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RAPID COMMUNICATION

Novel Acoustic Stimuli can Alter Locomotor Speed to Hippocampal Theta Relationship

Lauren L. Long,[1] James R. Hinman,[1] Chi-Ming A. Chen,[1] Ian H. Stevenson,[1] Heather L. Read,[1,2] Monty A. Escabi,[1,2,3] and James J. Chrobak[1]

ABSTRACT: Hippocampal theta (6–12 Hz) plays a critical role in synchronizing the discharge of action potentials, ultimately orchestrating individual neurons into large-scale ensembles. Alterations in theta dynamics may reflect variations in sensorimotor integration, the flow of sensory input, and/or cognitive processing. Previously we have investigated septotemporal variation in the locomotor speed to theta amplitude relationship as well as how that relationship is systematically altered as a function of novel, physical space. In the present study, we ask, beyond physical space, whether persistent and passive sound delivery can alter septal theta local field potential rhythm dynamics. Results indicate pronounced alterations in the slope of the speed to theta amplitude relationship as a function of sound presentation and location. Further, this reduction in slope habituates across days. The current findings highlight that moment-to-moment alterations in theta amplitude is a rich dynamic index that is quantitatively related to both alterations in motor behavior and sensory experience. The implications of these phenomena are discussed with respect to emergent cognitive functions subserved by hippocampal circuits. © 2014 Wiley Periodicals, Inc.

KEY WORDS: locomotion; oscillations; field potential; auditory; rat

The hippocampal theta rhythm has been linked to cognitive operations across several species (Winson, 1978; Hasselmo, 2005; Ulanovsky and Moss, 2007; Jeewajee et al., 2008; Montgomery et al., 2009) where its dynamics strongly correlate with the strength of encoding as indicated by subsequent memory performance (Sederberg et al., 2003; Rizzuto et al., 2003; Jutras et al., 2010; Nyhus and Curran, 2010). Traditionally, instantaneous variations in the theta signal are associated with alterations in ongoing sensorimotor integration, specifically locomotor speed of the rodent (Teitelbaum and McFarland, 1971; McFarland et al., 1975; Bland and Oddie, 2001). Although locomotor indices have been the focus of variations in hippocampal theta signal (Teitelbaum and McFarland, 1971; McFarland et al., 1975; Bland and Oddie, 2001), there exists a different, albeit related, literature linking theta rhythm alterations to visual (Givens, 1996), tactile (Itskov et al., 2011), odor (Wood et al., 1999; Wiebe and Stäubli, 1999; Martin et al., 2007, Komorowski et al., 2009; Gourévitch et al., 2010), gustatory (Ho et al., 2011), and auditory cues (Redding, 1967; Parmeggiani and Rapisarda, 1969; Parmeggiani et al., 1982), with a sparsity of reports linking the effect of sensory variables on locomotor indices. Investigations into the relationship between the hippocampus and auditory stimuli reveal sensitivity of hippocampal single units to sound stimuli (Tamura et al., 1992; Vinnik et al., 2012), especially when the sound stimulus is behaviorally relevant or attended to (McEchron et al., 2003; Kropotov et al., 2000; Liberman et al., 2009; Itskov et al., 2012). A different body of work examines the effect of sensory variables not only on single neurons, but on large-scale network activity, such as hippocampal theta oscillation (Liberman et al., 2009). Liberman et al. (2009) demonstrates that novel, time-varying auditory stimuli produce transient temporal phase correlations between the hippocampal theta rhythm and single neuron responses in the central nucleus of the inferior colliculus (Liberman et al., 2009). Altogether, these results suggest a correlation between theta power and the detection of novel, auditory stimuli.

While the aforementioned reports lack data with regards to how novel sensory (e.g., auditory) stimuli affect the prominent speed to hippocampal theta amplitude relationship, other studies highlight alterations in this relationship as a function of novel, physical space (Jeewajee et al., 2008; Kemere et al., 2013; Penley et al., 2013; Wells et al., 2013). The current study attempts to bridge these gaps in the literature and investigates how exposure to a passive (e.g., behaviorally irrelevant) and persistent novel auditory stimulus in a familiar physical environment affects the relationship between locomotor speed and hippocampal theta amplitude.

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[1] **Department of Psychology, University of Connecticut, Storrs, Connecticut;** [2] **Biomedical Engineering, University of Connecticut, Storrs, Connecticut;** [3] **Electrical and Computer Engineering University of Connecticut, Storrs, Connecticut.**

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Hinman JR is currently at Center for Memory and Brain, Department of Psychology, Boston University, Boston, MA, 02215.

*Correspondence to: James J. Chrobak, Department of Psychology, University of Connecticut, 406 Babbidge Rd U-1020, Storrs, CT 06269-1020. E-mail: james.chrobak@uconn.edu

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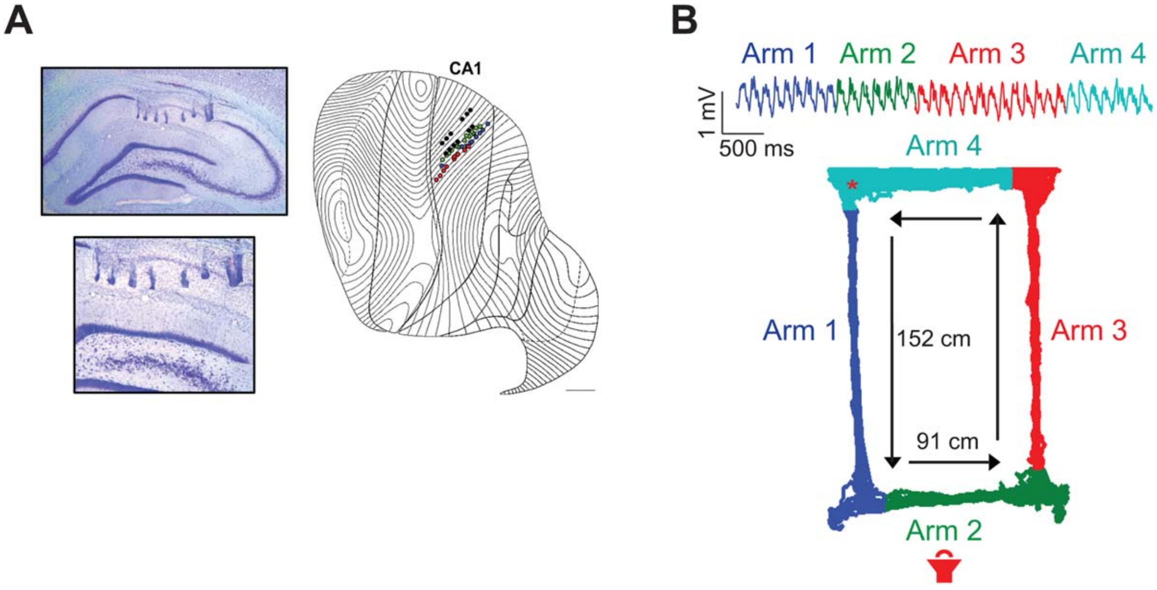

FIGURE 1. Methodological specifications. A. Representative photomicrographs of CA1 recording sites. Bottom photomicrograph is the same as top but close-up (20×). Flatmap representation of the hippocampal formation. Electrode placements are indicated as dots, where each color denotes one animal. B. Using a position threshold, the rectangular maze (152 × 91 cm^2) was discretized into four arms (arms 1–4; different colors). Animals were trained to run counter clockwise (arrows) and were rewarded in one corner of the maze (red asterisk; arm 4). A speaker was localized at the opposite end of the maze (red speaker cartoon; arm 2). Continuous representative theta traces are shown for each arm. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Overall, like novel physical space, we hypothesize that a novel and behaviorally irrelevant acoustic stimulus will not alter the slope of the speed-theta relationship, but will rather produce a parallel, positive shift of the speed-theta amplitude function, suggesting an overall increase in theta amplitude regardless of locomotor speed (but see Wells et al., 2013). Further, we hypothesize that this alteration in the relationship habituates across multiple sound exposures. Surprisingly, results indicate that persistent and passive presentation of a novel auditory stimulus decreased the slope of the speed to theta amplitude relationship, while in other cases, this relationship remained constant. Further, this diminished relationship habituated over subsequent sound presentations across days. Together, these results highlight the dynamic relationship between theta amplitude and locomotor speed as a function of novel sound presentation.

Four adult male Long Evans rats were used in this study. Four electrode arrays were constructed and yielded 16 electrodes per animal. During surgery (see Hinman et al., 2011; Penley et al., 2013), electrode arrays were chronically implanted and each array was positioned to target septal hippocampus using the following coordinates: AP: −3.0 to −4.0 mm; ML: 2.0–3.0 mm; DV: 2.0–3.0 mm relative to bregma. The current analyses included $n = 47$ electrodes across four animals. Animals were transcardially perfused with ice-cold saline followed by 4% paraformaldehyde in 0.1M phosphate buffer. Brains were sliced using a vibratome, mounted, and Nissl stained using thionin. Distances between electrodes were verified by placing each electrode position on a flatmap representation of the hippocampus (Swanson et al., 1978). Photomicrographs of electrode tracks were taken, digitized and prepared for presentation. Different colored dots represent electrode positions for each animal (Fig. 1A). It is important to note that there were no obvious proximo-distal differences in speed modulation of theta amplitude. Using a Neuralynx data acquisition system (Bozeman, MT), wide-band electrical activity was recorded (1–1894 Hz, with a sampling rate of 3787 Hz) and downsampled by a factor of six during offline analysis (631.3133 Hz). The raw signal was bandpass filtered between 6 and 12 Hz and the theta envelope was extracted as the Hilbert transform magnitude. Additionally, light emitting diodes attached to the headstage were tracked by a camera (33 Hz) located above the rectangular track in order to track the rats' position on the maze. The tracking data was up-sampled to 631.3133 Hz using a cubic spline interpolator in order to match the local field potential (LFP) data sampling rate. Speed was computed by taking the finite difference between successive tracking (position) samples, normalized by the sampling period, and followed by a low-pass filter (cutoff = 0.25 Hz) to minimize head movements and other movement related artifacts.

Rats were trained to run counter clockwise on a highly familiar (~ 3 months of exposure) rectangular track (152 × 91 cm^2) for a chocolate chip food reward located in one corner of the maze (red asterisk; Fig. 1B) and a speaker (Yamaha MSP5A, speaker schematic; Fig. 1B) at the opposite end. The speaker was elevated and set back from the maze as to not obstruct and confound the animals' view (30–40° above and 0.69 m away from Arm 2 of the maze; see Fig. 1B). The speaker output at 6 in. distance was flat (+/−7.5 dB) from 1 to 38 kHz). The sound was delivered continuously across all maze arms, but as the rat traversed the maze the rats' distance from the sound source varied. Using a position threshold, we discretized the rectangular track into four arms (Fig. 1B) in order to visualize the speed to theta amplitude relationship as a function of position (Fig. 1B). Representative theta traces are shown for each arm (Fig. 1B). Recordings consisted of two, 10-min sessions separated in time within a single day. During the first baseline session, the animals ran for a chocolate chip food reward. After the baseline session, the animal was placed in its home cage for 10 min. Then, the animal was placed back on the maze to complete the same behavioral task, but in the presence of broadband (1–38 kHz) white noise (Tucker Davis Technologies, Alachua FL; Yamaha MSP5) at 54–58 dB SPL (variable due to rats' distance from sound source; SPL for frequency above 1.0 kHz, which is the audible frequency range for rats) that was triggered at the onset of the recording session and played continuously to the animal as it traversed the rectangular maze. On day 2, animals received another sound presentation of the same stimulus.

The time-varying theta envelope was computed for each recording electrode. We then applied multiple regression analysis that included speed in order to assess the relationship between locomotor speed and theta amplitude. Thus, each electrode yielded a standardized regression coefficient (beta, β) that evaluated the linear association between speed and theta envelope (Cohen et al., 2003). Beta coefficients indicate how many standard deviations a measured variable (in this case theta amplitude) will change with a one standard deviation increase in a given explanatory variable (e.g., speed) and thus can be interpreted as representing the normalized slope of the function (Cohen et al., 2003; Cohen, 2008). Thus, beta coefficients describe which predictor variable has a greater effect on a given response variable, and each beta-value for a given electrode serves as parameters of the regression model that can be used to predict theta amplitude from locomotor speed (see Hinman et al., 2011; Long et al., 2014 for detailed analysis). One-way repeated measures ANOVAs were conducted to assess differences in baseline beta coefficients across four maze arms as well as the difference in beta coefficients for all arms as a function of three experimental sessions. All ANOVAs were followed by post hoc Tukey LSD tests. All data and statistical analyses were conducted with custom-written programs in MatLab or SPSS.

Regression lines for representative and simultaneously recorded electrode examples are plotted as a function of arm and recording session (Fig. 2A). The first presentation of passive sound sharply reduced the speed to theta amplitude relationship from baseline only on arm 2 (Fig. 2A; bottom, red line) and evidence habituation over subsequent sessions across days. The slope of the speed to theta amplitude relationship on all other arms remained consistent across recording sessions and days (Fig. 2A). These data suggest that novel and passive sound presentation initially reduces the relationship between motor variables and theta amplitude in a location specific manner and that repeated sound presentations can habituate this relationship across days.

Summary data support the above examples. The slope (β) of the speed to theta amplitude relationship was significantly reduced from baseline (no sound) to the novel sound session (day 1) only on the arm that was in closest proximity to the speaker, arm 2 (Fig. 2B; $F(1.63,74.91) = 227.41$, $P < 0.001$), where all three recording sessions significantly differed from each other (P values < 0.001, Tukey tests). A break down of the observed effect into the first and last half of the recordings reveals that the reduction in slope is pervasive throughout the entire recording session, where repeated sound presentation habituates this effect (Fig. 2B, bottom). R-squared values follow a similar trend as the beta coefficients. Variability explained by speed decreased from the baseline session to the novel sound session for arm 2, such that all three recording sessions significantly differed from each other (data not shown; $F(1.93,88.59) = 83.005$, $P < 0.001$). The current result suggests that when a novel sensory stimulus is present, speed is less predictive of theta amplitude. Overall, these data suggest that despite its omnipresence across arms, passive but novel sound presentation initially reduced the slope of the locomotor speed to theta amplitude relationship in a location specific manner such that multiple sound presentations can habituate this relationship. These findings indicate that the theta signal can carry information with regards to novelty, but appears to depend on the spatial location of that novel stimulus.

The relationship between speed and theta amplitude on arms 1 and 3 remained consistent within a day and across days (Fig. 2B; arm 1: $F(1.72,78.99) = 0.446$, $P = 0.612$; arm 3: $F(1.81,83.27) = 1.66$, $P = 0.198$). Moreover, the relationship between speed and theta amplitude differed across sessions on arm 4 (Fig. 2B; arm 4: $F(1.22,56.11) = 18.41$, $P < .001$) where differences could partially be attributed to food motivation, speed, or approach to food reward. Significant changes in the speed-theta amplitude relationship were observed between baseline and novel sound day 2 ($P < 0.001$, Tukey tests) as well as novel sound day 1 and novel sound day 2 ($P < 0.001$, Tukey tests). These results suggest that the speed to theta amplitude relationship can be altered (e.g., arm 2) and at the same time remain relatively similar (arms 1, 3) across sessions and days.

It is important to note that differences in maze arm length can result in different distributions of speed across arms. These potential differences led us to examine beta coefficients (β) for the slope of the speed to theta amplitude relationship across arms during baseline conditions. There were significant differences in beta coefficients across arms during the baseline session (Fig. 2B; $F(2,91.76) = 196.99$, $P < 0.001$). There were significant differences between arms 1 and 4 and all other arms ($P < 0.01$, Tukey tests). The only arms that were not different from each other were arms 2 and 3 ($P = 0.05$, Tukey tests). In order to understand how behavioral differences across arms, experimental session, and days could contribute to the current results, we pseudorandomly matched the speed distributions across all relevant parameters (arm, session, day) such that changes in slope cannot be a result of differences in running speed across arms, conditions, and days. For each animal we created three large cell arrays: one for speed, theta amplitude

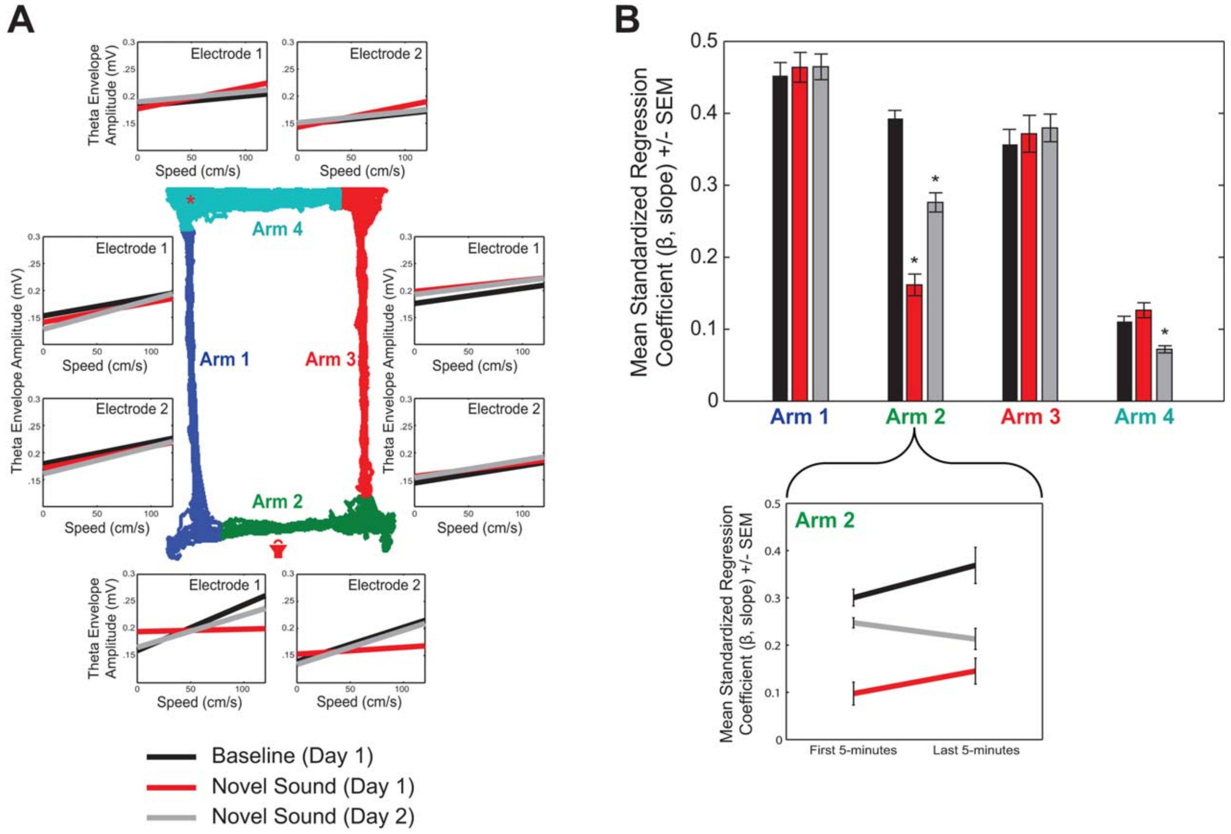

FIGURE 2. Speed and theta amplitude relationship as a function of novel sound. A. Regression lines plotted for simultaneously recorded electrodes (electrode 1; electrode 2) across all arms (1–4) for the baseline condition (no sound; day 1; black lines), the first presentation of the novel sound (day 1; red lines) and the second presentation of the same sound (day 2; light gray lines). As can be seen, the slope of the speed to theta amplitude relationship remains fairly consistent across conditions and days on some arms (1, 3, 4), but is highly dynamic on arm 2, which is the arm that is in closest proximity to the speaker (red speaker cartoon). B. Mean standardized regression coefficients (β, slope) +/− SEM are shown for the relationship between locomotor speed and theta amplitude and plotted as a function of arm (1–4) for the baseline condition on the first day (no sound; black) as well as the first presentation of the novel sound (day 1; red bar) and the second presentation of the same sound (day 2; light gray bar). As can be seen, there is a sharp reduction in the slope of the speed to theta amplitude relationship specific to arm 2 that habituates over days. The microstructure of this effect is denoted in the bottom part of B. As can be seen the effect is robust and fairly consistent over time (e.g., first 5 min vs. last 5 min of recordings). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

and time. A given cell array (e.g., speed), contained all speed trajectories across experimental sessions (2), days (2) all the while discretized by arm (4). Thus, for every animal each of the three cell arrays (speed, theta, and time) was 1 × 16 (2 × 2 × 4). These cell arrays were then fed into a custom written MatLab program that searched across all speed trajectories and found when the speeds matched (subsample approach). In this way, roughly half of the data was removed from the analysis. During points of matched speeds, timestamp information was also obtained such that it could be used to index theta amplitude values.

Importantly, when we matched speed distributions across arms, conditions, and days, there still exists a sharp reduction in the slope of the speed to theta amplitude relationship only on arm 2 ($F(1.80, 82.83) = 164.98$, $P < .001$). Moreover, there were significant differences across all experimental conditions on arm 2, as in the original (nonmatched) data (P values < 0.01, Tukey tests). Thus, the results do not reflect differences in locomotor speed of the animal across arms, conditions, and days, as all of these distributions were matched.

Historically, the theta LFP signal has often been considered limited as an information source and the speed to theta amplitude relationship, a constant. Here we show baseline variability in the speed to theta amplitude relationship and how environmental manipulations alter such relationships. These data support heterogeneity in the transformation of locomotor speed, likely reflecting either feedback from sensory circuits or direct input from motor control mechanisms (van Vugt et al., 2012). Thus, sensory input consequent to locomotion could modify hippocampal theta indices by multiple sources. First, medial thalamic nuclei (Vertes, 2006) are implicated in the initiation of movements (Vanderwolf, 1971). Further, vestibular input to the hippocampus is implicated in the stabilization of place cells (Russell et al., 2003) and spatial memory (Baek et al., 2010) such that vestibular disruptions lead to decreases in theta activity (Smith et al., 2005). Moreover, motor, proprioceptive, and visual information can indirectly reach the hippocampus through the entorhinal cortex and/or the medial septum (Smith et al., 2005). More than likely speed information reaches the hippocampus through the dynamic interaction of multiple sensory and motor systems.

The current results indicate that alterations in the sensory environment can profoundly modulate the dynamics of the speed to theta amplitude relationship. Further, our results reveal that presentation of a novel acoustic stimulus in a familiar environment modifies the speed to theta amplitude relationship in a location specific manner. Thus, the speed to theta amplitude relationship is a rich index: providing information with regards to not only novelty detection, but where that novel stimulus is located in space. Further, our data indicate that repeated experience with the acoustic stimulus habituates the previously altered speed to theta amplitude relationship. These results are consistent with previous findings that indicate significant alterations in the theta power to locomotor speed relationship during performance of cognitive (e.g., memory) tasks (Montgomery et al., 2009; Schmidt et al., 2013). Thus, these results suggest that alterations in sensory or contextual parameters may account for as much of the variability in theta indices as cognitive variables. Given previous and current results, it is important to identify and quantify such relationships as a means for understanding variability in theta indices as it relates to cognition.

Of particular importance is the comparison of alterations in the speed to theta amplitude relationship as a function of novel sensory variables (the current study) and novel, physical space (Jeewajee et al., 2008; Kemere et al., 2013; Penley et al., 2013; Wells et al., 2013). While both novel, their effects on the speed to theta amplitude relationship are strikingly dissimilar and important to consider. Penley et al., (2013) showed that novel physical space induces a parallel shift increase in the speed to theta amplitude function, suggesting an increase in the intercept and ultimately a DC (direct current) shift in theta amplitude (see Penley et al., 2013 Fig. 2). This shift may be provided by an increase in one or more modulatory inputs (e.g., cholinergic, noradrenergic) as indicated by an overall increase in theta amplitude independent of locomotor speed. In contrast, the current results reveal that sensory signals can exert a fundamentally different effect on the speed to theta amplitude relationship. Specifically, presentation of a passive, novel auditory stimulus in a familiar space induces a sharp reduction in the slope of the speed to theta amplitude relationship (Fig. 2) in a location specific manner, despite the omnipresence of the acoustic stimulus. These results suggest that during stationary epochs or low speeds, where theta amplitude may be relatively minimal, novel sensory variables may exert their greatest effect (sensory-evoked theta). This idea is not inconsistent with previous reports linking theta induction and phase reset at the encoding onset of particular sensory variables (Berry and Thompson, 1978; Rizzuto et al., 2003; Griffin et al., 2004).

Overall, these data indicate that a novel auditory stimulus exerts a fundamentally different effect on the locomotor speed to theta amplitude relationship as compared to novel physical space (but see Wells et al., 2013 for the effect of environmental novelty on speed-theta slope). Further, novel auditory tone presentation reduced the slope of the speed to theta amplitude function whereas novel, physical space does not alter the speed to theta amplitude function, but rather increases theta at all given locomotor speeds. Similar to novel physical space, the initial reduction in the speed-theta relationship habituated across days of sound delivery. An important question to further explore is whether not only passive, but active and thus behaviorally relevant sound presentation induces similar alterations in large-scale network dynamics across the septotemporal axis of the hippocampus.

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