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Sex differences in sleep-dependent perceptual learning

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ABSTRACT

Sex differences in learning and memory suggest differences between men and women in mechanisms of neural plasticity. Such differences have been reported in a variety of explicit memory tasks, but implicit memory has not been studied in this context. We investigated differences between men and women in offline consolidation of perceptual learning (PL) of motion direction discrimination. Initially, discrimination thresholds were measured for two opposite directions of motion, followed by approximately 40 minutes of training on one of the directions. During a post-training consolidation period, subjects either took a nap or remained awake. Thresholds were then reassessed for both directions of motion. We found that rapid eye movement (REM) sleep facilitates consolidation of PL but that the pattern of specificity in the REM condition differed between men and women. PL for men whose naps contained REM sleep was highly specific to the trained direction of motion, whereas REM sleep in women resulted in generalized learning to the untrained direction as well as to a novel direction that was not previously tested. Moreover, for subjects in the REM condition, men exhibited greater PL than women for the trained direction. Our findings provide the first evidence of sex differences in the magnitude and specificity of PL and in the role of REM sleep in implicit learning. Our results have important implications for optimization of educational and training strategies designed for males and females.

1. Introduction

Cognitive performance is influenced by a variety of psychological and biological factors, including sex. In the domain of episodic memory, there are systematic differences between men and women in performance of hippocampal-dependent tasks (reviewed in Herlitz, Airaksinen, & Nordstrom, 1999). In particular, women outperform men on episodic memory tasks, including word recall, word recognition, story recall, name recognition, face recognition, and concrete picture recall and recognition (Lewin, Wolgers, & Herlitz, 2001). Women also have better memory for emotional stimuli than men (Canli et al., 2002). In contrast, men excel on visuospatial episodic memory tasks (Herlitz, Airaksinen, & Nordstrom, 1999; Lewin, Wolgers, & Herlitz, 2001). Although complete mechanistic explanations of sex differences in cognition are still lacking, there are many biological dimorphisms that could account for these differences, such as dimorphisms in brain structure, sex hormones and neurotransmitters, and differing responses to stress hormones (reviewed in Cahill, 2006). In particular, no studies have determined whether sex differences exist for implicit learning and whether such differences interact with the documented effects of sleep on implicit learning. In the present study, we directly measure sex differences in sleep-dependent implicit learning of a visual perceptual skill.

Perceptual learning (PL) is the long-term improvement of performance on a sensory task. One of the hallmarks of PL is that it is specific to the physical features of the trained stimulus. That is, the performance improvement does not fully generalize to stimuli that are not used during training. In the visual system, specificity of PL has been demonstrated for spatial location (Ball & Sekuler, 1987; Nishina, Kawato, & Watanabe, 2009), orientation (Ahissar & Hochstein, 1997), spatial frequency (Fiorentini & Berardi, 1980), and ocularity, when training is monocular (Fahle, Edelman, & Poggio, 1995; Karni & Sagi, 1991), suggesting that the mechanism of training effects is a change in encoding in early stages of visual processing and/or decoding of activity in these early stages by higher-order areas involved in perceptual decisions. In particular, visual PL of motion direction discrimination is

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specific to the direction of motion and visual field location used for training (Ball & Sekuler, 1987; Rokem & Silver, 2010). In the present study, we assessed sex differences in the magnitude and specificity of PL of motion direction discrimination following sleep-dependent consolidation.

Offline consolidation during sleep has substantial effects on the magnitude and specificity of PL (Mednick, Nakayama, & Stickgold, 2003; Mednick et al., 2002). For example, post-training improvement of texture discrimination is dependent on both slow wave sleep and rapid eye movement (REM) sleep (Karni et al., 1994; Stickgold et al., 2000). A recent study reported sex differences in motor and verbal learning following a nap and found that sleep-dependent learning effects in women were mediated by the phase of the menstrual cycle (Genzel et al., 2012). However, PL was not examined in this study.

In the current study, we examined the effects of sleep during the consolidation period on the magnitude and specificity of PL of motion direction discrimination. We also assessed sex differences in these sleep effects. We utilized a nap paradigm that controls for circadian confounds and daytime interference. Our nap paradigm also allows for exquisite control of sleep stages (i.e., naps with and without REM sleep) and can produce the same magnitude of PL as a full night of sleep (Mednick, Nakayama, & Stickgold, 2003; Mednick et al., 2002). The experimental design includes a group of subjects that rested quietly during the consolidation period but were electroencephalographically monitored to insure they did not fall asleep (quiet wake) and a group that conducted their normal daily activities (without sleep or rest) during consolidation (active wake). Our results reveal a novel interaction between sex and sleep that affects both the magnitude and specificity of PL. This interaction demonstrates differences in the mechanisms of offline consolidation of PL between men and women.

2. Methods

2.1. Subjects

150 healthy non-smoking adults between the ages of 18 and 35 gave informed consent to participate in the study. All experimental procedures were approved by the University of California, San Diego Human Research Protections Program. Exclusion criteria included: (a) irregular sleep–wake schedule; (b) sleep disorder; (c) significant psychopathology in immediate family; (d) current use of any psychotropic medications; (e) history of head injury and/or seizures; (f) history of substance dependence; (g) any other major medical condition. These exclusion criteria were evaluated based on subject self-report.

Subjects were asked to maintain their usual sleep–wake schedule during the week prior to the experiment and to refrain from consumption of caffeine, alcohol, and all stimulants for 24 h prior to the beginning of the experiment as well as throughout the study day. Heavy caffeine users were not enrolled to exclude the possibility of significant withdrawal symptoms during the experiment. Subjects completed sleep diaries during the entire week prior to the experiment and wore actigraph wrist monitors (Actiwatch-64, Respironics) the night before the experiment to provide subjective and objective measures of sleep–wake activity, respectively. We also assessed trait daytime sleepiness with the Epworth Sleepiness Scale (Johns, 1991) and evaluated circadian phase preference for morningness or eveningness with the Horne–Ostberg Morningness–Eveningness Questionnaire (Horne & Ostberg, 1976).

2.2. Stimulus and task

Visual stimuli for the motion direction discrimination (MDD) task have been previously described (Rokem & Silver, 2010) and were created using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Random dot kinetograms were presented within an annulus subtending 1.5–3.1 degrees of visual angle and centered at the fixation point (Fig. 1A). The radius of each dot was 0.03 deg, and the dot density was 17 dots/deg^2. The dots were moving at a speed of 8 deg/s, and each dot moved continuously for two monitor frames (approximately 27 ms at the 75 Hz refresh rate used) before being reassigned to another random location within the annulus. The dots were displayed at full luminance (158.9 cd/m^2). Two quadrants of the annulus, located on opposite sides of the fixation point, contained 100% coherent dot motion, and the remaining quadrants contained 0% coherent motion (Fig. 1A).

In each trial, subjects reported whether the dots in two sequentially-presented stimuli were moving in the same or in different

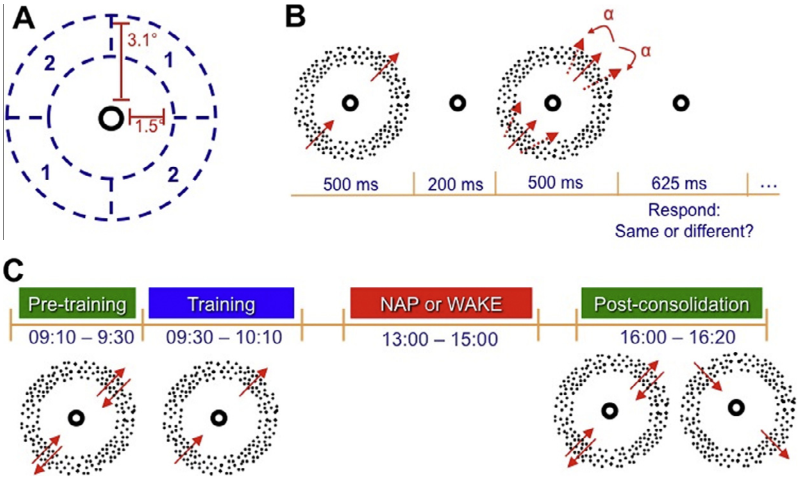

Fig. 1. Experimental procedures. (A) Stimulus configuration. Coherent motion was presented in one of two pairs of spatial locations (1 or 2), and the other pair of spatial locations contained dots with 0% motion coherence. (B) Motion direction discrimination task. In each trial, two fields of dots with 100% coherent motion were sequentially presented. The two stimuli contained either the same or slightly different directions of motion. Direction of motion is indicated by the arrows, and angular difference in motion direction is denoted here by α. (C) Experimental timeline. At 9:10, pre-training thresholds were obtained for two oblique directions of motion (in this example, 45° and 225° in location 1). One of these directions (here, 45° in location 1) was then randomly chosen to be the trained direction, and subjects performed the task with this direction/location combination for 1000 trials. Subjects then either napped or remained awake from 13:00 to 15:00. At 16:00, post-consolidation thresholds were obtained for the two directions of motion used in the pre-training measurements as well as a novel direction/location combination (in this example, 135° in location 2).