

The effects of circadian phase, time awake, and imposed sleep restriction on performing complex visual tasks: Evidence from comparative visual search

Marc Pomplun

Department of Computer Science,
University of Massachusetts Boston,
Boston, Massachusetts, USA



Edward J. Silva

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital,
Boston, Massachusetts, USA



Joseph M. Ronda

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital;
Division of Sleep Medicine, Harvard Medical School,
Boston, Massachusetts, USA



Sean W. Cain

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital;
Division of Sleep Medicine, Harvard Medical School,
Boston, Massachusetts, USA



Mirjam Y. Münch

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital;
Division of Sleep Medicine, Harvard Medical School,
Boston, Massachusetts, USA
Current address: Solar Energy and Building
Physics Laboratory,
Swiss Federal Institute of Technology Lausanne,
Lausanne, Switzerland



Charles A. Czeisler

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital;
Division of Sleep Medicine, Harvard Medical School,
Boston, Massachusetts, USA



Jeanne F. Duffy

Division of Sleep Medicine, Department of Medicine,
Brigham & Women's Hospital;
Division of Sleep Medicine, Harvard Medical School,
Boston, Massachusetts, USA



Cognitive performance not only differs between individuals, but also varies within them, influenced by factors that include sleep-wakefulness and biological time of day (circadian phase). Previous studies have shown that both factors influence accuracy rather than the speed of performing a visual search task, which can be hazardous in safety-critical tasks such as air-traffic control or baggage screening. However, prior investigations used simple, brief search tasks requiring little use of working memory. In order to study the effects of circadian phase, time awake, and chronic sleep restriction on the more realistic scenario of longer tasks requiring the sustained interaction of visual working memory and attentional control, the present study employed two comparative visual search tasks. In these tasks, participants had to detect a mismatch between two otherwise identical object distributions, with one of the tasks (mirror task) requiring an additional mental image

transformation. Time awake and circadian phase both had significant influences on the speed, but not the accuracy of task performance. Over the course of three weeks of chronic sleep restriction, speed but not accuracy of task performance was impacted. The results suggest measures for safer performance of important tasks and point out the importance of minimizing the impact of circadian phase and sleep-wake history in laboratory vision experiments.

Keywords: circadian rhythm, neurobehavioral performance, biological rhythm, visual attention, visual working memory

Citation: Pomplun, M., Silva, E. J., Ronda, J. M., Cain, S. W., Münch, M. Y., Czeisler, C. A., & Duffy, J. F. (2012). The effects of circadian phase, time awake, and imposed sleep restriction on performing complex visual tasks: Evidence from comparative visual search. *Journal of Vision*, 12(7):14, 1–19, <http://www.journalofvision.org/content/12/7/14>, doi:10.1167/12.7.14.

Introduction

Numerous factors can influence cognitive performance. For instance, the impact of sleep-wakefulness has been studied extensively on measures of attention, subjective alertness, and cognitive throughput (Bonnet, 1986; Dijk, Duffy, & Czeisler, 1992; Gillberg, Kecklund, Axelsson, & Åkerstedt, 1996; Silva, Wang, Ronda, Wyatt, & Duffy, 2010; Wilkinson, Edwards, & Haines, 1966). Time-of-day factors also significantly influence performance (Dijk et al., 1992; Silva et al., 2010; Wyatt, Ritz-De Cecco, Czeisler, & Dijk, 1999). The circadian timing system (biological clock) produces a rhythmic drive for wakefulness (and sleep) across the 24-hour day, and under normal conditions that rhythmic drive interacts with a sleep-wake homeostatic process to produce stable and high levels of alertness and cognitive performance across the roughly 16-hour waking day (Czeisler, Dijk, & Duffy, 1994; Dijk et al., 1992). Understanding how these processes independently and interactively influence performance, and the consequences of disrupted circadian rhythmicity and inadequate sleep on performance, are critical for 24-hour operations, occupations with long-duration work shifts, and safety-sensitive activities. Studying these influences may be particularly important with regard to safety-critical visual tasks such as driving a motor vehicle, performing a maintenance inspection, or monitoring a display (as required for air-traffic control and baggage screening). While the number of prior studies that have investigated how circadian phase and time awake influence visual search tasks is limited, one previous study showed that the sleep deprivation and circadian misalignment associated with night shift work impair visual selective attention in a visual search task (Santhi, Horowitz, Duffy, & Czeisler, 2007). Furthermore, in a separate study, both circadian phase and duration of time awake were found to influence visual search performance (Horowitz, Cade, Wolfe, & Czeisler, 2003). The results from those two studies suggest that during adverse circadian phases and after an extended time awake, participants do not slow down their task performance, but instead their proportion of incorrect responses increases. This finding could be

interpreted as participants being unaware of their reduced cognitive resources, despite the fact that they were receiving immediate feedback on the accuracy of their responses.

Those prior studies demonstrated that both circadian phase and time awake are important factors influencing performance on visual search, but raised additional issues that need to be addressed in order to understand better the impact of sleep-wake and circadian influences on real-world visual tasks. First, the previous studies focused on visual search tasks in which participants had to detect a pre-specified target. While such a search is a very common and natural task, it does not involve substantial encoding and retrieval of working memory content. Once memorized, the same target information is compared with the visual display data throughout the experimental session(s). Most demanding complex visual tasks, such as air-traffic control or computer-aided surgery, involve comparison and verification processes that require repeated, quick memory encoding and retrieval, together with higher cortical functions such as decision-making. Without any knowledge about the effects of circadian phase and sleep variables on such complex tasks, the applicability of laboratory results to real-world scenarios is limited.

The observation from prior studies that error rate rather than response time is affected by circadian phase and time awake has substantial practical implications and requires explicit investigation. There is now an extensive literature demonstrating that response time on a simple visual attention task is profoundly affected by both time awake (Dinges & Powell, 1985; Doran, Van Dongen, & Dinges, 2001; Wyatt et al., 1999) and circadian phase (Lee et al., 2009; Silva et al., 2010; Wyatt et al., 1999). Thus, the finding that on visual search tasks response time is relatively unaffected by time awake and circadian phase suggests that a more complex visual search task that requires working memory encoding and retrieval should be investigated to understand whether the inclusion of higher-level cognitive operations in such a task impacts response time (as in simple visual attention tasks), accuracy (as in simple search tasks), or both. This would not only advance the interpretation of findings on speed vs. accuracy tradeoffs in prior sleep/circadian rhythm

studies, but it may also help to develop approaches for error reduction in safety-critical visual search tasks.

The present work addresses both points—studying complex visual tasks and analyzing the relationship between speed and accuracy of task performance—by employing two tasks from the paradigm of comparative visual search (Fuller et al., 2006; Gottlob, 2006; Pomplun, 1998; Pomplun, Reingold, & Shen, 2001; Pomplun, Sichelschmidt et al., 2001). In a typical comparative visual search task, the stimulus display shows two nearly identical image panels side-by-side. The participant's task is to find the only difference between the two panels, such as the shape or orientation of one of the objects. In order to perform such a task, the participant has to repeatedly memorize information from one of the panels, switch his or her attention and gaze to the corresponding area in the other panel, and then compare the local display content with the memorized information. If the participant fails to detect a difference, s/he has to memorize new information, switch his or her gaze between panels again, and perform another comparison. This process is repeated until either the mismatch has been found, the participant determines that there is no mismatch (if this was an option), or the trial times out.

The comparative search task thus involves both a global search process aimed at scanning the entire display for the mismatch, and the local comparison processes required to detect the mismatching objects. This combination of attentional control with rapid visual working memory encoding and retrieval over an extended period of time qualifies comparative visual search as a paradigm for studying the performance of demanding real-world tasks. Comparative search has been used to study the relationship between attention and working memory (Hardiess, Gillner, & Mallot, 2008; Inamdar & Pomplun, 2003), cognitive impairment in schizophrenia (Fuller et al., 2006), and age-related cognitive decline (Gottlob, 2006).

In the present work, we used two variants of a comparative visual search task, termed the *copy task* and the *mirror task*, to address the questions outlined above. Both tasks use displays of solid triangles as stimuli, each of which point either to the left or to the right (see Figure 1). In the copy task, the right display panel is a translational copy of the left one, except for exactly one mismatch. In the mirror task, the right panel is a mirror image of the left one, i.e., it is horizontally flipped. As in the copy task, the mismatch in the mirror task consists in a single flipped triangle. Based on previous research using comparative visual search (Pomplun, 1998), we expected participants' performance to be slightly poorer in the mirror task than in the copy task, due to the additional operations on mental imagery required in the mirror task. In the copy task, participants only need to memorize local

image information superficially and look for any difference *popping out* at them when they switch their gaze between display panels. Because there is a constant horizontal offset between corresponding triangles and the display content—except for the mismatch—is identical in each panel, it is easy to mentally superimpose the memorized information with the corresponding display objects and check for any discrepancies.

However, in the mirror task, deeper memorization is necessary in order to mentally flip the visual working memory content. This flipping operation is required to match a local configuration of objects with its counterparts because no direct matching of display information is possible—both the relative locations and orientations of triangles differ between display panels. Such operations on mental imagery have been extensively studied, particularly with regard to mental rotation, which can be considered among the most prominent experimental paradigms in cognitive psychology, e.g., Shepard and Metzler (1971); see Shepard and Cooper (1982) for a review. In their original study, Shepard and Metzler (1971) presented participants with two side-by-side line drawings of three-dimensional objects. The participant's task was to decide whether these objects were identical or mirror images of each other. This task was non-trivial because the two images would usually show the objects from different viewing angles, and this angular disparity was along the x -, y -, or z -axis. The crucial finding from these studies was that the participants' response time increased linearly with greater disparity in the viewing angle, suggesting that participants mentally rotated one of the images to align it with its counterpart. These results imply that mental image transformations are actually carried out in a way similar to physical object manipulations. Regarding the mirror task in the present study, we assume that participants need to complete a mental *flip* operation before any comparison of local display content can occur. If this operation were affected by circadian phase, time awake, or both, it is possible that completing this mental flip could take longer at adverse circadian phases or longer durations awake. In the copy task, on the other hand, we hypothesized that the feasibility of superficial matching may lead to results similar to those from previous visual search studies (Horowitz et al., 2003; Santhi et al., 2007), in which adverse circadian phase or time awake conditions did not lead to slower performance but instead led to less accurate task performance.

Our study design involved circadian manipulation in a month-long controlled laboratory environment, during which time there were 3 weeks of limited sleep opportunity in order to accumulate chronic sleep restriction. The design allowed us to independently study the effects of circadian phase, time awake, and

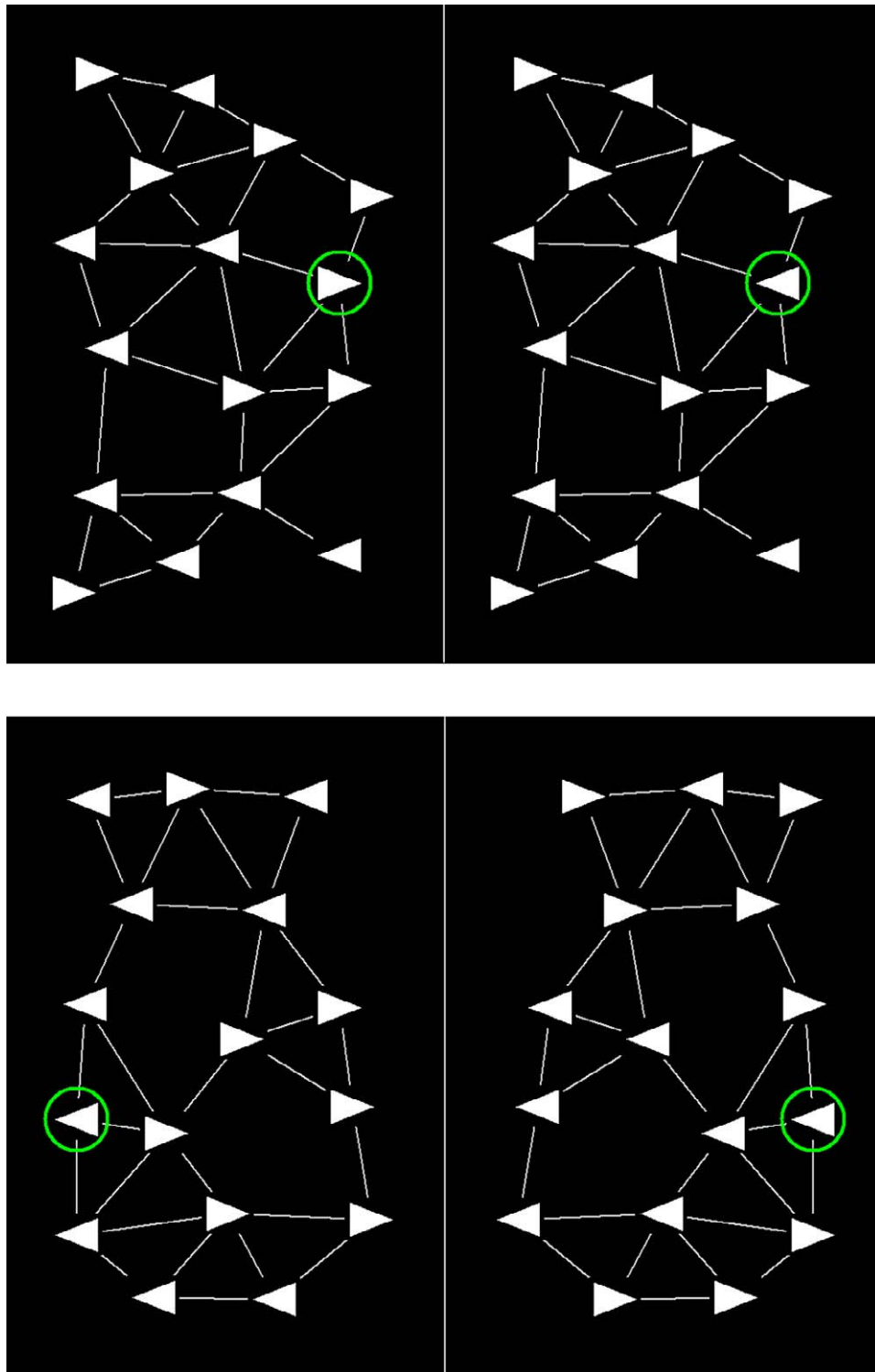


Figure 1. Example stimuli for the comparative visual search task, with green circles indicating the target objects. These circles were not shown during the task but were used to provide feedback to the participants after they had responded by button press. Upper panel: In the copy task, participants were instructed to detect the only mismatch between two translational copies of the same display, which consisted of one of the triangles pointing in a mismatching (opposite) direction (left vs. right). Lower panel: In the mirror task, participants were instructed to find the only mismatch between two mirrored copies of the same display, which consisted of one of the triangles pointing in a mismatched (same) direction (left vs. right).

prolonged sleep curtailment on performing each of the comparative search tasks—one that demanded mental image transformation (mirror task) and one that did not (copy task) to determine the influence of those variables on complex visual tasks involving the interaction of attention and working memory. We hypothesized that with increasing time awake and at adverse circadian phases, performance would slow, as has been shown for several types of performance tasks (Lee et al., 2009; Wyatt et al., 1999). We further hypothesized that as chronic sleep restriction accumulated over the three weeks, performance at adverse circadian phases and at longer wake durations would be further slowed (Cohen et al., 2010; Silva et al., 2010).

Methods

Participants

Included in these analyses are data from 12 healthy young adults (age 22.8 ± 2.3 years, range 19–27 years; six men, six women). The participants were medically and psychologically healthy as assessed during a screening evaluation prior to study, which included a physical examination, clinical biochemical tests on blood and urine, and an electrocardiogram to rule out current acute or chronic medical illness; psychological questionnaires and a screening interview with a clinical psychologist or psychiatrist to rule out current or past psychopathology; and an overnight polysomnographic sleep screen to rule out sleep disorders. None were regularly taking medications, and for at least one week prior to the study the participants were instructed to abstain from caffeine, nicotine, alcohol, and all prescription and over-the-counter medications. Compliance was verified by comprehensive toxicological analysis of their urine at laboratory admission.

Participants with a history of night shift work within the past year were excluded, as were participants who had traveled across more than two time zones in the three months prior to the study. To ensure that participants were well-rested before the start of the study, all participants were instructed to maintain a regular (± 30 minutes) sleep-wake schedule with 10 hours in bed per night for the three weeks prior to study; compliance with this regular schedule was verified with a wrist activity monitor (Actiwatch-L, Philips Respironics, Murrysville, PA).

The studies were conducted in accordance with the principles outlined in the Declaration of Helsinki and were reviewed and approved by the Human Research Committee of the Partners HealthCare System. Each

participant provided written informed consent prior to starting the study.

Apparatus and procedure

The inpatient study began with six baseline days during which the participants were scheduled to 16 (first 3 days) or 10 (following 3 days) hours per day in bed. The baseline was followed by three weeks of chronic sleep restriction (CSR), during which time participants lived on 28-hour “days” (6.5 hours in bed per 28 hours, equivalent to 5.6 hours in bed per 24 hours) with sleep episodes beginning 4 hours later each CSR-day (see Figure 2). The CSR was followed by a nine-day recovery segment (data not included in the present analysis). During the study, each participant lived in an environment free of time cues in a private study room in the Intensive Physiological Monitoring Unit of the Brigham and Women’s Hospital Center for Clinical Investigation, part of the Harvard Catalyst Clinical and Translational Science Center. Ambient light intensity during all scheduled wake episodes was dim [0.0087 W/m^2 (roughly 3.3 lux) at 137 cm from the floor facing towards the white walls, with a maximum of 0.048 W/m^2 (roughly 15 lux) at 187 cm from the floor facing towards the ceiling-mounted light fixtures] to minimize the ability of the circadian system to entrain to the imposed sleep-wake schedule and to minimize the alerting effects of light. In order to ensure the participants remained awake throughout their scheduled wake episode, during the three weeks of CSR there was a technician present in the participants’ rooms throughout each scheduled wake episode. During free time between tests, participants were allowed to pursue sedentary activities in their study room, which typically included reading, listening to music, watching videos, pursuing hobbies, or interacting with the technician.

Beginning approximately 3 hours after scheduled waketime, participants were administered roughly 25-minute computerized neurobehavioral performance test batteries at 2-hour intervals. Every other test battery (beginning with the second test battery) included a session of the Comparative Visual Search (CVS) task, resulting in four CVS test sessions per CSR-day, at approximately 5, 9, 13, and 17 hours after scheduled wake time. Test batteries also included other performance tests, whose data will be reported elsewhere.

Participants were oriented to study procedures and were trained on the performance battery tests on the admission day; that training included instructions pertaining to posture and positioning at a standard workstation during the testing. In a seated position, participants were approximately 60 cm from the

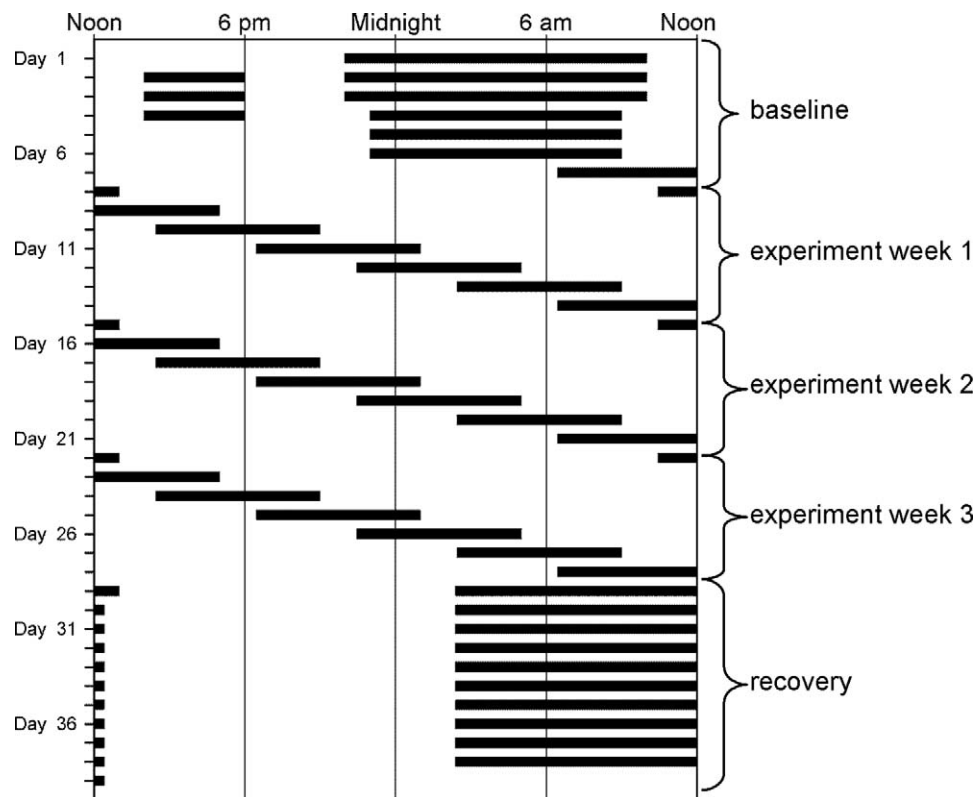


Figure 2. Raster plot of the inpatient study. Horizontal axis represents time of day and is 24 hours in length. Each line represents one study day and each day is plotted beneath the previous day. Black boxes indicate scheduled sleep opportunities. Following six baseline days (10–16 hours of scheduled sleep opportunity per 24 hours), participants were scheduled to live on 28-hour “days” for 3 weeks, with each day scheduled to begin 4 hours later than the previous day. During these 3 weeks, chronic sleep restriction was imposed, with 6.5 hours of scheduled sleep opportunity each day (equivalent to 5.6 hours/24 hours) and 21.5-hour wake episodes. After the chronic sleep restriction segment, a 9-day recovery segment (10 hours of scheduled sleep opportunity per 24 hours) was scheduled.

monitor screen, which was 32.4×24.2 cm ($32^\circ \times 24^\circ$ of visual angle) with a resolution of $1,024 \times 768$ pixels.

Stimuli

In the CVS task, each half of the display contained 16 objects, which were randomly distributed over a rectangular area of 12.8° of visual angle horizontally and 21.2° vertically, with a separation of 3.1° between the halves (see Figure 1). The objects were white triangles (1.5° wide and 1.2° tall) that pointed either to the left or to the right, had a minimum distance of 3° between their centers, and were presented on a black background. Each object in the left half had a counterpart at the corresponding position in the right half. Neighboring objects were connected by gray lines to facilitate comparison of the two halves. In the copy trial type, the two display halves were perfect translational copies of each other, except for one triangle that pointed in a different direction (left vs. right) than its counterpart in the other half. In the mirror trial type,

the halves were mirrored copies of each other, and again one triangle was mismatched, that is, it pointed in the same direction as its counterpart. The stimulus displays were created by first generating one stimulus half with 16 triangles (eight triangles pointing in each direction), then placing a perfect (translational or mirrored) copy in the other half and finally flipping the direction of one triangle that was randomly chosen from the entire display. The display was (invisibly) divided vertically into four equal-sized intervals, and there were always four objects in each interval and display half. In the 16 trials of the same trial type within a session, the target occurred four times in each of the four intervals.

Procedure

Each session of the CVS task started with written task instructions on the screen, followed by a total of 34 trials. Before the first trial of each type in a given session, one practice trial was administered. Each

session of the task consisted of four blocks of eight trials (two blocks of the copy task, two blocks of the mirror task), and started with a randomly chosen trial type, followed by blocks of alternating types. If participants responded too quickly (< 400 ms) to any trial, it was counted as an anticipation rather than an actually performed trial and was repeated within the same block. If participants did not respond within 30 seconds, the trial timed out, and the next trial was started.

In each trial of the CVS task, participants were first informed about the trial type by the word “copy” or “mirror” at the top of the screen. After 1 second, this text was replaced by the stimulus display. Participants were instructed to search the display from top to bottom, and if they did not detect the mismatch, to start again at the top. Once they detected the mismatch, they were to report the direction of the mismatching triangle in the right display half by pressing one of two buttons labeled “LEFT” and “RIGHT.” After responding, a pair of circles that indicated the target object in both display halves was shown. If the participant had reported the correct orientation, these circles were green, otherwise they were red (see [Figure 1](#)).

Data analysis

Time awake

In cases when scheduled tests were delayed due to technical problems, we used in our analyses the actual time that the test was taken rather than the scheduled time. Each test was coded with an elapsed time since scheduled wake time, and tests were then binned into four 4-hour bins of approximately 5, 9, 13, and 17 hours awake.

Circadian phase

All tests from the CSR segment of the study were also coded with the circadian phase. To do this, we collected core body temperature data at 1-minute intervals throughout the CSR segment. After the study was complete, these data were assessed for intrinsic circadian period (Czeisler et al., 1999; Duffy et al., 2011), and the first core body temperature nadir was identified and assigned a circadian phase of 0° . Using this information, together with the intrinsic circadian period, each minute of the CSR segment was then assigned a circadian phase between 0° and 359° from which the circadian phase of each test was estimated. The tests were then binned in 60° circadian phase bins (equivalent to 4 hours) centered on the assigned bin (e.g., the 0° circadian phase bin covered the range of 330° to 30°).

Experiment week

Each test was also binned by experiment week. Each week consisted of six 28-hour “days” (equivalent to 7 calendar days), with each week beginning at the same clock hour (see [Figure 2](#)).

Adjusted response time

When evaluating task performance in psychophysical tasks, both response time (RT) and response accuracy need to be considered. In the present study, three types of response outcomes could occur in each trial: (a) a correct response (left vs. right); (b) an incorrect response; or (c) no response (the trial timed out). Because time-outs could be due to the participant’s inattention or briefly falling asleep, we excluded them from analysis; time-outs accounted for 2.1% of the trials. After this exclusion, 25,720 trials remained in the dataset for analysis. Response accuracy was computed as the proportion of correct responses among the analyzed trials, with an overall average of 95.8%.

A common problem in performance analysis is the possibility that participants may, under some conditions, respond faster at the cost of accuracy or respond more accurately at the cost of response time. In the current study, the correlation between RT and the proportion of trials with correct responses across tasks and participants was $r = -0.353$, which argues against a strong prevalence of a consistent speed-accuracy trade-off. Due to this finding and the generally high response accuracy, we did not separately analyze accuracy but instead combined accuracy with RT into a single performance measure (Smilek, Enns, Eastwood, & Merikle, 2006; Watson, Brennan, Kingstone, & Enns, 2010). For each participant, we divided the average RT for correct responses by the proportion of trials with correct responses. The resulting *adjusted RT* equaled RT if a participant gave 100% correct responses and it increased with lower accuracy. All RT analyses reported below are based on the adjusted RT measure. The use of this measure did not change the pattern of results compared to RT alone.

Search speed and proportion of target misses

In the comparative visual search task, response accuracy is not indicative of the thoroughness or efficiency of a participant’s search. Because participants knew that every display contained a target, they should have kept searching until they found it. Therefore, response accuracy is not related to whether participants found the target in their first top-to-bottom scan or had to search the display more than once. For example, some participants may scan the display very quickly and consequently miss the target quite often during their first scan of the display, while others may proceed

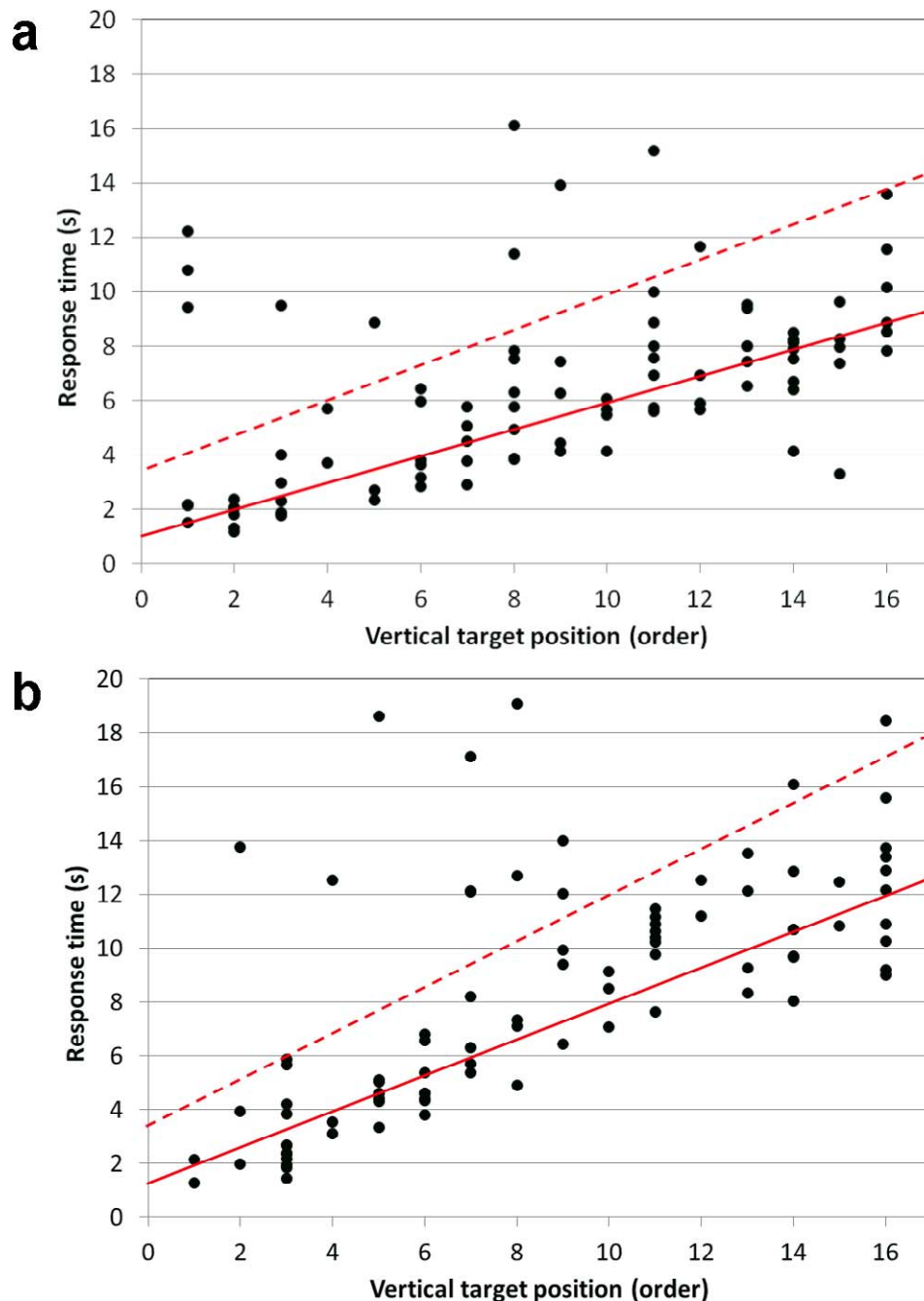


Figure 3. Two examples of RT, taken from the same participant and different experimental conditions, plotted against the vertical order (from top to bottom) of the target among the 16 search items. The straight lines indicate the result of the linear regression, and samples above the dotted lines are estimated to include target misses. (a) Copy task, 5 hours awake, circadian phase 240° , week one; estimated processing time per item: 481 ms, estimated misses: 11%; (b) mirror task; 5 hours awake, circadian phase 60° , week one; estimated processing time per item: 675 ms, 12% misses.

more slowly and rarely miss the target during the first scan. In order to obtain a more fine-grained insight into how participants perform the task, we measured these characteristics, search speed and proportion of target misses, and how they might be influenced by the independent variables.

The experimental procedures did not allow us to record the participants' eye movements, which would have enabled a direct measurement of search speed and target misses. Because participants were instructed to search the displays from top to bottom, we estimated search speed and the proportion of target misses by analyzing RT as a function of the vertical target position. To

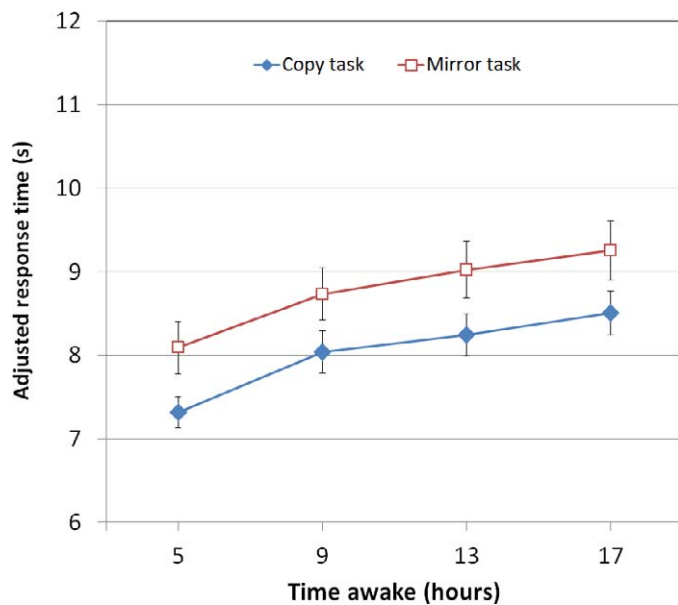


Figure 4. Adjusted RT (mean \pm standard error of the mean) for the four levels of Time Awake in the copy (filled blue diamonds) and mirror (open red squares) versions of the task.

derive a speed estimate, we computed a linear regression of (nonadjusted) RT as a function of the vertical order of the target on the screen within the set of 16 search items. If the target were the topmost search item on the screen, its assigned position was one, and if it were the bottom item, its assigned position was 16. In order to avoid outliers influencing the regression, particularly trials with target misses, a modified regression algorithm determined from a regression line that included a maximum of the data points within a tolerance range

(minimizing the mean square error) was applied. The tolerance range increased linearly with greater order, i.e., longer searches. Because the number of samples for each participant and condition was relatively small (< 100) for estimating individual tolerance ranges, common ranges for the entire dataset were determined by visual inspection of the data (Pomplun, 1998; Pomplun, Sichelschmidt et al., 2001). The most plausible results were found for the following tolerance:

$$\text{Tolerance} = 1000 \text{ ms} + \text{vertical target order} \cdot 100 \text{ ms}$$

Trials whose RT exceeded the regression line by twice the tolerance were considered to include at least one target miss (that is, the response time for a correct response suggested that the participant missed the target on the first search path and had to begin the search again). Figure 3 shows two examples of this analysis for the same participant under different experimental conditions (copy task, 5 hours awake, circadian phase 240° , week one vs. mirror task, 5 hours awake, circadian phase 60° , week one). While there is a linear trend in the data, the results of this analysis can only be considered rough estimates of search speed and proportion of target misses. To reduce the noise in the data, only those regressions that included more than 50% of trials within its double-tolerance range were included in further analysis.

Statistical tests

The participants' performance, indicated by adjusted RT, was first assessed through analyses of variance

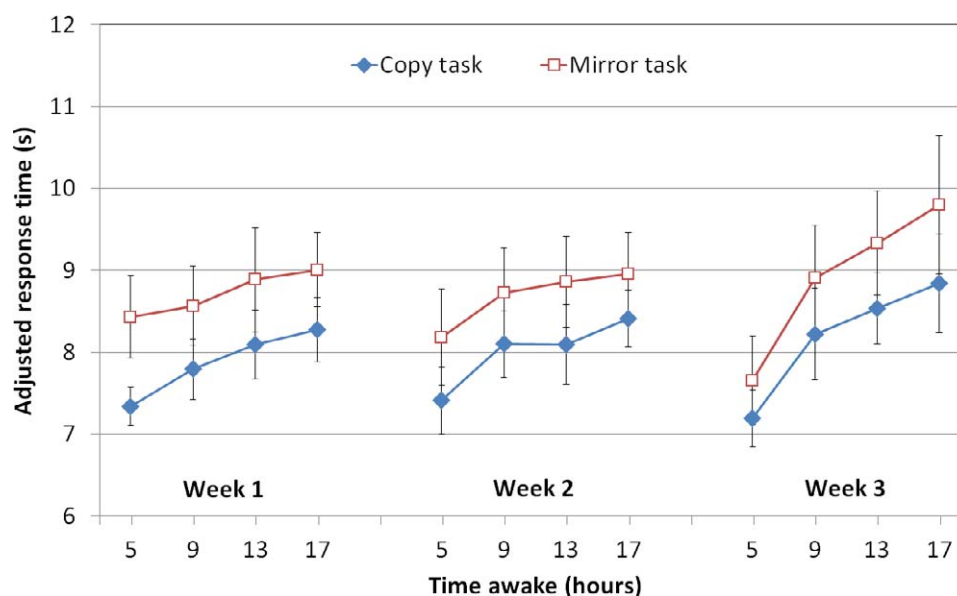


Figure 5. Adjusted RT for the four levels of time awake for each of the three experiment weeks for the copy (filled blue diamonds) and mirror (open red squares) versions of the task.

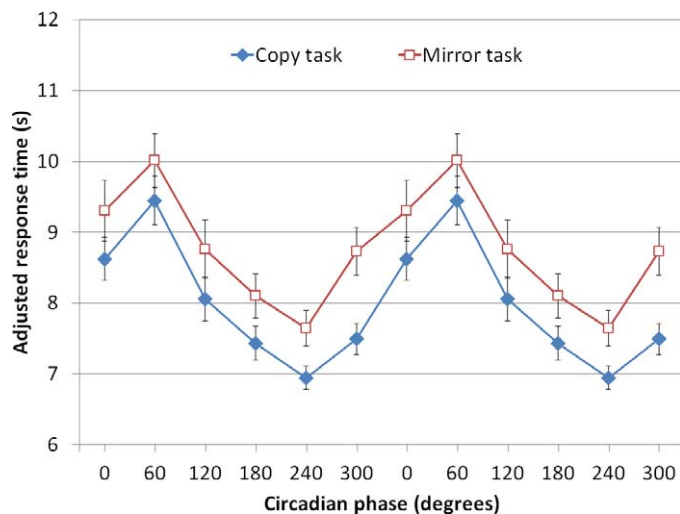


Figure 6. Adjusted RT with respect to circadian phase from 0–360°, with 0° corresponding to the core body temperature nadir, which under normal entrained conditions occurs approximately 2 hours before usual wake time in young adults. For better illustration, the data are double plotted with respect to circadian phase. Filled blue diamonds (mean \pm SEM) indicate copy task, while open red squares indicate mirror task.

(ANOVAs) testing for the main effects of time awake (a sleep-wake homeostatic process), circadian phase (circadian process), and experiment week, all of which were treated as categorical, rather than continuous, variables. We also tested all possible two-way interactions.

Additional ANOVAs were conducted to test specific hypotheses and to assess the magnitude of the effects of

sleep-wake dependent and circadian variables on the participants' performance. In most of our analyses, we intended to demonstrate the maximum impact that sleep-wake dependent and circadian variables can have under laboratory conditions in order to demonstrate the potential benefit of controlling for these influences. In most laboratory vision experiments, the participants are students who often have irregular sleep schedules and thus at the time of their experiment session may vary greatly in their circadian phase, time awake, or recent sleep-wake history. Therefore, in our analyses we focused on the extreme values of time awake (5 hours vs. 17 hours), circadian phase (60° vs. 240°), and experiment week (week one vs. week three). These post-hoc comparisons were made using paired *t*-tests.

Results in all figures are presented as mean \pm standard error, with all observations first averaged within and then across participants. For all statistical tests, the critical significance level is defined as $\alpha = 0.05$. All reported degrees of freedom and *p*-values are from the final statistical model for each measure. All statistical analyses were conducted using SPSS Statistics V17.0 (SPSS, Inc., Chicago, IL; www.spss.com).

Results and discussion

Adjusted response time

Adjusted RT was analyzed using a four-way repeated-measures ANOVA with the factors Task, Time Awake, Circadian Phase, and Experiment Week.

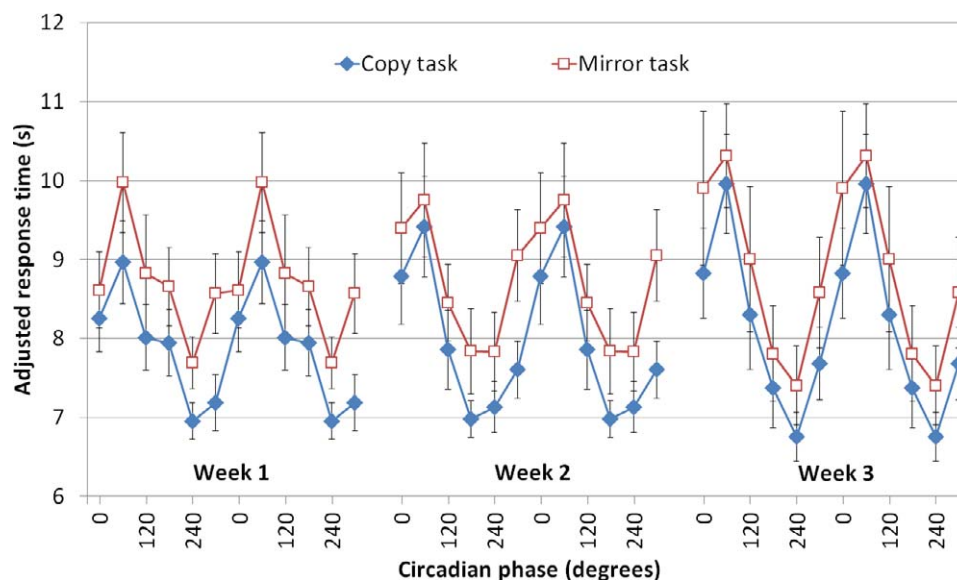


Figure 7. Adjusted RT as a function of circadian phase for each of the three experiment weeks. For better illustration, the data for each week are double plotted with respect to circadian phase. Filled blue diamonds (mean \pm SEM) indicate copy task, while open red squares indicate mirror task.

The copy task had shorter adjusted RTs than the mirror task (8.00 vs. 8.75 s), $F(1, 11) = 6.42$, $p < 0.05$, with no interaction between the factors Task and Experiment Week, $F(2, 10) < 1$, $p > 0.5$. There was an overall significant effect of elapsed time between waking up and performing the task (Time Awake), $F(3, 9) = 13.10$, $p = 0.001$, which did not interact with the Task, $F(3, 9) < 1$, $p > 0.5$. As shown in Figure 4, adjusted RT increased monotonically with longer Time Awake, with the largest increase occurring between 5 and 9 hours awake.

The pattern of increased adjusted RT with longer Time Awake varied significantly across Experiment Weeks, as demonstrated by a significant interaction of the factors Time Awake and Experiment Week, $F(6, 6) = 14.35$, $p < 0.005$. Figure 5 suggests that this interaction is due to the effect of Time Awake on adjusted RT increasing over the course of the experiment, i.e., with longer exposure to sleep restriction. Post-hoc tests revealed that the increase in adjusted RT between 5 and 17 hours awake was not significantly different between weeks one and three in the copy task, $t(11) = 1.1$, $p > 0.2$, but was significantly greater in week three than in week one in the mirror task, $t(11) = 2.39$, $p < 0.05$. These results suggest that sustained sleep restriction (between weeks one and three) amplifies the performance degradation caused by longer time awake within a day (between 5 and 17 hours awake), and this degradation in performance may be greater for tasks involving higher-level processes such as mental image transformation (as in the mirror task).

The factor Circadian Phase (levels 0° , 60° , 120° , 180° , 240° , and 300°) had a significant main effect on adjusted RT, $F(5, 55) = 14.92$, $p < 0.001$ (see Figure 6). Consistent with previous studies in which performance across all circadian phases was examined (Cohen et al., 2010; Dijk et al., 1992; Duffy, Dijk, Klerman, & Czeisler, 1998; Lee et al., 2009; Silva et al., 2010; Wyatt et al., 1999), performance was worst at approximately 60° , i.e., near usual wake time under entrained conditions, and best at approximately 240° , i.e., approximately 12 hours opposite that time. The interaction of Task type and Circadian Phase was not significant, $F(5, 55) = 1.51$, $p > 0.2$, indicating that performance on both versions of the Task was affected similarly by Circadian Phase.

In order to test whether the Circadian Phase effect on performance was influenced by Experiment Week, we performed an analysis similar to the corresponding one for Time Awake, again focusing on the extreme values of Circadian Phase and Experiment Week. For each task and for weeks one and three of the experiment, the influence of Circadian Phase was measured as the difference in adjusted RT between phases 60° (typically worst performance) and 240°

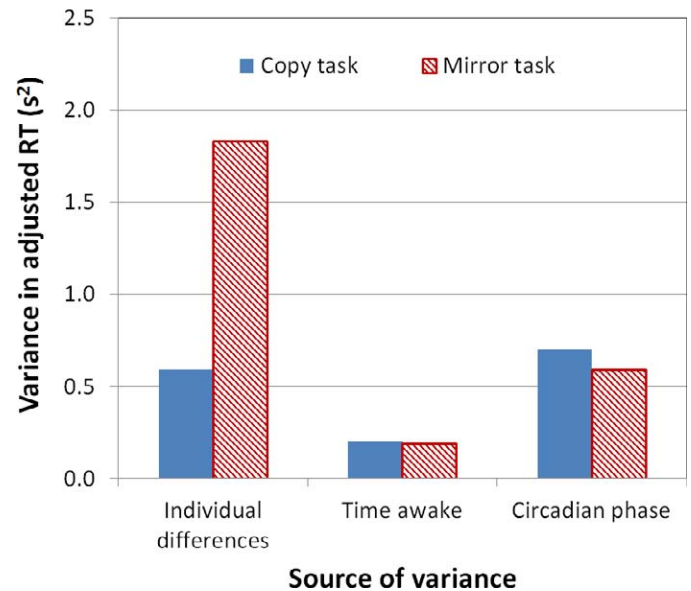


Figure 8. Amount of variance in adjusted RT attributable to individual differences (from baseline data only), time awake (from the three experiment weeks), and circadian phase (from the three experiment weeks) for the copy (blue) and mirror (red) tasks.

(typically best performance). While there was a tendency toward greater influence of Circadian Phase in week three as compared to week one, $F(1, 11) = 3.76$, $p = 0.079$, neither the main effect of Task nor the interaction of the two factors reached significance, both $F_s(1, 11) < 1$, $p_s > 0.5$. Figure 7 illustrates adjusted RT as a function of both Experiment Week and Circadian Phase. Finally, we found that there was no significant interaction between the factors Circadian Phase and Time Awake, $F(15, 165) < 1$, $p > 0.5$.

Intersubject variance in performance

In order to estimate the magnitude of the intersubject variance in performance due to individual differences, we used data from baseline day trials only in order to minimize potential individual differences in response to imposed sleep restriction. Observations from baseline days one through three were excluded from analysis in order to account for an adjustment period to laboratory conditions and also for orienting participants to the CVS tasks. After this exclusion and the exclusion of time-outs, the baseline data set consisted of 2,259 trials. As illustrated in Figure 8, the performance variance across participants for the copy and mirror tasks was 0.59 and 1.83 s², respectively.

We next compared these intersubject baseline variance estimates to variance estimates associated with Time Awake and Circadian Phase from the three CSR

Experiment Weeks. Variance along the levels of Time Awake and Circadian Phase was computed for the three CSR Experiment Weeks based on the four or six values of adjusted RT, respectively, averaged across all participants and all other factors. The performance variance introduced by the four levels of Time Awake was 0.20 and 0.19 s^2 for the copy and mirror tasks, respectively (Figure 8). Finally, the variance induced by Circadian Phase was 0.70 and 0.59 s^2 for the copy and mirror tasks, respectively (Figure 8). In all cases, the differences in variance between the factors failed to reach statistical significance, all $ps > 0.1$, likely due to the small sample sizes (for Circadian Phase only 6; for Time Awake only 4). Nevertheless, the variance data suggest that in the copy task, similar amounts of variance were induced by individual differences and by circadian phase.

Effect of vertical target position on adjusted response time

In order to examine whether the effects of circadian and wake-dependent influences on performance are particularly strong in trials involving the comparison of many objects, and thus demanding sustained operation of visual attention and working memory, we divided all of the experimental trials into two groups based on whether the search target was located in the upper half or the lower half of the stimulus screen. In this analysis, copy and mirror trials were merged. Because participants were instructed to search the display from top to bottom, the trials with targets in the lower half should have induced longer response times, and this was confirmed, as the average adjusted RT was 6.7 and 10.2 s for upper- and lower-half targets, respectively, $F(1, 11) = 89.30$, $p < 0.001$. Except for the absolute difference in adjusted RT between the trials with targets in the upper and lower half, their dependence on Time Awake, Circadian Phase, and Experiment Week and their interactions did not differ significantly, all $Fs < 1.43$, $ps > 0.2$ (see Figure 9). Thus, our findings suggest that performance of slightly longer tasks does not disproportionately deteriorate under adverse conditions.

Effect of horizontal target position on adjusted response time in the mirror task

To address whether making individual cognitive operations more demanding, rather than increasing their number, will lead to particularly strong deterioration of performance under adverse circadian and prior wakefulness conditions, we studied how performance was influenced by the horizontal position of the search target in the mirror task. In this task, if the target is on the left

side of the left stimulus panel, its counterpart is on the right side of the right stimulus panel, i.e., there is a large spatial separation between the targets. If, on the other hand, the target is on the right side of the left stimulus panel, its counterpart is on the left side of the right panel, leading to a small target separation.

Detecting targets with larger separation imposes greater demands on both attentional control and working memory because switching attention between corresponding objects across panels involves a greater visual angle and longer saccade duration (Hardies et al., 2008; Inamdar & Pomplun, 2003). We therefore examined mirror-task trials with small vs. large separation (25% of all trials with smallest or largest separation, respectively) for influences of Time Awake, Circadian Phase, and Experiment Week.

A four-way ANOVA with factors Target Separation, Time Awake, Circadian Phase, and Experiment Week indicated that Time Awake only slightly affected adjusted RT for mirror trials with small Target Separation (7.3 s for 5 hours awake vs. 7.9 s for 17 hours awake, $F(1, 11) = 1.96$, $p = 0.076$) but significantly influenced adjusted RT for trials with large separation (9.0 s for 5 hours awake vs. 10.7 s for 17 hours awake, $F(1, 11) = 4.90$, $p < 0.05$, see Figure 10a). There was no differential effect of Circadian Phase on adjusted RT for small vs. large target separation trials, $F(1, 11) < 1$, $p > 0.5$, and no effect of Experiment Week on small vs. large Target Separation trials, nor any significant interactions, all $Fs(1, 11) < 1$, $p > 0.5$. While Experiment Week did not have a significant main effect on adjusted RT, $F(2, 22) < 1$, $p > 0.5$, it showed a tendency toward an interaction with Target Separation, $F(2, 22) = 2.83$, $p = 0.08$. This finding was due to the fact that for small target separation, adjusted RT improved from 8.0 s in week one to 7.6 s in week three, whereas for large separation, it deteriorated from 9.6 to 10.5 s (Figure 10b).

All together, we found that increasing the working memory and attentional control demands of the task (large vs. small target separation) led to a tendency toward greater degradations in performance with longer sleep restriction and longer time awake, but did not amplify the effect of circadian phase.

Search speed and proportion of target misses

Our final analysis tested whether the additional, higher-level mental *flip* operation in the mirror task would slow search under adverse time awake and circadian phase conditions and thereby keep accuracy more stable than in the copy task. For this analysis we examined the processing time per item and the percentage of missed targets (with *missed*

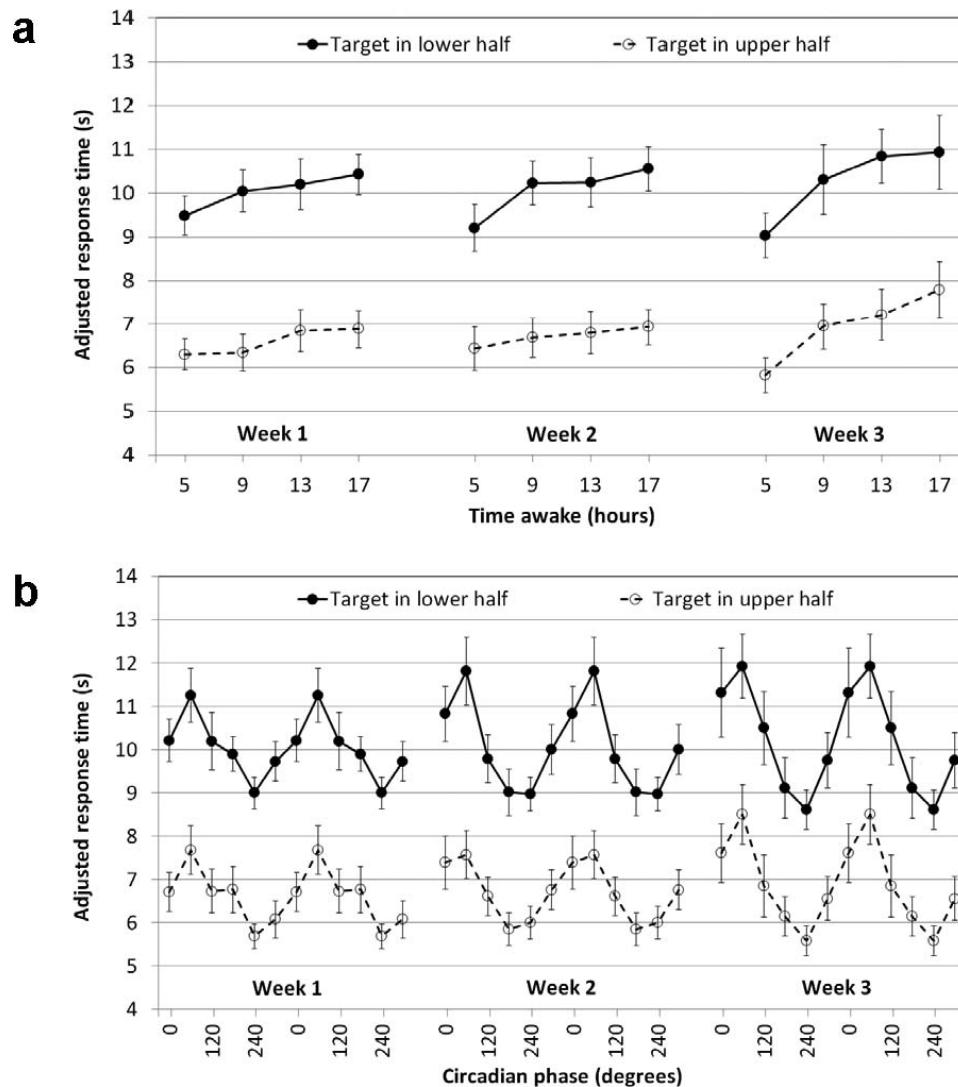


Figure 9. Adjusted RT according to target location, averaged over the two tasks. Open symbols and dashed line represent targets located in the upper half of the display, filled symbols and solid line represent targets in the lower half of the display. (a) Adjusted RT according to target location as a function of time awake for each of the three experiment weeks; (b) adjusted RT according to target location as a function of circadian phase for each of the three experiment weeks. The data are double plotted with respect to circadian phase for each week.

targets defined as those correct responses that had RT longer than two times the expected duration; see [Methods](#)). Overall, processing took significantly less time per item for the copy task (536 ms) than the mirror task (637 ms), $F(1,11) = 7.25$, $p < 0.05$, but there was no difference in the proportion of missed targets between the copy task (0.186) and the mirror task (0.195), $F(1, 11) = 1.23$, $p > 0.2$. There was an increase of processing time per item with longer Time Awake, $F(3, 9) = 6.11$, $p < 0.05$, with no significant interaction of Time Awake and Task, $F(3, 9) < 1$, $p > 0.5$ (see [Figure 11](#)). There was no significant effect of time awake on the proportion of missed targets, $F(3, 9) = 1.21$, $p > 0.3$ and no

interaction between Time Awake and Task, $F(3, 9) < 1$, $p > 0.5$.

When we compared the processing time per item between the extreme circadian phases (60° and 240°), there was no significant impact of Circadian Phase on the copy task, $F(1, 11) < 1$, $p > 0.5$, and a trend toward an influence of Circadian Phase on processing time per item in the mirror task, $F(1, 11) = 1.87$, $p = 0.088$ (see [Figure 12a](#)). When we examined the proportion of missed targets, we found no influence of Circadian Phase in the mirror task, $F(1, 11) = 1.15$, $p > 0.2$, but a significant influence of Circadian Phase on missed targets in the copy task, $F(1, 11) = 4.82$, $p < 0.001$ (see [Figure 12b](#)). There were no

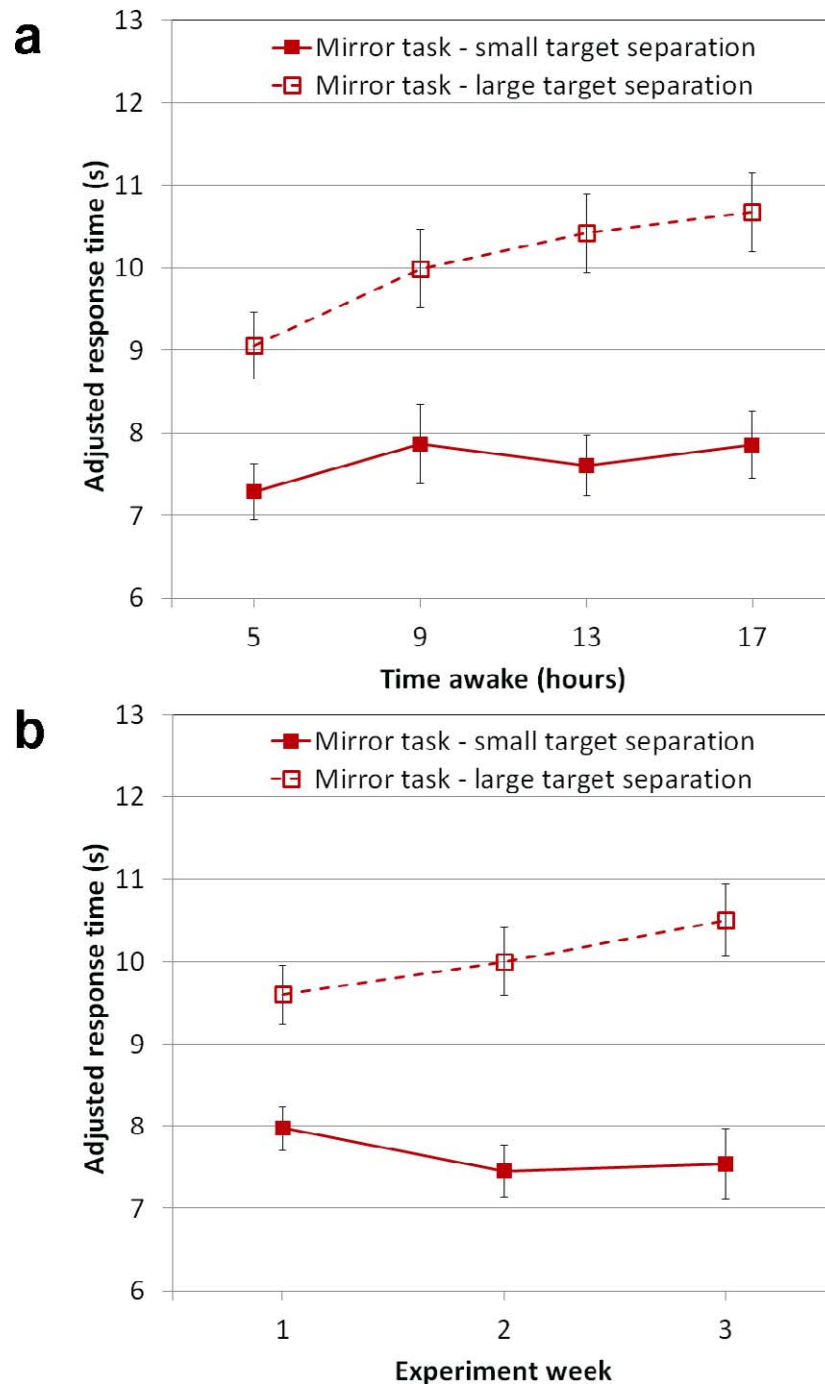


Figure 10. Adjusted RT in mirror-task trials with small (solid symbols and lines) and large (dashed symbols and lines) target separation as a function of (a) experiment week and (b) time awake (mean \pm SEM).

interactions of Circadian Phase with Experiment Week, $F(2, 10) = 1.22$, $p > 0.2$, or Time Awake, $F(1, 11) < 1$, $p > 0.5$. Finally, Experiment Week did not have a main effect on processing time or proportion of missed targets, nor an interaction with Task for these variables, all $F_s(2, 10) < 1.30$, $p_s > 0.2$.

General discussion

The results of the present study provide further evidence for the impact of sleep-wake and circadian-dependent influences on visual attention task performance (Horowitz et al., 2003; Santhi et al., 2007). Unlike previous studies, in the current experiment we

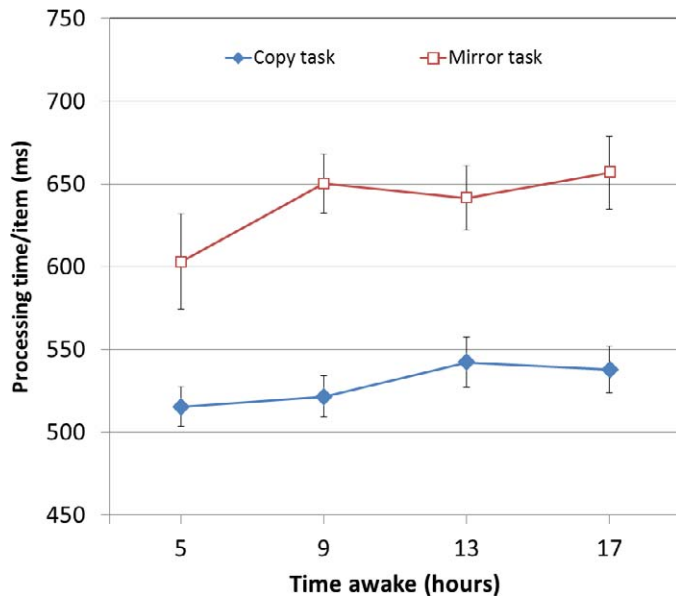


Figure 11. Processing time per item according to time awake for the copy (filled blue diamonds) and mirror (open red squares) tasks.

used a protocol that allowed us to separate the influences of circadian phase and time awake so as to examine their independent and interactive impacts on performance in a visual search task. Furthermore, the current study examined performance over three weeks of chronic sleep restriction, which enabled the additional investigation of cumulative sleep restriction effects on visual search task performance. The current study also employed two comparative search tasks that required extensive interaction of visual attention and working memory. One of these tasks—the mirror task—additionally required mental image transformations that not only increase task difficulty but also make a qualitative difference, because such transformations are assumed to mimic physical object manipulations (Shepard & Cooper, 1982; Shepard & Metzler, 1971). According to our hypothesis, these mental image transformations need to be carried out fully in order for them to be effective. This differs from the other processes involved in comparative search, particularly the superficial memorization of local image information and detection of any difference popping out, whose performance can range along a continuum of speed-accuracy tradeoffs.

Performance on both tasks was found to deteriorate substantially with longer time awake, and this effect increased during the course of the experiment with longer exposure to sleep restriction. This influence of sleep restriction was stronger for the mirror task than for the copy task, indicating that the additional mental image transformation required by the mirror task was particularly affected by continued inadequate sleep. This finding corroborates previous research showing

that acute sleep deprivation impairs performance, especially in more difficult tasks (Blatter, Opwis, Munch, Wirz-Justice, & Cajochen, 2005). Similarly, circadian phase strongly affected performance on both tasks. In accordance with other such studies (Cohen et al., 2010; Dijk et al., 1992; Duffy et al., 1998; Lee et al., 2009; Silva et al., 2010; Wyatt et al., 1999), performance was worst at a circadian phase of approximately 60° (near or just after habitual wake time under normal, entrained conditions) and best at approximately 240° (about 12 hours opposite, during the *wake maintenance zone* [Strogatz, Kronauer, & Czeisler, 1987]). There was a tendency toward greater influence of circadian phase later in the experiment (with increasing exposure to sleep restriction), but this influence did not differ between the two task versions.

The current results demonstrate the impact of circadian phase and wake duration on the types of data routinely collected in human vision experiments. In the majority of such experiments, researchers typically schedule experimental sessions throughout the work day and without any knowledge about the participants' sleep-wake history. However, as the present data show, such approaches are likely to add unnecessary noise to the resulting visual performance data. Both time awake and, particularly, circadian phase significantly affect performance on comparative visual search tasks, with circadian phase in the copy task even leading to an amount of variance in performance similar to that induced by inter-participant differences. While it may be difficult (if not impossible) to perfectly control circadian phase and sleep-wake history outside of specialized laboratories where specific sleep conditions can be imposed and both circadian phase and sleep can be monitored, it is possible to implement procedures to minimize the impact of circadian phase and sleep-wake history. Participants can be asked about the times when they typically go to bed and get up, about recent travel across time zones, and about recent night work or staying up all night. They can also be asked to keep a regular and adequate (8+ hours/night) sleep schedule prior to study, and to document their bed and wake times. Such information would allow vision researchers to exclude candidates with inconsistent or unusual sleep patterns and to schedule the remaining candidates in such a way that their circadian phase and time awake at the time of their experimental session are as similar across participants and conditions as possible. This includes avoiding morning experimental sessions for most young adult (college student) participants and ensuring all participants have adequate sleep durations for several nights prior to testing. Based on the current results, such procedures could substantially diminish some of the noise typically found in visual search

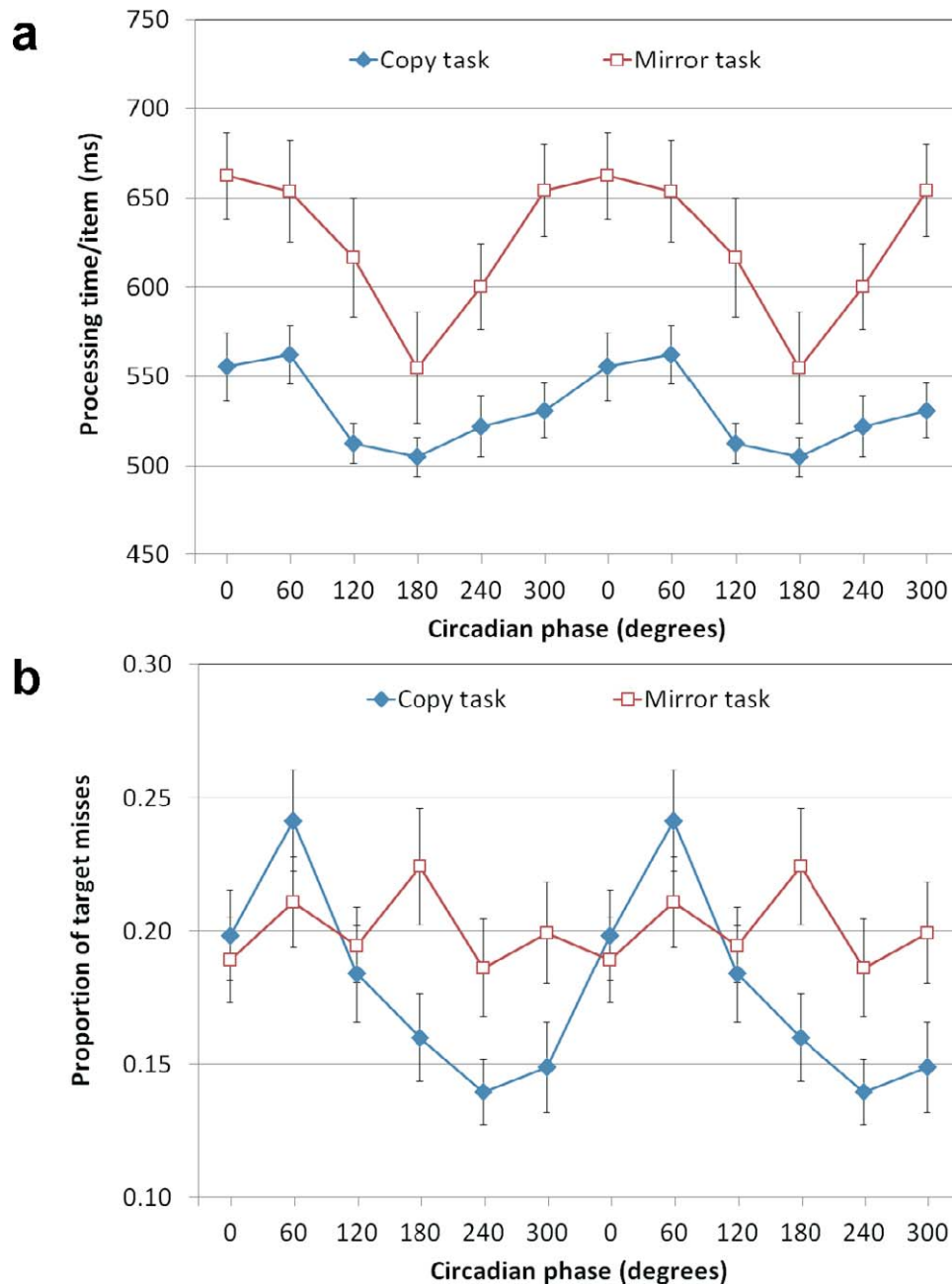


Figure 12. (a) Processing time per item and (b) proportion of trials with *missed* targets (with missed targets defined as those correct responses that had RT longer than two times the expected duration) for the copy (filled blue diamonds) and mirror (open red squares) tasks as a function of circadian phase. For better illustration, the data are double plotted with respect to circadian phase.

performance data, thereby reducing the number of participants required for testing a given hypothesis.

Another important feature of the comparative search tasks we employed in the present study is that they require participants to perform repeated operations of visual attention and working memory over an extended interval of typically 5 to 13 seconds (Pomplun, Sichelschmidt et al., 2001). This demand resembles real-world tasks that arise, for example, in baggage screening or air-traffic control, covering a much longer timespan than the visual search tasks with rapid

presentation-and-response trials used previously (Horowitz et al., 2003; Santhi et al., 2007). Studying whether time awake and circadian phase affect longer duration tasks—demanding sustained control of visual attention and working memory—especially strongly, yielded a counterintuitive result: Trials requiring the processing of more objects were not affected more strongly by time awake, circadian phase, or experiment week than were trials with fewer objects. However, increasing the demands of individual mental operations did seem to make participants' performance more susceptible to

influence by sleep-wake history because we found an increased influence of time awake and experiment week (duration of sleep restriction) when there was a greater horizontal distance between target objects in the mirror task. In summary, the results from comparing the two tasks, trials with few and many object comparisons and mirror task trials with small and large target separation suggest that a longer duration visual task does not make performance on the task more susceptible to circadian phase or time awake. Instead, it is greater difficulty in the individual cognitive operations involved in the task that leads to more pronounced performance deterioration with greater time awake and longer exposure to sleep restriction. The influence of circadian phase on performance did not increase with greater difficulty of individual mental operations, at least for the manipulations and measures used in the present study. Loosely speaking, while circadian phase seems to influence a wide range of attentional and working memory operations to a large but similar extent, sleep-wake history particularly affects more demanding operations.

Previous studies employing visual search tasks (Horowitz et al., 2003; Santhi et al., 2007) have reported that adverse circadian phase and acute sleep deprivation induced by prolonged wakefulness led to decreased accuracy, leaving the speed of responses largely unaffected. In other words, even though participants in those studies received immediate feedback regarding their response accuracy, they did not adapt their search speed to their reduced cognitive resources. Such behavior could be due to participants being unaware of deterioration in their cognitive resources such as visual working memory capacity and attentional control, which could have important negative consequences for individuals performing visual search tasks in safety-sensitive occupations. The present comparative search tasks allowed us to study effects of chronic sleep restriction in the absence of prolonged wakefulness on the speed vs. accuracy tradeoff from a more natural perspective of longer-duration tasks. Relating participants' response times to the vertical target positions across trials made it possible to derive useful estimates of the speed with which participants processed the given information and the frequency with which they overlooked the target objects when scanning through them.

For the copy task, we found an influence of both time awake and circadian phase on search speed and target misses that was largely consistent with previous visual search studies: Longer time awake and adverse circadian phase had minimal influence on search speed but led to a significantly higher proportion of missed targets. In contrast, in the mirror task, both time awake and circadian phase had substantial effects on search speed—slowing it down with prolonged wakefulness

and at adverse circadian phases—while influencing accuracy only minimally. This finding is consistent with our hypothesis that completing the mental image flip in the mirror task slowed participants' search pace during testing conditions and led to accuracy being rather invariant with regard to time awake and circadian phase.

The findings from the mirror task suggest that a strategy of imposing a mental image transformation could be tested for use in safety-critical tasks where workers are required to work during the night (at adverse circadian phases) or for long durations awake. In the present study, the mental image transformation only slightly reduced performance speed (9.4% increase in adjusted RT) while keeping accuracy nearly constant. Therefore, a trained observer who makes very few mistakes in such a task might maintain this low error rate even under adverse circadian and time awake conditions, as long as the task involves high-level mental image transformations. However, in our study the participants did not have to perform such a task for extended durations as such workers would and our findings therefore might not translate to such a real-world situation. Such a strategy can be tested for a variety of visual tasks, task manipulations, and time-on-task durations. While the present study has provided an assessment of wake-dependent and circadian effects on the performance of complex visual tasks, it is important to note that the current findings may not generalize across all varieties of such tasks. The data presented here may nonetheless serve as a starting point for further research on this topic and its many important practical implications.

Acknowledgments

We wish to thank the study participants; T. Okada and K. Berkenbush for subject recruitment and screening and the staff of the Center for Clinical Investigation (CCI), the Chronobiology Core, and the Sleep Core at Brigham and Women's Hospital (BWH) for assistance with carrying out the study.

This study was funded by NIH grant P01 AG09975 and was conducted in the BWH CCI, part of the Harvard Catalyst Clinical and Translational Science Center (UL1 RR025758-01), formerly a GCRC (M01 RR02635). Development and implementation of the CVS was supported in part by NIH grant R21 AT002571. JFD was supported in part by the BWH-BRI Fund to Sustain Research Excellence; MM was supported by fellowships from the La-Roche and Novartis Foundations (Switzerland) and Jazz Pharmaceuticals (USA); SWC was supported in part by a fellowship from the Natural Sciences and Engineering Research Council of Canada.

Commercial relationships: none.
 Corresponding author: Marc Pomplun.
 Email: marc@cs.umb.edu.

Address: Department of Computer Science, University of Massachusetts Boston, Boston, Massachusetts, USA.

References

- Blatter, K., Opwis, K., Münch, M., Wirz-Justice, A., & Cajochen, C. (2005). Sleep loss-related decrements in planning performance in healthy elderly depend on task difficulty. *Journal of Sleep Research, 14*, 409–417.
- Bonnet, M. H. (1986). Performance and sleepiness as a function of frequency and placement of sleep disruption. *Psychophysiology, 23*, 263–271.
- Cohen, D. A., Wang, W., Wyatt, J. K., Kronauer, R. E., Dijk, D. J., Czeisler, C. A., & Klerman, E. B. (2010). Uncovering residual effects of chronic sleep loss on human performance. *Science Translational Medicine, 2*(14), 14ra13.
- Czeisler, C. A., Dijk, D. J., & Duffy, J. F. (1994). Entrained phase of the circadian pacemaker serves to stabilize alertness and performance throughout the habitual waking day. In R. D. Ogilvie, & J. R. Harsh (Eds.), *Sleep onset: Normal and abnormal processes* (pp. 89–110). Washington, D.C.: American Psychological Association.
- Czeisler, C. A., Duffy, J. F., Shanahan, T. L., Brown, E. N., Mitchell, J. F., Rimmer, D. W....Kronauer, R. E. (1999). Stability, precision, and near-24-hour period of the human circadian pacemaker. *Science, 284*, 2177–2181.
- Dijk, D. J., Duffy, J. F., & Czeisler, C. A. (1992). Circadian and sleep/wake dependent aspects of subjective alertness and cognitive performance. *Journal of Sleep Research, 1*, 112–117.
- Dinges, D. F., & Powell, J. W. (1985). Microcomputer analyses of performance on a portable, simple visual RT task during sustained operations. *Behavior Research Methods, Instruments & Computers, 17*, 652–655.
- Doran, S. M., Van Dongen, H. P. A., & Dinges, D. F. (2001). Sustained attention performance during sleep deprivation: Evidence of state instability. *Archives Italiennes de Biologie, 139*, 253–267.
- Duffy, J. F., Cain, S. W., Chang, A. M., Phillips, A. J. K., Münch, M. Y., Gronfier, C., Czeisler....C. A. (2011). Sex difference in the near-24-hour intrinsic period of the human circadian timing system. *Proceedings of the National Academy of Sciences of the United States of America, 108*(Supplement 3), 15602–15608.
- Duffy, J. F., Dijk, D. J., Klerman, E. B., & Czeisler, C. A. (1998). Later endogenous circadian temperature nadir relative to an earlier wake time in older people. *American Journal of Physiology, 275*, R1478–R1487.
- Fuller, R. L., Luck, S. J., Braun, E. L., Robinson, B. M., McMahon, R. P., & Gold, J. M. (2006). Impaired control of visual attention in schizophrenia. *Journal of Abnormal Psychology, 115*, 266–275.
- Gillberg, M., Kecklund, G., Axelsson, J., & Åkerstedt, T. (1996). The effects of a short daytime nap after restricted night sleep. *Sleep, 19*, 570–575.
- Gottlob, L. R. (2006). Aging and comparative search for feature differences. *Aging, Neuropsychology, and Cognition, 13*, 435–457.
- Hardiess, G., Gillner, S., & Mallot, H. A. (2008). Head and eye movements and the role of memory limitations in a visual search paradigm. *Journal of Vision, 8*(1):7, 1–13, <http://www.w.journalofvision.org/content/8/1/7>, doi:10.1167/8.1.7. [PubMed] [Article]
- Horowitz, T. S., Cade, B. E., Wolfe, J. M., & Czeisler, C. A. (2003). Searching night and day: A dissociation of effects of circadian phase and time awake on visual selective attention and vigilance. *Psychological Science, 14*, 549–557.
- Inamdar, S., & Pomplun, M. (2003). Comparative search reveals the tradeoff between eye movements and working memory use in visual tasks. In R. Alterman & D. Kirsh (Eds.), *Proceedings of the Twenty-fifth Annual Meeting of the Cognitive Science Society* (pp. 599–604). Boston, Massachusetts.
- Lee, J. H., Wang, W., Silva, E. J., Chang, A. M., Scheuermaier, K. D., Cain, S. W. et al. (2009). Neurobehavioral performance in young adults living on a 28-h day for 6 weeks. *Sleep, 32*, 905–913.
- Pomplun, M. (1998). *Analysis and models of eye movements in comparative visual search*. Göttingen: Cuvillier.
- Pomplun, M., Reingold, E. M., & Shen, J. (2001). Investigating the visual span in comparative search: The effects of task difficulty and divided attention. *Cognition, 81*, B57–67.
- Pomplun, M., Sichelschmidt, L., Wagner, K., Clermont, T., Rickheit, G., & Ritter, H. (2001). Comparative visual search: A difference that makes a difference. *Cognitive Science, 25*, 3–36.
- Santhi, N., Horowitz, T. S., Duffy, J. F., & Czeisler, C.

- A. (2007). Acute sleep deprivation and circadian misalignment associated with transition onto the first night of work impairs visual selective attention. *PLoS ONE*, 2, e1233.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.
- Silva, E. J., Wang, W., Ronda, J. M., Wyatt, J. K., & Duffy, J. F. (2010). Circadian and wake-dependent influences on subjective sleepiness, cognitive throughput, and reaction time performance in older and young adults. *Sleep*, 33, 481–490.
- Smilek, D., Enns, J. T., Eastwood, J. D., & Merikle, P. M. (2006). Relax! Cognitive strategy influences visual search. *Visual Cognition*, 14, 543–564.
- Strogatz, S. H., Kronauer, R. E., & Czeisler, C. A. (1987). Circadian pacemaker interferes with sleep onset at specific times each day: Role in insomnia. *American Journal of Physiology*, 253, R172–R178.
- Watson, M. R., Brennan, A. A., Kingstone, A., & Enns, J. T. (2010). Looking versus seeing: Strategies alter eye movements during visual search. *Psychonomic Bulletin & Review*, 17, 543–549.
- Wilkinson, R. T., Edwards, R. S., & Haines, E. (1966). Performance following a night of reduced sleep. *Psychonomic Science*, 5, 471–472.
- Wyatt, J. K., Ritz-De Cecco, A., Czeisler, C. A., & Dijk, D. J. (1999). Circadian temperature and melatonin rhythms, sleep, and neurobehavioral function in humans living on a 20-h day. *American Journal of Physiology*, 277, R1152–R1163.