

SPECIAL ISSUE: BEHAVIORAL NEUROSCIENCE OF SLEEP

Ventromedial Prefrontal Theta Activity During Rapid Eye Movement Sleep is Associated With Improved Decision-Making on the Iowa Gambling Task

Corrine J. Seeley
Queen's University

Carlyle T. Smith
Trent University

Kevin J. MacDonald
Brock University

Richard J. Beninger
Queen's University

Recent research is beginning to reveal an intricate relationship between sleep and decision-making. The Iowa Gambling Task (IGT) is a unique decision-making task that relies on the ventromedial prefrontal cortex (vmPFC), an area that integrates and weighs previous experiences with reward and loss to select choices with the highest overall value. Recently, it has been demonstrated that a period of sleep can enhance decision-making on this task. Our study investigated the sleep mechanisms (sleep stages and cortical activity) that underlie this improvement. We recorded electrophysiology for 3 consecutive nights: a habituation, baseline, and acquisition night. On acquisition night participants were administered either a 200-trial IGT (IGT group; $n = 13$) or a 200-trial control (IGT-control group; $n = 8$) version of the task prior to sleep. Compared with baseline, the IGT group had a significant increase in theta frequency (4 Hz–8 Hz) on sites located above vmPFC and left prefrontal cortex during REM sleep. This increase correlated with subsequent performance improvement from deck B, a high reward deck with negative long-term outcomes. Furthermore, presleep emotional arousal (measured via skin conductance response) toward deck B correlated to increased theta activity above the right vmPFC during REM sleep. Overall, these results suggest that insight into deck B may be enhanced via vmPFC theta activity during REM sleep and REM sleep may have distinct mechanisms for processing decision-making information.

Keywords: decision-making, deck B phenomenon, Iowa Gambling Task, rapid-eye movement sleep, ventromedial prefrontal cortex

“Sleep on it” are common words of advice given to individuals making important or difficult decisions. When decisions are complex and involve weighing multiple risks and benefits of several options, many believe that a night of sleep can help sort through information to provide a clear answer upon awakening. Recently, research using the Iowa Gambling Task (IGT), a task designed to mimic real life decision-making, has revealed an intricate relationship between sleep and decision-making. Studies show evidence

that decision-making on the IGT is disrupted by periods of sleep deprivation (Killgore et al., 2006, 2012). Furthermore, research has emerged to suggest that the reverse relationship exists and that a period of postlearning sleep can help enhance IGT decision-making (Pace-schott et al., 2012; Seeley, Beninger, & Smith, 2014). Currently, it is unknown what sleep-related mechanism underlies this effect.

IGT decision-making relies on a unique set of cognitive and neural mechanisms. In the IGT, individuals choose from four decks (A, B, C, D). Each deck delivers consistent monetary rewards and inconsistent monetary punishments of different magnitude and frequencies. Decks A and B are “bad decks,” with high reward (\$100 per draw) but relatively high punishments, resulting in a negative expected value (EV; $-\$250$) per 10 card selections. Decks C and D are “good decks,” with a small reward (\$50 per draw) but relatively small punishments, resulting in a positive EV (\$250) per 10 card selections. Recent studies suggest that decision-makers initially prefer the low-probability ($p = .1$) punishment decks (B and D) and avoid the high-probability punishment ($p = .5$) decks (A and C; Chiu et al., 2008; Lin et al., 2007; Singh & Khan, 2009). Thus, successful performance relies on shifting choice away from bad deck B by integrating the large infrequent

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Corrine J. Seeley, Centre for Neuroscience, Queen's University; Carlyle T. Smith, Department of Psychology, Trent University; Kevin J. MacDonald, Department of Psychology, Brock University; Richard J. Beninger, Centre for Neuroscience and Department of Psychology, Queen's University.

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Correspondence concerning this article should be addressed to Corrine J. Seeley, Centre for Neuroscience, Queen's University, 99 University Avenue, Kingston, Ontario, Canada K7L 3N6. E-mail: corrineseeley@gmail.com

\$1,250 punishment into its value estimate (Fernie & Tunney, 2006; Seeley et al., 2014; Wasserman et al., 2012). Recent evidence suggests that individuals who show patterns of this shift prior to sleep have enhanced decision-making on the task compared with those who show no evidence of learning prior to sleep (Seeley et al., 2014).

A key brain area important for guiding shifts in choice in the IGT is the ventromedial prefrontal cortex (vmPFC). The vmPFC integrates and weighs previous emotional experience toward reward and loss through reciprocal connections to areas that process emotion, including the striatum, insula and amygdala (Bechara et al., 1999; Fellows & Farah, 2003; Lawrence, Jollant, O'Daly, Zelaya, & Phillips, 2009; Linnet, Møller, Peterson, Gjedde, & Doudet, 2011), and areas that process cognitive information including the hippocampus and dorsolateral prefrontal cortex (Ernst et al., 2002; Gupta et al., 2009; Li, Lu, D'Argembeau, Ng, & Bechara, 2010; Manes et al., 2002). As learning develops, a common marker of task insight is the development of an "anticipatory" skin conductance response (SCR) that occurs in the 5 s preceding choice from bad decks (Bechara & Damasio, 2002; Bechara et al., 1996; Crone et al., 2004; Guillaume et al., 2009; Wagar & Dixon, 2006). This emotional arousal is often a physiological marker that precedes learning and is thought to be generated by the vmPFC through reciprocal connections to underlying brain areas including the amygdala, insula and striatum (Bechara et al., 2002, 1999; Li et al., 2010; Lin et al., 2008). Although a wide body of literature has identified the vmPFC and subcortical areas as important for online learning, it is currently unknown what sleep-related mechanisms underlie offline learning of the task.

Sleep plays a critical role in memory consolidation and brain plasticity. Higher-order cognitive procedural tasks, like the IGT, are enhanced by postlearning REM sleep (Djonlagic et al., 2009; Peigneux et al., 2003; Smith, 2010; Smith & Peters, 2011; Yordanova et al., 2008), whereas motor procedural tasks are commonly linked to Stage 2 sleep and sleep spindles (Fogel, Smith, and Beninger, 2009; Smith & Macneill, 1994; Tweed et al., 1999; Walker et al., 2003). Furthermore, REM sleep has been implicated in the consolidation of tasks that involve memory for stimuli that evoke negative emotions (Baran et al., 2012; Hu et al., 2006; Nishida et al., 2009). Many areas that underlie IGT learning, including the amygdala, hippocampus, striatum, and prefrontal cortex are active during REM sleep (Hobson & Pace-Schott, 2002; Maquet et al., 2000; Nofzinger, 2005; Perogamvros & Schwartz, 2012; Peigneux et al., 2003) and have been linked to REM sleep-dependent consolidation of emotional memories (Hobson & Pace-Schott, 2002; Peigneux et al., 2003; Perogamvros & Schwartz, 2012). One particular electrophysiological feature of REM sleep that is linked to this process is the 4 Hz–8 Hz theta rhythm (Deliens et al., 2014; Diekelmann et al., 2009; Nishida et al., 2009; Popa et al., 2010). Theta oscillations are commonly reported in REM sleep. They appear in areas of the limbic system and PFC and are often linked to retention of emotional memories (Deliens et al., 2014; Diekelmann et al., 2009; Nishida et al., 2009; Popa et al., 2010). Interestingly, the vmPFC is also shown to be active during periods of REM sleep; however, there has yet to be a study to investigate the potential role of this activity in sleep-related memory processing (Hobson & Pace-Schott, 2002; Perogamvros & Schwartz, 2012).

Overall, our goal was to investigate the sleep architecture (i.e., sleep stages) and sleep-stage properties (i.e., spectral frequencies and topographic location) that may underlie postlearning processing of deck B. Because postlearning REM sleep facilitates learning of both complex cognitive tasks and tasks of an emotional nature, we suggest that REM sleep may increase following learning of the task and correlate with task improvement. Furthermore, given that the vmPFC is largely involved in IGT learning, and has heightened activity during REM sleep, we predicted an increase in theta power on sites above the vmPFC during postlearning REM sleep. We expected sleep-related changes to be correlated with improvement from deck B rather than deck A, C, D, or good decks (C and D) combined. Finally, because presleep insight is imperative for sleep-related enhancement of the IGT (Seeley et al., 2014), we expected that individuals who developed anticipatory SCRs to deck B would have larger sleep-related changes.

Method

Subjects

Participants were recruited through poster advertisements on Trent University campus and were initially screened using telephone and online questionnaires. Participants were included if they reported the following criteria: average of 7–8 hr of uninterrupted sleep per night, sleep time occurring between 22:00–24:00 and 07:00–09:00, no daytime napping or shift work, limited daily caffeine use (<3 cups a day prior to 15:00), limited alcohol use (<10 drinks a week) and no nicotine use. All participants were right-handed, scored below 10 on the Beck Depression Inventory (Beck et al., 1961), had no history of concussions or traumatic brain injuries, seizures, and no current psychological conditions, medication use, or sleep problems that could disrupt sleep maintenance or sleep architecture. Sleep and activity diaries were used to verify that participants maintained this status beginning the week prior to participation and until the study was complete. In total, 21 participants [mean ($\pm$ SEM) age = 20.1 $\pm$ 0.3 years; female = 17] met these criteria and successfully completed the study. All participants showed healthy normal sleep (<15 arousals per hour of sleep) during their acclimatization night (Williams et al., 1974). This research was approved by the Trent University Ethics Board.

General Procedure

Following a week of stabilization, participants came into the lab to have polysomnogram (PSG) recordings taken during three consecutive nights of sleep. The first night was an acclimatization night where participants got used to sleeping with electrodes on and while in a new environment. Participants arrived to the lab at 21:00 and had an electrode montage (see below) applied prior to a night of sleep. The second night was a baseline night, used to provide a measure of baseline sleep so changes in sleep architecture could be identified following administration of the task on the third night. Participants arrived at 20:30 and had the same electrode application, followed by a night of sleep. The third night was the acquisition night that introduced the learning task prior to sleep. Participants arrived at 20:00 and had the electrode application. Participants were randomly administered

the IGT ($n = 13$) or IGT-control ($n = 8$) task between 21:00–22:00, followed by a night of sleep. The IGT-control was used to ensure any sleep related changes on acquisition night were specific to IGT learning. In the morning, the IGT group was readministered the IGT (Session 2) at 09:00 after having an opportunity to shower and eat a light breakfast. Following session two, participants were debriefed and paid \$75 for their time.

On all nights, lights-out was encouraged before 23:30 and lights-on was at 08:00. During the day, participants left the lab and were reminded to adhere to the sleep and wake guidelines. On days with scheduled PSG recordings, participants were instructed to refrain from alcohol use and if possible, avoid engaging in new forms of learning (e.g., video games, musical instruments). All participants provided written and informed consent during participation.

Task Versions

Iowa Gambling Task (IGT). For the IGT group, we administered the same 200-trial shuffled version as previously reported in Seeley, Beninger, and Smith (2014). This version maintained the same reward and punishment structure as the original (Bechara et al., 1996), with a more difficult “shuffled” deck placement (C, A, B, D; Li et al., 2010; Preston et al., 2007; Seeley et al., 2014). Instructions for the task were given as previously reported in Seeley et al. (2014). To allow for the collection of anticipatory SCRs the task was modified to have a 10-s delay between trials (Bechara et al., 1996; Crone et al., 2004; Wagar & Dixon, 2006) and timing signals were used to identify anticipatory SCRs.

The task began with a green light that signaled participants to make a deck selection. Following the selection the light turned red for 5-s and the screen displayed the monetary reward, monetary punishment, net gain and cumulative net total. The light then turned yellow, signaling participants to place the mouse over their next choice. It remained yellow for a 5-s “anticipatory period.” Electrodermal activity during this time was used to score anticipatory SCRs. Following the 5-s anticipatory period the light turned green, signaling participants to make their preestablished choice. This procedure continued for 200 trials. Decks were recycled after 40 trials allowing for unlimited choice from each deck. Prior to administration of the task, a five-trial practice task was administered, to ensure participants understood the timing signals. All participants showed active SCRs during task administration.

Iowa Gambling Task control task. The IGT control task was designed to mimic the IGT without the learning or complex decision-making component. It maintained the same timing signals, number of deck choices, and visual output as the IGT task, however, participants did not receive monetary reward or punishment for their selections. This design ensured that the control participants spent an equivalent amount of time watching a computer screen, monitoring timing signals, and making deck selections (i.e., motor movements) as the IGT group. Participants were instructed that they would not receive feedback for their choice, and to continue making deck selections until the task was over.

Polysomnogram Recordings

PSG recordings were done using Neuroscan (Version 4.5.1). The electrode hook-up included an 18-channel standard montage

that recorded electroencephalogram (EEG), electromyogram (EMG), and electrooculogram (EOG) signals. EOG (left and right ocular canthus), EMG (left and right chin), cortical EEG (C3, C4, CZ, FZ, F3, F4, F7, F8 FP1, and FP2), a ground (FPZ), reference (AFZ) and bipolar A1/A2 channels were placed according to the International 10–20 system (Jasper, 1958). FP1 and FP2 sites were used as best-guess surfaced EEG estimates of vmPFC lobe activity. EEG and EOG signals were high- and low-pass filtered at 100 Hz and 0.05 Hz, respectively and a bipolar mastoid channel was recorded from A1 and A2. All signals were $<5 \text{ k } \Omega$ and recorded at a rate of 250 Hz using a 60 Hz notch filter.

Skin Conductance Response

During Session 1, electrodermal activity was collected using Biopac MP36 (Biopac Systems, CA). Two Ag-AgCl electrodes filled with isotonic gel were placed on the medial phalanx of the index and middle finger of the left hand. SCR activity was recorded and displayed on a computer screen in a separate room. Each time a card selection was made, the deck choice was simultaneously marked on the recording to ensure that deck selections could be identified. To minimize signal artifacts, participants were instructed to rest their left hand on the desk and keep it still until the task was complete.

Data Processing and Statistical Analyses

Task performance.

Initial learning session one. To investigate initial learning in the IGT group, the 200 trials of session one were split into blocks of 50 trials (Overman & Pierce, 2013; Seeley et al., 2014). Proportion of choices (total draws chosen/total number of possible draws) was calculated for the good decks (decks C and D) combined as well as each individual deck. To investigate whether deck preferences changed across the 200 trials we performed a one-way repeated measures analyses of variance (ANOVA) of block (1, 2, 3, 4). The dependent variable was proportion of choices from the good decks combined. Greenhouse–Geisser corrections were used to avoid the effects of sphericity violations.

Improvement across sessions. To investigate whether improvement occurred from Session 1 to Session 2, the overall proportion of draws per 200 trials was calculated for session one and session two in the positive EV decks (C and D) and each individual deck (A, B, C, D). A paired t test was performed with session (1, 2) as the independent variable and proportion of draws from good decks combined (C and D) as the dependent variable.

Sleep architecture. PSG recordings were visually scored in PRANA (Version 9.9; Phi Tools) in 30-s epochs using standard procedures from Rechtschaffen and Kales (1968). A computer algorithm previously reported by Fogel, Smith, and Beninger (2009) was used to detect and mark high-frequency movement artifact. Each subject was scored blind to their night and condition and inter- and intrarater reliability was at least 85%. The sleep architecture values obtained from the PSG recordings on baseline and acquisition night were total min of sleep period time (SPT), total sleep time (TST), sleep efficiency (SE; TST/SPT), Stage 1, Stage 2, slow-wave sleep (SWS), and REM. The SPT value reflected the time interval from the initial detection of Stage 1 to lights-on. The TST reflected the min asleep during this time.

The dependent variables used for analyses were SPT, TST, and percentage of SPT spent in Stage 1, Stage 2, SWS and REM during baseline and acquisition night. To investigate whether sleep architecture changed following administration of the IGT, a mixed two-way Night (Baseline, Acquisition) $\times$ Group (IGT, IGT-control) ANOVA was performed for each dependent variable. We hypothesized that individuals in the IGT group would increase in % REM sleep from baseline to acquisition and that individuals in the IGT-control group would not. We expected no changes in SPT, TST, % Stage 1, % Stage 2, and % SWS in the IGT or IGT-control group.

Power spectral analysis. Power spectral analysis was done using the scored artifact-free 30-s epochs reported above. The absolute power spectrum at each EEG site was calculated using fast Fourier transform for delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), sigma (12–16 Hz), beta (16–35 Hz), and gamma (35–45 Hz) frequency bands. All data were referenced to A1/A2 reference electrodes prior to analysis. Hanning window with 2-s overlap was applied and data were averaged into 30-s epochs. The absolute spectral power values for each frequency band were averaged across each sleep stage separately (REM, SWS, and Stage 2) for each individual electrode site (CZ, FZ, F3, F4, F7, F8, FP1, FP2) and log transformed calculations were applied.

Within each sleep stage a mixed three-way Night (baseline, acquisition) $\times$ Group (IGT, IGT-control) $\times$ Site (CZ, FZ, F7, F8, F3, F4, FP1, FP2) ANOVA was performed with spectral power value as the dependent variable. Significant interactions were followed up with a mixed two-way Night (baseline, acquisition) $\times$ Group (IGT, IGT-control) ANOVA for each site, then one-way simple effects repeated measures ANOVA of night for each group and Tukeys tests for multiple comparisons. We hypothesized the IGT group would show increased theta activity during REM sleep in sites FP1 and FP2 which are located above the vmPFC. We expected no change in either group during Stage 2 or SWS.

To investigate whether changes in power spectral values correlate with postsleep IGT improvement we performed Pearson correlations between change in power spectral value and IGT improvement score. Power spectral change scores were calculated for each significant variable by subtracting the acquisition night from baseline night value. IGT improvement scores were calculated for good decks combined (C and D) and each deck separately (A, B, C, D) by subtracting the proportion of choices in Session 2 from the proportion of choices in Session 1. For each deck and good decks combined, Pearson correlations were performed between the power spectral change value and IGT improvement score.

Anticipatory skin conductance response. As a means to investigate whether presleep insight is related to sleep-related changes, we analyzed anticipatory SCR activity toward deck B during Session 1. Analysis was done using Acqknowledge 3.9.0 software. All recordings were screened for movement artifact prior to analysis. Baseline measures were removed using a high pass IIR filter set to 0.05 Hz. The SCR was defined as the peak-to-peak amplitude difference (microseimens) during the 5-s interval prior to each deck selection (Crone et al., 2004; Miu et al., 2008; Wagar & Dixon, 2006). Because the participants had large interindividual variability in SCRs, each participant's average anticipatory response for each deck was normalized to the average anticipatory

response of all decks (A, B, C, D) combined. Pearson correlations were performed to investigate whether average anticipatory SCRs toward deck B correlated with significant sleep-related changes. To evaluate whether learning was specific to deck B we performed the same analysis on decks A, C, and D but did not expect significant results.

Results

Task Performance

Initial learning in Session 1. The IGT group did not show evidence of initial learning during Session 1. Results revealed no increase in choices from the good decks (decks C and D) combined and a nonsignificant effect of trial block, $F(1.6, 28.4) = 1.2, p = .31$. Figure 1A illustrates that participants preferred low-frequency penalty bad deck B, and did not shift choice toward good decks C and/or D across four trial blocks.

Improvement between sessions. Despite no behavioral evidence of initial learning in Session 1, improvement between sessions was equivalent to the sleep-related improvement previously reported by Seeley et al. (2014; Figure 1B). The paired t test of session (1, 2) on the good decks combined revealed that mean

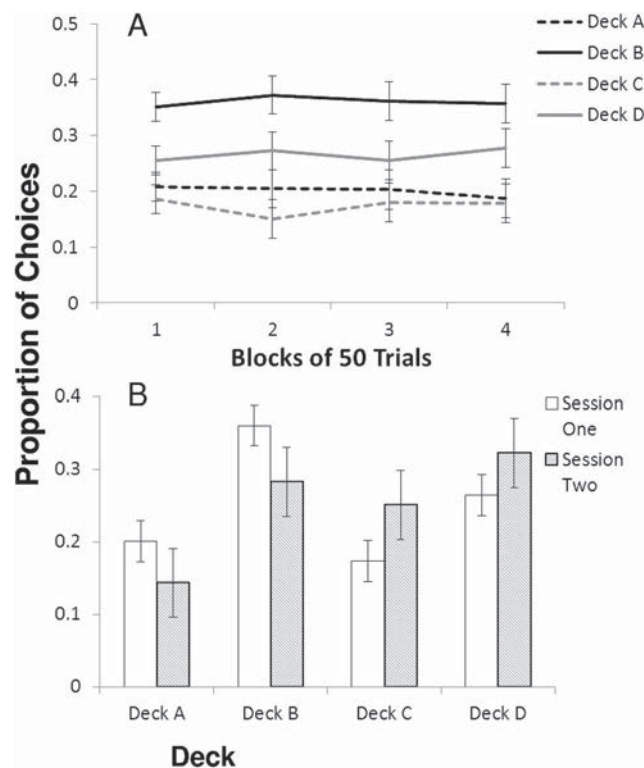


Figure 1. Session 1 deck choice and subsequent improvement in Session 2 following a period of sleep. (A) Session 1 mean ($\pm$ SEM) proportion of draws from each deck (A, B, C, D) in four blocks of 50 trials each ($N = 13$). Solid lines represent low-frequency penalty decks and dashed lines represent high-frequency penalty decks; black lines represent negative expected value (EV) decks and gray lines represent positive EV decks. (B) Mean ($\pm$ SEM) proportion of choices from each deck (A, B, C, D) in Session 1 and Session 2 ($N = 13$).

($\pm$ SEM) proportion of choices from the good decks significantly improved from Session 1 (0.44 ± 0.04) to Session 2 (0.60 ± 0.05); $F(1, 12) = 5.7, p = .03$, in the IGT group. Overall, participants increased choices from good decks by 16.1%, which is comparable with the 12%–15% sleep-related improvement previously reported by Seeley et al. (2014). Figure 1B illustrates that participants reduced choices from bad decks A and B and increased choice toward good decks C and D.

Sleep Architecture Changes

There were no significant differences in sleep architecture from baseline to acquisition night in the IGT or IGT-control group. The Night $\times$ Group interactions for SPT, TST, SE, and sleep stages were not significant as summarized in Table 1.

Power Spectral Changes

Power spectral changes: REM Sleep. In the IGT group, theta activity appeared to increase during REM sleep in the left and right medial prefrontal cortex (FP1 and FP2) as well as the left lateral prefrontal cortex (F7) following IGT training on the acquisition night compared to baseline (Figure 2A); no comparable increases were seen on any sites in the IGT-control group. The Night $\times$ Group $\times$ Site ANOVA revealed a significant 3-way interaction effect for the theta frequency band only, $F(7, 147) = 2.1, p = .045$. Three-way interactions from ANOVA for delta, $F(7, 147) = 1.2, p = .35$; sigma, $F(7, 147) = 0.8, p = .61$; beta, $F(7, 147) = 0.2, p = .99$; alpha, $F(7, 147) = 0.3, p = .95$; and gamma, $F(7, 147) = 0.4, p = .92$, frequencies were not significant (data not shown). Interactions in follow-up Night $\times$ Group ANOVA on the theta frequency band were significant for sites FP1, $F(1, 19) = 4.7, p = .04$; FP2, $F(1, 19) = 4.8, p = .04$; and F7, $F(1, 17) = 7.4, p = .015$, but nonsignificant for sites F8, $F(1, 18) = 2.1, p = .16$ and the remaining sites: CZ, $F(1, 18) = 0.1, p = .78$; FZ, $F(1, 18) = 1.4, p = .30$; F3, $F(1, 19) = 0.1, p = .83$; and F4, $F(1, 19) = 0.1, p = .75$. Post hoc comparisons revealed a significant increase in theta power from baseline to acquisition night on sites FP1, $F(1, 12) = 3.8, 0.04$; FP2, $F(1, 12) = 4.5, p = .03$; and F7, $F(1, 11) = 3.4, p = .04$ in the IGT group only. The IGT-control subjects (Figure 2B) showed no significant change at FP1, $F(1, 7) = 1.8, p = .22$; FP2, $F(1, 7) = 1.4, p = .28$; or F7, $F(1, 6) = 5.5, p = .09$ (see Figure 2B). Overall, these results reveal that theta power

on prefrontal cortex sites (FP1 and FP2), as well as left prefrontal cortex (F7) significantly increases during REM sleep after exposure to the IGT.

Theta correlation with deck improvement. In the IGT group, Pearson correlations revealed that individuals with increased theta power in FP1, FP2, and F7 during REM sleep, had a larger reduction in choice from deck B during session two. Improvement (a decrease) in choices from deck B significantly correlated with theta power change scores for sites FP1 ($p = .017$; Figure 3B), FP2 ($p = .017$; Figure 3A), and F7 ($p = .022$; Figure 3C). Improvement in choice from deck A, C, and D or good decks (decks C and D) combined did not significantly correlate with theta power change scores on these sites.

Power spectral changes: SWS and Stage 2. As expected, power spectral activity showed little change at any site during SWS or Stage 2 from baseline to acquisition night in the IGT or IGT-control groups. The Night $\times$ Condition $\times$ Site ANOVA revealed nonsignificant 3-way interaction effects during both SWS and Stage 2 sleep. During SWS, delta, $F(7, 147) = 1.7, p = .12$; theta, $F(7, 147) = 0.9, p = .47$; sigma, $F(7, 147) = 0.7, p = .69$; alpha, $F(7, 147) = 0.6, p = .75$; beta, $F(7, 147) = 0.9, p = .99$; and gamma, $F(7, 131) = 0.4, p = 1.0$ were not significant (data not shown). During Stage 2, delta, $F(7, 147) = 1.3, p = .28$; theta, $F(7, 147) = 1.3, p = .24$; sigma, $F(7, 147) = 1.1, p = .39$; alpha, $F(7, 147) = 0.9, p = .48$; beta, $F(7, 147) = 0.2, p = .99$; and gamma, $F(7, 131) = 0.008, p = 1.0$ were not significant (data not shown). Overall, power spectral activity did not change significantly during SWS or Stage 2.

Anticipatory skin conductance response: Session 1. Individuals with higher anticipatory SCRs for deck B during Session 1 exhibited larger changes in theta power on site FP2 during REM sleep (see Figure 4). The average anticipatory SCRs toward deck B significantly correlated with change in FP2 theta ($p = .04$), but did not significantly correlate with change in FP1 ($p = .12$) or F7 ($p = .32$) theta activity (data not shown). As expected, we found no evidence that anticipatory response to deck A, C, or D correlated with increased theta activity on sites FP1, FP2, or F7 ($p > .05$). These results reveal that anticipatory SCRs toward deck B are linked to increased theta activity in the right prefrontal cortex (PFC) during postle-arning REM sleep.

Table 1
Sleep Architecture ($\pm$ SEM) on Baseline and Acquisition Night in the IGT and IGT Control Group

Sleep stage characteristics	IGT		IGT control		<i>F</i>	<i>p</i>
	Baseline	Acquisition	Baseline	Acquisition		
SPT (minutes)	514.7 $\pm$ 5.4	495.2 $\pm$ 9.9	523.3 $\pm$ 6.9	518.5 $\pm$ 12.7	.88	.36
TST (minutes)	478.2 $\pm$ 8.7	464.6 $\pm$ 15.0	491.5 $\pm$ 11.1	484.3 $\pm$ 19.0	.72	.80
Sleep efficiency (TST/SPT)	92.9 $\pm$ 1.3	93.7 $\pm$ 1.6	93.9 $\pm$ 1.7	93.0 $\pm$ 1.9	.43	.54
Stage 1 sleep (% SPT)	1.2 $\pm$.4	1.2 $\pm$.3	2.1 $\pm$.5	1.9 $\pm$.4	.11	.78
Stage 2 sleep (% SPT)	50.0 $\pm$ 2.1	49.2 $\pm$ 2.2	53.7 $\pm$ 2.7	53.2 $\pm$ 2.9	.02	.88
Slow wave sleep (% SPT)	22.6 $\pm$ 1.8	22.0 $\pm$ 2.2	18.0 $\pm$ 2.3	17.7 $\pm$ 2.8	.36	.85
REM sleep (% SPT)	19.1 $\pm$ 1.1	21.4 $\pm$ 1.6	20.1 $\pm$ 1.4	19.9 $\pm$ 2.0	.95	.34

Note. There were no significant differences in sleep architecture from baseline to acquisition in the IGT or IGT-control group ($p > .05$). IGT = Iowa Gambling Task; SPT = sleep period time; TST = total sleep time.

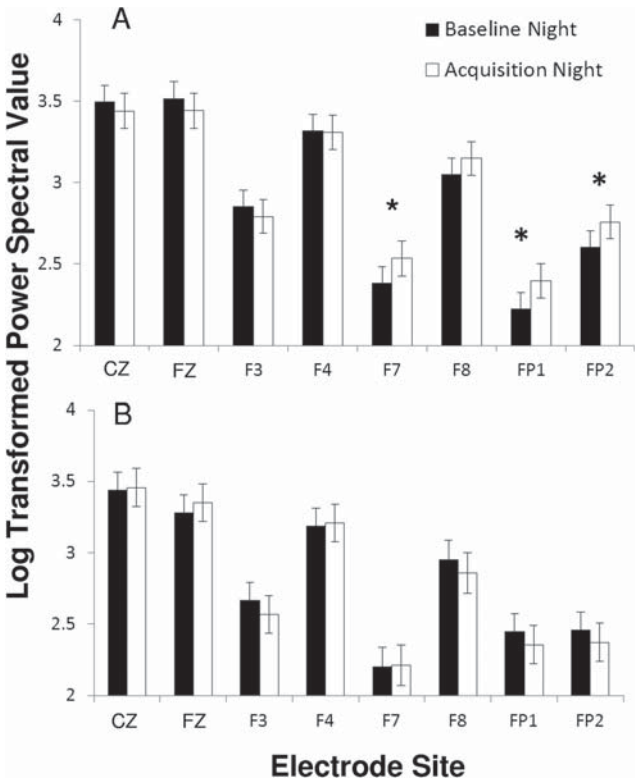


Figure 2. Theta power spectral (dB) activity during REM sleep on baseline and acquisition night in the Iowa Gambling Task (IGT) and IGT control groups. Log transformed absolute power spectral values for theta frequency range (4 Hz–8 Hz) on sites CZ, FZ, F3, F4, F7, F8, FP1, and FP2 during REM sleep on baseline and acquisition night. Results revealed a significant three-way interaction in analysis of variance (ANOVA) of Night $\times$ Group $\times$ Site, followed by a significant two-way ANOVA of Night $\times$ Group on sites FP1, FP2, and F7 only. Simple effects one-way ANOVA of night on each site revealed (A) significant effects in the IGT group ($N = 13$), that increased activity from baseline to acquisition on sites FP1, FP2, and F7, and (B) nonsignificant effects in the IGT-control group. *Significant increase ($p < .05$) by Tukeys test for multiple comparisons.

Discussion

The main finding of our study suggests that theta activity on sites above the vmPFC (FP1 and FP2) and left PFC (F7) during REM sleep may be linked to offline processing of deck B. We found no evidence that the amount of time spent in REM sleep increased following learning of the IGT (see Table 1); however, we did find that during REM sleep, theta frequencies were heightened on sites above the vmPFC and left lateral PFC regions. Compared with baseline sleep, individuals who were administered the IGT had a significant increase in theta power on sites above the left and right vmPFC and the left lateral PFC during postlearning REM sleep (Figure 2A). Each of these increases correlated with reduced choice from bad deck B (see Figure 3). These changes were not found in the IGT-control group (Figure 2B). Overall, our results confirm our previously reported “deck B sleep effect” (Seeley et al., 2014) and suggest that specific mechanisms during postlearning REM sleep may actively process deck B information. Furthermore, our findings show that presleep anticipatory SCRs

toward deck B correlate with increased theta activity on sites above the right vmPFC during postacquisition REM sleep (see Figure 4). Overall, these results have several implications for understanding the possible role of REM sleep and REM sleep theta in facilitating cognitive-emotional decision-making.

This is the first study to link activity on sites located above the vmPFC (FP1, FP2) and lateral PFC (F7) to sleep-related improvement of a task. Observed changes were specific to prefrontal sites and not found in other frontal areas (Figure 2A). Because these sites were best guess estimates, future work should be done to determine the exact source of the activity and the underlying neural circuitry involved in its generation. In rodents, theta is generated in the hippocampus and has been phase-locked to activity in the amygdala, striatum and prefrontal cortex (Buzsaki, 2002; Leung, 1998). This phase-locked activity is thought to play

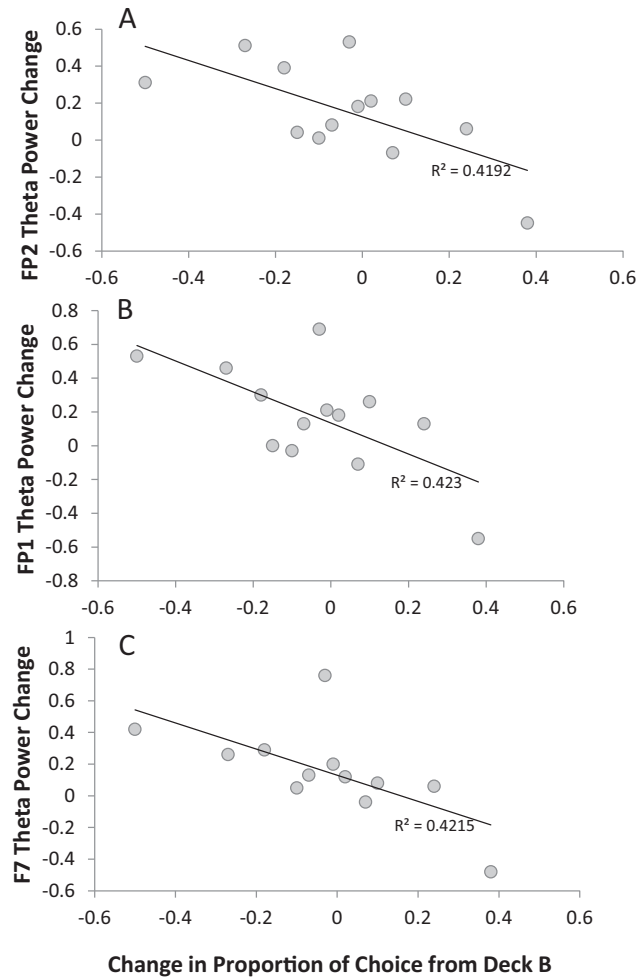


Figure 3. Relationship between deck B improvement across sessions and REM sleep-related changes in power spectral theta during postlearning sleep. The correlation between the improvement (a decrease) in deck B choice (proportion of draws in Session 1 – proportion of draws in Session 2) and the change (baseline – acquisition night) in log transformed absolute power spectral theta activity (4 Hz–8 Hz) on sites (A) FP2, (B) FP1, and (C) F7 in the Iowa Gambling Task group. The line of best fit and R squared (R^2) is shown. All correlations are significant ($p < .025$).

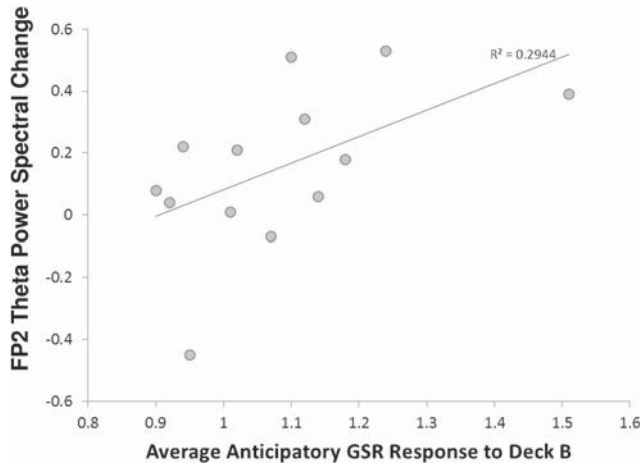


Figure 4. Relationship between deck B anticipatory skin conductance response (SCR) during session one and REM sleep-related changes in FP2 power spectral theta. The Pearson correlation of the average anticipatory GSR response (microseimens) prior to deck B selections during session one and the change (baseline – acquisition night) in log transformed absolute power spectral theta (4 Hz–8 Hz) activity on site FP2 was significant ($p = .04$). The line of best fit and R squared (R^2) is shown.

a critical role in decision processing during REM sleep (Louie & Wilson, 2001; Popa et al., 2010). In humans, theta generation during REM sleep is not well understood. It has been suggested that theta activity in the hippocampus and prefrontal cortex are driven by separate generators (Cantero et al., 2003; Nishida et al., 2009). Future work should be done to identify the source of theta generation in prefrontal areas during REM sleep. It is possible that theta activity was generated independently in the vmPFC and reflects top-down processing on decision-making systems. It is also possible that theta activity was generated by the hippocampus and reflects a bottom-up coupling with underlying brain areas including the amygdala, striatum and vmPFC, as suggested by the rodent literature (Hobson & Pace-Schott, 2002; Perogamvros & Schwartz, 2012). REM sleep theta activity in the hippocampus has also been shown to reflect a reactivation of areas that were previously involved in online learning (Hennevin et al., 1998; Louie & Wilson, 2001). Thus, it is possible that heightened theta on sites above the vmPFC and left lateral PFC reflects a synchronization with subcortical areas and/or a reactivation of cortical-subcortical pathways that were active while performing the task. Interesting future work could be done to identify the online neural circuitry involved in deck B learning and whether the observed theta activity during REM sleep reflects a reactivation of these areas. Overall, future research needs to be done to identify the source of the theta activity on sites FP1, FP2, and F7 during REM sleep, and the offline neural and cognitive processing this activity represents.

Because the IGT is a complex cognitive-emotional task, the mechanisms that underlie our REM sleep enhancement of deck B remain unknown. On a behavioral level, REM sleep has a generalized role in integrating information to provide insight into complex problems (Djonlagic et al., 2009; Smith, 2010; Smith & Peters, 2011). It is possible that vmPFC theta has a generalized role in higher-order cognitive processing. It is also possible that REM sleep helps people consider long-term EV goal outcomes, as

opposed to short-term goal outcomes, a process disrupted by sleep deprivation (Olson et al., 2014). However, because the result was specific to deck B, rather than all decks, we suggest that more distinct mechanisms may be involved.

Deck B learning is unique and requires integrating a large infrequent \$1,250 loss into its value estimate to discover its negative EV. Often, learning of the task is preceded by the development of anticipatory SCRs toward bad decks (Bechara et al., 1997; Suzuki et al., 2003) and it is currently thought that anticipating the negative loss of deck B is crucial to IGT learning. Our results show that individuals with higher presleep anticipatory SCRs toward deck B showed larger changes in theta power on sites above the right vmPFC site during REM sleep (see Figure 4). We suggest that the right vmPFC may have a distinct role in processing insight into the loss of deck B that was gained prior to sleep. During IGT learning the right vmPFC has been linked to expectancy of negative punishments (Christakou et al., 2009) and generation of anticipatory SCRs (Tranel et al., 2002), whereas left PFC activity precedes shifts in choice (Lawrence et al., 2009) and is linked to monitoring of unsteady outcomes (Windmann et al., 2006) and reversal learning (Fellows & Farah, 2003). Thus, it is possible that the right vmPFC theta may be specifically involved in processing emotional insight into the task, where the left vmPFC may reflect online monitoring of unexpected outcomes (i.e., unexpected punishment) and more general cognitive processes involved in IGT learning. It is also possible that the right vmPFC processed information that was below levels of conscious awareness to the subject. Some work suggests that anticipatory SCRs during early stages of learning are generated below levels of conscious awareness (Bechara et al., 1997; Suzuki et al., 2003; for review see Turnbull et al., 2014). Because we found no obvious shifting of deck B during Session 1 (Figure 1A), the anticipatory SCRs may reflect early learning and be below levels of conscious awareness to the subject. Given that REM sleep has been linked to enhancement of implicit cognitive tasks (Djonlagic et al., 2009; Ellenbogen et al., 2007; Yordanova et al., 2008) it is possible that vmPFC theta may be an underlying mechanism for sorting out decision problems below levels of conscious awareness. Interesting future work could be done to investigate the participants presleep and postsleep awareness of deck B, as well as how SCRs and insight develop in our shuffled, more difficult version of the task.

A limitation to our results is that it is unclear whether these results generalize across different stages of IGT performance and deck B insight. It is possible that REM sleep has a generalized role in processing all stages of IGT learning. However, it is also possible that sleep-related mechanisms change as IGT learning progresses. For example, it has been suggested that as IGT learning progresses, associations become declarative (explicit) in nature (Bechara et al., 1997; Bowman et al., 2005) and are stored in long-term memory via connections to hippocampal memory systems (Gupta et al., 2009). However, it has also been suggested that hippocampal/declarative learning is not necessary for IGT learning (Turnbull et al., 2014). Declarative tasks are enhanced with SWS and through hippocampal cortical synchronized activity (Gais & Born, 2004; Smith & Peters, 2011). Due to the complexity of the IGT, future research should investigate whether these results apply to all stages of IGT learning. Another limitation to our results is that, given our small sample size, it is unclear whether our results can be generalized to a larger population and across various

population groups, including gender. Within the 13 individuals in the IGT group, the majority of participants were female ($N = 10$). Within the IGT it has been suggested that males perform slightly better on the IGT than females (for review see van den Bos et al., 2013). Performance differences have been linked to greater activation of the right lateral vmPFC and a heightened ability in dealing with irregular patterns and updating choice based on punishments. We found no evidence that the three males performed better during session one compared to females. Furthermore, it does not appear that sleep-related improvement in deck B choice was driven by males or females separately. However, given our small sample of males it is difficult to draw any firm conclusions. Studies suggest that females have more theta activity at baseline (Wada et al., 1994) and during REM sleep (Liscombe et al., 2002) compared with males. Whether females have larger sleep-related changes in theta during postlearning sleep is currently unknown. Interesting future research could investigate potential differences in sleep-related improvement in males and females separately.

Future work should also investigate whether sleep-related changes generalize across various subgroups and clinical populations. For example, IQ has been found to predict both IGT performance (Webb et al., 2014) and REM sleep-related changes in memory (Smith et al., 2004). It is possible our results may be restricted to or enhanced in those with higher IQ. It is also possible that our effects are different across clinical populations that are known to have altered cognitive and/or emotional strategies during IGT choice. For example, individuals with depression move away from bad decks faster than normal controls (Smoski et al., 2008), as well as have heightened reactivity toward emotionally negative stimuli (Nofzinger et al., 1994), and a higher prevalence of REM sleep disorders (Rasch & Born, 2013). Thus, it is possible that individuals with depression have more pronounced or altered changes in theta activity following IGT learning. Overall, it would be interesting to see how these results apply to clinical populations with altered cognitive or emotional strategies during IGT choice.

Conclusion

The goal of this article was to provide neural evidence for our previously reported “deck B sleep effect.” We suggest that insight into deck B may be enhanced via prefrontal cortex theta during REM sleep. More specifically we found that theta recorded above the right vmPFC may contribute to enhancing emotional insight into the negative nature of deck B. These findings suggest that mechanisms during REM sleep may help aid decision processing and underlie the common practice to “sleep on it.”

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