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Keeping time in your sleep: Overnight consolidation of temporal rhythm

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ABSTRACT

Temporal processing forms the basis of a vast number of human behaviours, from simple perception and action to tasks like locomotion, playing a musical instrument, and understanding language. Growing evidence suggests that these procedural skills are consolidated during sleep, however investigation of such learning has focused upon the order in which movements are made rather than their temporal dynamics. Here, we use psychophysics and neuroimaging to explore the possibility that temporal aspects of such skills are also enhanced over a period of sleep. Behaviourally, our examinations of motor (tapping a finger in time with a temporal rhythm) and perceptual (monitoring a temporal rhythm for deviants) tasks reveal post-sleep improvements in both domains. Functionally, we show that brain-state during retention (sleep or wake) modulates subsequent responses in the striatum, supplementary motor area, and lateral cerebellum during motor timing, and in the posterior hippocampus during perceptual timing. Our data support the proposal that these two forms of timing draw on different brain mechanisms, with motor timing using a more automatic system while perceptual timing of the same rhythm is more closely associated with cognitive processing.

1. Introduction

Humans spend a large proportion of their waking lives performing skilled tasks which require little attention. These include movement based activities like walking or riding a bicycle and perceptual activities like reading, understanding speech, or judging the depth of a visual scene. Careful analysis has demonstrated that many of these tasks can be broken down into independently learned temporal and ordinal elements (Ullen & Bengtsson, 2003). Furthermore, many such procedural skills have been shown to improve across periods of sleep (Born, Rasch, & Gais, 2006; Dang-Vu, Desseilles, Peigneux, & Maquet, 2006; Fenn, Nusbaum, & Margoliash, 2003; Fischer, Drosopoulos, Tsen, & Born, 2006; Fischer, Hallschmid, Elsner, & Born, 2002; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; Laureys, Peigneux, Perrin, & Maquet, 2002; Maquet et al., 2000; Maquet, Schwartz, Passingham, & Frith, 2003; Plihal & Born, 1997; Rauchs, Desgranges, Foret, & Eustache, 2005; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000; Walker & Stickgold, 2004; Walker & Stickgold, 2006). Most examinations of such off-line enhancement have focussed on the order of responses (Cohen, Pascual-Leone, Press, & Robertson, 2005; Robertson, Pascual-Leone, & Press, 2004; Spencer, Sunm, & Ivry, 2006; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). Consolidation of the temporal aspects of these tasks therefore remains largely unexplored, though one study (Maquet et al., 2003) demonstrated that the emergent timing in visuomotor tracking is strengthened over sleep. In the current report, we aim to build on this work by determining whether the event timing in skilled rhythm processing (Spencer, Zelaznik, Diedrichsen, & Ivry, 2003; Zelaznik, Spencer, & Doffin, 2000; Zelaznik, Spencer, & Ivry, 2002) also undergoes overnight consolidation, and to examine the neuroplasticity associated with such changes.

Studies of procedural learning have shown that the brain areas in which responses are enhanced as learning progresses (Doyon et al., 2009) commonly exhibit greater activity when the task is performed after sleep. This is true for both motor (Albouy et al., 2008; Walker, Stickgold, Alsop et al., 2005) and perceptual (Walker, Stickgold, Jolesz, & Yoo, 2005) forms of learning. A wide range of evidence suggests that different temporal processing mechanisms are recruited in different forms of timing task (Lewis & Miall, 2003; Rammsayer, 1999; Wiener, Turkeltaub, & Coslett, 2010; Zelaznik et al., 2002). Meta-analysis of neuroimaging studies of time perception (Lewis & Miall, 2003) shows that areas of the motor system, including striatum, cerebellum, and SMA are recruited for tasks in which timing is performed more or less automatically (e.g.,

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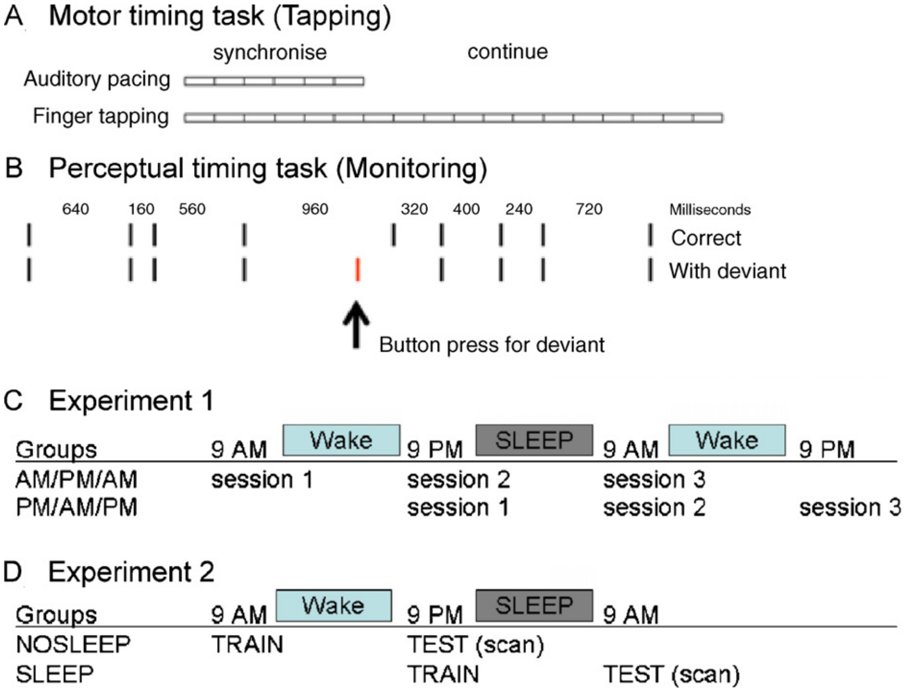

Fig. 1. Tasks and paradigms. (A) The tapping task: in each trial, participants tapped their right index finger in time with an auditory rhythm, then continued to tap the same temporal rhythm once the auditory cues had ceased. Each oblong box represents a repetition of the full rhythm sequence (or 'bar'). (B) The Monitoring task: participants listened to a repeating auditory rhythm and pressed a key when they detected a temporal deviant. Deviants were rare and consisted of an auditory beep which occurred 200 ms too early or too late, disrupting the timing of the two adjacent intervals in the rhythm. (C) The testing schedule for AM/PM/AM and PM/AM/PM groups in Experiment 1. (D) The testing schedule for sleep and wake groups in Experiment 2.

continuous, repetitive motor timing of intervals less than one second), while prefrontal and parietal regions are recruited for the more cognitively demanding timing in tasks with the opposite characteristics (e.g., discontinuous, non-motor timing of intervals greater than one second). Because many tasks encompass a combination of these characteristics, it has been proposed that elements of both timing systems can be recruited simultaneously (Lewis & Miall, 2003). The distinct yet potentially overlapping brain regions recruited during motor and perceptual timing provide a prime example of this (Bueti, Walsh, Frith, & Rees, 2008; Clarke, Ivry, Grinband, & Shimizu, 1996; Lewis & Miall, 2003; Wiener et al., 2010). Here, we explore the distinction between motor and perceptual timing by studying offline consolidation of brain activity during both types of task.

To allow examination of both motor and perceptual timing, we elected to use auditory rhythms akin to those found in music as our stimuli. In our motor paradigm, 'Tapping' (Wing & Kristofferson, 1973), participants synchronised button presses with a rhythm of auditory beeps which occurred in a repeating temporal pattern, then continued to tap the same temporal rhythm without external cues (Fig. 1A). In our perceptual paradigm, 'Monitoring', participants listened to an equivalent auditory rhythm and monitored it for rare temporal deviants (Fig. 1B), pressing a button when these were detected. We performed two experiments using these paradigms: one which examined the interaction between sleep and behavioural performance in the Tapping task, and a second which used functional magnetic resonance imaging (fMRI) to monitor sleep-related alterations in the brain responses associated with both Tapping and Monitoring tasks.

Based upon a prior analysis of the systems used in automatic and cognitively controlled timing (Lewis & Miall, 2003), we expected consolidation across sleep to modulate learning-related alterations in brain response within the movement control system (particularly the supplementary motor area (SMA), cerebellum, and striatum) during motoric rhythm tapping (Wiener et al., 2010), and in higher cognitive areas (potentially including prefrontal and parietal cortices) during perceptual rhythm Monitoring (Lewis & Miall, 2006).

2. Materials and methods

2.1. Participants

All participants were consenting, healthy, right handed, and had no history of psychiatric illness. 14 of these (7 male and 7 female, mean age 27) participated in Experiment 1, and 24 (12 male and 12 female, mean age 25, ±SEM 1 year) in Experiment 2. All participants were instructed to abstain from alcohol, caffeine, and other drugs during, and for twenty-four hours prior to, the experiment. Experiments were approved by the Liverpool research ethics committee.

2.2. Behavioural tasks

2.2.1. Experiment 1: behavioural testing

Participants performed a motor synchronisation continuation task (Wing & Kristofferson, 1973) (Fig. 1A, Tapping) in three sessions. The rhythm they learned was based on those in Lewis, Wing, Pope, Praamstra, and Miall (2004) and consisted of eight temporal intervals: 107, 429, 214, 1065, 536, 643, 321, and 857 ms, in that order, with each bar (repeating sequence of intervals) lasting 4172 ms. Each trial was initiated by a press to the spacebar, and contained a synchronisation phase immediately followed by a continuation phase. During synchronisation, the rhythm was presented via auditory beeps (250 Hz for 25 ms) and was repeated 6 times (25 s total), during continuation auditory presentation stopped and participants were exposed to 47 s of silence, terminated by a high pitched beep. Participants were instructed to synchronise right index finger button presses with the beeps during synchronisation (6 bars), then continue to press the button in the same temporal sequence during continuation (11 bars). There were 8 synchronisation/continuation trials in every session.

Fourteen participants were randomly divided into two groups, determined by the time of day at which they were trained and tested: an AM/PM/AM group (seven participants) and a PM/AM/PM group (seven participants). In the AM/PM/AM group, Session 1 was performed in the morning of day 1, Session 2 that evening, and Session 3 in the morning of day 2 (Fig. 1C). In the PM/AM/PM group, the order was reversed: Session 1 was performed on the evening of Day 1, Session 2 the next morning (Day 2), and Session 3 that evening. For these two groups, all experimental sessions began between 8:00 and 11:00 AM or 20:00 and 23:00 PM, and delays between sessions were always 12 h (±1).