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REVIEW

Individual differences in working memory efficiency modulate proactive interference after sleep deprivation

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Abstract
Whether and how sleep loss affects executive functioning are still under debate. In this study, we examined the role of individual differences in determining the levels of working memory (WM) efficiency and proactive interference (PI) after sleep deprivation. Fifty-two participants performed a test battery included a modified Sternberg task and the Jonides' 2-back task under two sleep conditions: baseline (BL, a night of regular sleep), and total sleep deprivation (SD, 24 h of wakefulness). In general, we replicated Tucker and colleagues' (2010) results. However, when we divided the subjects into two groups according to WM efficiency after SD, participants that showed a greater efficiency were more susceptible to PI, while those with lower WM efficiency showed a level of resistance to PI similar to BL. These results indicate that resistance to PI after SD is dependent on WM efficiency, highlighting the importance of individual differences in sleep deprivation studies.

Abbreviations

BL	Baseline
SD	Sleep deprivation
M	Mean
std	Standard deviation
SSS	Stanford Sleepiness Scale
GVAS	Global Vigor–Affect Scale
VAS	Visual Analog Scale
NT	Non-target
T	Target
ANOVA	Analysis of variance
Mdn	Median
RT	Reaction times
PE	Preserved-efficiency group
WE	Worsened-efficiency group
WM	Working memory
PI	Proactive interference

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Introduction

Among several questions still unsettled in sleep research, one of the main debates is whether and how executive functions are affected by sleep deprivation (Harrison & Horne, 1998; Tucker, Whitney, Belenky, Hinson, & Van Dongen, 2010). The term "executive functions" refers to a set of cognitive functions including reasoning, problem solving, attentional control, working memory and inhibitory control. They allow anticipating, planning, setting goals, modifying behaviour to adapt to a new condition and inhibiting prepotent responses (Chan, Shum, Toulopoulou, & Chen, 2008). In our daily routine, many tasks such as socializing, working and managing household, require an efficient executive functioning (Alvarez & Emory, 2006; Damasio, 1994; Grafman & Litvan, 1999). Hence, understanding whether and to what extent sleep deprivation impairs executive functions has important implications.

Previous studies on the effects of sleep loss on executive functioning produced inconsistent results. For instance, ability to inhibit a prepotent response was found impaired after sleep loss in some studies (Chuah, Venkatraman, Dinges, & Chee, 2006; Drummond, Paulus, & Tapert, 2006; Slama et al., 2018), but preserved in others, under both sleep restriction (Schaedler et al., 2018) and sleep deprivation (Fournier, Hansen, Stubblefield, & Van Dongen, 2018; Sagaspe et al., 2006).

In 2010, Tucker et al. (2010) ascribed the issue of the inconsistency of results to the measure used to investigate executive functioning, to what is known as "the task impurity problem" (Miyake et al., 2000). Executive functions operate on other cognitive processes, and any task that targets executive functioning also implicates non-executive cognitive processes which are not easily singled out. A low score on a test for executive functioning could be the result of an impairment of other non-executive cognitive components. Tucker et al. (2010) examined the hypothesis that only non-executive components are vulnerable to deterioration after sleep deprivation. Using a modified Sternberg task (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Sternberg & Sternberg, 1966), they were able to dissociate non-executive components (i.e., probe encoding, response selection and motor execution of the response) from two distinct components of executive functioning, working memory scanning efficiency and resistance to proactive interference. Working memory allows the temporary storage of items while processing at the same time incoming information or retrieving them from long-term memory (Baddeley, 2003). In the modified Sternberg task, working memory scanning efficiency is calculated as the amount of time taken to access items held in working memory. Instead, proactive interference is the intrusion of traces of events that occurred before the target material (Friedman & Miyake, 2004; Keppel & Underwood, 1962). It refers to the difficulty to remember new items when previous ones are too similar. In everyday live, intrusions of previous materials happen often, for example when one changes the password of the email account and the old one interferes during the retrieval process. Experimentally, the ability to resist interference is calculated by the difference between conditions with and without interfering items. Tucker et al. (2010) found that after 62 h of continuous wakefulness the non-executive components were impaired while working memory scanning efficiency and resistance to proactive interference were not significantly affected.

A number of studies have shown that working memory and proactive interference are strongly correlated, and that resistance to proactive interference is sensitive to the ability to store information in working memory (Keppel & Underwood, 1962; Lustig, May, & Hasher, 2001). More importantly, individual differences in working memory efficiency correspond to differences in individual susceptibility to proactive interference (Bunting, 2006; Rosen & Engle, 1998). Participants with high working memory capacity as assessed by operation span tasks, perform better on a proactive interference task than participants with low capacity (Chiappe, Hasher, & Siegel, 2000; Kane & Engle, 2000; Lilienthal, Rose, Tamez, Myerson, & Hale, 2015; Rosen & Engle, 1998).

These results obviously refer to non-sleep-deprived participants. Hence, it is legitimate to wonder if even after sleep deprivation/reduction, this difference between high and low working memory capacity individuals is maintained or it is altered by sleep loss. Moreover, the recent emphasis on interindividual differences in vulnerability to sleep loss (Tkachenko & Dinges, 2018) might pose the question: are the results obtained by Tucker et al. (2010) due to a real no-effect of sleep deprivation on resistance to proactive interference or rather to an average no-effect caused by mixing up participants with increased and decreased level of resistance to proactive interference?

Based on these considerations, we hypothesized that individual differences in working memory after sleep deprivation might modulate the resistance to proactive interference. For these reasons, we decided to use two independent tests to measure working memory and proactive interference: the N-back task (Jonides, Schumacher, & Smith, 1997) and the modified Sternberg task (Bunge et al., 2001; Sternberg & Sternberg, 1966), respectively. The N-back task is a well-established test for evaluating working memory (Owen, McMillan, Laird, & Bullmore, 2005), it requires high demand on central executive resources (Smith et al., 1999) and is reportedly impaired after sleep deprivation (Choo, Lee, Venkatraman, Sheu, & Chee, 2005; del Angel et al., 2015; Gerhardsson et al., 2018; Lythe, Williams, Anderson, Libri, & Mehta, 2012; Martínez-Cancino, Azpiroz, & Jiménez-Angeles, 2015).

We expected to replicate Tucker's results (Tucker et al., 2010) so long as, in a first overall analysis, our sample would be treated as a whole. We anticipated, however, that, once classified based on their differential decline in working memory, participants characterized by a working memory efficiency degraded by sleep loss would behave significantly differently from those who maintained a level of efficiency comparable to that of baseline.

Methods

Participants

Fifty-eight students at the University of Trieste were selected to participate in this study by means of a battery of web-based questionnaires. To be recruited, they had to be: right-handed, with normal or corrected to normal vision, psychologically and physically healthy, not being on medication, with no history of brain injury or psychiatric illness, with normal scores at the Beck depression scale (Steer, Ball, Ranieri, & Beck, 1997), with no sleep or circadian disorders, good sleepers with a score less than or equal to 6 at the Pittsburgh Sleep Quality Index Questionnaire (Buysse, Reynolds, Monk, Berman, & Kupfer, 1989).

Moreover, the Morningness–Eveningness Questionnaire (Horne et al., 1976) was administered to avoid confounding effects of extreme chronotypes: extreme morning

(> 70) and extreme evening (< 31) chronotypes were not included in this study. During the experiment, participants were requested to maintain regular sleep habits evaluated by subjective sleep diary. They were requested to abstain from alcohol, caffeine and other stimulants for at least 24 h before the experimental sessions. For their participation in the study, they received course credits.

Six individuals had to be discarded at the end of data collection because they either slept significantly less than the minimum of 6 h required in the baseline condition (two participants) or assumed caffeine and/or alcohol (four participants). Hence, the current sample consists of fifty-two participants (36 female; age range 19–28 years, $M = 21.6$, std = 2.36; habitual sleep duration: $M = 466$ min, std = 38 min).

Prior to the experiment, written informed consent was collected from each participant in agreement with the Declaration of Helsinki. The study was previously approved by the University Ethic Committee.

Materials

Stanford Sleepiness Scale

The Stanford Sleepiness Scale (SSS—Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973) is a self-rating scale used to quantify subjective level of sleepiness. It consists of seven numbered statements ranging from 1 (very alert) to 7 (very sleepy).

Global Vigor–Affect Scale

The Global Vigor–Affect Scale (GVAS—Monk, 1989) consists of eight questions used to assess changes in mood and subjective activation. Each question is directly followed by a Visual Analog Scale (VAS) that is a horizontal straight line of 100 mm anchored at either end by a short verbal description, “very little” on the left and “a great deal” on the right. Participants had to mark the line to indicate the degree of their current subjective state. Each scale (Global Vigor and Global Affect) ranges from 0 to 100.

Modified Sternberg task

The modified Sternberg task is a task that allows the dissociation of non-executive from executive components (Bunge et al., 2001; Sternberg & Sternberg, 1966; Tucker et al., 2010). The task version we used foresees a total of 128 trials preceded by 20 training trials. Stimuli are presented electronically using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). In each trial, participants views on screen a set of items that they have to hold in working memory, followed by a probe item. They are instructed to respond as quickly and accurately as possible using a mouse. If the probe item is present in the current memory set they had to press the left button, else the right button. The size of memory set is of two or four items, 50% each. The training items are numbers, while in testing they are consonant letters. Half of the probes are positive, meaning that they are in the current memory set thus the correct response is “yes” and the other half is negative, so the correct response is “no” (Fig. 1). Subjects are required to respond within a 1500 ms window.

The ability to resist proactive interference is evaluated by manipulating the recency of negative probes. In half of the trials, the negative probe is recent meaning that it has been seen in the memory set of the previous trial and in the other half it is non-recent. The difference in RTs between recent and non-recent is a measure of resistance to proactive interference. The linear relationship between RTs and memory set size which is determined by two versus four item conditions, and is represented by intercept and slope. The intercept measures the non-executive components involved in performing the task (motor speed), while the slope is a measure of working memory scanning efficiency. Also, the number of lapses is counted. Lapses are defined as slow trials characterized by delayed behavioural responses, rather than a complete absence of response, as typically used in the SD psychomotor vigilance test (PVT) literature (Basner & Dinges, 2011; Doran, Van Dongen, & Dinges, 2001; Lim & Dinges, 2008). Threshold for lapses in the PVT (Dinges et al., 1997), a simple reaction time task, is classically set at 500 ms (Basner & Dinges, 2011). However, in the case of the modified Sternberg task, a choice reaction time task, we decided to set it longer, as response times greater than or equal to 750 ms for all conditions.

N-back task

The *N*-back task (Jonides et al., 1997) is a well-established test for evaluating working memory (Owen et al., 2005). The task version we used foresees a total of 135 trials, 45 per block, for a total of three blocks, preceded by 20 training

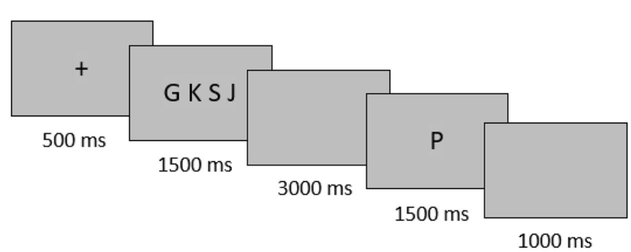

Fig. 1 The modified Sternberg task. Example of a trial in which participants have to answer “no”, not present in the current memory set

trials. Stimuli for training are numbers, while for testing are consonant letters. The order of the three blocks is counterbalanced. Stimuli are presented electronically using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

This block-designed task requires on-line monitoring, updating and manipulation of the information held in memory. Participants have to monitor a series of stimuli appearing one at a time on the screen. They are instructed to use a mouse to respond as fast and as accurate as possible within a 1500 ms window pushing the left button whenever a stimulus presented is the same as the one presented *n* previous items and pushing the right button if not. In the current study, *n* could be equal to 0, 1 or 2. For example, in the 0-back condition, participants are required to respond pushing the left button of the mouse whenever a pre-specified stimulus (“V” letter) is presented. Thus, subjects have to hold one item in memory. In the 1-back condition, participants are instructed to press the left button of the mouse whenever the letter that appears on the screen is the same as the previous one. For instance, the correct answer to the last letter of the sequence “SWW” is “yes”, the correct answer to the sequence “GQS” is “no” (right button). Finally, in the 2-back condition (Fig. 2), the correct answer to the last letter of the sequence “WGW” is “yes” (left button), while the correct answer to the sequence “WGG” is “no” (right button).

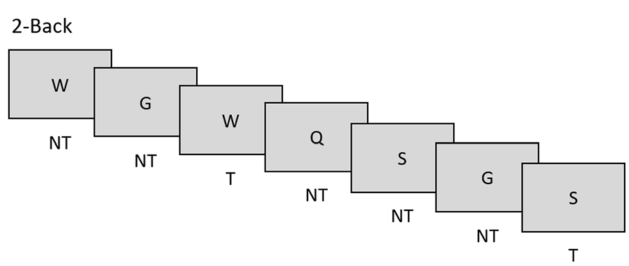

Fig. 2 Jonides’ 2-back task. Schematic representation of the 2-back task. Participants had to press the left button of the mouse whenever a letter appeared on the screen two steps before was the same. *NT* non-target, *T* target

Procedure

The experiment was conducted in a controlled environment of the Sleep Psychophysiology Laboratory at the University of Trieste. The evening before each experimental session (at 8 pm), participants came to the laboratory to undergo a training phase to familiarize with the tasks. The training was crucial to avoid possible confounding learning effects. The morning after (at 9 a.m.), participants were tested. Sleep conditions were counterbalanced across participants with an interval of 1 week between the two to avoid carry over effects. Participants were tested under the following sleep conditions (see Fig. 3):

(a) Baseline (BL)—participants came back to the laboratory around 8:30 a.m. after a regular night of uninterrupted sleep at their own homes under actigraphic control. We checked that all subjects had slept at least 6 h. However, after recording and checking all the sleep files, due to a problem with storage we lost a part of data (10 subjects). Moreover, subjective sleep diary was used to confirm that they had slept at least 6 h per night ($M = 426$ min.; std $= 27$ min.). The 42 subjects whose actigraphic records were available, slept on average 450 ± 52 min.

(b) Total sleep deprivation (SD)—participants were monitored in the laboratory from 8:00 p.m. onward. One day preceding the deprivation night, they received precise instructions to keep their regular bedtimes and not to nap during the day. They spent the entire night awake under the continuous monitoring of trained research assistants. As per standard sleep deprivation protocols, they could study, socialize, play board games, watch movies, and surf the internet. They were not allowed to drink beverages containing stimulants like alcohol, coffee or tea throughout the whole night. Overall, participants stayed awake for a total of 24 consecutive hours.

Participants were run in group sessions with half undergoing sleep deprivation first and the other half in the

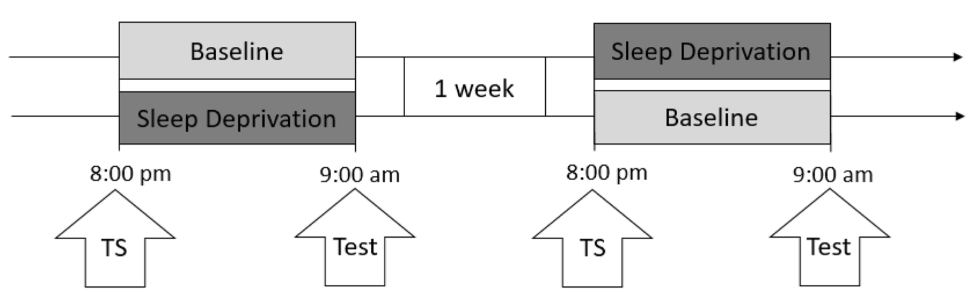

Fig. 3 Timeline of the study. Participants underwent a training session (TS) in the evening before testing. Then, they underwent two sleep conditions, baseline (regular night of sleep) or sleep deprivation (24 h of wakefulness) with a week in between, in a counterbalanced order (for the first session, half of participants underwent a night of normal sleep and the other half a sleep deprivation night)

opposite order (23 participants completed the BL–SD order and 29 the reverse). In both conditions, the experimental session started at 9 a.m. to preclude circadian confounds. First, participants rated their sleepiness and mood by means of the SSS and the VGAS. The subjective scales were always presented before the behavioural tests to verify the participants' state of vigilance at the beginning of each experimental session. Then, they sat in front of an individual computer and performed the modified Sternberg and N-back tasks. The order of behavioural tasks was counterbalanced between subjects to control for carryover effects from one task to the next.

Data analysis

The Wilcoxon matched-pairs test was used to analyse responses to the SSS. GVAS data, reaction time and accuracy rate data were analysed by multiple repeated measure analysis of variance (ANOVA). First, a group level analysis was performed on both the modified Sternberg task and the N-back task. Then, an individual level analysis was carried out. Previous studies used two methods to compute individual vulnerability to SD. One method is based on the degree of change in cognitive performance after SD (Chee & Tan, 2010), the other one is based on the extent of individual's change after SD taking into account their performance at BL (Chuah et al., 2006). In this study, to better investigate whether individual differences in working memory performance after SD modulate the resistance to proactive interference, the second method was used. Participants were divided in a preserved-efficiency (PE) group and worsened-efficiency (WE) group according to their performance in accuracy at the 2-back task from BL to SD, using an arbitrary cut-off of 60% that allowed us to get two nearly balanced groups. Therefore, in the PE group we included: (a) participants whose baseline performance was above 60%, and + it did not fall below the cut-off after sleep deprivation and (b) participants who performed below the cut-off in baseline but surpassed it after sleep deprivation. In the WE group we included: (a) participants who had a performance below 60% in both sleep conditions, (b) participants who improved their performance after sleep deprivation, but did not reach the 60% of correct responses, and (c) those whose performance was good at baseline, but dropped below the threshold after sleep deprivation.

In the PE group, there were 12 participants of the BL–SD order and 21 of SD–BL. For the WE group, 11 participants accomplished the BL–SD order and 8 the SD–BL.

Finally, we performed ANOVAs on the modified Sternberg task with group as factor.

Planned comparisons were run using least squares means method. All analyses were carried out using Statistica software (v 13.0, StatSoft, Inc., Tulsa, OK, USA).

Results

Group level

Subjective measures

The SSS analysis showed that perceived sleepiness following 24 h of sleep deprivation was significantly higher than in baseline condition (Mdn 5 vs 2 respectively; $p<0.05$).

The vigor and the affect indexes were calculated for each sleep condition and then analysed with two one-way ANOVAs. Both vigor (68 ± 5 in BL vs 33 ± 6 after SD; $F_{1,51}=123.65$, $p<0.001$ $\eta^2_G=0.44$) and affect (77 ± 4 in BL vs 67 ± 5 after SD; $F_{1,51}=13.5$, $p<0.001$ $\eta^2_G=0.08$) were characterized by a significant decrease following sleep deprivation.

Modified Sternberg task

Overall performance on this task was significantly affected by sleep deprivation. Following sleep deprivation, reaction times were significantly slower ($F_{1,51}=18.9$, $p<0.001$, $\eta^2_G=0.06$), accuracy significantly decreased ($F_{1,51}=14.04$, $p<0.001$, $\eta^2_G=0.07$), the number of both misses and lapses significantly increased ($F_{1,51}=9.05$, $p<0.01$, $\eta^2_G=0.08$; and $F_{1,51}=28.01$, $p<0.001$, $\eta^2_G=0.12$).

The analysis on the dissociated components of the task revealed that our results substantially replicate those of Tucker and colleagues (Table 1). For the RT, the intercept, which measures non-executive components of the task, was significantly higher in the sleep deprived condition compared to the baseline ($F_{1,51}=13.44$, $p<0.001$, $\eta^2_G=0.06$). The slope, measure of working memory scanning efficiency was not significantly different after sleep deprivation ($F_{1,51}=0.11$, ns, $\eta^2_G<0.004$). Proactive interference, measured as the difference in RT between recent and non-recent negative probes with four-item condition, did not significantly differ ($F_{1,51}=0.13$, ns, $\eta^2_G<0.004$).

As for accuracy (Table 1), there was no significant effect on intercept ($F_{1,51}=1.51$, ns, $\eta^2_G<0.01$) and slope ($F_{1,51}=1.12$, ns, $\eta^2_G<0.004$). Likewise, the difference in accuracy between recent and non-recent negative probes with four-item condition was not significant ($F_{1,51}=0.12$, ns, $\eta^2_G<0.004$).

Jonides "N-back" task

A repeated measure ANOVA with sleep condition as factor was run per each condition of the N-back task on the accuracy. While the difference between baseline and sleep deprivation in the 0-back condition was not

Table 1 Means and standard deviations (in parenthesis) of reaction times (RT) and accuracy percentages on the modified Sternberg task, for Tucker et al 2010 and the present study

Experiment	Sleep condition	Intercept	Slope	Proactive interference
RT (ms)				
Tucker et al. (2010)	CG	588 (45)	60 (8)	70 (25)
	DG	675 (46)	56 (8)	70 (24)
Riontino and Cavallero (present study)	BL	447 (18)	19 (4)	41 (11)
	SD	490 (27)	20 (4)	39 (15)
Accuracy (%)				
Riontino and Cavallero (present study)	BL	98.9 (6.8)	− 1.4 (2.3)	− 4.5 (6.4)
	SD	97.0 (12)	− 1.9 (3.5)	− 4.0 (7.6)

CG control group, *DG* deprived group, *BL* baseline, *SD* sleep deprivation

significant (0.90 ± 0.10 vs 0.89 ± 0.11; $F_{1,51} = 0.04$, $p = \text{ns}$, $\eta^2_G = 0.0004$) in the 1-back condition, it approached significance (0.92 ± 0.09 vs 0.88 ± 0.15; $F_{1,51} = 3.07$, $p = 0.086$, $\eta^2_G = 0.023$). In the 2-back condition, which is our critical measure, there was a significant impairment after sleep deprivation compared to baseline (0.73 ± 0.16 vs 0.68 ± 0.20; $F_{1,51} = 4.32$, $p = 0.043$, $\eta^2_G = 0.020$). When participants had to hold in memory two items and constantly update them, they were significantly less accurate after sleep deprivation, as already reported in previous studies (del Angel et al., 2015; Martínez-Cancino et al., 2015). For the purpose of this study, accuracy at the 2-back condition was taken as critical measure to assess individual differences in working memory efficiency. Participants were divided in two groups (PE and WE) based on their performance after sleep deprivation as described in the data analysis section. The PE group ($n = 33$) did not show significant difference in accuracy between BL and SD (0.79 ± 0.05 and 0.81 ± 0.04 respectively), while the WE group ($n = 19$) had on average lower accuracy after SD (0.47 ± 0.05) compared to BL (0.63 ± 0.07) (Fig. 4).

Individual level

There was no significant difference between the two groups in terms of subjective sleepiness, vigor and affect scores. We re-analysed data from the modified Sternberg task with group (PE and WE) as categorical predictor variable in ANOVAs. There was not significant interaction between the two groups and sleep conditions on overall reaction times ($F_{1,50} = 0.008$, ns, $\eta^2_G < 0.004$), accuracy ($F_{1,50} = 0.60$, ns, $\eta^2_G < 0.004$), number of misses ($F_{1,50} = 0.02$, ns, $\eta^2_G < 0.004$) and number of lapses ($F_{1,50} = 0.45$, ns, $\eta^2_G < 0.004$). The analysis on the dissociated components of the task (Table 2) revealed that,

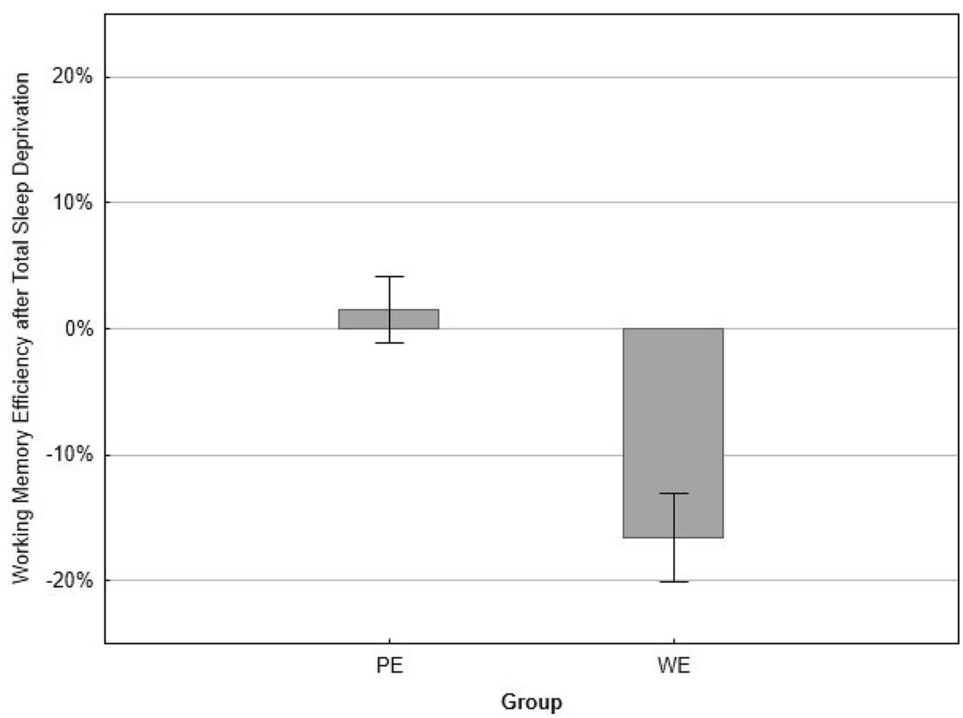

Fig. 4 Difference in working memory efficiency after sleep deprivation on the Jonides' 2-back task for the preserved-efficiency (PE) and the worsened-efficiency (WE) groups

Table 2 Means and standard deviations (in parenthesis) of reaction times (RT) and accuracy percentages for preserved-efficiency group and worsened-efficiency group on the modified Sternberg task

Group	Sleep condition	Intercept	Slope	Proactive interference
RT (ms)				
PE	BL	441 (23)	21 (5)	32 (13)
	SD	485 (34)	20 (5)	48 (19)
WE	BL	458 (30)	18 (6)	57 (17)
	SD	500 (45)	18 (7)	22 (24)
Accuracy (%)				
PE	BL	98.8 (5.1)	– 0.8 (1.6)	– 2.8 (5.2)
	SD	97.0 (11.9)	– 1.5 (2.3)	– 3.4 (7.3)
WE	BL	99.2 (9.2)	– 2.4 (4.0)	– 7.2 (5.0)
	SD	95.2 (15.1)	– 2.6 (5.0)	– 4.9 (8.2)

PE preserved-efficiency group, *WE* worsened-efficiency group, *BL* baseline, *SD* sleep deprivation

for RTs, there was no significant interaction between group and condition of sleep (SD vs BL) for intercept ($F_{1,50}=0.003$, ns, $\eta^2_G<0.004$) and slope ($F_{1,50}=0.10$, ns, $\eta^2_G<0.004$), while, there was a significant interaction for the proactive interference ($F_{1,50}=15.75$, $p<0.001$, $\eta^2_G=0.07$).

Planned contrasts showed that the PE group had significantly more difficulties to control proactive interference after SD ($F_{1,50}=4.32$, $p<0.05$, $\eta^2_G=0.03$, see Fig. 5). Instead, the WE group showed what looks like a diminished susceptibility to proactive interference ($F_{1,50}=11.59$, $p<0.001$, $\eta^2_G=0.08$).

For accuracy (Table 2), there was no significant group by sleep condition interaction for intercept ($F_{1,50}=0.09$, ns, $\eta^2_G<0.004$), slope ($F_{1,50}=0.29$, ns, $\eta^2_G<0.004$) nor proactive interference ($F_{1,50}=1.02$, ns, $\eta^2_G<0.004$).

Finally, to entirely rule out the possibility of order effects, we performed an ANCOVA analysis on RTs for proactive interference with order of sleep condition as covariate. There was still a significant interaction for proactive interference ($F_{1,49}=12.78$, $p<0.001$, $\eta^2_G=0.05$) while the order effect was not significant ($F_{1,49}=0.85$, ns, $\eta^2_G=0.01$).

Discussion

Our results show that sleep deprivation differentially affects individual storage of interfering material and that resistance to proactive interference after SD is dependent on individual differences in a working memory task. Previous findings on executive functioning support the existence in waking of a positive relationship between working

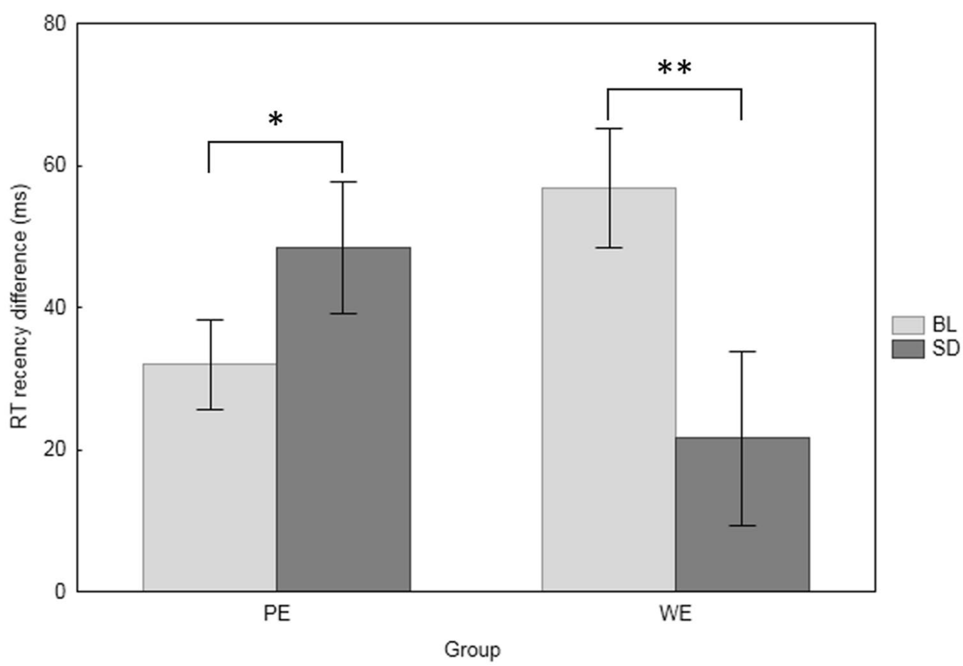

Fig. 5 Difference in RT between recent and non-recent negative probes on the modified Sternberg task, in sleep deprivation (SD) and baseline (BL) for preserved-efficiency (PE) and worsened-efficiency (WE) groups. Lower value on the ordinate represents greater resistance to proactive interference. *$p<.05$; **$p<.001$

memory efficiency and resistance to proactive interference (Kane & Engle, 2000; Rosen & Engle, 1998). We found that sleep loss reverses this relationship (Fig. 5). Individuals characterized by (a) a high level of working memory efficiency, and (b) no WM efficiency degradation after SD, displayed deteriorated abilities to manipulate information within the memory buffer and to control inhibition of interfering materials. Conversely, individuals characterized at Baseline by a poor working memory efficiency, and after SD, a significantly diminished WM efficiency, were apparently not affected by interference and even showed a significantly enhanced resistance to it. This last result, far from being described as an improvement of their ability to control the effect of interfering material, might be more easily explained by considering the significant worsening, after SD, of their ability to store material in working memory. It is reasonable to maintain that these individuals showed significantly less proactive interference after SD because the encoding of the interfering material was compromised by SD resulting in a lower strength of the memory trace (Kareken, Moberg, & Gur, 1996; Rohrer, 1996; Kliegl, Pastötter, & Bäuml, 2015).

It's worth noting that a similar phenomenon has been evidenced by Kareken and colleagues (1996) in schizophrenia: the patients in their study "did not develop PI nearly as much as controls". […..] Reduced susceptibility to PI [….] implicate[s] deficient semantic processing of information to be remembered, which may contribute to impaired encoding and retrieval (Kareken et al., 1996).

A completely different story is to try to explain the results of the PE group that was characterized by no WM efficiency degradation after SD but showed, contrary to the expectations, deteriorated abilities to manipulate information within the memory buffer and to control inhibition of interfering materials. For these individuals, SD selectively impairs distinct components of executive functions differentially: while WM scanning efficiency is not affected by sleep loss, resistance to PI is significantly degraded in comparison with BL levels. We face the paradoxical situation that those individuals who were more efficient in WM efficiency and thus more resistant to PI in BL, following SD become the most prone to suffer PI.

What is it that makes an individual who is not sleep deprived and shows a high level of memory scanning efficiency, more resistant to PI?

Three hypothesis have been put forward:

(a) According to the controlled attention view, it would be "the ability to maintain attention for the goal at hand while avoiding distractions" (Bunting, 2006) that accounts for individual differences in working memory capacity. Since individuals with high WM would be more capable to limit their attention on relevant information they would be more resistant to PI (Hasher & Zacks, 1988; Engle, 2002).

(b) According to the inhibition view, a purely "inhibitory mechanism that deletes irrelevant information from WM" would be the crucial variable (Bunting, 2006). For example, high-WM individuals would be more able to accurately inhibit or suppress irrelevant information, resulting in a better resistance to interference; and.

(c) According to the source monitoring view, the cause of individual differences in WM would be the ability to monitor the source of information to remember rather than the ability to limit attention and/or inhibit irrelevant information. In this view, high-WM individuals are not more capable to inhibit or control irrelevant information in memory than low-WM individuals. Rather, they are significantly better at identifying such information as irrelevant, excluding it at the time of retrieval and consequently to endure interference (Lilienthal et al., 2015).

As evidenced by a large number of research results, SD affects both attention and inhibition, while less, if anything, is known about its influence on memory source monitoring. It remains to clarify which one (or more) of these processes is responsible for modulating performance after SD. In light of our results, this is particularly relevant to explain why following SD the PE group fails to resist interfering material. One possibility is that their WM efficiency is preserved after SD in terms of resolution of representations that can be held in an active state, at the expense of the ability for protecting the activation from interference.

Further research is needed to investigate the role of sleep loss in reversing the relationship between working memory and proactive interference, and this could result in a better comprehension of the mechanism underlying their interaction.

One could have expected to find effect of poorer working memory on other Sternberg measures, mainly on accuracy. However, accuracy rate was considerably high in both groups and sleep conditions, as shown in Table 2. This indicates that, although susceptible to SD, the task is relatively effortless to accomplish. As a matter of fact, the modified Sternberg task is cognitively straightforward as it has separate periods for encoding, retention and recognition, unlike the 2-back task which is more engaging, as at each new item, participants must encode, execute a memory scanning, respond and erase previous items. This suggests that the modified Sternberg task is not likely to bring out group differences in terms of working memory vulnerability after sleep loss.

These data add up to previous findings pointing out that individuals have differential neurocognitive vulnerability to SD (Chuah et al., 2006; Cui et al., 2015; Lim, Choo, & Chee, 2007; Rupp, Wesensten, & Balkin, 2012; Tkachenko & Dinges, 2018; Van Dongen, Baynard, Maislin, & Dinges, 2004; Yeo, Tandi, & Chee, 2015), highlighting the importance of assessing interindividual differences in investigating the effects of SD on executive functioning (Chuah et al., 2006). Indeed, the fact that Tucker et al. (2010) overlooked these differences could be the reason why they did not find impairments in executive functioning. Here, at first, we replicated their findings, but after dividing participants based on their individual differences, we obtained opposite results. Still, there are several differences between these studies that make difficult to compare them. For example, in their study, the length of SD was much longer, 51 h. This extended wakefulness could account for much longer RTs compared to what we found (see Table 1). Further research is required to establish if variability among individuals in sleep vulnerability related to working memory is a stable trait; therefore, possibly used as a phenotypic trait. Attempts to identify factors responsible of individual difference in vulnerability to SD were made in various behavioural and neuroimaging studies (Chee et al., 2006; Cui et al., 2015; Lythe et al., 2012; Yeo et al., 2015). This could be crucial to avoid negative consequences on health and prevent accidents. Additional studies with more refine measures are needed to disentangle this question and to investigate possible correlation between neural activity and behavioural individual differences on executive functioning after SD.

Finally, this study is consistent with the theory that the prefrontal cortex is particularly affected by SD (Harrison & Horne, 2000). The prefrontal cortex is one of the main brain structures underling executive functioning (Thomas et al., 2000; Wu et al., 2006; Xu et al., 2016), activated during the N-back task (Owen et al., 2005) and also involved in interindividual differences in response to sleep loss (Chuah et al., 2006). An fMRI study would be necessary to further investigate neural impairments linked with our paradigm.

In conclusion, these results indicate that: (1) sleep deprivation differentially affects individual storage of interfering material; (2) the relationship between working memory efficiency and proactive interference is reversed following a night of total sleep deprivation; (3) individual differences must be considered in investigating the effects of sleep deprivation. Current findings contribute to the research of the effects of SD in identifying individuals more vulnerable to sleep loss and clarifying inconsistencies in the literature in relation to the effects of SD on executive functions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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