

Title: Temporal dynamics of object location processing 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.

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

Introduction

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).

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 (M G Packard & McGaugh, 1996; Mark G. Packard & Goodman, 2013). Our study was based on this

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

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

Although the NT170 is interpreted as a correlate of egocentric reference frame use, the experimental design of Baker and Holroyd (2009, 2013) did not enable differentiation between egocentric and allocentric coding since the alleys were only approached from one direction (either left or right). Nevertheless, the design of Baker and Holroyd was possibly more conducive to response learning, because participants started each trial from the same alley and thus egocentric path 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.

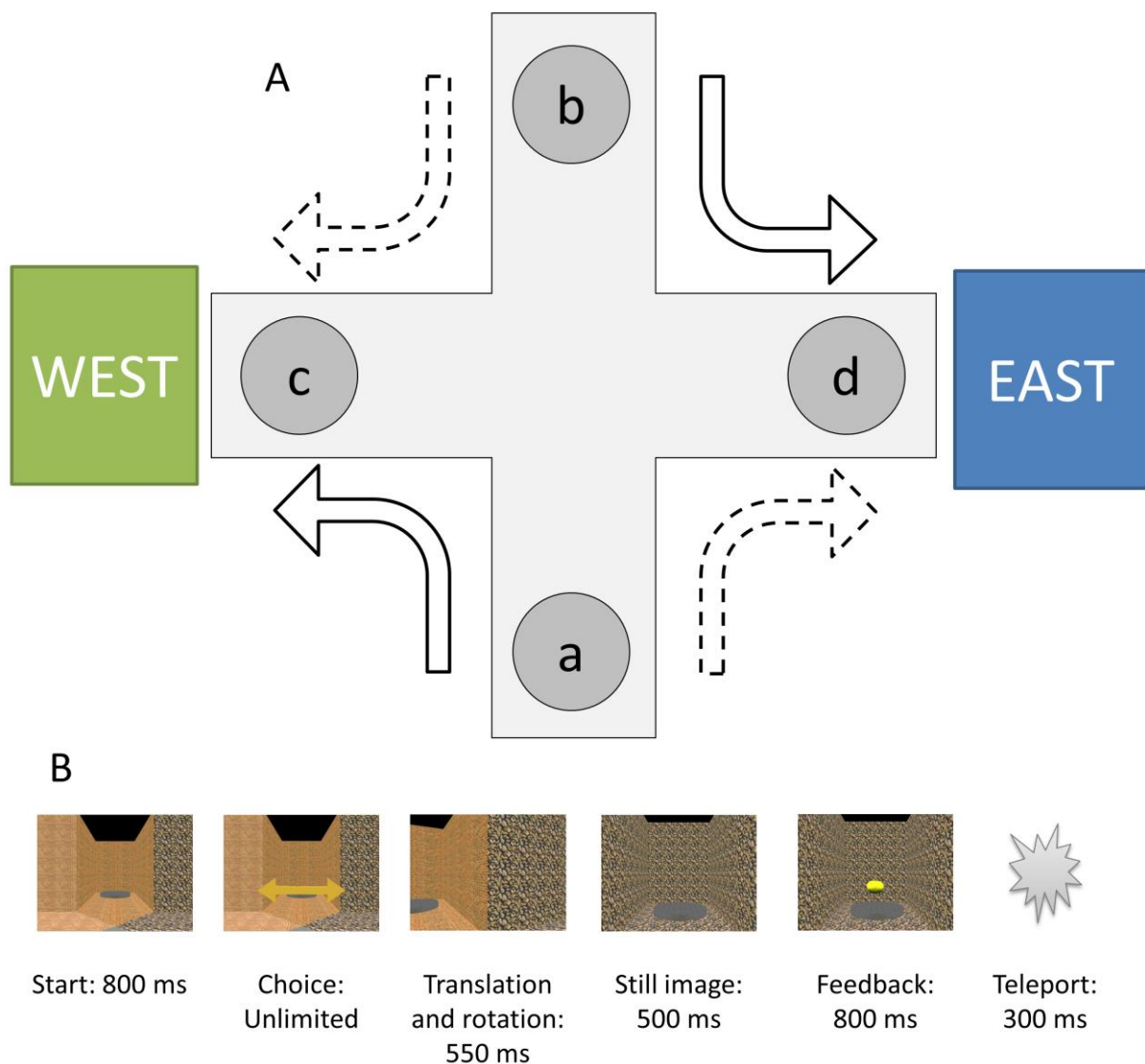


Figure 1. The layout of the cross maze and the trial timeline. A. Participants started either in point a or b and were told to choose between the two horizontal alleys. After they chose, they were translated and rotated to look into the chosen alley where the reward object appeared (point c and d). In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

Method

Participants

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

Apparatus and stimuli

The experiment was run at the CAVE-like virtual reality arena (Cruz-Neira, Sandin, & DeFanti, 1993) of the 3DICC Laboratory, MTA SZTAKI (Fig S1-S2). Participants sat in a comfortable chair in the center of the virtual environment; they were surrounded by three screens (3(w) by 2(h) m each) from the front and the two sides. They wore stereoglasses (Infitec) and 3D

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

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

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

Procedure

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

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

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

Statistical analyses

Behavioral data

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

EEG data

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

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

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

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

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

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

Results

Behavioral results

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 .

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 ($M_{\text{diff}} = 8.824$, $t(33) = 0.869$, $p = .391$, $BF_{01} = 3.840$, 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.

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

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

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

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

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

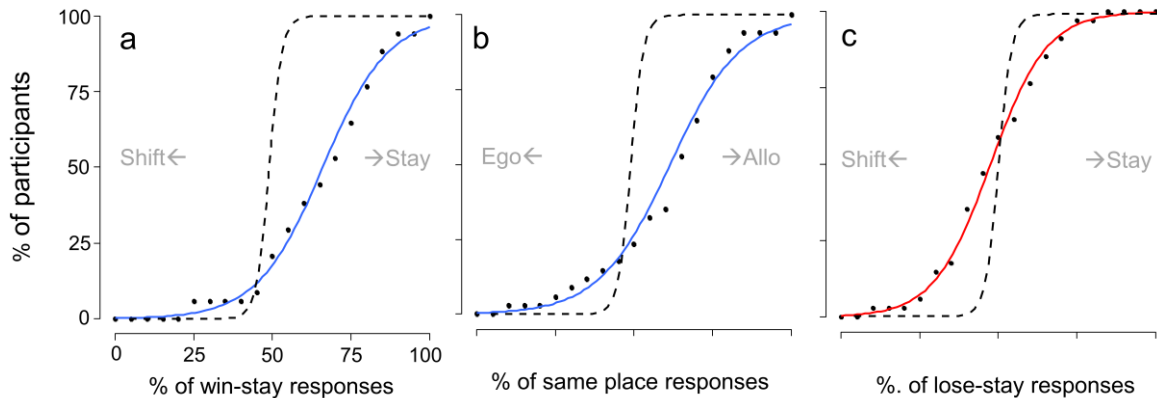


Figure 2. Reward dependent strategies in the experiment. We found (a) that most of the participants showed win-stay preference in more than 50% of the cases in the next trial, which behaviour (b) was specific to the rewarded alley. (c) Also, we found a smaller lose-shift preference. Black dots indicate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

EEG analysis

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

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

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

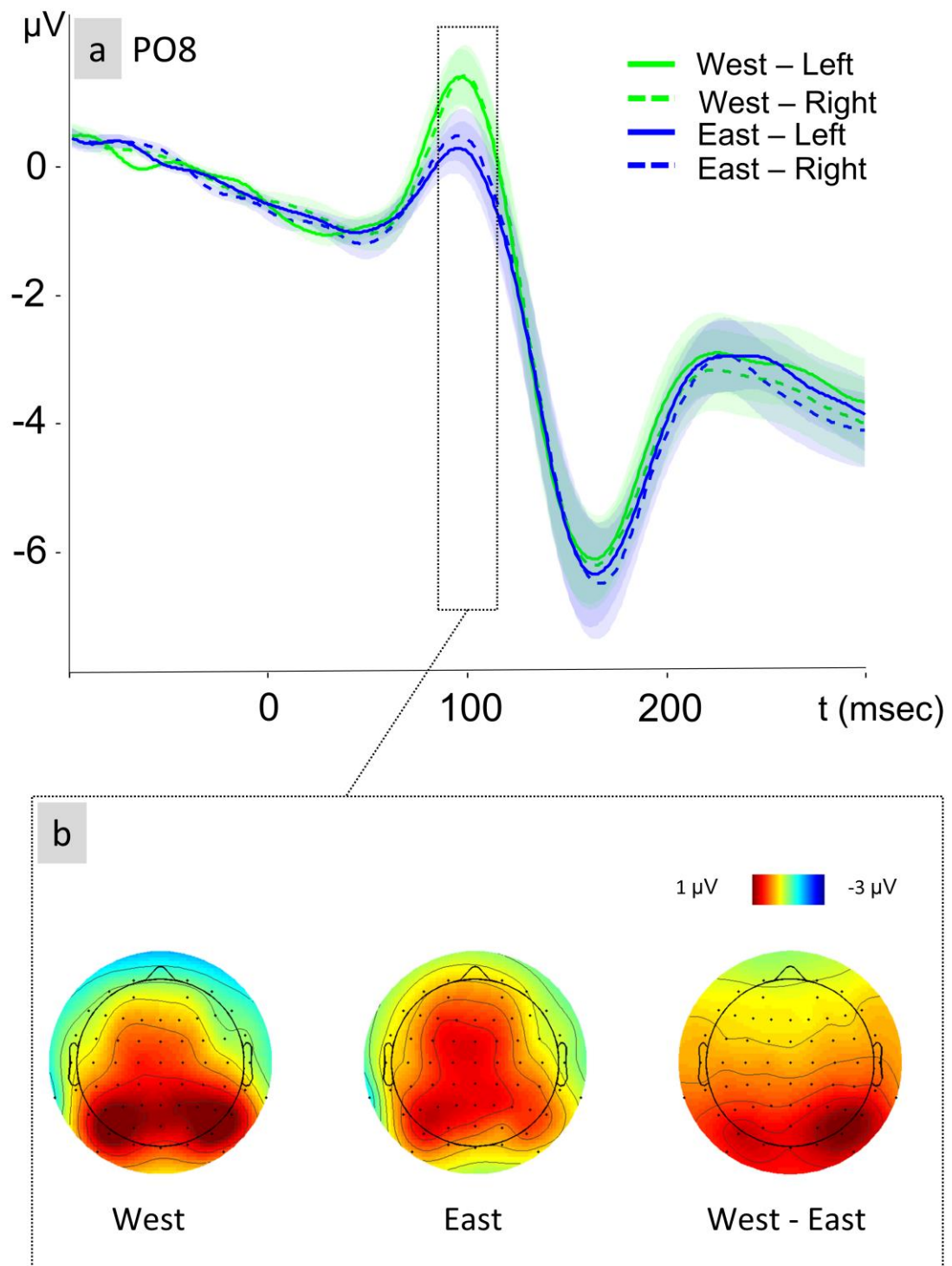


Figure3. Processing of the location of feedback objects in allocentric reference frame.(a) The topographic dissimilarity analysis showed difference between West and East object locations but not between Left and Right in the P1 time window (between 90-110 msec). We show the difference

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.

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

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

>> INSERT TABLE 1 HERE <<

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Tables

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

		PO8		PO7	
Allocentric	Egocentric	P1	NT170	P1	NT170
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)

Figure captions

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.

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.