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Authors

Cellini, Nicola
Goodbourn, Patrick T
McDevitt, Elizabeth A
[et al.](#)

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Sleep after practice reduces the attentional blink

Nicola Cellini¹, Patrick T. Goodbourn², Elizabeth A. McDevitt³, Paolo Martini⁴, Alex O. Holcombe², and Sara C. Mednick³

Sara C. Mednick: smednick@ucr.edu

¹Department of General Psychology, University of Padova, Via Venezia 8, Padova 35131, Italy

²School of Psychology, University of Sydney, Brennan MacCallum Building (A18), Sydney 2006, New South Wales, Australia

³Department of Psychology, University of California Riverside, 900 University Avenue, Riverside, CA 92521, USA

⁴Department of Psychology, Harvard University, 52 Oxford Street, Cambridge 02138, MA, USA

Abstract

The attentional blink (AB) is an impairment in detecting the second of two targets that appear in close temporal succession. We investigated the effect of practice and a nap on the magnitude of the AB deficit. We found evidence that sleep boosts practice-dependent reduction of the AB. Participants reported two target letters embedded in a rapid serial visual presentation display. After two morning sessions, half the participants took a polysomnographically recorded nap, while the others remained awake. Comparing two afternoon sessions to the two morning sessions, we observed a decreased AB only within the group who napped. The improvement was due to increased efficacy of the attentional selection of T2 (the probability of reporting a T2-relevant item). There was no change in selection's latency or temporal precision. The magnitude of improvement was positively associated with the duration of N2 sleep and the number of N2 sleep spindles. Our results suggest that sleep, particularly N2 sleep and sleep spindles, improves attentional selection in time.

Keywords

Attentional blink; Daytime naps; N2 sleep; Selective attention; Sleep spindles

Correspondence to: Sara C. Mednick, smednick@ucr.edu.

Nicola Cellini and Patrick T. Goodbourn contributed equally to this work.

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Author contributions N. Cellini and P. T. Goodbourn contributed equally to this work and share first authorship. S. C. Mednick, A. O. Holcombe, and P. Martini developed the study concept. S. C. Mednick, A. O. Holcombe, P. Martini, P. T. Goodbourn and E. A. McDevitt contributed to the study design. A. O. Holcombe programmed the experiment. Testing and data collection were performed by N. Cellini and E. A. McDevitt. N. Cellini, P. T. Goodbourn and E. A. McDevitt performed the data analysis and interpretation. All authors drafted the manuscript, provided critical revisions, and approved the final version for submission.

Introduction

The attentional blink (AB) may reflect a failure of attentional selection. Observers often fail to detect a second target (T2) that closely follows a first target (T1) in a series of stimuli presented sequentially in a single location (Raymond, Shapiro, & Arnell, 1992). Accuracy for target detection is high when there is only one target, or when T2 is the next item in the stream after T1 (lag-1 sparing; Hommel & Akyürek, 2005). However, when T2 appears between 100 and 500 ms after T1, detection of T2 is markedly impaired (Choi, Chang, Shibata, Sasaki, & Watanabe, 2012). Several theories suggest that the AB occurs because the cognitive resources available for conscious processing are limited: processing T1 leaves fewer resources available for T2 (for reviews, see Dux & Marois, 2009; Martens & Wyble, 2010). Equally, the AB could reflect a failure of attentional control: delays or increased temporal variance in the allocation of attentional resources could result in difficulties in reporting T2 (Di Lollo et al. 2005; Olivers & Meeter, 2008; Taatgen et al. 2009).

Practice can reduce the magnitude of the AB. Maki and Padmanabhan (1994) reported improvement in an AB task after several days of training. Braun (1998) observed that T2 accuracy in an AB task was at or near chance in novice observers, whereas trained observers showed a smaller AB effect. It also has been reported that 3 months of intensive meditation training (Slagter et al., 2007) or specific color-salient attentional training (Choi et al., 2012; Tang et al. 2014; Willems et al. 2014) can reduce the AB. Importantly, in these studies, training sessions took place across days or even months, with sleep periods occurring between training sessions. While it has been suggested that sleep may mediate the effect of training on the AB (Tang et al., 2014), the role of sleep between training sessions has not been investigated.

Past research suggests that sleep can facilitate the consolidation of declarative and procedural information (for reviews, see Diekelmann & Born, 2010; Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011; Stickgold & Walker, 2013; Toniai & Cirelli, 2014). Specific features of sleep, such as slow wave activity (0.5–4 Hz) and sleep spindles, which are short bursts (0.5–3 s) of oscillatory activity in the frequency range of approximately 11–16 Hz (De Gennaro & Ferrara, 2003) are associated with improved memory performance (Mednick et al., 2011). In particular, sleep spindles correlate with the consolidation of episodic memory (Mednick et al., 2013) and motor skills (Nishida & Walker, 2007), and spindle activity is associated with visual perceptual learning (Bang et al. 2014). In addition, sleep can reverse detrimental effects of within-day over-training on visual perceptual learning (Censor, Karni, & Sagi, 2006; Mednick, Nakayama, & Stickgold, 2003; Mednick et al. 2005; Mednick et al., 2002).

To our knowledge, no prior study has investigated the role of sleep on attentional selection. Here, we tested the effect of sleep on changes in AB task performance associated with repeated testing. In addition, we aimed to explore which sleep features, if any, contributed to the changes. We investigated changes not only in overall performance, but also in three specific aspects of attentional selection in time (Vul, Nieuwenstein, & Kanwisher, 2008): efficacy (the ability to report an item in temporal proximity to the target), latency (the

position of the reported item relative to the target), and precision (the width of the distribution of reported item positions).

Materials and methods

Participants

Eighty-eight healthy young adults (mean age = 19.4 years, $SD = 1.2$ years; 40 female) participated in the study, for which they received financial compensation or course credit. The planned sample size of 80 participants was informed by the sizes of the effects found in previous studies of the psychophysical and sleep literatures on learning and memory (Diekelmann, Biggel, Rasch, & Born, 2012; Mednick, et al., 2003; Nishida & Walker, 2007). All participants gave their informed consent. The study was approved by the University of California at Riverside Human Research Protections Program. Participants were monitored for 1 week prior to the study using sleep diaries and Actiwatch-64 actigraph wristwatches (Respironics, Murrysville, PA) ensuring regular sleep-wake activity and between 6–8 h of sleep every night. In addition, participants had at least 7 h of sleep the night before the experimental day. Participants were excluded for irregular sleep-wake schedules, sleep or mental disorders, smoking, or a history of substance dependence.

Procedure

The study took place at the Sleep and Cognition Lab in the Department of Psychology at the University of California, Riverside. Each participant completed four sessions of a rapid serial visual presentation (RSVP) task, which occurred at 9:00 a.m., 12:00 p.m., 3:00 p.m. and 5:00 p.m. At the end of the second session, participants were randomly assigned to a *Nap* or *Wake* condition. Individuals were unaware of group assignment until this time. At about 1:00 p.m., participants in the Nap group ($n = 47$) took a nap, which was recorded by polysomnography (PSG; mean nap duration = 63.39 min, $SD = 21.15$ min). A trained sleep technician monitored all naps in real-time and the nap ended when participants obtained 90 min of sleep, reached 2 h in bed or awakened and remained awake for more than 20 min without falling asleep again. In the Wake condition, about half of the participants went about their normal daytime activities with wakefulness monitored by an actigraph (*Active-wake*; $n = 18$), and the other half sat in a room quietly resting while monitored by PSG (*Quiet-wake*; $n = 23$). Since preliminary analyses showed no differences between participants in Active- and Quiet-wake conditions, data were pooled into a single Wake group.

We excluded the data of those in the Nap condition who slept less than 10 min ($n = 2$), and of participants in the Quiet-wake condition who showed sleep intrusions ($n = 3$). We excluded five participants (in various conditions) owing to technical difficulties during their testing or recording sessions, and an additional four participants with near-floor performance in all sessions. The final sample comprised 74 individuals (mean age = 19.4 years, $SD = 1.2$ years; 32 female), 40 in the Nap group and 34 in the Wake group.

Sleepiness scale

Subjective sleepiness was measured before each session using the Karolinska Sleepiness Scale (KSS; Åkerstedt & Gillberg, 1990), which assesses an individual's momentary state of

alertness to sleepiness, on a scale of 1 (*extremely alert*) to 9 (*extremely sleepy*). This self-report questionnaire has been validated against behavioral and EEG measures of sleepiness (see Kaida et al., 2006).

RSVP task

An RSVP stream of all 26 letters of the English alphabet, in an order generated randomly on each trial, was presented in the center of a screen at 12 items s⁻¹. The monitor resolution was 1024×768 pixels with a refresh rate of 60 Hz. The letters were drawn in white Courier font on a black background. Each letter subtended 2.5° of visual angle at a viewing distance of 57 cm. Each letter was displayed for 34 ms (two refreshes), followed by an empty interval of 50 ms (three refreshes) before the onset of the subsequent letter (see Fig. 1).

Two of the letters were targets, identified by a cue. The cue was a white circle with a diameter of 12.0° centered on the target letter. The first cue appeared in one of five possible serial positions in the stream (6, 7, 8, 9, or 10) varying across trials. The number of items between the first target (T1) and second target (T2) was varied to yield a lag of 2 (stimulus onset asynchrony [SOA]: 168 ms), 5 (SOA: 420 ms) or 10 (SOA: 840 ms) items.

At the end of each trial, participants used the keyboard to report which letters were cued, in order of appearance. No feedback was provided. Each session consisted of 210 trials. The experiment was programmed in Python using PsychoPy2 (Peirce, 2007, 2008). The code that generated the stimuli and controlled the experiment is available at <https://github.com/alexholcombe/attentional-blink>.

For each participant we computed the probability of correctly reporting the second target given correct report of the first target (contingent T2 accuracy, or T2|T1). In addition, we computed efficacy, latency and precision of selection using a method similar to that used by Vul, Nieuwenstein, and Kanwisher (2008) and Martini (2013). The method is based on the analysis of *serial position error* of the reported letters at different lags. Serial position errors are expressed in number of items from the target; for example, reporting the item immediately prior to T2 in the RSVP stream is an error of -1, while reporting the item immediately following T2 is an error of +1. By collapsing across trials, we compiled a distribution of serial position errors for each participant, session and lag (Fig. 2, left panels).

Efficacy, latency and precision are three separable aspects of T2 selection that might be affected by the AB (Vul et al., 2008). *Efficacy* estimates the proportion of trials on which the observer successfully reports an item in the vicinity of T2. (On other trials, the observer might guess randomly, or mistakenly report an item in the vicinity of T1 rather than T2). Thus successful trials are not only those on which the observer reports T2 correctly, but also those on which the observer reports a temporally proximal item that was selected in response to the T2 cue. *Latency* can be defined as the average serial position error on successful trials; and *precision* can be defined as the trial-to-trial variability in serial position error on successful trials.

To better understand efficacy, latency, and precision, consider two hypothetical observers. On every trial, Observer A reports the item that immediately followed T2 in the RSVP

stream. By standard scoring methods, she has low accuracy, because T2 is never reported correctly. However, her T2 selection efficacy is high, because she consistently reports an item close to T2. Her T2 selection latency is +1, because she consistently reports the item following T2; and her precision is high, because the serial position error of her report is the same on every trial. In contrast, observer B usually reports T2 correctly, but sometimes reports the item that preceded T2, and just as often reports the item that followed T2. Observer A has the same efficacy of selection as Observer B, as both consistently report items close to T2. However, Observer B's selection latency is lower than Observer A's, because his average serial position error is zero. Observer B's precision is poorer than Observer A's, because the serial position error of his report varies from trial-to-trial.

To quantify efficacy, latency and precision of selection, we fit a mixture model to the probability density histogram of serial position error, separately for T1 and T2 position errors for each lag (Fig. 2, right panels). The mixture had three components: (1) a Gaussian target distribution, which could vary in total area (i.e., total proportion of trials accounted for, ρ_1), mean (μ_1) and standard deviation (σ_1); (2) a secondary Gaussian distribution with free parameters ρ_2 , μ_2 and σ_2 ; and (3) a uniform guess distribution, which made up the remaining proportion of trials ($1 - \rho_1 - \rho_2$). This is a straightforward extension of Goodbourn and Holcombe's (2015) mixture model for single-target selection in RSVP, with the addition of a secondary Gaussian distribution to account for T1-related items mistakenly reported as T2 (or, for distributions of T1 position errors, T2-related items mistakenly reported as T1). The full model is thus given by

$$f(x, p_1, p_2, \mu_1, \mu_2, \sigma_1, \sigma_2) = W(x) \left[\left(\frac{p_1}{C_N} \right) N(x, \mu_1, \sigma_1) + \left(\frac{p_2}{C_N} \right) N(x, \mu_2, \sigma_2) + \left(\frac{1 - p_1 - p_2}{C_U} \right) U(x) \right],$$

where x is serial position error, \mathcal{N} is the Gaussian distribution, U is the uniform distribution, W is a windowing function that accounts for the effects of restricting T1 and T2 to particular serial positions, and C_N and C_U are normalizing constants for the Gaussian and uniform distributions, respectively (Goodbourn & Holcombe, 2015). For the T1 model fit, μ_1 was constrained to $[-1, +1]$, and μ_2 was constrained to $[(\text{lag}-1), (\text{lag}+1)]$. For T2, μ_1 was constrained to $[-1, +1]$, and μ_2 was constrained to $[(-\text{lag}-1), (-\text{lag}+1)]$. We calculated efficacy of selection as the proportion of trials on which a target-related item was selected (ρ_1 , the total area of the Gaussian target distribution). We also computed the latency of selection as the center of mass of target reports (μ_1 , the mean of the Gaussian target distribution). Finally, we calculated the precision of selection as the temporal dispersion of target reports (σ_1 , the standard deviation of the Gaussian target distribution).

Sleep recording

Polysomnographs were recorded using Grass Heritage Model 15 amplifiers with Grass Gamma software (Astro-Med, West Warwick, RI). Three unipolar electroencephalogram (EEG) channels (C4–A1, C3–A2, O1–A2), two unipolar electrooculograms (EOG) referenced to opposite mastoids, and chin bipolar electromyogram (EMG) were recorded using the International 10–20 system (Jasper, 1958). Raw data were digitized at a sampling

rate of 256 Hz and passed to the Grass Gamma software, where the data were filtered (EEG and EOG: 0.3–35 Hz; EMG: 10–100 Hz) and visually scored in 30-s epochs according to the American Academy of Sleep Medicine guidelines (Iber, Ancoli-Israel, Chesson, & Quan, 2007). The following sleep parameters were calculated: total sleep time (TST), defined as the number of minutes scored as sleep between lights off and lights on; sleep-onset latency (SL), the number of minutes between lights out and the first epoch scored as sleep; wake after sleep onset (WASO), the number of minutes scored as wake after sleep onset; sleep efficiency (SE), the ratio between TST and total time in bed (i.e., minutes from lights out to lights on); and the total number of minutes in each of N1, N2, slow wave sleep (SWS), and rapid eye movement (REM) sleep stages. We also used BrainVision Analyzer 2.0 (Brain Products, Gilching, Germany) to determine the number of sleep spindles, spindle density (spindles min^{-1}), spindle peak frequency and spindle amplitude during N2 sleep, following Wamsley et al. (2012; see also Warby et al., 2014).

Data analysis

Preliminary analyses revealed no significant differences between sessions 1 and 2 (morning), or between sessions 3 and 4 (afternoon). Thus, to reduce the error of our parameter estimates, performance data and subjective sleepiness data (see Fig. 3) for each participant were pooled across the two morning sessions and across the two afternoon sessions.

We performed repeated-measures ANOVAs with Group as a between-subjects factor and Session as a within-subjects factor. Separate ANOVAs were performed for T1 and contingent T2 accuracy, and for each lag (lag 2, lag 5 and lag 10). Tukey's HSD test was used for post-hoc comparisons, and partial eta squared (η^2_p) is reported for effect size. Note that we considered changes in lag 2, which is the center of the AB period, as a measure of AB changes, whereas lag 5 and lag 10 (which sit at the edge and outside the temporal window in which the AB operates, respectively) were considered as control conditions to test the specificity of any possible improvement.

To separate the effect of change in sleepiness across the sessions from the non-sleepiness-related effects of napping, we entered change in sleepiness as a covariate in our ANOVAs. But rather than using difference in sleepiness between the morning and afternoon as the covariate, we used residuals from a linear regression of afternoon sleepiness values on morning values. Difference scores are undesirably correlated with the baseline measure (in this case, morning sleepiness); by using the residuals from a regression analysis, we removed the variance in afternoon sleepiness that could be accounted for by morning sleepiness. The residuals were thus a pure measure of change in sleepiness, uninfluenced by differences in baseline values (see DeGutis et al. 2013).

We also examined the relationship between changes in selective attention and specific sleep features. Using the same method we applied to sleepiness scores, we first regressed afternoon performance (i.e., T2/T1) on morning performance; the residuals of this analysis provided a measure of task improvement uncorrelated with baseline values. Pearson correlations examined associations between task improvement and sleep features.

Results

AB performance

The ANOVA on KSS showed a significant interaction between Session and Group [$F(1, 72) = 11.72, P = 0.001, \eta^2_p = 0.14$]. Sleepiness decreased significantly from the morning to the afternoon sessions only in the Nap group ($P = 0.003$, Fig. 3).

The ANOVAs on AB accuracy (T2|T1) revealed a significant main effect of Session on contingent T2 accuracy for lag 2 [$F(1, 71) = 13.12, P < 0.001, \eta^2_p = 0.16$], and a significant interaction between Session and Group [$F(1, 71) = 9.13, P = 0.003, \eta^2_p = 0.11$] (Fig. 4). In the Nap group only, contingent T2 accuracy increased significantly from morning to afternoon ($P < 0.001$). Specifically for lag 2, T2 accuracy in the afternoon was higher in the Nap group compared to the Wake group ($P = 0.016$). These effects were only present for lag 2; there were no significant effects for lags 5 or 10 (all $P > 0.2$; Fig. 5). For T1 accuracy, there was no significant effect of Session or Group, and no interaction between Session and Group, at any lag (all $P > 0.1$).

Relationship between T2 accuracy change and attentional features

To test which aspects of attentional selection accounted for the change between morning and afternoon sessions in the Nap group, we calculated the Pearson correlation coefficient between contingent T2 accuracy residual scores for lag 2, and the corresponding regression residuals (that control for baseline performance) for efficacy, latency and precision. The results showed a significant correlation between improvement in lag 2 accuracy and improvement in the efficacy of selection ($r = .41; P = .008$), suggesting that the Nap group's changes in lag 2 accuracy were driven by changes in selection efficacy.

Relationship between sleep features and change in AB performance

Which features of sleep are associated with changes in the AB? Summary statistics for overall sleep characteristics, and their correlation with contingent T2 accuracy (T2|T1) residuals for lag 2, are reported in Table 1. No overall sleep characteristics appear to be associated with changes in the AB.

Moving from gross measures of sleep to assessment of sleep stages, Table 2 presents sleep stage durations and correlations with contingent T2 accuracy residuals for lag 2. There was a significant association between N2 sleep and change in the AB, whereby more time spent in N2 was associated with a greater improvement in contingent T2 accuracy at lag 2. The association between lag-2 performance improvement and N2 sleep remains after controlling for TST ($r = .36, P = .02$) and SE ($r = .41, P = 0.01$).

N2 sleep is characterized by the occurrence of sleep spindles, which already have been associated with learning (Schabus et al., 2006) and memory (Mednick et al., 2013). Accordingly, we investigated the possibility of a relationship between N2 sleep spindles and change in AB performance. Exploratory *t*-tests revealed no difference between the left (C3) and right (C4) hemispheres for any spindle feature, so we conducted analyses with data averaged over C3 and C4 electrodes. Table 3 presents summary statistics for the number,

density, amplitude and peak frequency of sleep spindles during N2, along with their correlation with contingent T2 accuracy residuals for lag 2. Improvements in the AB appear to be associated with the total number of spindles during N2 sleep (Fig. 6), but not with their density, amplitude or peak frequency.

Discussion

Here we found that practice reduced AB only when accompanied by daytime sleep. Sleep affects learning in several ways (for reviews, see Stickgold & Walker, 2013; Tononi & Cirelli, 2014), including improving extraction of the implicit rules of a task, strengthening specific cortical connections (for example, visual pathways) in response to environmental demands (such as a specific task), and perhaps generally increasing neural signal-to-noise ratios. The current findings provide the first evidence, to our knowledge, that sleep also benefits attentional selection in time. Specifically, participants who had a nap were better than participants who remained awake at reporting the second of two target letters presented within a brief temporal window. To statistically control for the effect of napping on sleepiness, we included as a covariate a measure of change in reported sleepiness between morning and afternoon sessions. Thus, although we cannot completely exclude the possibility that sleepiness influenced AB performance, it is unlikely that sleep affects selective attention simply by modulating sleepiness.

Sleep modulates practice-dependent changes in the AB

Our results indicate that the observed change in performance was not driven by a general improvement: we did not observe an improvement in first-target (T1) performance and second-target (T2) performance was not improved for trials where the targets were well separated in time (lags 5 and 10). Rather, sleep appears to specifically facilitate selective temporal attention inside the AB window. We observed performance improvements only at lag 2, which is at the center of the AB period (168 ms). We observed no changes at lag 5 (420 ms), which is at the edge of the AB temporal window, nor at lag 10 (840 ms), which is well outside the window.

Because lag 5 is an edge case, we had no strong prediction of whether it should improve when AB is reduced. In some previous AB studies, 420 ms may be within the AB, although at our relatively fast rate of presentation, previous research found this lag to be exactly at the edge (Vul et al., 2008) or even outside (Dale & Arnell, 2013) the AB window. But our findings offer some insight into why we observed no improvement. As can be seen in the response error distributions pictured in Fig. 2, the proportion of *almost*-correct T2 responses at lag 5 (Fig. 2c) is nearly as high as at lag 10 (Fig. 2a). That is, *efficacy* at lag 5 is closer to that at lag 10 than to that at lag 2; in contrast, efficacy at lag 2 is very low (Fig. 2e). However, the most common response at lag 5 is the item *after* T2. Thus the reason for low accuracy (exactly correct T2, contingent on exactly correct T1) differs between lag 2 and lag 5: at lag 2, low accuracy is driven by low efficacy; at lag 5, low accuracy is driven by *high latency* (see also Vul et al., 2008, for similar results). Since nap-related improvements appear to be driven only by changes in efficacy, we should not expect performance at lag 5 to benefit from a daytime nap.

In the current study we employed a repeated-testing design to elicit practice-dependent changes. Although we might expect some amount of learning in both groups, we observed an improvement only in the Nap group. We did not observe a significant difference between the two tests within a morning, or the two tests within an afternoon, in either group. This raises the possibility that previous findings of improvement with practice may have occurred only because participants slept.

Previous published evidence indeed appears to be consistent with a requirement that participants sleep in order to realize the benefits of practice. Maki and Padmanabhan (1994) showed that the AB was ameliorated across 15 days of practice. Similarly, Slagter and colleagues (2007) found that participants exhibited a reduced AB in the second of two sessions separated by 3 months, with a greater reduction in a group who undertook intensive meditation training than in a control group. The present data suggest that the improvements observed in these studies may have depended on sleep between training sessions. Garner and colleagues (Garner, Tombu, & Dux, 2014) tested the effect of two training regimens on AB performance: participants underwent either a training regimen known to improve psychological refractory period (PRP) performance, or a visual search training regimen. After 2 weeks (during which they presumably slept), and independent of the training regimen, AB performance improved. Dale and Arnell (2013) compared performance between two sessions separated by 7–10 days. They found an increase in T2 accuracy across all lags, with no significant interaction between lag and testing session, which they took to indicate a general improvement in T2 accuracy rather than an improvement specific to the AB period. Visual inspection of their results, however, shows that the improvement was most pronounced for lags 2 and 3 (210 and 315 ms, respectively) in the second session (their Figure 1a), with very little difference for lag 1 and for longer lags.

Improvements in accuracy are driven by efficacy of selection

Attentional selection can vary in its efficacy, latency, and temporal precision, with changes in any of these causing changes in the usual metric of AB performance: conditional T2 accuracy (Vul et al., 2008). Along with calculating conditional T2 accuracy, we used a mixture model to extract the specific aspects of attentional selection underlying performance. We found that improvements in lag-2 accuracy were associated with improvements in efficacy of selection, but were not associated with other aspects. This indicates that the improved performance was driven by an increased probability of reporting from a T2-relevant attentional sample, rather than by improved temporal precision or reduced latency. Previous studies of the effect of practice have not distinguished between these possibilities, and this result should inform future theories of training and the AB. The result seems consistent with previous suggestions that training improves T2 reports owing to increased attentional control (Choi et al., 2012). It is also consistent with the notion that training improves temporal expectation (Tang et al., 2014; Willems et al., 2014), in as much as temporal expectation improves efficacy of selection, as reported by Martini (2013).

N2 sleep and attentional improvement

Correlational studies have suggested that specific sleep features play a role in facilitating aspects of human cognition (Diekelmann & Born, 2010). Experimental studies have

demonstrated critical roles for slow wave activity (Marshall, Helgadóttir, Mölle, & Born, 2006) and sleep spindles (Mednick et al., 2013) in the consolidation of episodic memory. Our exploratory analyses suggest that N2 sleep and its hallmark feature (the spindle) play a role in improving attentional selection during the AB. This result remains significant when controlling for total sleep time and sleep efficiency, supporting the claim that it is not the overall length of sleep influencing performance, but rather a specific sleep stage and its related feature that is beneficial for performance on the task. It should be noted that time spent in N2 sleep and number of spindles are very highly correlated ($r = .88, p < .001$), so it is not possible to dissociate minutes of N2 and number of spindles to determine if one of these variables is more critical for changes in the AB.

The association between performance improvement and N2 sleep and spindles might provide some insight into the mechanism responsible for the improvement. According to Hommel and colleagues (2006), an attentional network involving occipital, infero-temporal, posterior parietal and fronto-lateral regions is responsible for processing stimuli in an RSVP stream. Within this network, synchronization between left frontal and right parietal areas has been associated with the absence of an AB (Gross et al., 2004). During N2 sleep, cortico-cortical connectivity is relatively intact compared to other stages of sleep, allowing the global brain interactions important for synchronizing local and global network activity, without the interference of an active waking state (Genzel, Kroes, Dresler, & Battaglia, 2014). Moreover, during N2 sleep, connectivity is strengthened within the dorsal attentional network (Larson-Prior et al., 2009). It is thus plausible that the fronto-parietal network involved in the AB is shaped during N2 sleep.

We also found some (non-significant) evidence for a relationship ($r = 0.28, p = 0.08$) between N1 sleep and performance improvement. As pointed out by Genzel and colleagues (2014), active synaptic potentiation may occur during light sleep (N1 and N2). However, this effect is stronger during N2 because that stage is characterized by the presence of sleep spindles, which facilitate local plasticity (Bang et al., 2014). Indeed, sleep spindles can modulate membrane potential in cortical neurons and induce short- and long-term potentiation in neocortical pyramidal cells (for a review, see Genzel et al., 2014). Spindles, which are generated in the thalamocortical network, may improve selective attention in the AB task by strengthening the thalamocortical loop, thereby increasing its effectiveness in allocating attentional resources (Portas et al., 1998; Schiff et al., 2013). In other words, it is possible that during a period of sleep following the AB training, active potentiation of relevant information (e.g., the temporal structure and contents of an AB task) can strengthen the attentional network for that information, enhancing the ability to allocate attentional resources in time. The result is higher efficacy of selection, which drives the AB improvement. The other aspects of T2 selection, latency and precision, are believed to be set by a previous stage of processing, perhaps more perceptual (Goodbourn & Holcombe, 2015).

The specific association of the improvement with N2 sleep speaks against a mechanism based on homeostatic regulation of synaptic connections, as that is associated with slow-wave sleep (the *synaptic homeostasis hypothesis*; Tononi & Cirelli, 2014).

For some tasks, researchers have found that repeated practice without sleep results in a *decrease* in performance. One example is perceptual learning tasks, for which the performance decrease has been termed perceptual deterioration (Censor et al., 2006; Mednick et al., 2002, 2003, 2005). This effect does not appear to occur in the AB task, as we did not observe it here nor was it observed by Kelly & Dux (2011), who gave participants two sessions of four blocks each. Clearly, performance can decline on a variety of tasks with prolonged wakefulness (Lim & Dinges 2008) and such decreases may have been due to sleepiness, resulting in lapses of vigilance (Durmer & Dinges, 2005). However, our participants were well rested, and this may explain why we observed a performance maintenance in across a day of testing.

Conclusion

We report the first evidence that sleep can facilitate improvements in the temporal allocation of selective attention. We found that a daytime nap reduces the AB by modulating efficacy (the probability of reporting a T2-relevant item), with no change in latency or temporal precision. These improvements were specifically associated with stage N2 sleep and sleep spindles. Further studies, perhaps using a pharmacological or brain stimulation design, should replicate and expand our findings.

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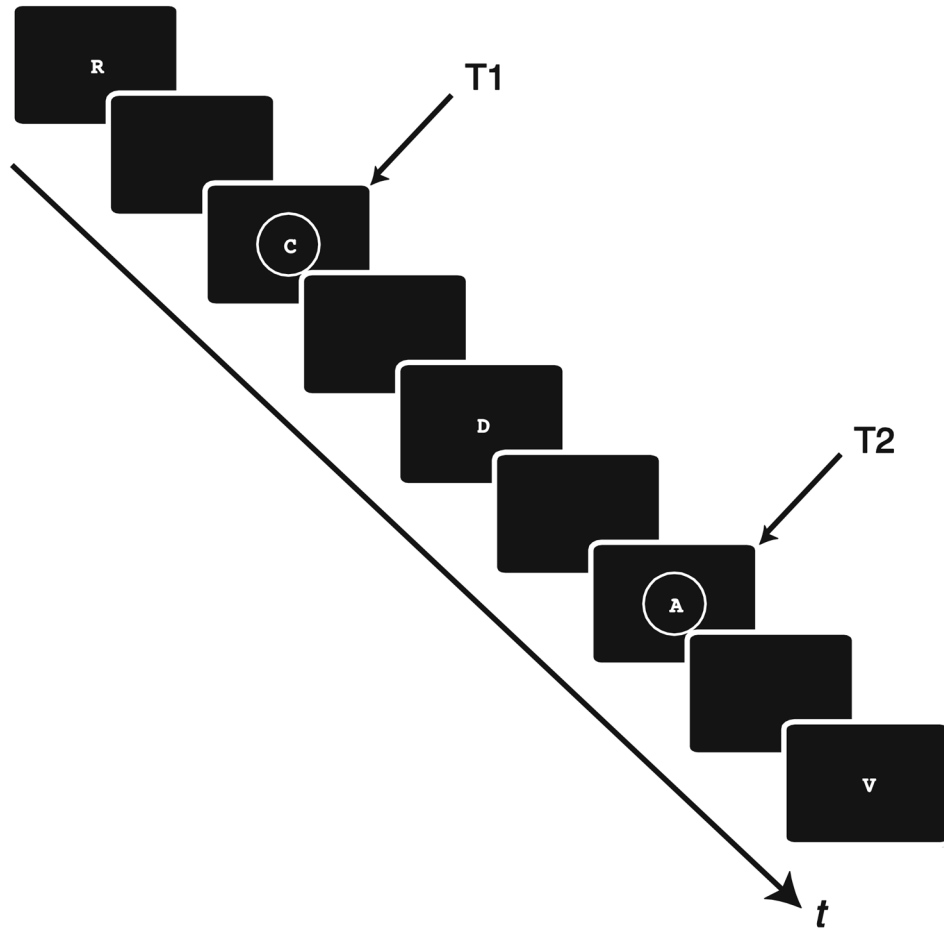


Fig. 1. Excerpt from one trial of the rapid serial visual presentation (RSVP) task. On each trial, a stream of all 26 letters of the English alphabet, in an order generated randomly on every trial, was presented in the center of the screen. Two of the letters were targets cued by an annulus ($T1$ and $T2$). Participants reported the two cued letters. The lag (number of letters from $T1$ to $T2$) varied across trials. This example shows a lag-2 trial

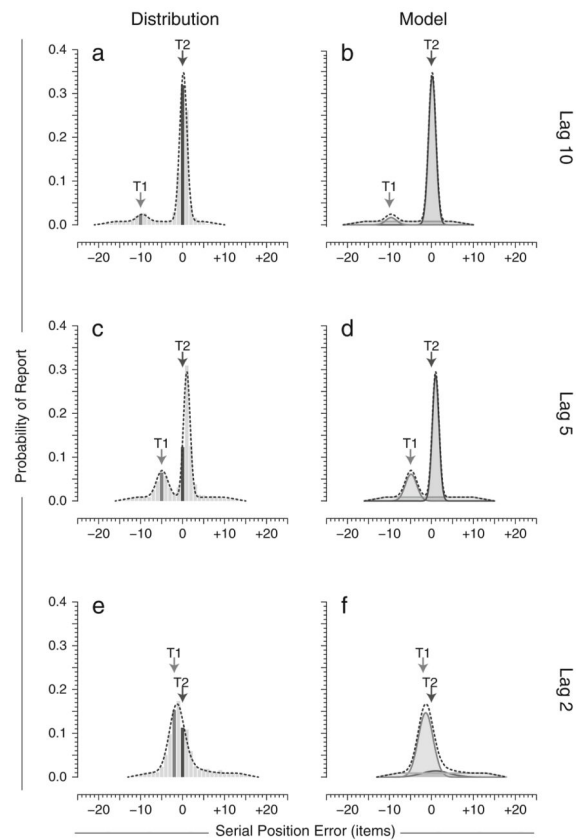


Fig. 2.

a–f To extract efficacy, latency and precision of selection, a mixture model was fit to distributions of T2 serial position error for one participant in a single session. *Left panels* Distribution of serial position error in T2 reports for **a** lag 10, **b** lag 5, and **c** lag 2. Error is expressed in items from T2. *Right panels* Mixture model fit to the data for **d** lag 10, **e** lag 5, and **c** lag 2. The model comprises a mixture of three distributions: a Gaussian distribution accounting for T2-related items, a second Gaussian distribution accounting for T1-related items mistakenly reported as T2, and a uniform distribution accounting for random guesses and errors caused by letter confusions. In all panels, the dashed line is the sum of the three distributions

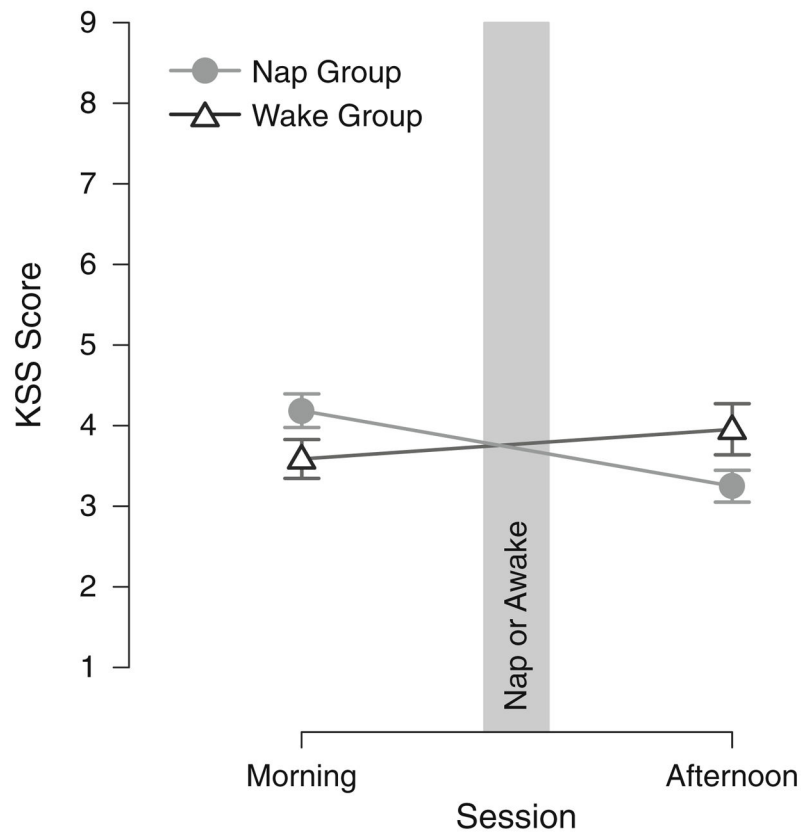


Fig. 3. Mean Karolinska sleepiness scale (KSS) scores for the *Nap* and *Wake* groups. Error bars ± 1 standard error of the mean (SEM). Participants in the *Nap* group ($n = 40$) napped between morning and afternoon sessions, while participants in the *Wake* group ($n = 34$) either rested quietly or went about their usual activities

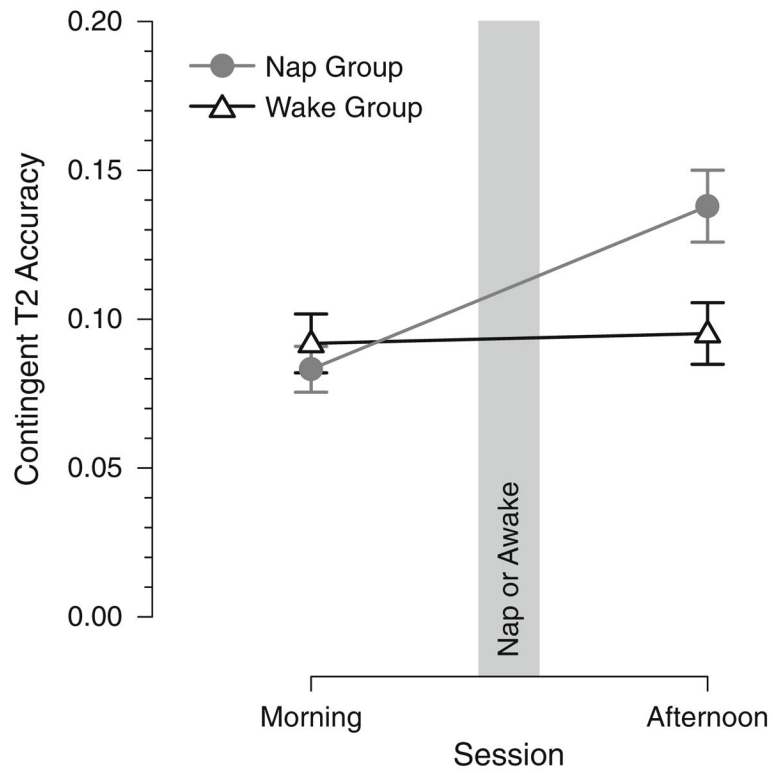


Fig. 4. Mean lag-2 contingent T2 accuracy for the *Nap* and *Wake* groups. Contingent T2 accuracy is defined as the probability of a correct report for T2 given a correct report for T1, $p(T2|T1)$. Error bars ± 1 SEM. Participants in the *Nap* group ($n = 40$) napped between morning and afternoon sessions, while participants in the *Wake* group ($n = 34$) either rested quietly or went about their usual activities

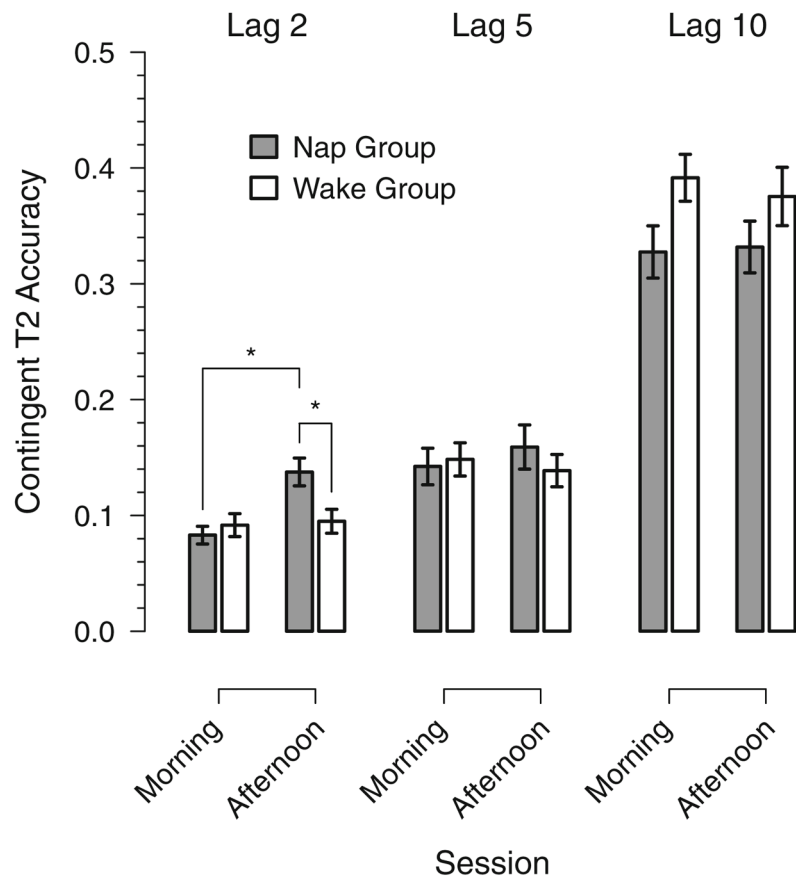


Fig. 5. Mean contingent T2 accuracy as a function of session and lag. There was a significant increase in contingent T2 accuracy between morning and afternoon sessions, only for the *Nap group* and only for *lag 2*. Conventions are the same as in Fig. 4

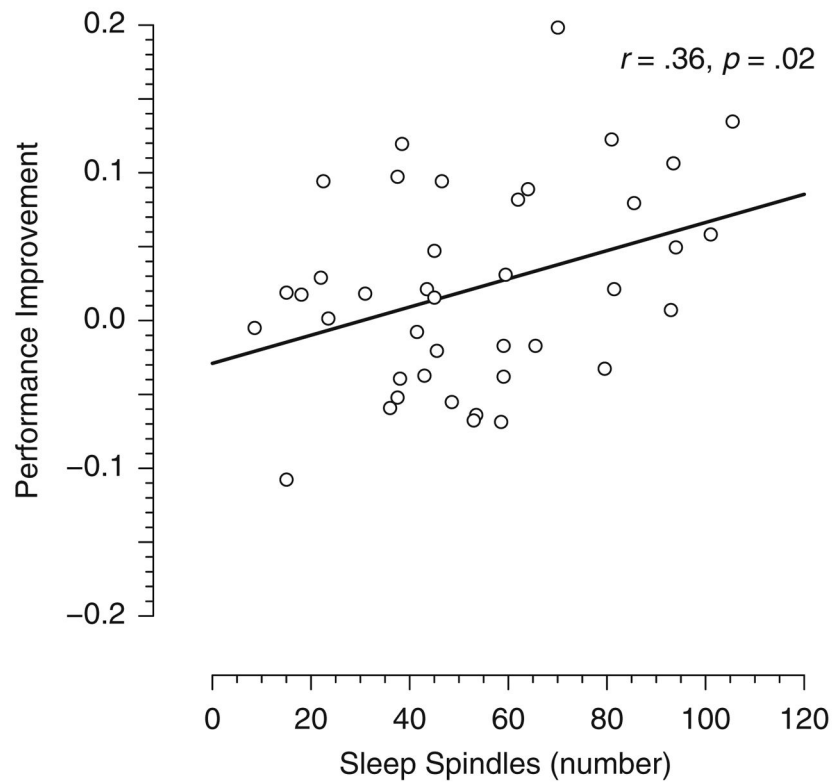


Fig. 6. Performance improvement as a function of number of N2 sleep spindles. A participant's performance improvement is the corresponding residual of a linear regression of afternoon on morning contingent T2 accuracy for lag 2. The solid line shows the best fit by linear regression of performance improvement on number of N2 sleep spindles

Table 1

Sleep characteristics and correlation with T2/T1 residuals. *SE* Sleep efficiency, *TST* total sleep time, *WASO* wake after sleep onset

	Mean \pm SD	T2/T1 residual correlation
TST (min)	62.5 \pm 20.8	$r = .21, P = .20$
Sleep latency (min)	10.4 \pm 10.2	$r = -.13, P = .42$
WASO (min)	12.6 \pm 14.0	$r = .08, P = .64$
Sleep efficiency (%)	74.1 \pm 19.4	$r = .09, P = .59$

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Table 2

Sleep stage polysomnography and correlation with T2/T1 residuals. *REM* Rapid eye movement, *SWS* slow-wave sleep

	Mean \pm <i>SD</i>	T2/T1 residual correlation
N1 (min)	9.5 \pm 6.6	$r = .28, P = .08$
N2 (min)	26.3 \pm 11.3	$r = .41, P = .01$
SWS (min)	18.9 \pm 15.6	$r = -.16, P = .34$
REM (min)	7.9 \pm 9.4	$r = .04, P = .81$

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Table 3

N2 spindle analysis and correlation with T2/T1 residuals

	Mean \pm SD	T2/T1 residual correlation
Number	53.0 \pm 25.4	$r = .36, P = .02$
Density (spindles/min)	2.1 \pm 0.7	$r = .02, P = .92$
Amplitude (3V)	18.8 \pm 5.2	$r = -.23, P = .14$
Peak frequency (Hz)	13.5 \pm 0.4	$r = -.01, P = .97$

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