

A history of adolescent binge drinking in humans is associated with impaired self-movement cue processing on manipulatory scale navigation tasks



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HIGHLIGHTS

- A history of adolescent binge drinking was associated with performance deficits on spatial tasks.
- Binge drinking impaired self-movement cue processing and spared use of environmental cues.
- Performance deficits were not mediated by motor coordination or motivational factors.
- These results further describe the behavioral impairments associated with adolescent binge drinking.

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ABSTRACT

A binge drinking pattern of alcohol consumption has been shown to have an impact on brain structures that continue to develop into late adolescence. These same brain structures have been implicated in processing self-movement cues. The current study applies an array of existing and novel kinematic analysis techniques to characterize performance on manipulatory scale tasks to assess spatial orientation deficits associated with a history of adolescent binge drinking. Using kinematic analysis techniques, a history of adolescent binge drinking in university students was associated with disruptions in outward segment movement organization and less accurate direction and distance estimation in a dead reckoning task. Similar disruptions in performance were found in the bead maze task in the first training block; however, no group differences were observed on subsequent blocks of place training. This is the first study to demonstrate a relationship between adolescent binge drinking in humans and impaired processing of self-movement cues. This pattern of results demonstrates the potential of manipulatory-scale spatial tasks to detect differences in information processing associated with factors known to disrupt normal central nervous system development.

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1. Introduction

Animals use multiple sources of information to maintain spatial orientation [17]. One source of information originates from environmental cues (i.e., visual, auditory, olfactory), and animals can learn to use these cues or relationships between them to guide movement. Although researchers have traditionally focused on environmental cue use, self-movement cues (i.e., vestibular, proprioception, optic flow) offer another source of information that is generated as the animal moves through an environment. These self-movement cues can be used for

dead reckoning (also referred to as path integration). Dead reckoning is an online navigational strategy that involves processing internally generated self-movement cues while moving through an environment to estimate direction and distance to the point movement originated. [4,13,15,17,36,40,44,53]. Dead reckoning tasks have been adapted for multiple species [33,35,42] and across different scales of human movement [21,26,28,54]. Specifically, human participants have been shown to use dead reckoning-based navigation at virtual [20,60], manipulatory [21,54], and ambulatory [26,39,52] scales. Each scale of movement provides access to different sources of self-movement cues. For example, during ambulatory dead reckoning tasks participants are provided access vestibular, proprioceptive, and motor efferent copies. In contrast, manipulatory scale dead reckoning scale tasks restrict participants to proprioceptive and motor efferent copies sources of self-movement

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cues, whereas participants are restricted to optic flow in virtual reality tasks. Integration of this multi-sensory information depends on the activity of a network of brain structures.

Recent work has provided evidence of a role for the hippocampus, entorhinal cortex, and medial prefrontal cortex in self-movement cue processing. For example, hippocampal damage in humans ([39]; however, see [45]) and rats ([23,27,30]; however see [2]) has been shown to disrupt performance on dead reckoning tasks. This relationship has been supported by functional magnetic resonance imaging work demonstrating hippocampal and prefrontal cortex activation while participants engaged in a virtual dead reckoning task with increased hippocampal activation being associated with the more accurate direction estimation [60]. In addition, similar impairments in self-movement cue processing have been observed in rats subsequent to damage focused on the entorhinal cortex [38,56]. Finally, increased medial prefrontal activation has been observed while human participants engaged in a virtual dead reckoning task [60]. Changes in the function of this network of brain structures may contribute to the age related decline of accuracy observed on dead reckoning tasks [20,28]. Therefore, it is possible to use dead reckoning tasks to investigate other developmental experiences that may influence the function of this network of structures.

Recent work has demonstrated an association between adolescent (12 to 25 years) binge drinking pattern of alcohol consumption (4 to 5 standard alcohol drinks in a 2 h period at least once a month [37]) in humans and deficits in central nervous system function [11,41]. Animal models have complemented this research by demonstrating adolescent binge drinking produces structural changes in structural changes in hippocampus, entorhinal cortex, and medial prefrontal cortex [7,8,12,50]. In addition, adolescence is a developmental period marked by decreased sensitivity to the sedative effect of alcohol [25] and increased sensitivity to the neurotoxic effects of alcohol [12]. These observations are especially troubling considering that the prevalence of binge drinking has been shown to progressively increase throughout adolescence culminating in >40% of university students in the US reporting a history of this pattern of alcohol consumption [55]. This trend has prompted researchers to investigate whether cognitive deficits are associated with this pattern of alcohol consumption during adolescence. Recent work has not shown a relationship between binge drinking and performance on analogous place-learning tasks in humans [46] or rodents [8]; however, this lack of deficit may reflect the inability of traditional place-learning tasks to dissociate between environmental and self-movement cue processing. As of yet, no studies have investigated self-movement cue processing deficits associated with a history of adolescent binge drinking.

The current study uses three human manipulatory-scale tasks to assess spatial orientation in adolescent participants reporting or not reporting a history of binge drinking in the previous six months. Rodent analogues of these tasks have previously been shown to dissociate impaired processing of self-movement cues (dead reckoning task) from spared use of environmental cues (place learning and matching-to-place) associated with damage to the hippocampal formation [23]. The dead reckoning task is a manipulatory scale analogue [54] of the rodent food-hoarding task conducted under dark conditions [27]. Blindfolded participants use their index finger to search the surface of a table for a small piece of Velcro tape. Upon finding the tape, they are instructed to return to the start location. The accuracy in estimating direction and distance to the start location assesses self-movement cue processing in participants. The bead maze-place task is a manipulatory scale analogue of the water maze place-learning task [22]. Participants use their index finger to search for a piece of Velcro tape attached to the bottom of a shallow well of beads. Although the start position varies across trials, the position of the Velcro tape remains fixed. The progressive improvement in estimating direction and distance to the Velcro tape assesses a participant's use of environmental cues, self-movement cues, or a combination of both to encode the direction and

distance to a fixed goal position. The bead maze-matching-to-place task is a manipulatory scale analogue of the matching-to-place task in the water maze [22]. Participants are given two trials to find the Velcro tape after it has moved to a new position. The improved performance observed between trials characterizes a participant's ability to update the encoded position of the goal. This collection of manipulatory scale tasks combined with kinematic analysis provides a novel approach to examine the spatial information processing deficits associated with adolescent binge drinking.

2. Methods

2.1. Participants

Northern Illinois University undergraduate students were provided supplemental course credit for their participation in the study. Responses to the Alcohol Use Disorder Identification Test (AUDIT)[3] administered during mass testing at the start of the semester were used to screen for potential Binge Drinkers (BD) and Non-Binge Drinkers (NB). BD participants were contacted if they responded between 6 and 9 on the measures of hazardous alcohol use domain and between 0 and 3 on both dependence symptoms and harmful alcohol domains. NB participants were contacted if they reported responses between 0 and 2 on all three domains. Based on the above criteria, a total of 26 participants were contacted and were run through the tasks. Participants were excluded from the study if they reported a history of traumatic brain injury ($n = 5$), neurological disorder ($n = 1$), or if they failed to follow the instructions ($n = 4$). The resulting sample of NB (3 female, 4 male) participants were an average age of 19.6 (SEM: 0.68) years old and had an average MMSE-2 score of 28.1 (SEM: 0.46). The resulting sample of BD (5 female, 4 male) participants were an average age of 18.9 (SEM: 0.35) years old and had an average MMSE-2 score of 29.4 (SEM: 0.18). All participants self-identified as being right handed. Consistent with previous work ([32]; for a review, see [31]), prevalence of tobacco smoking was higher in the BD (5 of 9) than the NB group (1 of 7).

2.2. Apparatus

2.2.1. Dead reckoning task

Participants were seated in an adjustable chair, such that their forearms rested comfortably on the surface of a rectangular table (0.61 m × 0.91 m). A bullet security camera was positioned perpendicular and above the participant, such that the entire table surface was within the view of the camera (see Fig. 1a). The camera was connected to a DVD recorder. A small piece of Velcro tape (2.5 cm × 2.5 cm) was attached to the surface of the table. The location of the Velcro tape varied across trials. Both a sleeping mask and a black silk scarf were used to blindfold the participants.

2.2.2. Bead maze

The same chair, table, and camera set up was used for the bead maze. The bead maze was a shallow circular well (48.3 cm in diameter and 2.5 cm deep) cut into two sheets of foam board with a third sheet of foam board serving as the base. The well was filled with small (~3 mm diameter) plastic beads, such that the piece of Velcro attached to the base of the well was not visible to the participant.

2.3. Procedure

All procedures were approved by the Northern Illinois University Institutional Review Board. Upon entering the lab, participants provided written consent prior to experiencing any tasks. Next, participants completed the MMSE-2 (PAR, Inc. Lutz, FL, USA), and general medical history was collected. Next, participants were taken into the testing room and instructed to adjust the seat such that their arms were resting

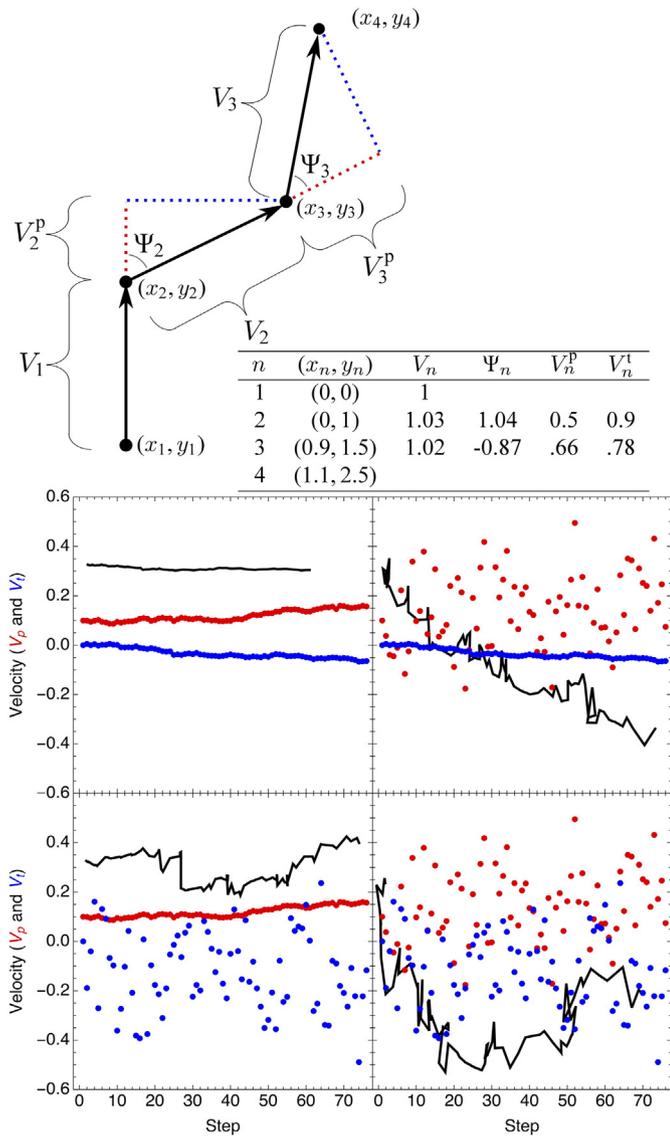


Fig. 1. The top panel diagrams vector quantities for a three-segment path. Under the assumption of constant time step length, the V_n represent point-to-point speeds. The Ψ_n are the (signed; clockwise is positive) angle in radians between the n and $n-1$ direction vectors, and V_n^P and V_n^T are the turning and persistence speeds given by $V_n^P = V_n \sin(\Psi_n)$ and $V_n^T = V_n \cos(\Psi_n)$, but for example, V_n^P can be thought of as the length of the projection of the second velocity vector onto the direction of the first and V_n^T as the projection of the second velocity vector in the direction normal to the first vector. The bottom panels plot simulated paths (black lines) in which ρ_t and ρ_p were systematically varied. The decomposed orthogonal velocities V^P (red circles) and V^T (blue circles) are plotted for all steps of each path. Varying the magnitude of ρ_t and ρ_p differentially influences the topographical organization of the path. The top left panel plots a path with ρ_t and ρ_p set at 0.98. The top right panel has ρ_t set at 0.98 and ρ_p set at 0.20. The bottom left panel has ρ_t set at 0.20 and ρ_p set at 0.98. The bottom right panel has ρ_t set at 0.20 and ρ_p set at 0.20. Changes in either ρ_t or ρ_p are associated with differences in the path topography. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

comfortably on the table. Once the individual was comfortable, he or she was instructed on the procedure of the searching task.

2.3.1. Dead reckoning task

Prior to being blindfolded, a practice trial was conducted. During the practice trial, the individual's finger and the Velcro were placed in different random positions. The participant was then instructed to find the Velcro. Upon finding the Velcro, the participant was asked to return as directly as possible to the original location where his/her finger was placed. Following the practice trial, the participant was blindfolded.

After the participant was blindfolded, the Velcro tape was attached to the table and the participant's finger was placed at one of three start locations. The participant was then instructed to find the Velcro and stop on the Velcro when it was found. When the participant encountered the Velcro, he/she was asked to return as directly as possible back to the starting location. When the participant's finger stopped in an area of the table, the trial was completed. This procedure was continued over 12 trials with both the starting location and the Velcro location varying across trials.

2.3.2. Bead maze task - place training

Following the searching task, participants experienced the bead maze task. Once the bead maze was placed on the table, participants were instructed to use their index fingers to search the well for a piece of Velcro while maintaining contact with the base of the apparatus. Upon finding the Velcro, the finger was removed from the apparatus, and participants were asked to put their hands in their laps. In between trials, participants were blindfolded and the experimenters feigned lifting and moving the Velcro tape and made a noise similar moving the Velcro location after each trial. This was done to prevent any auditory cues that would distinguish the place training phase from the matching-to-place phase. After the bead maze was reset for the next trial, the participant was able to remove the blindfold and his/her finger was placed in the next starting location by the experimenter. Place training consisted of 20 trials in which starting locations varying across trials while the location of the Velcro remained the same.

2.3.3. Bead maze task - matching-to-place

Following the first 20 trials of place training, participants were tested in a matching-to-place task. Matching-to-place consisted of 6 trials, starting from trial 21, in which the location of the Velcro tape shifted to the center of a new quadrant every two trials.

2.4. Data analysis

Videos of participants' behavior were converted to digital files using the Peak Performance (Vicon/Contemphas, Kempten Germany) motion capture system. Participants' movements were tracked by selecting one pixel every frame that corresponded to the proximal knuckle of the index finger for their preferred hand. The resulting xy -coordinates were scaled to real world units and used to calculate moment-to-moment speeds.

Each trial on the dead reckoning task was divided into outward and homeward segments. The outward segment was defined as all movements from the initiating search until finding the piece of Velcro tape. Several measures were used to characterize performance on the outward segment. First, time elapsed, distance traveled, and maximum moment-to-moment speed were recorded for each outward segment. Next, path circuitry was calculated for each outward segment by finding the ratio of the distance between the start point and the Velcro tape and the total distance traveled. Path circuitry values approaching zero represent highly circuitous paths, whereas values approaching one reflect direct paths.

Kinematic analysis of movement provides additional insight to potential processing differences between groups. In fact, there have been a number of approaches to analyze animal movement paths outlined in the literature. Specifically, tortuosity is the quantification of the intuitive idea that path "straightness" corresponds to searching strategy. Previous work has reviewed a number of different metrics of tortuosity and animal movement, including a "straightness index" equal to the start-to-finish distance divided by total distance traveled (a quantity used in the present study and known in the psychological literature as "path circuitry") and a summation of accumulated directional errors [5]. Benhamou then shows how these may be derived from random and correlated random walk models. The current study included an adaptation to a recent approach from the ecological literature that draws from the correlated random walk literature to analyze movement

kinematics on the outward segments of the dead reckoning trials. The approach was developed to analyze movement kinematics for foraging and resting animals and has been applied, for example, to sea otter trajectories [18,19]. In particular, velocities are decomposed into mutually orthogonal and scalar valued “persistence” and “turning” velocities (V^p and V^t , respectively) that are assumed to draw from normally distributed Weiner processes, and their associated moment-to-moment autocorrelations ρ^p and ρ^t give a measure of the tendency to respectively move in straight line segments or frequently turn. This analysis is powerful as it allows the determination of the autocorrelation on any scale of the trajectory and comparisons among and within trajectories using maximum likelihood ratio. This method has been previously used to look for significant changes in this autocorrelation that indicate behavioral change points within searching trajectories [19]. Although detailed discussion of this metric is available [18], we summarize the steps here.

Suppose the j th trial of the i th participant consists of a vector $\vec{Z} = \{Z_n\}_{n=1}^{l_{ij}}$ of l_{ij} equally temporally spaced xy -pairs, that we transform to the vectors speed

$$\vec{V} = \{V_n\}_{n=1}^{l_{ij}} \stackrel{\text{def}}{=} \{\|Z_n - Z_{n-1}\|\}_{n=1}^{l_{ij}},$$

and turning angle

$$\vec{\Psi} = \{\Psi_n\}_{n=1}^{l_{ij}} \stackrel{\text{def}}{=} \{\phi_n - \phi_{n-1}\}_{n=1}^{l_{ij}},$$

where ϕ_n is the compass direction at the n th step, and Z_0 is the starting position and $\Psi_0 = 0$. We then follow Gurarie et al. by decomposing speed and turning angle components into the orthogonal vectors persistence velocity

$$\vec{V}^p = \{V_n^p\}_{n=1}^{l_{ij}} = \{V_n \cos(\Psi_n)\}_{n=1}^{l_{ij}},$$

and turning velocity.

$$\vec{V}^t = \{V_n^t\}_{n=1}^{l_{ij}} = \{V_n \sin(\Psi_n)\}_{n=1}^{l_{ij}}.$$

As Gurarie et al. note, this captures tendencies to head in the same direction (\vec{V}^p) versus heading in an orthogonal direction (\vec{V}^t ; see Fig. 1). Gurarie et al. show that these vectors are well modeled by stationary, Gaussian, autoregressive time series models.

The persistence metric is the autocorrelation ρ of a Weiner process drawing on the normal distribution. In particular, for the j th trial of the i th participant we let the vector \vec{W} consist of l_{ij} equally spaced ($(t_k - t_{k-1}) = \text{constant}$) observations normalized to $\mu = E[\vec{W}] = 0$ and $\sigma = \text{Var}[\vec{W}] = 1$. We then assume that the process is governed by $W_k = \rho W_{k-1} + \epsilon_k, k = 1, \dots, l_{ij}$, where $\rho = \text{Corr}[W_k, W_{k-1}]$ is the autocorrelation and ϵ_k is the error term. We define the likelihood function to be

$$L(\rho | \vec{W}) = \prod_{k=1}^{l_{ij}} f(W_k | W_{k-1}) \stackrel{\text{def}}{=} \prod_{k=1}^{l_{ij}} \frac{1}{\sqrt{2\pi(1-\rho^2)}} \exp\left(-\frac{(W_k - \rho W_{k-1})^2}{2-2\rho^2}\right),$$

which can be used to find the autocorrelation for the j th trial of the i th participant: $\rho_{ij} = \text{argmax}_{0 \leq \rho \leq 1} LL(\rho, \vec{W}) \stackrel{\text{def}}{=} \text{argmax}_{0 \leq \rho \leq 1} \ln(L(\rho, \vec{W}))$. Therefore, each trial is assigned a correlation that was then compared among groups (e.g. Binge vs. Non Binge, see Fig. 2 for two examples of the LL function for two different trajectories evaluated over a range of values of ρ) via standard repeated measures ANOVA.

The homeward segment was defined as all movement after the participant initiated movement away from the Velcro tape and concluded when his/her hand stopped. Several measures were used to quantify performance on the homeward segment. First, accuracy of direction

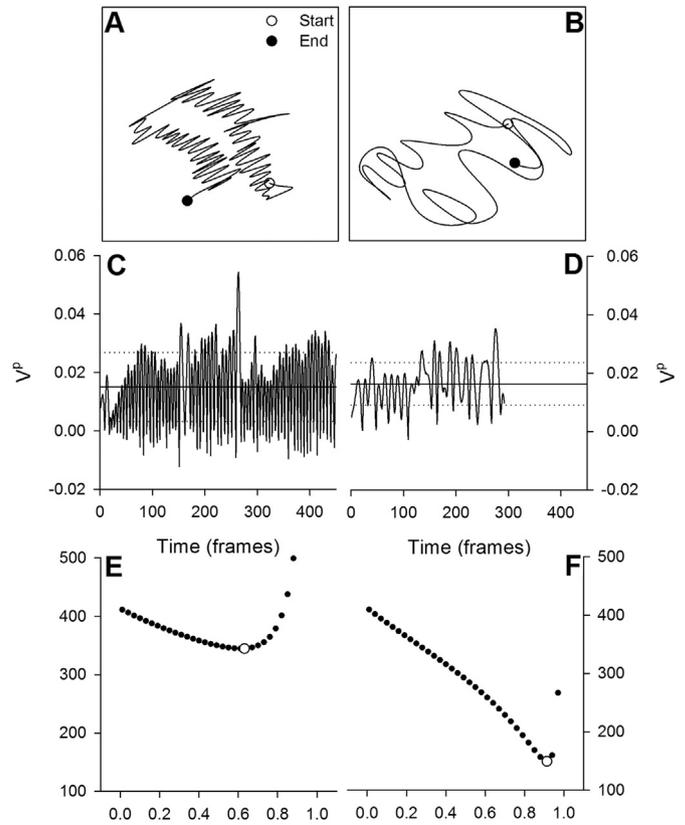


Fig. 2. Outward segment movement characteristics are presented for NB (left column) and BD (right column) participants. Path topographies (panels A & B) are plotted for representative paths. The persistence velocity as a function of time is shown for both representative outward paths (panels C & D). The solid and dashed horizontal lines indicate the mean and mean \pm the standard deviation of the persistence velocity over the entire outward trajectory. Note that mean persistence velocity and, to an extent, the corresponding standard deviation are very similar (0.0131 ± 0.0119 and 0.0138 ± 0.0095 , for panels C and D, respectively). Panels E and F show the negative of the Log Likelihood function ($LL(\rho, \vec{W})$) for the trajectory evaluated as a function of the autocorrelation parameter, ρ , and the value that minimizes this quantity is shown by the white dot. The differences in path characteristics are captured by the much larger difference in ρ compared with the mean or standard deviation of velocity.

estimation was indexed by calculating heading error for each trip. Heading error was defined as the angle subtended by the start location, location of the Velcro tape, and peak speed on the homeward segment. Next, accuracy of distance estimation was indexed by calculating the absolute distance error for each trip. The absolute distance error was calculated by finding the absolute difference between the distance traveled and the distance between the start point and the Velcro tape. Finally, the maximum moment-to-moment speed was recorded for each homeward segment.

Several measures were used to characterize performance on the bead maze task. Time elapsed, distance traveled, and maximum moment-to-moment speed were recorded for each trial. During place training, performance was averaged into blocks of five trials. During matching-to-place testing, performance was averaged into two blocks. Block one averaged performance across the first trials with the new Velcro position. Block two averaged performance across the second trials with the new Velcro position.

3. Results

3.1. AUDIT

Table 1 presents the group response characteristics to the Hazardous, Dependence, and Harmful categories on the AUDIT. Groups significantly

Table 1
Participant characteristics.

Group	Hazardous alcohol use**	Dependence symptoms	Harmful alcohol use*
NB (4F,3M)	0.43(0.16)	0.10(0.10)	0.00(0.00)
BD (5F,4M)	2.37(0.09)	0.41(0.18)	0.33(0.14)

Note: Means and Standard Error of the Mean are provided for AUDIT response categories.

* Indicates $p < 0.05$.

** Indicates $p < 0.001$.

differed in their responses to the Hazardous [T (14) = -11.431, $p < 0.001$, $d = 5.58$] and Harmful [T (14) = -2.143, $p = 0.05$, $d = 1.15$] response categories. The responses elicited by the BD group were consistent with the National Survey on Drug Use and Health [49] definition of binge drinking behavior (i.e., 5 or more alcoholic drinks on the same occasion, at least once a month). The significant difference observed on the Harmful category was related to an elevated number of reported incidents of blacking out. Groups did not significantly differ in their responses to the Dependence category.

3.2. Dead reckoning task

Group differences in performance were observed during the dead reckoning task. Fig. 2 plots several characteristics of outward segments from representative NB and BD participants. Groups did not differ in outward segment path circuitry; however, variability in this characteristic was observed across participants' 12 trials. Similar to previous work examining the influence of outward segment path circuitry on homeward segment performance [54], each participant's trials were sorted into three sets of decreasingly less complex outward segments: High circuitous (M: 0.02; SD: 0.01), Medium circuitous (M: 0.08; SD: 0.05), and Low circuitous (M: 0.28; SD: 0.16). A 2 (group) \times 3 (path circuitry) mixed ANOVA was conducted on all dependent measures.

3.2.1. Outward segment

In general, performance on the outward segment was similar between groups (see Fig. 3). The ANOVA conducted on average time revealed a significant effect of path circuitry [$F(2, 28) = 63.17$, $p < 0.001$, $\eta_p^2 = 0.819$]. Groups did not significantly differ in time to find the Velcro tape [$F(1, 14) = 1.13$, $p = 0.305$, $\eta_p^2 = 0.075$]. The Group \times Path circuitry interaction was not significant [$F(2, 28) = 1.24$, $p = 0.303$, $\eta_p^2 = 0.082$]. The ANOVA conducted on the average distance traveled revealed a significant effect of path circuitry [$F(2, 28) = 67.52$, $p < 0.001$, $\eta_p^2 = 0.828$]. Groups did not significantly differ in distance traveled while searching for the Velcro tape [$F(1, 14) = 0.370$, $p = 0.553$, $\eta_p^2 = 0.026$]. The Group \times Path circuitry interaction was not significant [$F(2, 28) = 1.67$, $p = 0.207$, $\eta_p^2 = 0.107$]. The ANOVA conducted on the average peak speed revealed a significant effect of path circuitry [$F(2, 28) = 26.00$, $p < 0.001$, $\eta_p^2 = 0.650$]. Groups did not significantly differ in peak speed while searching for the Velcro tape [$F(1, 14) = 0.317$, $p = 0.582$, $\eta_p^2 = 0.022$]. The Group \times Path circuitry interaction was not significant [$F(2, 28) = 1.40$, $p = 0.262$, $\eta_p^2 = 0.091$]. These results demonstrate that as the outward segment became less circuitous, participants took less time, followed shorter paths, and exhibited lower peak speeds while searching for the Velcro tape. These differences were not related to group membership.

One exception to the previous pattern of results was observed during the kinematic analysis of movement organization. Recall that the persistence (\bar{V}^p) metric indexes the tendency to head in the same direction; whereas the turning (\bar{V}^t) metric indexes the tendency to head in an orthogonal direction [19]. Significant differences in the persistence metric were observed on the outward segment (see bottom right panel of Fig. 3). The ANOVA conducted on the average persistence metric revealed a significant effect of path circuitry [$F(2, 28) = 25.78$, $p < 0.001$, $\eta_p^2 = 0.684$] and a significant Group \times Path circuitry interaction

[$F(2, 28) = 11.10$, $p < 0.001$, $\eta_p^2 = 0.442$]. The main effect of group was not significant [$F(1, 14) = 2.56$, $p = 0.132$, $\eta_p^2 = 0.155$]. Post hoc analysis revealed that the BD group only had significantly higher persistence values when outward segments were highly circuitous (LSD $p < 0.05$). In contrast, no significant differences were observed in the turning metric. The ANOVA conducted on the average turning metric failed to reveal a significant effect of path circuitry [$F(2, 28) = 2.458$, $p = 0.104$, $\eta_p^2 = 0.149$], group [$F(1, 14) = 2.490$, $p = 0.137$, $\eta_p^2 = 0.151$], and Group \times Path circuitry interaction [$F(2, 28) = 0.713$, $p = 0.499$, $\eta_p^2 = 0.048$]. These results demonstrated that BD participants exhibited changes in movement organization selective to the persistence metric relative to the NB group when the paths were highly circuitous.

3.2.2. Homeward segment

A history of adolescent binge drinking was associated with less accurate performance on the homeward segment (see Fig. 4). The ANOVA conducted on average heading error (top panel Fig. 5) revealed a significant effect of path circuitry [$F(2, 28) = 13.79$, $p < 0.001$, $\eta_p^2 = 0.496$], group [$F(1, 14) = 11.98$, $p < 0.005$, $\eta_p^2 = 0.461$], and Group \times Path circuitry interaction [$F(2, 28) = 8.47$, $p = 0.001$, $\eta_p^2 = 0.377$]. Post hoc analysis revealed that the BD group only had a significantly higher homeward segment heading error when outward segments were highly circuitous (LSD, $p < 0.05$). The ANOVA conducted on average absolute distance error (middle panel Fig. 5) revealed a significant effect of path circuitry [$F(2, 28) = 4.72$, $p < 0.05$, $\eta_p^2 = 0.252$] and group [$F(1, 14) = 6.89$, $p < 0.05$, $\eta_p^2 = 0.330$]; however, the Group \times Path circuitry interaction [$F(2, 28) = 1.44$, $p = 0.255$, $\eta_p^2 = 0.093$] was not significant. The ANOVA conducted on average peak speed (bottom panel Fig. 5) revealed a significant effect of path circuitry [$F(2, 28) = 4.80$, $p < 0.05$, $\eta_p^2 = 0.255$]; however, neither the effect of group [$F(1, 14) = 0.23$, $p = 0.64$, $\eta_p^2 = 0.016$] nor the Group \times Path circuitry interaction [$F(2,$

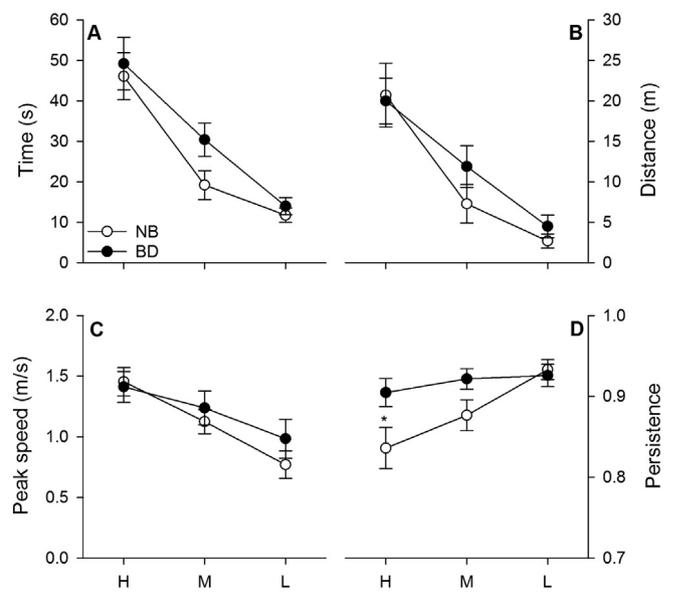


Fig. 3. Average outward segment time to find the Velcro tape (A), distance traveled (B), peak speed (C), and persistence (D) is plotted for each group's high, middle, and low categories of path circuitry. * $p < 0.05$.

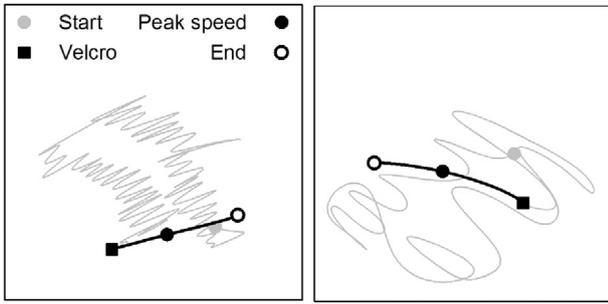


Fig. 4. Homeward segments are plotted for the representative NB (left hand panel) and BD (right hand panel) trips. The black square represents the location of the Velcro tape, the black circle represents the location of the homeward segment peak speed, and the white circle represents the end of the homeward segment. The gray circle and line represent the outward segment start position and path, respectively.

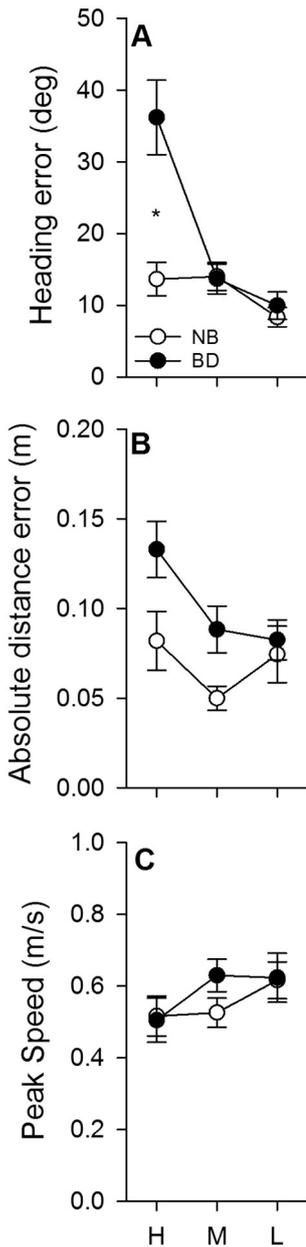


Fig. 5. Homeward segment average heading error (panel A), absolute distance error (panel B), and peak speed (panel C) are plotted for each group. These characteristics are plotted relative to high (H), middle (M), and low (L) levels of outward segment path circuituity. * $p < 0.05$.

28) = 1.52, $p = 0.236$, $\eta_p^2 = 0.098$] were significant. The BD group was significantly less accurate in estimating direction and distance to the start location, relative to the NB group. Direction and distance estimation improved with more direct searching paths. These improved direction and distance estimations were associated with an increase in peak speed.

3.3. Bead maze task - place training

Both groups became more accurate in locating the Velcro tape across training trials (see Fig. 6). The ANOVA conducted on average time to locate the Velcro tape revealed a significant effect of block [$F(3, 42) = 34.90$, $p < 0.001$, $\eta_p^2 = 0.714$] and Group \times Block interaction [$F(3, 42) = 5.48$, $p < 0.005$, $\eta_p^2 = 0.282$]. The main effect of group [$F(1, 14) = 3.25$, $p = 0.09$, $\eta_p^2 = 0.188$] was not significant. Post hoc analysis revealed that group differences in time to find the Velcro tape was restricted to the first block (LSD, $p < 0.05$). The ANOVA conducted on average distance traveled while searching for the Velcro tape revealed a significant effect of block [$F(3, 42) = 46.88$, $p < 0.001$, $\eta_p^2 = 0.770$] and Group \times Block interaction [$F(3, 42) = 6.46$, $p < 0.005$, $\eta_p^2 = 0.316$]. The main effect of group [$F(1, 14) = 2.80$, $p = 0.117$, $\eta_p^2 = 0.167$] was not significant. Post hoc analysis revealed that group differences in travel distance while searching for the Velcro tape was restricted to the first block (LSD, $p < 0.05$). The ANOVA conducted on the average peak speed revealed a significant effect of block [$F(3, 42) = 12.25$, $p < 0.001$, $\eta_p^2 = 0.467$]; however, neither the main effect of group [$F(1, 14) = 0.244$, $p = 0.629$, $\eta_p^2 = 0.017$] nor the Group \times Block interaction [$F(3, 42) = 2.75$, $p = 0.054$, $\eta_p^2 = 0.164$] were significant. These results demonstrate that the group differences in performance were restricted to early place training trials.

3.4. Bead maze task - matching-to-place

Both groups became more accurate in locating the Velcro tape from the first block to the second block (see Fig. 7). The ANOVA conducted on average time to locate the Velcro tape revealed a significant effect of block [$F(1, 14) = 10.11$, $p < 0.01$, $\eta_p^2 = 0.419$]; however, neither group [$F(1, 14) = 0.005$, $p = 0.942$, $\eta_p^2 = 0.000$] nor Group \times Block interaction [$F(1, 14) = 3.70$, $p = 0.08$, $\eta_p^2 = 0.209$] were significant.

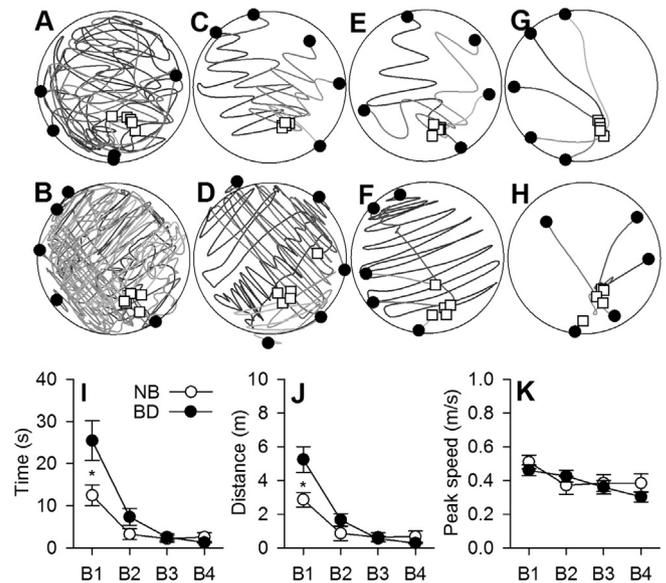


Fig. 6. Start locations (black circle), paths followed (lines), and stop locations (white squares) are plotted for a representative NB (A, C, E, G) and BD (B, D, F, H) participant across the four blocks of place training trials. Average time to find the Velcro tape (panel I), distance traveled (panel J), and peak speed (panel K) are plotted for both groups across place training blocks. * $p < 0.05$.

The ANOVA conducted on the average distance traveled revealed a significant effect of block [$F(1, 14) = 7.29, p < 0.05, \eta_p^2 = 0.342$]; however, neither group [$F(1, 14) = 0.013, p = 0.912, \eta_p^2 = 0.001$] nor Group \times Block interaction [$F(1, 14) = 3.50, p = 0.082, \eta_p^2 = 0.200$] were significant. The ANOVA conducted on average peak speed did not reveal a significant effect of block [$F(1, 14) = 4.07, p = 0.063, \eta_p^2 = 0.225$], group [$F(1, 14) = 0.061, p = 0.808, \eta_p^2 = 0.0004$], or Group \times Block interaction [$F(1, 14) = 1.83, p = 0.198, \eta_p^2 = 0.115$]. These results are consistent with both groups exhibiting similar levels of improved performance across blocks.

4. Discussion

This study examined the influence of adolescent binge drinking on three manipulatory scale spatial tasks. Group differences were observed on several aspects of performance across the spatial tasks. First, differences in movement organization were observed on the outward segment of highly circuitous paths during the dead reckoning task. To be specific, participants with a history of binge drinking exhibited paths with higher levels of persistence. Next, groups differed in estimating direction and distance to the start location during the dead reckoning task. A history of binge drinking was associated with less accurate direction and distance estimations. The impaired direction estimation was most pronounced following highly circuitous outward segments. Finally, performance varied between groups early in the acquisition of a place response in the bead maze. During the first block of five trials, participants with a history of binge drinking required more time and traveled longer distances while searching for the hidden Velcro tape. The following sections discuss potential factors that could mediate the observed differences in performance between groups.

4.1. Spatial orientation deficits

Spatial orientation can be derived from environmental and self-movement cues. Participants were restricted to using self-movement cues during the dead reckoning task. The pattern of group differences

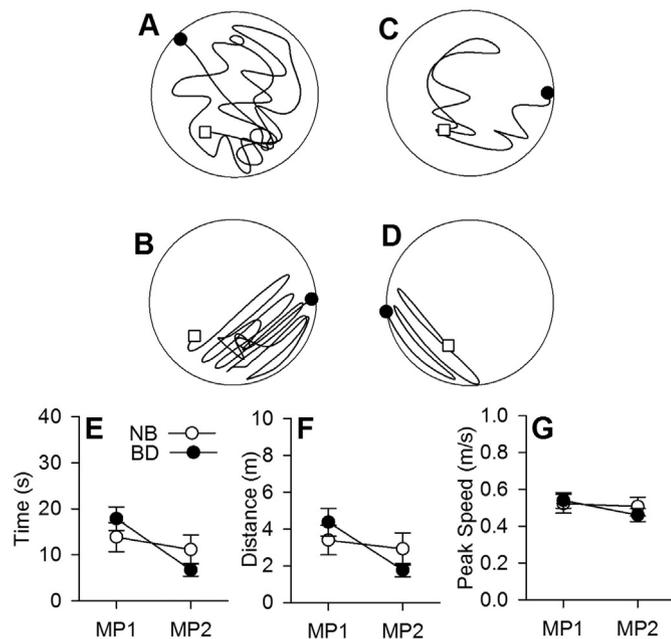


Fig. 7. Start locations (black circle), paths followed (lines), and stop locations (white squares) are plotted for the first (A, B) and second (C, D) trials of matching-to-place testing for a representative ND (A, C) and BD (B, D) participants. The average time to find the Velcro tape (panel E), distance traveled (panel F), and peak speed (panel G) are plotted for both groups collapsed across the first and second trials with the new Velcro tape position.

observed on the manipulatory scale dead reckoning tasks is consistent with selective impairment in self-movement cue processing. Specifically, participants with a history of adolescent binge drinking were less accurate in estimating direction and distance when restricted to using self-movement cues. Dead reckoning, or using self-movement cues to estimate direction and distance, has been posited to depend on multiple stages of information processing [26]. Impairments in one or multiple stages of self-movement cue processing may have contributed to the increase in direction and distance errors observed in participants with a history of binge drinking.

One source of dead reckoning error reflects a decrease in the accuracy of detecting self-movement cues while updating the representation of current position [16,21]. Detection of changes in heading and translations are most accurate if they occurred sequentially rather than simultaneously. Previous work has shown that simultaneous changes in heading during translations on an outward segment were associated with the disruptions in direction estimation [52,54]. In the current study, the parameter of persistence [19] was applied to describe the movement organization observed on the outward segment. Participants with a history of binge drinking exhibited higher persistence values on highly circuitous paths. This difference in movement organization may have attenuated the precision of updating the representation of the current position; therefore, estimating direction and distance to the refuge was less accurate.

Another possible source of error in self-movement cue processing has been attributed to a stepwise decay of the representation of the current position, or leaky integration [20,24]. In general, as the representation of the start position is updated with self-movement cues, there is a progressive reduction or leak in the values that represent direction and distance. Observing that participants increasingly underestimate distance as the distance to the start position increases has been taken as evidence for leaky integration as a basis for errors in distance estimation [20,24]. Differential rates of leaky integration may have contributed to performance on the homeward segment observed in the current study. Highly circuitous outward segments (integration over longer distances) were associated with larger heading and distance errors. Interestingly, while this effect was most evident in the heading error in participants with a history of binge drinking, a similar magnitude effect was not observed in distance error. These results are consistent with behavioral studies demonstrating that direction and distance estimations are derived from distinct processing systems [14]. It is possible that a history of binge drinking may be more associated with increased leaky integration related to direction estimation; however, procedural differences may limit this conclusion. For example, in the current study, the size of the table top restricted the range of distances between the start location and Velcro tape relative to the range of distances used in previous studies [20,24]. This restricted range may have limited the ability to see larger distance errors in participants with a history of binge drinking subsequent to highly circuitous outward segments. Future work using virtual or ambulatory scale dead reckoning tasks in participants with a history of binge drinking may provide insight to the selectivity of the processing deficit.

Multiple sources of information were available to guide performance in the bead maze tasks. Although participants had access to environmental and self-movement cues throughout place training and matching-to-place trials, group differences were restricted to the first block of place learning trials. Early in training, self-movement cue processing provides an important bridging strategy for encoding relationships between landmarks [57]. Previous work has shown that disruptions in self-movement cue processing attenuate learning relationships between environmental cues [6,43,48]. Therefore, it is possible that group differences in locating the Velcro tape in the first block of place training were mediated by impaired self-movement cue processing associated with a history of binge drinking. In contrast, performance on subsequent blocks of place training did not differ between groups. This demonstrates, given sufficient training, both groups were

equivalent in encoding direction and distance to a fixed location. In general, similar results have been observed in human and rodent studies examining the relationship between an adolescent binge drinking pattern of alcohol consumption and place learning. For example, a history of binge drinking in adolescent humans was not observed to influence place learning in a virtual water maze task [46]. Rodent models of adolescent binge drinking have failed to disrupt performance during place training in the water maze task; however, disruptions in performance were observed during platform reversal trials [8]. There are multiple factors that may have contributed to the absence of this effect during matching-to-place testing in the current study. For example, the difference in scale between the rodent and human spatial tasks may have fostered a differential tendency to perseverate at the former goal location. It is possible that shifting searching strategies at the human manipulatory scale is easier relative to the scale of a rodent in the water maze. The level of alcohol exposure is another potential difference between human and rodent studies. In the current study this level may have been sufficient to disrupt self-movement cue processing in the absence of environmental cues, but our bead maze data suggest that the presence of additional environmental cues provides a compensatory mechanism to correct for accumulating errors. Higher levels of alcohol exposure in rodent models may preclude this compensatory mechanism. Future work examining performance of human participants with higher levels of alcohol exposure would provide insight to this possibility.

The performance of participants with a history of binge drinking is consistent with impaired self-movement cue processing and spared use of environmental cues. Although this pattern of impaired and spared cue use parallels observations in the rodent literature (see Section 4.3. Neurobiology of spatial orientation deficits), factors may have influenced group differences in performance.

4.2. Other contributing factors

Participants with a history of adolescent binge drinking likely differ on a number of factors. Differences in cognitive function could be one factor that may have influenced performance in the current study. Although no group differences were observed on the MMSE in the current study, more subtle cognitive deficits may have influenced performance. First, previous work has demonstrated an association between a history of binge drinking and impaired episodic memory [34]. Interestingly, rodent dead reckoning has been posited to be homologous to episodic memory in humans [59]. The results of the current study provide further evidence of a potential relationship between dead reckoning and episodic memory. Second, disruptions in executive function have been observed in participants with a history of adolescent binge drinking [34]. These deficits reflect an increase in perseverative errors on the Self-Ordered Pointing Task. This tendency to continue a response pattern may be related to the group difference in movement organization observed on the outward segment. Finally, adolescent binge drinking has been associated with changes in brain activity elicited by working memory based tasks ([10,11,47]). The trial-unique or online nature of dead reckoning would likely depend on working memory systems. In contrast, group differences in errors or latency are not typically observed on these working memory tasks ([10,11,47,34]). Therefore, it is possible that the performance deficits reported in the current study are reflective of the sensitivity of the behavioral tasks to detect subtle working memory deficits. Further work is needed to evaluate the extent that dead reckoning depends on these different cognitive domains.

Both motivational and motor coordination factors could have contributed to group differences in performance. First, adolescents with a history of binge drinking may have been less motivated to engage with the spatial tasks. For example, this differential level of motivation could have translated to longer searching times. During the dead reckoning task, longer outward segment times would result in more challenging self-movement cue processing episodes; thereby less accurate

direction and distance estimation. Observing that groups exhibited equivalent search times and traveled distances to find the Velcro tape during the dead reckoning task discounts the role of motivational factors. Next, generating the homeward segment depends on fine motor control. Group differences in fine motor control may have limited individuals with a history of adolescent binge drinking from accurately estimating direction and distance in the spatial tasks. Peak speed is one aspect of performance that would likely be sensitive to impaired fine motor control. The absence of group differences in peak speed in either spatial task limits the role of motor coordination in mediating disruptions in performance. These results are evidence that neither task engagement nor motor coordination were factors mediating group differences in direction and distance estimation during the dead reckoning task.

4.3. Neurobiology of spatial orientation deficits

Spatial orientation depends on multiple neural systems. Disruption in any one neural system will produce a specific pattern of spatial orientation deficits, or topographical disorientation [1]. Binge drinking has been shown to influence a network of brain structures that have been implicated in self-movement cue processing. The hippocampus is one structure within this network in which a binge drinking pattern of alcohol use has been shown to influence function. For example, a history of adolescent binge drinking has been shown to alter hippocampal activation in human participants while engaged in a verbal encoding task [41]. In addition, changes in hippocampal anatomy have been observed in nonhuman primates [50] and rodents [7–9]. A growing number of studies have implicated a role for the hippocampus in processing self-movement cues. First, humans with damage to the right hippocampus are impaired in an ambulatory scale dead reckoning task [39]. Next, human participants engaging in a virtual dead reckoning task exhibit hippocampal activation that is related to task accuracy [60]. Finally, complete hippocampal lesions [27], selective cholinergic deafferentation [30], or selective GABAergic deafferentation [23,29] have been shown to impair performance in a food hoarding task when restricted to using self-movement cues. These studies provide evidence that disruptions in hippocampal function may contribute to the impaired direction and distance estimation observed in the current study; however, the hippocampus might not be the only structure impacted by binge drinking.

The entorhinal cortex may also contribute to the relationship between binge drinking and self-movement cue processing. As of yet, no human studies have observed a relationship between binge drinking and entorhinal function; however, several rodent studies have demonstrated increased markers of neurodegeneration in the entorhinal cortex subsequent to models of binge drinking alcohol exposure [7,9,12]. Several studies have demonstrated a role for the entorhinal cortex in processing self-movement cues [38,51,56]. Recent work has suggested that the role of the entorhinal cortex may be more selective to deriving distance estimates from self-movement cues [56]. Therefore, it is possible that impaired distance estimation associated with a history of binge drinking may depend in part on attenuated self-movement cue processing in the entorhinal cortex. Further work is needed in both human and rodent subjects to better characterize the role of the entorhinal cortex in spatial deficits associated with a history of binge drinking.

The role of the frontal cortex in self-movement cue processing is less well characterized. For example, human imaging work has demonstrated medial prefrontal cortical activation during the outward segment of a virtual dead reckoning task [60]. In contrast, medial frontal lesions spare performance of rats in the food-hoarding tasks under dark conditions [58]. Nonetheless, a history of binge drinking in adolescent participants has been associated with reductions in prefrontal cortex activation during a visual working memory task [11]. In addition, rats exposed to the 4 day binge ethanol treatment exhibited increased neurodegeneration in frontal cortical regions [9,12]. Considering these observations, it is

possible that the frontal cortex may be involved in the structured encoding or segmented generation of self-movement cues. As discussed in the previous section, behavior on the outward segment is typically segmented into stops and progressions, with most of the changes in heading occurring during stops. In the current study, group differences on the outward segment were limited to the persistence measure on highly circuitous paths. Failure to segment movements (indicated by higher persistence values) limits the gain associated with detecting changes in direction and affords a greater accumulation of error. This effect is compounded as path length increases. Therefore, it is possible that the frontal cortex mediates the relationship between binge drinking and impaired self-movement cue processing by disrupting movement segmentation. Future work systematically varying outward segment movement segmentation (i.e., triangle completion task) may provide further evidence for the role of the frontal cortex in processing self-movement cues.

4.4. Self-movement cue processing across scales

Access to self-movement cues varies across scales of human movement. At the ambulatory scale, blindfold participants have access to vestibular, proprioceptive, and motor efferent copies; whereas participants are restricted to proprioceptive and motor efferent copies at the manipulatory scale. In addition, virtual reality restricts participants to optic flow. Although each scale of movement is associated with a different set of self-movement cues, the processing demands of dead reckoning do not change across scales. Therefore it is likely that dead reckoning based self-movement cue processing is a centralized process that is independent of scale.

Factors that influence performance on dead reckoning tasks provide evidence consistent with this centralized view of self-movement cue processing. When presented with equivalent patterns of self-movement cues across varied scales of movement, similar distance error profiles have been observed. Specifically, participants exhibit a tendency to overestimate distance after following paths with short Euclidian distances and underestimate distance after following paths with long Euclidian distances. This relationship between Euclidian distance and distance estimation has been observed in human participants at the ambulatory [26], manipulatory [21], and virtual [20] scales of movement. These observations are consistent with self-movement cue based distance estimates derived from processing that is centralized.

Outward segment movement segmentation has been shown to influence accuracy of self-movement cue based direction estimation across multiple scales of movement. In general, outward segment movement can be characterized as a sequence of relatively fast non-circuitous progressions punctuated by periods of relatively slow movement and high path curvature. Decreases in the strength of relationship between linear speeds and path curvature have been shown to be associated with more error in direction estimation at the ambulatory [52] and manipulatory [54] scales. These observations are consistent with centralized processing of self-movement cues to estimate direction; however, one difference in direction estimation has been observed across scales of movement. Ambulatory scale triangle completion tasks elicit direction estimation bias that varies as function of the angle experienced on the outward segment [26]. In contrast, no change in directional bias was observed across angles of varied magnitude in a manipulatory scale triangle completion task [21]. It is possible that the small scale of movement (4, 8, 12 cm) was not sufficient to elicit differences in movement segmentation across angles of varied magnitude. Therefore a directional bias was not observed as a function of the angle experienced on the outward segment. Results from an experiment using longer triangle legs (25 cm) are consistent with this view [54]. Specifically, increasing the angle between triangle legs increased the strength of movement segmentation and was associated with decreases in heading error. These observations demonstrate a relationship between movement segmentation and direction estimation that is

conserved across scales of movement. Dead reckoning based distance and direction estimation depends on centralized processing of self-movement cues that is independent of movement scale.

4.5. Conclusions

The current study adds to a growing literature demonstrating a role for the hippocampus, entorhinal cortex, and medial prefrontal cortex in processing self-movement cues. This network of brain structures continues to develop late into adolescence and is sensitive to the effects of a binge drinking pattern of alcohol consumption. The quasi-experimental design of the study precludes inferring a causal relationship between adolescent binge drinking and self-movement cue processing deficits; however, these spatial tasks are analogues to rodent spatial tasks that have previously been shown to detect deficits in self-movement cue processing [23,27,30]. Given the relatively small sample size used in the current study, there may be concern regarding the generalizability of the current study's results. However, the selectivity of the behavioral deficits combined with the magnitude of group differences (considered large effects for partial eta squared) provide compelling evidence for an association between a history of adolescent binge drinking and impaired self-movement cue processing. Further work is needed to examine whether these observations extend to navigational tasks in humans at the ambulatory and virtual scales. This work will establish a foundation to evaluate rodent models of adolescent binge drinking and may provide insight to the neural basis of this relationship.

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