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How does one night of sleep deprivation affect the internal clock?

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ABSTRACT

Twelve subjects performed two temporal tasks, one explicit (Experiment 1) and one implicit (Experiment 2) after one night of sleep deprivation and after one night of normal rest. Experiment 1 involved a 1100-ms duration production task, and in Experiment 2 subjects performed a word identification task requiring implicit estimation of vowel duration (around 150 ms). One night of sleep deprivation had the same pattern of effect on explicit timing in the suprasecond range and implicit timing in the millisecond range. Specifically, sleep deprivation induced productions of shorter intervals in the duration production task and estimation of segmental durations as being longer in the word identification task. Both results are consistent with an acceleration of pacemaker rate.

Moreover, in both experiments, we found a correlation between the alertness level of participants and the size of the effect. Therefore, sleep deprivation, which physiologically manipulates cortical arousal level, produced similar performance modulation in suprasecond explicit and subsecond implicit tasks suggesting a common mechanism.

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1. Introduction

Humans, as other animals, have the ability to perform behaviorally relevant time measurement across a wide range of intervals (for review, see Buhusi & Meck, 2005). The perception of time in the hundreds of seconds to minutes range is often referred to as interval timing and has to be differentiated from timing in the circadian range. For many years, the prevalent guiding theoretical framework for understanding how we measure the duration of intervals has proposed that we time intervals using an internal clock functioning as a stopwatch, with a clock stage composed of a pacemaker-counter device. An interval is specified by the accumulation of pulses emitted at a regular rate from a pacemaker. The more pulses that are accumulated, the longer the subjective estimation of duration.

One way of studying the clock component of the pacemaker-accumulator type is to attempt to change the rate at which the pacemaker runs. Different manipulations have already been mentioned to affect the speed of pacemaker (for review, see Wearden & Penton-Voak, 1995). In 1933, Hoagland was one of the first who reported that increases in body temperature yield to an acceleration of pacemaker rate. Later, Treisman and collaborators (Treisman, Faulkner, Naish, & Brogan, 1990; Treisman, Faulkner, & Naish, 1992) modeled a temporal pacemaker and proposed that external stimuli influence pacemaker rate, the more arousing the stimuli, the more the pacemaker rate increases. They presented participants with a train of repetitive stimulation (clicks or flashes), whilst they performed a time judgment task, and observed that participants behaved as if their internal clock had increased in speed. Similar results were later obtained by preceding stimulus presentation by a train of clicks in various tasks (Penton-Voak, Edwards, Percival, & Wearden, 1996). The same effect was found whatever the modality (visual or auditory) of the stimuli and it was more marked at longer stimulus durations, which was consistent with an acceleration of pacemaker rate. Burle and Casini (2001) demonstrated that presenting a train of clicks with strong intensity produced greater acceleration of pacemaker rate than presentation of clicks with weak intensity. In all of these experiments, it was supposed that increasing cortical arousal level with entraining sensory inputs speed up the rate of the pacemaker.

Another convenient way of modifying cortical arousal is to use sleep deprivation. Sleep deprivation is known to deteriorate a wide range of cognitive, behavioral and physiological measures (Dinges, 1992; Mertens & Collins, 1986; Pilcher & Huffcutt, 1996). For example, significant effects have been demonstrated on the Sternberg working memory task (Mu et al., 2005), Raven's matrices (Linde & Bergstrom, 1992), verbal fluency (Horne, 1988) and Tower of London (non-verbal planning) (Horne, 1988). Deteriorations in vigilance and activation, which frequently cause industrial or automobile accidents, are also often consecutive to

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sleep deprivation (Connor et al., 2002; Fairecloughand Graham, 1999). Very recently, Vyazovskiy et al. (2011) demonstrated that as sleep deprivation increases in rats, the amount of cortical neurons switching from ON state (awake-like activity) to OFF state (NREM sleep-like activity) also increases. But on the contrary, some other recent studies performed in rats or in humans, suggest that instead of decreasing cortical arousal, moderate sleep deprivation increases the excitability of cortical neurons (Huber et al., 2012; Liu, Faraguna, Cirelli, Tononi, & Gao, 2010; Vyazovskiy et al., 2009).

A decrease in cortical arousal level, which slows the pacemaker rate, should manifest as underestimation of subjective time due to fewer accumulated pulses while an increase in cortical excitability should lead to the opposite manifestation, that is overestimation of subjective time due to more accumulated pulses. The objective of the present study was to investigate the effect of sleep deprivation on the internal clock.

To this aim, two different timing tasks were used, involving either explicit (Experiment 1) or implicit (Experiment 2) temporal judgment. As proposed by Coull and Nobre (2008), "the crucial distinction between explicit and implicit timing is whether or not the task instructions require subjects to provide an overt estimate of duration (p. 137)." In the first experiment, participants performed a temporal production task where they had to explicitly time a 1100 ms interval. In the second experiment, participants perform a speech perception task. Speech perception, in which the role of segmental duration is of particular importance, is a good example of an implicit temporal task. Indeed, in many languages, it is observed that the variation in vowel duration depends on whether the following consonant is voiced or voiceless (Kingston & Diehl, 1994). For example, the /ɛ/ lasts longer in *bed* (voiced consonant) than in *bet* (*voiceless consonant*). This context-dependent variation in vowel duration has been shown to influence the perception of post-vocalic consonant voicing: following longer vowels, consonants are more often perceived as voiced than voiceless (Casini, Burle, & Nguyen, 2009; Fischer & Ohde, 1990). Moreover, the segmental durations involved in speech perception are in the range of tens to hundreds of milliseconds, whereas the temporal production task in Experiment 1 required estimation of a 1100 ms duration. In the field of the psychology of time, a distinction is often made between the processing of durations superior or inferior to one second. Some authors propose that time estimation of hundreds of milliseconds to seconds (supra-seconds durations) would be cognitively mediated whereas measurement of tens to a few hundreds of milliseconds (sub-second durations) is supposed to be of a highly perceptual nature and not accessible to cognitive control (Karmakar & Buonomano, 2007; Michon, 1985; Rammsayer & Lima, 1991). However, some behavioral data also suggest that common mechanisms are involved for both short and long durations (Rammsayer & Ulrich, 2005). As a consequence, the issue of timescale specificity is still debated and it appears relevant to check whether sleep deprivation affects the two duration ranges in a similar manner. As the segmental durations involved are around 150 ms, speech perception seems well-suited to tackle this question.

The duration production task and the speech perception task were carried out either after a normal night of rest (rest condition) or after one night of sleep deprivation (deprivation condition).

2. Experiment 1: Temporal production under sleep deprivation

Participants performed a temporal production task either after a rest night or after one sleep deprived night. Moreover, to investigate whether sleep deprivation specifically affects pacemaker rate, we also manipulated the attention level of participants. Since in a previous study (Burle & Casini, 2001) we have demonstrated that attention specifically acts on the switch device, our aim was to verify whether sleep deprivation and attention manipulations do not interact but rather are additive, which would suggest that sleep deprivation affects a different component of the internal clock, presumably the pacemaker rate. Participants therefore performed the temporal production task either as a single task or in a dual-task concurrent with a reaction time (RT) task. We also delivered click trains during duration production, as in Burle and Casini (2001). This would have allowed for the comparison of the effect of sleep deprivation, which tonically modifies brain activation level, to the effect of click trains, which are believed to phasically modify brain activation level. However, due to technical difficulties, the sound intensities applied did not match those intended. As a result, no effect of this variable was obtained even in the rest condition, and we will not refer to it further. Two factors were then crossed for results analysis in the present experiment: sleep conditions (rest or deprivation) and attentional resources (single or dual-task).

2.1. Material and method

2.1.1. Participants

Twelve participants were paid for their participation in the experiment (6 women and 6 men, mean age: 26 years, range: 21–37 years). All participants were volunteers and gave informed consent to the experimental procedure, following the Helsinki declaration (1964). The study was approved by the French Ethical Committee.

2.1.2. Procedure

Participants were seated comfortably in a dimly lit and sound-shielded room, facing a black video screen located 1 m away. A device with two response keys was available. The left index and middle fingers were used for the RT task and the right thumb was used on a single keypress for the duration production task (for a figure of the device, see Burle & Casini, 2001). All stimuli and responses were controlled by a computer running t-scope (Stevens, Lammertyn, Verbruggen, & Vandierendonk, 2006). Time production and RTs were recorded to the nearest millisecond.

Each participant performed two experimental sessions, one after one sleep deprived night and the other after a normal night's rest. Each of these sessions contained six blocks of 50 trials corresponding to two blocks of each task. The three tasks tested were: a 1100-ms duration-production task, a RT-only task, and a dual-task in which the participants simultaneously performed the duration-production task and the RT task. The order of blocks was counterbalanced across participants.

One day before the first experimental session (sleep deprived or rest night session, depending on participants), a training session for each task was performed by each participant in order to obtain reliable performance during experimental blocks. It was also important that subjects were trained on the standard duration and then build a representation of the standard duration before the sleep deprivation.

2.1.2.1. Training session

2.1.2.1.1. Duration-production training. The training session consisted of two parts. For the first five trials, a central red circle appeared on the screen indicating the beginning of the trial. Then a 600 Hz tone sounded during 1100 ms. At the end of the sound, participants reproduced the duration of the sound by pressing the keypress with the right thumb. When participants released the keypress, an auditory feedback was delivered. Five different feedbacks were used. If the produced interval was correct (less

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