decomposed by independent component analysis to help artifact removal (Delorme &  
190 Makeig, 2004). For each participant, the ICA returned 63 components. We rejected components  
191 carrying eye blinks and muscle artifacts, then, recomposed the channel based data. Moreover, we  
192 rejected every epoch where the EEG signal exceeds a +/- 100  $\mu$ V limit within the -100 to 500 msec  
193 time window. Baseline potential was calculated using the -100 – 0 msec window.

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

206           Second, in two separate tests, we analyzed whether ERPs differed when an object (regardless  
207 of its value) appeared in the left vs. right alley (i.e., coding in an egocentric reference frame) and in the  
208 East vs. West alley (i.e., coding in an allocentric reference frame). Due to the cross maze design and  
209 the different starting points, the current paradigm made it possible to differentiate between these two  
210 reference frames. Since there exists previous ERP literature on the topic (Baker & Holroyd, 2009,  
211 2013; Simon-Thomas et al., 2003; van Hoogmoed et al., 2012), we were able to make specific  
212 hypotheses of when we expect the earliest spatial location dependent ERP differences. These time  
213 windows were those in which the P1 (Simon-Thomas et al., 2003) and the NT170 (Baker & Holroyd,  
214 2013) ERP components usually appear. We identified the time window for the topographic analysis  
215 for the P1 between 90 and 110 and for the NT170 between 180 and 200 msec. The FRN was identified  
216 between 200-300 msec.

217           Statistical analysis of scalp topographies was done in Ragu (Koenig, Kottlow, Stein, Melie-  
218 García, & Melie-garc, 2011), where randomization tests were done on the averaged data in the above  
219 specified time intervals. We performed 1000 randomization runs and applied a 5% significance

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

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## Results

### Behavioral results

239 We analyzed the participants’ choices to see whether they show preference to an allocentric  
240 reference frame in the task. First, we calculated the simple place (allocentric) and action (egocentric)  
241 preference scores. These were quantified by counting choices of the West and East alley and the left  
242 and right turn, respectively, and taking the more frequent for both. Participants reported more  
243 complex, feedback dependent strategies during the debriefing, thus we hypothesized that a simple  
244 preference would not describe adequately their performance in the task. Therefore we tested whether

245 the collected data favored the null hypothesis ( $H_0$ , i.e. the simple preference scores did not reveal any  
246 systematic preference for one alley or turn), or the alternative hypothesis ( $H_1$ ) using a Bayesian paired-  
247 sample  $t$ -test. Following the objective Bayes analysis routine (Berger, 2006); we specified 0.707 as the  
248 width of the half-Cauchy distribution prior. According to Wagenmakers et al. (Wagenmakers,  
249 Wetzels, Borsboom, & van der Maas, 2011),  $BF_{01}$  values between 1 and 3 indicate anecdotal evidence  
250 for  $H_0$ , while values between 3 and 10 indicate substantial evidence for  $H_0$ .

251 Participants showed 53.88 (3.29) % simple preference for one egocentric choice and 55.03  
252 (5.83) % for one allocentric alley. The analysis showed moderately strong evidence that the simple  
253 preference scores were the same in both egocentric and allocentric reference frames ( $M_{diff} = 8.824$ ,  
254  $t(33) = 0.869$ ,  $p = .391$ ,  $BF_{01} = 3.840$ , error % < 0.001). This pattern shows that simple preference  
255 scores were not describing adequately the response strategies in the task. We also inspected if there  
256 were any participants showing an extreme preference for one specific alley/choice, which would have  
257 biased the ERP calculation due to the low number (< 50) of trials in the condition. Only 6 participants  
258 showed preference for one alley or choice in at least 62.5 % (250/400) of the cases. Importantly, none  
259 of them had less than 120 trials in any condition, which enabled us the reliable calculation of ERP  
260 averages in the latter analysis. In the next step, we examined whether participants' choices depended  
261 on the rewards.

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

269 Because the same place and same action choices are not distinguishable when the next trial  
270 started from the same alley, next, we took only the subset of trials where after a reward the next trial

271 started in the opposite alley. Analysis of these trials could show if the win-stay strategy found was  
272 specific to the rewarded place or to the rewarded action. According to the results, participants  
273 preferred the choice of an allocentric place over an egocentric response ( $\beta = .45$ ,  $z(33) = 13.95$ ,  $p <$   
274  $.001$ ,  $M_{\text{prop same place}} = .61 (.20)$  see Fig. 2) in the task. Based on these scores, we were able to classify  
275 participants to allocentric (22/34), unknown (7/34), and egocentric (5/34) groups (see Suppl. section  
276 4); this grouping also shows that the task was predominantly allocentric. Interestingly, a comparison  
277 between the first and second half of the experiment showed that allocentric win-stay preference  
278 became stronger during the experiment ( $t(33) = -2.23$ ,  $p = 0.03$ ,  $M_{1\text{st}} = .58(.22)$ ,  $M_{2\text{nd}} = .64(.20)$ ). This  
279 result may indicate a stabilization of strategy.

280         Lastly, we tested the participants' behavior after no-reward events. For this, like with the test  
281 of win-shift or win-stay strategies, we selected the trials without teleportation. Because according to  
282 the task, these events were not actual loss events but simple no reward events, we did not expect large  
283 no-reward dependent strategy. Indeed, we only found a small preference for lose-shift behavior ( $\beta$   
284  $= .09$ ,  $z(33) = 2.3$ ,  $p = .02$ ,  $M_{\text{prop lose shift}} = .52 (.17)$  see Fig. 2). Analysis of the trials with teleportation  
285 did not enable us to specify if the lose-shift strategy was specific to place or action ( $p = .44$ ).

286         Summarizing the analysis of the behavioral data, we found that (1) participants did not show  
287 simple preference for one place or action, but (2) they did follow a win-stay and (3) lose-shift  
288 strategies, and (4) chose often the same place after a rewarded trial. This strategy required them to  
289 encode and use the allocentric spatial coordinates of the object during the task. Importantly, because  
290 there was no association between the objects and alleys, they had to encode their ad-hoc spatial  
291 coordinates in each trial. Therefore, in the analysis of the EEG data, we aimed to identify the  
292 electrophysiological correlates of this process.

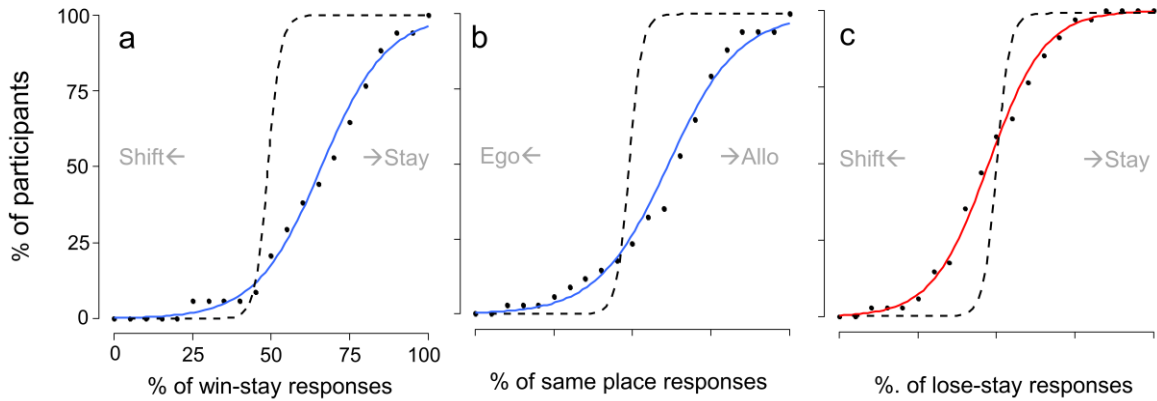


Figure 2. Reward dependent strategies in the experiment. We found (a) that most of the participants showed win-stay preference in more than 50% of the cases in the next trial, which behaviour (b) was specific to the rewarded alley. (c) Also, we found a smaller lose-shift preference. Black dots indicate 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 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.

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## 295 EEG analysis

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297 We started with analyzing whether reward and nonreward objects elicit FRN. According to  
 298 our analysis method, we explored differences in global field power and topographic dissimilarity using  
 299 randomization statistics. Significant differences were found between 200-300 msec in the global field  
 300 powers and in the topographies. These long-lasting differences signaled the processing of reward  
 301 information. Consistent with our expectations, the elicited negativity in the nonreward condition was  
 302 maximal over the FCz electrode. Here the difference was significant between 153 and 266 msec  
 303 (results are significant after cluster-threshold and FDR correction). This result shows that participants  
 304 were involved in the task and evaluated the rewards, in line with the behavioral results.

305 We, then, turned to the spatial processing related analysis to explore whether the feedback  
 306 objects were processed in an allocentric and possibly even in an egocentric reference frame. Because

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

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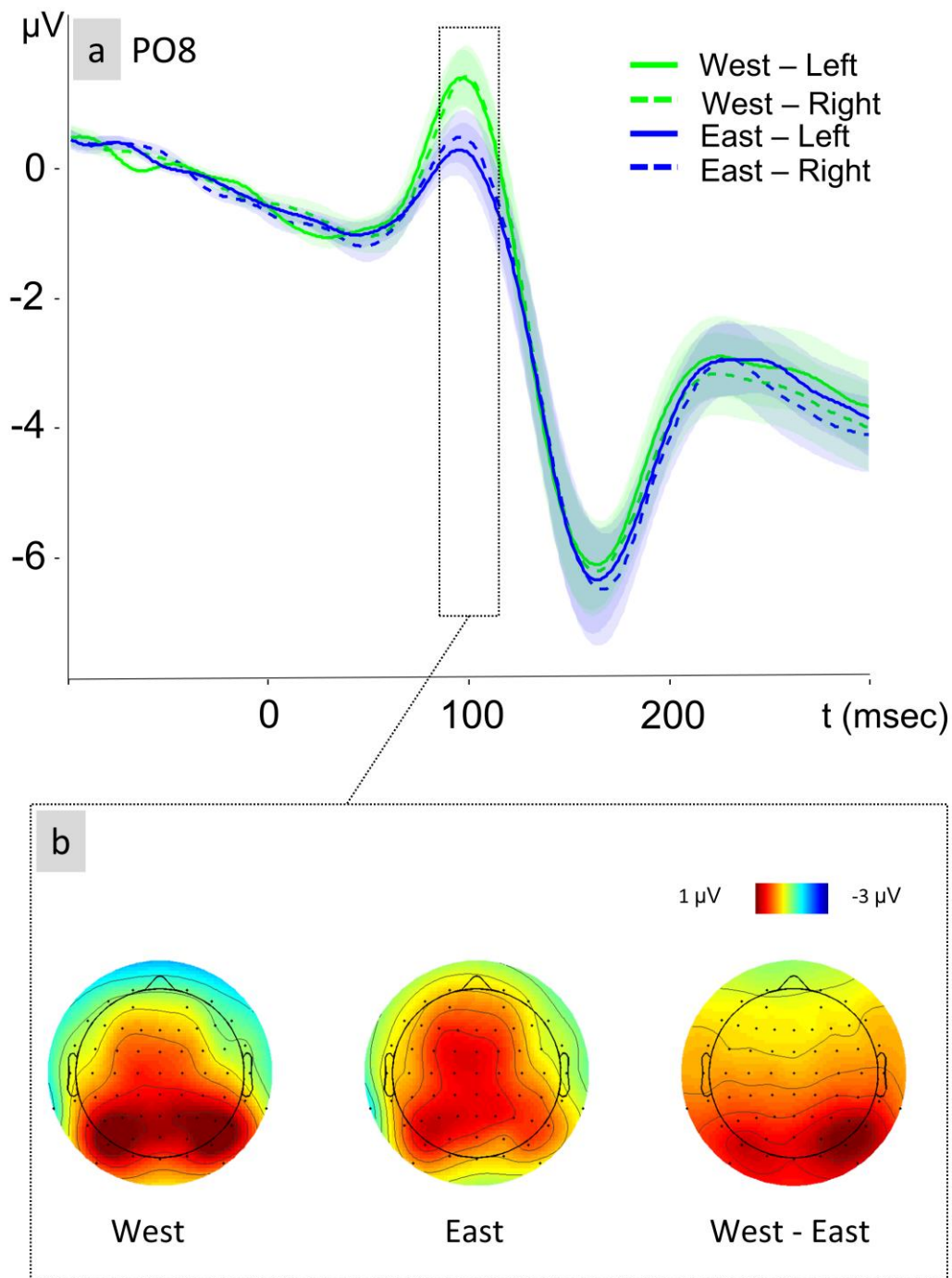


Figure 3. Processing of the location of feedback objects in allocentric reference frame. (a) The topographic dissimilarity analysis showed difference between West and East object locations but not between Left and Right in the P1 time window (between 90-110 msec). We show the difference in waveforms 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.



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

328           Lastly, we further analyzed the difference on PO8 electrode. For the purpose of comparison  
329 with the related findings, we followed the peak analysis method of Baker and Holroyd (Baker &  
330 Holroyd, 2009). That is, first, we identified the latency and amplitude of the P1 by finding the most  
331 positive value between 50 and 150 msec (see Table 1). Then, using this latency as the onset of the  
332 NT170, we identified the peak of the NT170 from here to 200 msec as the most negative point (see  
333 Table 1). Peak amplitudes and latencies were compared in the 2 by 2 repeated measures ANOVA  
334 separately for the P1 and for the NT170. We found a significant amplitude difference on the P1  
335 between the two allocentric places ( $F(1,33) = 4.46, p = .042, \eta^2_p = .12$ ), consistent with the results  
336 above. None of the other effects were significant, importantly, neither the amplitude ( $F(1,33) = 0.06, p$   
337  $= .806, \eta^2_p < .01$ ) nor the latency of the NT170 ( $F(1,33) = 0.02, p = .891, \eta^2_p < .01$ ) differed between  
338 left and right turns. Because the effect seemed to affect the P1 bilaterally, we tested the effect on the  
339 PO7 electrode, too. We found difference on tendency level ( $F(1,33) = 3.93, p = .056, \eta^2_p = .11$ ).  
340 Similarly to PO8, we did not find significant egocentric NT170 effect on the PO7. These results  
341 suggest that robust egocentric processing did not occur in the first 300 ms after the feedback object  
342 appeared.

343

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

|                                                    |            | PO8           |               | PO7           |               |
|----------------------------------------------------|------------|---------------|---------------|---------------|---------------|
| Allocentric                                        | Egocentric | P1            | NT170         | P1            | NT170         |
| Amplitude in $\mu\text{V}$ : 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) |

345

346

## Discussion

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

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

361 In the analysis of EEG data, we found that nonrewarding objects elicited an FRN after 150  
362 msec, a fronto-central negativity previously found to be related to feedback value processing (Baker &  
363 Holroyd, 2009, 2013). This effect indicated that participants were engaged in the reward finding task.  
364 This is in line with previous studies using similar designs (Baker & Holroyd, 2009, 2013). However,  
365 while in the studies of Baker and Holroyd (2009, 2013) object location was processed in egocentric  
366 reference frame, signaled by the latency modulation of the NT170, we did not find such effect in the  
367 cross maze. In contrast, we found that the amplitude and topography of the P1 component were  
368 sensitive to coding the object location in *allocentric* reference frame. Similarly to earlier results (Baker  
369 & Holroyd, 2013; Simon-Thomas et al., 2003), the P1 was maximal over the right parieto-occipital  
370 electrode sites. It is important to note that we did not find difference in global field power but in  
371 topographies. This means the larger P1 amplitude should not be interpreted as stronger processing of  
372 objects in the West alley, but as a different topographic distribution for the P1 in the West alley, which  
373 resulted in larger amplitude over parieto-occipital sites but smaller elsewhere. Importantly, we found  
374 that the spatial location related activity in the P1 window was not affected by the reward value of the  
375 object. This indicates a very early modulation of visual processing related ERPs by allocentric spatial  
376 information. P1 has been shown to be affected by spatial attention (Luck, Heinze, Mangun, &  
377 Hillyard, 1990; Martínez et al., 1999). Moreover, this component has been shown to be modulated by  
378 complex information, like the spatial location of a graspable object (Handy, Grafton, Shroff, Ketay, &  
379 Gazzaniga, 2003).

380 Our results extend the interpretation of Baker and Holroyd (2009) stating that the egocentric  
381 encoding of object location is conveyed in the latency effect of the NT170 component. Here we  
382 provide evidence that the allocentric encoding of an object is reflected in the topography of the P1  
383 component. Presumably, the allocentric coding, instead of egocentric, in the current task is partly due  
384 to the introduction of the teleportation and hence the disruption of continuous (or at least predictable)  
385 egocentric path integration. Path integration is an important part of the formation of egocentric spatial  
386 memory (Buzsáki, 2005; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006). More broadly, the  
387 spatio-temporal congruity of successive events has been shown to be important for episodic memory

388 formation in general (Buzsáki & Moser, 2013). These processes are strongly related to theta  
389 oscillations in the brain (Baker & Holroyd, 2013; Caplan et al., 2003; O'Keefe & Recce, 1993) and to  
390 the hippocampal-parahippocampal system (Baker, Umemoto, Krawitz, & Holroyd, 2015; Cornwell,  
391 Johnson, Holroyd, Carver, & Grillon, 2008). Normally, repeated experiences in an environment lead  
392 to the formation of semantic memory (Buzsáki, 2005), which is thought to be more of allocentric in  
393 nature (Buzsáki & Moser, 2013). Semantic memory is more related to alpha activity (Brötzner,  
394 Klimesch, Doppelmayr, Zauner, & Kerschbaum, 2014) and less dependent on hippocampal areas  
395 (Corkin, 2002; Vargha-Khadem et al., 1997; Winson, 1978). While the relationship between semantic  
396 vs. episodic memory and de facto spatial navigation is still an active research area (Buzsáki & Moser,  
397 2013), this duality helps the interpretation of current results. Alpha activity has been shown to play  
398 important role in allocentric navigation in previous studies too (Chiu et al., 2012; Lin, Chiu, &  
399 Gramann, 2015; Plank, Müller, Onton, Makeig, & Gramann, 2010). The importance of these  
400 frequencies from the perspective of ERPs is that phase-locking of alpha and theta oscillations are  
401 generating the P1-N1 complex (Klimesch et al., 2004), and the mean latency of the P1 lies in the alpha  
402 frequency range. Therefore, we hypothesize that while the NT170 is related to partial resetting of theta  
403 oscillatory activity (Baker & Holroyd, 2013), the P1 modulation found in the current study is more  
404 likely related to alpha activity changes. Further studies should explore the event-related spectral  
405 perturbations related to the P1-NT170 complex.

406         Also, future studies should use EEG-fMRI co-registration to identify the brain areas  
407 responsible for the allocentric processing in the current study and integrate them with the results  
408 regarding the egocentric NT170 difference (Baker & Holroyd, 2013; Baker et al., 2015). While the  
409 NT170 was related to a partial resetting of the ongoing theta rhythm in the parahippocampal cortex  
410 (Baker & Holroyd, 2013), we hypothesize that the allocentric P1 effect is more related to activity  
411 differences in the retrosplenial cortex. We form this assumption on the basis of previous results:  
412 Sulpizio and colleagues (Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013) showed that  
413 although both the retrosplenial cortex and the parahippocampal cortex code object locations in a stable  
414 environmental reference frame, only the retrosplenial cortex activation is modulated by the amount of

415 viewpoint change relative to that reference frame. EEG evidence from a recent study (Lin et al., 2015)  
416 also found that the retrosplenial cortex plays important role in translating egocentric experience into  
417 spatial representation in allocentric reference frame.

418         While the stochastic relocation due to teleportation is the most probable cause of the activity  
419 difference between the results of Baker and Holroyd (2009, 2013) and the recent study, there are other  
420 possible factors to consider (Mark G. Packard & Goodman, 2013). An important difference in the  
421 studies is that in the instructions Baker and Holroyd used the words ‘left’ and ‘right’, in contrast, we  
422 used neither these nor the words referring to the cardinal directions. The use of spatial references in  
423 language also modulates cognitive processing (Lee, 2002; Taylor & Tversky, 1996). Importantly, the  
424 fact that we found the same pattern of activity in the learning phase, where no teleportation happened,  
425 as in the experimental phase suggests that the instructions played an important role. Nevertheless, we  
426 cannot decide which part of our instruction facilitated the use of an allocentric reference frame in the  
427 cross maze: the lack of linguistic reference to egocentric coordinates or the mentioning of  
428 teleportation. This requires further explorations. Another potential factor that might influenced the  
429 pattern of results in the current study is that while Baker and Holroyd (Baker & Holroyd, 2009)  
430 motivated their participants by a more-reward-more-money received instruction, in the current  
431 experiment, participants were told to receive a fixed amount of compensation and only their score was  
432 affected by the choices. A study of Xu et al. (2016) showed behavioural and ERP evidence that real  
433 monetary losses are more aversive than hypothetical ones. Thus, one could argue that the earlier  
434 instruction was not only motivating but also more stressing since participants believed that their  
435 performance affected the reward they would earn by the end of the experiment. Stress, increased  
436 arousal, and anxiety are also factors that favor response learning (McGaugh, 2004; Wingard &  
437 Packard, 2008). Future studies should investigate what factors contribute to place and response  
438 learning in these tasks in humans.

439         Importantly, none of the ERP differences found in the current study can be attributed to a  
440 simple association between textures and reward objects because reward objects were present in both

441 alleys with equal probability. Furthermore, because the orientation of the cross maze also varied  
442 randomly between participants and we summed ERPs according to left/right and East/West alley turns,  
443 ERPs cannot reflect any texture related cognitive process. Note that earlier studies (Baker & Holroyd,  
444 2013) did not reveal a topographical modulation of the egocentric NT170 component when the task  
445 was presented in a nonspatial context. This suggests that the presented effects are indeed related to  
446 spatial processing. We also analyzed whether there were reward-related changes coinciding with the  
447 spatial differences and found that (1) reward based processing started only later in time and (2) with  
448 fronto-central topography.

449 We did not find difference in the presence of P1 modulation and lack of NT170 modulation  
450 between the allocentric, egocentric and unknown strategy groups (Fig S8-S9). One would have  
451 expected P1 amplitude modulation for the participants following allocentric and NT170 latency  
452 modulation for the participants following egocentric strategy. Here only a small fraction of  
453 participants showed egocentric win-stay responses more often (5/34) and they showed the same P1  
454 modulation pattern than the allocentric strategy followers. This could be due to several reasons, for  
455 example, it is possible that different neural correlates feature an egocentric strategy when that is the  
456 default based on the task specificities (like in the T-maze) versus when the task is predominantly  
457 allocentric and the strategy choice is motivated by the participant's aspiration to find out the aim of the  
458 experiment. Because the current data did not allow more in-depth analysis of EEG and strategy  
459 relationship, further studies are required to investigate any related hypothesis. Importantly, while in  
460 the current task reward was found with 50 % probability, future studies should manipulate the reward  
461 probability in ways that facilitate the use of different strategies, even with switches between different  
462 rewarding fashions during the experiment. This would help enlighten the relationship between strategy  
463 and ERP correlates.

464 A limitation of the current study is the use of only limited immersiveness in virtual reality.  
465 The current state-of-art enables not only button press interaction and sitting position, but also more  
466 direct interaction and even locomotion in virtual spaces while recording EEG (e.g., Snider, Plank,

467 Lynch, Halgren, & Poizner, 2013). Real locomotion would have possibly increased participants' use  
468 of egocentric reference frames, as well. Exploring how humans reorient after teleportation in a space  
469 where direct locomotion is also enabled would be essential for the development of virtual and  
470 augmented reality interfaces (Török, 2016).

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

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

483

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## **Figure captions**

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