



Research report

Impact of age, sleep pressure and circadian phase on time-of-day estimates

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ABSTRACT

Orientation and self-location within the temporal fabric of the environment involves multiple organismic systems. While temporal self-location on the physiological level has been known for some time to be based on a 'biological clock' located within the hypothalamus, the mechanisms that participate in temporal position finding on the cognitive level are not yet fully understood.

In order to probe the mechanisms that underlie this faculty, verbal estimates on time-of-day were collected at 3.75-h intervals from 16 young (7 males, 8 females; 20–31 years) and 16 older (8 males, 8 females; 57–74 years) subjects in a balanced crossover design during 40-h epochs of prolonged wakefulness and 40-h epochs of sleep satiation spent under constant routine conditions.

An overestimation of clock time during prolonged wakefulness was found in both age-groups, with significantly larger errors for the older group (young: 0.5 ± 0.2 h; older: 1.5 ± 0.2 h, $p < 0.05$). In both age-groups, estimation errors ran roughly parallel to the time course of core body temperature. However a significant interaction between time-of-day and age-group was observed (rANOVA, $p < 0.05$): younger subjects exhibited similar estimation errors as the older subjects after 16 h of prior wakefulness, whereas the latter did not manifest decrements under high sleep pressure.

Data collected under conditions of sleep satiation also displayed a diurnal oscillation in estimation errors and a general overestimation (young: 0.8 ± 0.2 h; older: 1.3 ± 0.3 h, $p < 0.05$). Here however, the age-groups did not differ significantly nor was there an interactive effect between time-of-day and age-group.

The effects of age, duration of wake time and circadian phase on temporal position finding are in line with predictions based on the idea that awareness about current position in time is derived from interval timing processes.

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1. Introduction

Orientation and self-location within the temporal environment plays a critical role in any organism's adaptive behavior. A well-characterized system serving this purpose on the *physiological* level is the circadian master oscillator situated within the suprachiasmatic nuclei of the hypothalamus. Drawing upon transcriptional and translational feedback loops, this structure provides the organism with information about its current position within the environmental daily light–dark cycle. Sensory inputs act as 'zeitgebers', i.e., as signals controlling the synchronized run of internal and external time (circadian entrainment) [1] and, via its neural and hormonal output signals, the master oscillator allows the organism to anticipate and prepare for changes in the physical environment

that are associated with day and night. It thereby ensures that the organism will 'do the right thing' at the right time-of-day, and it provides internal temporal organization so internal changes take place in coordination with one another [2]. Dislocations between external time and its physiological correlate as well as alterations in the phase relationships between different physiological parameters can have detrimental health-related consequences [3]. Among the many conditions that have been linked to circadian misalignment are cardiovascular, respiratory, endocrine, rheumatological, psychiatric and neurological diseases (for references see Ref. [3]).

The mechanisms that underlie temporal self-location and orientation on the *cognitive* level and their potential connections to the circadian system are still poorly understood [4–6]. Whereas some species employ information about time-of-day to anticipate food availability [7] and others use time-compensated sun compass orientation to navigate long distances [8], the competence of temporal self-location on the diurnal scale has seemingly become dispensable in humans with the advent and proliferation of precise time-telling devices. Its undiminished relevance can however

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be sensed from situations in which its function is compromised. Blatant dislocations between external time and its mental representation may occur, e.g., in association with organic and functional mental disorders (such as schizophrenia or strokes) [9] and are a hallmark of dementia [10,11], but milder and transient distortions in orientation for time and temporal self-location are part of everyday life. The bewilderment we may experience upon emerging from the fictional world of an absorbing film or the fleeting moments of perplexity we may undergo upon awakening from an unscheduled nap may serve as examples. Additional relevance for the topic arises from the proliferation of working environments in which the most important of natural time cues, illumination levels, no longer ensure reliable orientation. A better understanding of the mechanisms involved in temporal self-location may also help elucidate the basis of mental time travel (imagined projection of one's temporal position to the past or the future) and, more broadly speaking, the processes that interact to produce the distinct percept of having a stable and continuous 'self' located in – and moving across – time and space.

In spite of the diversity in approaches that address the issue of cognitive temporal orientation and self-location and that range from research on time–place learning in animals [12] to anthropological psychiatry [13], models of this faculty are coarse and little is known about the mechanisms and substrates that mediate it. The establishment of quantitative theories of temporal orientation/self-location in a diurnal context (judgments about time-of-day) is complicated by the fact, that a relationship between this capacity and interval timing, i.e., the appreciation of durations in the seconds-to-hours range is often implicitly presupposed in the human literature [14]. The assumption that humans and non-human animals in some way make use of duration judgments to infer their current location in time seems plausible. However, research on time–place learning in animals [12,15] and on timed awakening in humans [16] point to a critical involvement of entirely different processes in temporal self-location.

Here, we thus aimed at investigating the role of interval timing in temporal self-location. Specifically, we hypothesized that judgments about *durations experienced* serve a function for self-location within time which is reminiscent to the role estimates on *distances travelled* play for self-location within space. While navigating through space, humans and non-human animals continuously integrate cues from proprioception, inertial sensors and optical flow to infer distances covered and thus arrive at an estimate on their position relative to a starting point (spatial path integration). In moving through *time*, knowledge about one's current temporal location could be informed by judgments about stretches of time (i.e., durations) travelled with respect to a (temporal) starting point (temporal path integration). If this really were the case, then the inferences about temporal position drawn from duration judgments should be susceptible to factors known to modulate the latter.

Therefore, we chose to manipulate factors that are known to have a systematic impact on duration judgments and to test temporal self-location (operationalized as time-of-day judgments during temporal isolation) performed under the influence of these factors against the predictions that would ensue from the assumption of interval timing acting as sketched above (temporal path integration) in temporal position finding:

- **Circadian phase:** Based on the compression in subjectively perceived duration that reportedly accompanies decreased core body temperature [17], we expected subjects to underestimate the time spent in temporal isolation (and thus clock time) w.r.t. the average, during the lower part of the core body temperature cycle. Conversely, elevated core body temperature dilates a given interval's perceived duration, presumably leading to relatively positive deviations from actual clock time in time-of-day judgments.

- **Duration of wake time:** Increasing sleep pressure, which leads to a shortening in subjectively perceived duration [18], is expected to be reflected in a decreasing component in clock-time estimates across an epoch of extended wakefulness.
- **Age:** As a result of the expansion of subjectively perceived durations with age [19], we expect older subjects to display relatively more (w.r.t. the average) positive deviations in their clock-time estimates than younger subjects.

2. Methods

2.1. Participants

Sixteen healthy young (8 males, 8 females, mean age 25 ± 3.5 years, age range 20–31 years) and 16 healthy older volunteers (8 males, 8 females, mean age 65 ± 5.5 years, age range 57–74 years) successfully completed the study. All participants were non-smokers, free from medical, psychiatric, neurologic and sleep disorders (Pittsburgh Sleep Quality Index score ≤ 5) and average chronotypes (Horne-Ostberg Morningness-Eveningness score between 12 and 23) as assessed by screening questionnaires, a physical examination and a polysomnographically recorded screening night. An additional neuropsychological assessment ensured that none of the older volunteers suffered motor, attentional or memory impairments. Other exclusion criteria were: shift work within 3 months and transmeridian flights within 1 month prior to the study, excessive caffeine and alcohol consumption, drug use and excessive physical activity. Young female participants started the study on days 1–5 after menses onset in order to complete the entire study block within the follicular phase. All study participants gave signed informed consent; the local Ethics Committee approved the study protocol, screening questionnaires and consent form and all procedures conformed to the Declaration of Helsinki.

2.2. Protocol

The entire study consisted of two study legs of 5 days each with 2 weeks in between. During the week prior to each study leg (baseline week) participants were instructed to maintain a regular sleep–wake-cycle (bed and wake times within ± 30 min of a self-selected target time), which was verified via wrist activity monitors (Cambridge Neurotechnologies, UK) and sleep logs. The two study legs comprised two conditions: high sleep pressure (SD protocol) and low sleep pressure (NAP protocol), which were conducted in a balanced crossover design. Each study leg consisted of an adaptation night and a baseline night, followed by 40 h of either sleep deprivation or sleep satiation, and a recovery night. The sleep–wake schedules were calculated by centering the 8 h sleep episodes on the midpoint of each individual's habitual sleep time as assessed by actigraphy and sleep logs during the baseline week. Low sleep pressure was attained using 10 alternating cycles of 75 min of scheduled sleep (naps) and 150 min of scheduled wakefulness. In both the SD and the NAP protocol, wake episodes were spent under constant routine conditions (constant dim light levels, < 8 lx, semi-recumbent posture in bed, food and liquid intake at regular intervals, no cues on time-of-day. During scheduled sleep episodes, a minor shift to supine posture was allowed and lights were turned off (0 lx, for more information see Ref. [20]).

2.3. Measures

- **Temporal orientation:** Cognitive temporal orientation was assessed across the 40 h constant routine episode by prompting a verbal estimate about time-of-day every 3.75 h (centered within the phases of wakefulness during NAP and at equivalent positions during SD). A lab technician prompted the estimate via an interphone by asking the subject the standard question: "What time is it now according to your opinion?" Subjects were instructed to respond spontaneously and to avoid calculations or comparable cognitive strategies to infer actual clock time. We used a set interval as opposed to randomized intervals to sample time-of-day judgments in order to keep possible masking effects constant.
- **Core body temperature (CBT):** CBT was recorded at 20-s intervals using an indwelling rectal probe (Interstar, Cham, Switzerland; Therm, type 5500-3, Ahlborn, Holzkirchen, Germany). The temperature was displayed on a personal computer screen and continuously monitored by a lab technician. After the study, the recordings were visually inspected and artifacts resulting from removal or malfunction of the probe were excluded from further analysis.

2.4. Statistical analyses

Mean temporal orientation errors were calculated based on individual differences between clock-time estimate and actual clock time; one participant from the younger group (male, 28 years) had to be excluded from further analyses because he did not comply with the test procedure. Statistical analyses of the time course in temporal orientation errors and core body temperature respectively, were carried out using ANOVA for repeated measures (rANOVA) with Huynh-Feldt's statistics and Curran Everett's alpha-corrected *t*-test for post hoc tests. Correlations between

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