



Cognitive flexibility: A distinct element of performance impairment due to sleep deprivation



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ABSTRACT

In around-the-clock operations, reduced alertness due to circadian misalignment and sleep loss causes performance impairment, which can lead to catastrophic errors and accidents. There is mounting evidence that performance on different tasks is differentially affected, but the general principles underlying this differentiation are not well understood. One factor that may be particularly relevant is the degree to which tasks require executive control, that is, control over the initiation, monitoring, and termination of actions in order to achieve goals. A key aspect of this is cognitive flexibility, i.e., the deployment of cognitive control resources to adapt to changes in events. Loss of cognitive flexibility due to sleep deprivation has been attributed to “feedback blunting,” meaning that feedback on behavioral outcomes has reduced salience - and that feedback is therefore less effective at driving behavior modification under changing circumstances. The cognitive mechanisms underlying feedback blunting are as yet unknown. Here we present data from an experiment that investigated the effects of sleep deprivation on performance after an unexpected reversal of stimulus-response mappings, requiring cognitive flexibility to maintain good performance. Nineteen healthy young adults completed a 4-day in-laboratory study. Subjects were randomized to either a total sleep deprivation condition ($n = 11$) or a control condition ($n = 8$). A three-phase reversal learning decision task was administered at baseline, and again after 30.5 h of sleep deprivation, or matching well-rested control. The task was based on a *go/no go* task paradigm, in which stimuli were assigned to either a *go* (response) set or a *no go* (no response) set. Each phase of the task included four stimuli (two in the *go* set and two in the *no go* set). After each stimulus presentation, subjects could make a response within 750 ms or withhold their response. They were then shown feedback on the accuracy of their response. In phase 1 of the task, subjects were explicitly told which stimuli were assigned to the *go* and *no go* sets. In phases 2 and 3, new stimuli were used that were different from those used in phase 1. Subjects were not explicitly told the *go/no go* mappings and were instead required to use accuracy feedback to learn which stimuli were in the *go* and *no go* sets. Phase 3 continued directly from phase 2 and retained the same stimuli as in phase 2, but there was an unannounced reversal of the stimulus-response mappings. Task results confirmed that sleep deprivation resulted in loss of cognitive flexibility through feedback blunting, and that this effect was *not* produced solely by (1) general performance impairment because of overwhelming sleep drive; (2) reduced working memory resources available to perform the task; (3) incomplete learning of stimulus-response mappings before the unannounced reversal; or (4) interference with stimulus identification through lapses in vigilant attention. Overall, the results suggest that sleep deprivation causes a fundamental problem with dynamic attentional control. This element of performance impairment due to sleep deprivation appears to be distinct from vigilant attention deficits, and represents a particularly significant challenge for fatigue risk management.

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1. Introduction

In around-the-clock industries (health care, emergency response, protective services, energy production, resource extraction, transportation, etc.), nighttime and early morning work hours displace sleep, leading to reduced alertness and performance impairment (Åkerstedt, 2007). Attendant errors and accidents cost money, time, resources, or even lives (Rosekind et al., 2010). Fatigue risk management is concerned with eliminating or mitigating these adverse consequences of reduced alertness. Fatigue risk management strategies may include setting limits on work hours and time on task (Gander et al., 2011), adopting risk-reduction behaviors that improve the resilience of the work environment to alertness-related risks (Dawson et al., 2012), and/or application of various countermeasures (Satterfield & Van Dongen, 2013).

For effective and efficient approaches to fatigue risk management, however, it would be helpful to know what aspects of a job or task make it susceptible to adverse outcomes due to reduced alertness and how to counteract these effects. There is mounting evidence that performance on different tasks is differentially affected when alertness is reduced (Pilcher & Huffcutt, 1996; Killgore, 2010; Lim & Dinges, 2010; Jackson & Van Dongen, 2011), but the general principles underlying this differentiation are not well understood. One factor that may be particularly relevant is the degree to which tasks require executive control (Nilsson et al., 2005), especially tasks that (presumably) involve the prefrontal cortex (Harrison & Horne, 2000). This would include complex cognitive tasks (Jones & Harrison, 2001), flexible decision making tasks (Harrison & Horne, 1999), tasks with high levels of novelty (Harrison & Horne, 1998), as well as tasks requiring response inhibition (Harrison et al., 2007). However, the literature on this topic is quite mixed (Killgore, 2010), with multiple examples of such tasks that are remarkably resilient to reduced alertness (Lim & Dinges, 2010) - including specific counterexamples questioning the involvement of executive control as a generic aspect of sleep-deprived performance impairment (Pace-Schott et al., 2009; Tucker et al., 2010). To better understand the link between sleep deprivation and performance impairment, the literature on the effects of sleep deprivation on executive control needs to be clarified (Williamson et al., 2011). There appears to be a need for a more refined view on the aspects of cognition that are specifically affected by sleep deprivation (Jackson et al., 2013).

A key aspect of executive functioning that has been found to be very sensitive to reduced alertness is cognitive flexibility, i.e., the deployment of cognitive control resources to adapt to changes in events (Whitney et al., 2015). Cognitive flexibility is essential in many real-world settings where reduced alertness is also an issue. For instance, in emergency medicine the condition of a patient may suddenly change and care providers must be able to pick up on the relevant symptoms and adjust the treatment course. Similarly, in military settings warfighters must have good situational awareness and be able to update their understanding of the mission context as new information and feedback from prior actions become available. In such settings, individuals must identify and attend to information that is critical and avoid distraction by information that is, or becomes, irrelevant. It is in such critical contexts that the effects of sleep deprivation on cognitive flexibility have a major impact on performance and safety.

An earlier in-laboratory study (Whitney et al., 2015) provided evidence that cognitive flexibility is particularly vulnerable to the effects of sleep deprivation. In this study, one group of subjects was sleep-deprived for 55 h and another group served as a well-rested control group. All subjects performed a two-phase reversal learning decision task. This task was based on a *go/no go* task paradigm, in which two-digit numeric stimuli were assigned to either a *go* (response) set or a *no go* (no response) set. In each of the two phases of the task, subjects were presented with eight different stimuli, of which four were assigned to the *go* set and four were assigned to the *no go* set. Subjects had a 750-ms window after a stimulus was presented to respond (by pressing the

space bar) or decide to withhold their response. Accuracy feedback, which included hypothetical monetary rewards and punishments, was provided to the subjects after each trial. The second phase of the task was different from the first phase in that the *go* and *no go* sets of stimuli were unexpectedly reversed. The results of the study showed that in the first phase, before the reversal, sleep-deprived subjects exhibited a reduced ability to correctly learn and respond to stimulus-response mappings. Importantly, in the second phase, after the mappings were reversed unexpectedly, the sleep-deprived subjects lost all discriminability. They neither maintained the original stimulus-response mappings nor switched to the new stimulus-response mappings.

The loss of cognitive flexibility due to sleep deprivation that was seen in this study has been attributed to “feedback blunting.” This term describes the observation that behavioral outcome feedback for a sleep-deprived individual has reduced salience (Whitney et al., 2015). The feedback is therefore less effective at directing and modifying actions in a changing environment. Feedback blunting provides an explanation for sleep-deprived individuals showing perseverative behavior, loss of situational awareness, and poor decision making. However, the mechanisms underlying feedback blunting are unknown. Feedback blunting could be caused by general, downstream impairments from loss of vigilant attention due to sleep deprivation (Lim & Dinges, 2008). Alternatively, feedback blunting could be caused by specific problems with forming or maintaining associations between stimuli and response sets, and/or by degraded processing in affective pathways that contribute to salience of action outcomes and other significant events (Whitney et al., 2015). Here we present data from an experiment that investigated the effects of sleep deprivation on performance after an unexpected reversal of stimulus-response mappings in greater detail. Our objective was to elucidate the underlying mechanisms that lead to feedback blunting and the impairment of cognitive flexibility. This research is part of a larger effort to clarify the nature of performance deficits due to reduced alertness in order to be able to design better countermeasure strategies.

2. Methods

2.1. Subjects

Nineteen subjects (13 females) ages 22–36 (mean \pm SD: 26.2 \pm 5.1 years) completed a 4-day/3-night in-laboratory study. Subjects participated in groups of up to four and were randomized as a group to either a total sleep deprivation (TSD) condition ($n = 11$) or a control condition ($n = 8$). All subjects were carefully screened to be physically and psychologically healthy with no current medical or drug treatment, excluding oral contraceptives. They were between the ages of 22 and 40, were free of drugs and alcohol, had no history of a learning disability or moderate to severe brain injury, had no previous adverse reaction to sleep deprivation, were not vision or hearing impaired unless corrected to normal, and were not pregnant. Subjects reported having good habitual sleep, with 6–10 h of sleep daily, regular bed times and habitual wake times between 06:00 and 09:00, and no shift work or travel across time zones within 1 month of entering the study. Polysomnographic sleep recordings after the first night of sleep in the laboratory indicated no sleep disorders.

During the week prior to each subject’s in-laboratory study, subjects were instructed to refrain from using caffeine, alcohol, or drugs, refrain from napping, and to keep a consistent sleep/wake schedule. Compliance was assessed with a wrist actigraph to measure their sleep and wake schedule at home, as well as a sleep diary and calls to a time-stamped voicemail box every day prior to going to sleep and just after waking up.

The laboratory environment was shielded from outside influences, with no internet access, subject telephone access, or live television. Subjects were continuously monitored by trained staff members and no visitors were allowed. There were no windows and lights were fixed

at < 100 lx during all waking periods and off during scheduled sleep periods. Ambient temperature was maintained at 22 ± 1 °C. Subjects were assigned to individual, private bedrooms (monitored by camera and microphone), which were used for scheduled sleep periods and computer testing. Between testing and sleep periods, subjects were in a central suite area and could engage in non-vigorous activities such as board games and reading.

The study was approved by the Institutional Review Board of Washington State University. Subjects gave written informed consent and were paid for their time.

2.2. Study design

Subjects entered the laboratory at 17:30 on day 1 and went to bed at 22:00 for baseline sleep until 08:00 on day 2. Subjects in the TSD condition were then continuously awake for 38 h, from 08:00 on day 2 to 22:00 on day 3. Subjects in the control condition had another night with 10 h in bed on the second night (22:00–08:00). All subjects had a final 10-hour sleep opportunity from 22:00 on day 3 to 08:00 on day 4 before leaving the lab at 10:30.

The three-phase reversal learning decision task was administered twice: at 14:30 on day 2 as a baseline measure, when subjects had been awake for 6.5 h; and again at 14:30 on day 3, when the TSD subjects had been awake for 30.5 h (and control subjects had again been awake for 6.5 h). There were two equivalent versions of the task (with different sets of numbers as the stimuli). One version of which was administered on day 2 and the other on day 3, in randomized order.

2.3. Three-phase reversal learning decision task

The three-phase reversal learning decision task was a variation on the two-phase reversal learning decision task used previously (Whitney et al., 2015). The task was again based on a *go/no go* task paradigm, in which two-digit numeric stimuli were assigned to either a *go* (response) set or a *no go* (no response) set. In each phase of the task, subjects were presented with four different stimuli (compared to eight in the two-phase version of the task). Two of the four stimuli were assigned to the *go* set and two were assigned to the *no go* set. Subjects had a 750-ms window after a stimulus was presented to respond (by pressing the space bar) or decide to withhold their response. The 750-ms duration of the response window was such that subjects could not use speed/accuracy trade-off and slow down their responses to increase accuracy. As such, the primary index of task performance was response accuracy (rather than response speed). Accuracy feedback, which included hypothetical monetary rewards and punishments, was provided to the subjects after each trial. Specifically, “Correct!” or “Incorrect” was shown, and the hypothetical monetary tally was increased by \$0.20 for each correct response and reduced by \$0.20 for each incorrect response.

In phase 1 of the task, which was an additional phase compared to the design of the task in the previous study (Whitney et al., 2015), there were 32 trials. In this phase, subjects were explicitly shown (via on-screen instructions) which two stimuli were assigned to the *go* set and which two stimuli were assigned to the *no go* set. Each stimulus was presented an equal number of times (in randomized order). Each trial began with a message of “Get Ready” shown on the computer screen, followed by the presentation of one of the four numbers in the center of the screen. After the 750-ms window in which the subject made or withheld their response, an acknowledgement message of either “Response Detected” or “No Response Detected” was shown, followed by the accuracy feedback. At the end of each trial, after the accuracy feedback, subjects were prompted for probe recall (e.g., “Which stimulus was the one just presented on this trial? Press 1 for 13, Press 2 for 25, Press 3 for 78, Press 4 for 94”). They responded by typing a number from 1–4, corresponding to the four possible stimuli shown on-screen, and then the next trial began.

The next two phases were similar to the two-phase reversal learning

decision task, except that the set sizes were reduced from eight to four (as in phase 1 of the present task). New stimuli were used that were different from those used in phase 1 but kept the same between phases 2 and 3. Subjects were not explicitly told the *go/no go* mappings and were instead required to use feedback on the accuracy of their responses to learn which numbers were in the *go* and *no go* sets. For example, if the first stimulus presented was “64” and the subject withheld a response, a feedback message of “Correct!” would confirm that 64 was in the *no go* set and a message of “Incorrect” would indicate that 64 was in the *no go* set of numbers. To minimize distraction from the learning requirement, phases 2 and 3 did not have probe recall after each trial.

At the beginning of phase 2, which involved a new set of stimuli (different from phase 1), subjects were informed that at some point during the task the *go/no go* sets may be reversed, and that they should use the feedback to determine when to update their response pattern. Phase 2 consisted of either 40 or 48 trials, depending on the task version. The first 8 trials in the 48-trial version were not used for analysis.

Phase 3 continued directly from phase 2 with an unannounced reversal of the stimulus–response mappings. That is, the stimuli that were previously in the *go* set in phase two were now in the *no go* set and vice versa. Subjects had to use the accuracy feedback to detect the reversal and update their response set. For example, if a subject had previously learned that 64 was in the *no go* set of numbers, but their feedback was “Incorrect” after withholding their response to 64, they could learn that the sets had reversed and 64 was now in the *go* set of numbers. Phase 3 contained 40 trials.

2.4. Analyses

For analysis of performance within each phase of the task, the trials of the three-phase reversal learning decision task were grouped in blocks such that each phase contained four trial blocks with the same number of trials per block (8 trials per block in phase 1 and 10 trials per block in phases 2 and 3). A signal detection framework was used to convert hits (responses to *go* stimuli) and false alarms (FAs; responses to *no go* stimuli) into discriminability index values (Green & Swets, 1974) for each trial block. The discriminability index (or sensitivity index), d' , is a function of the difference between the probability of hits minus the probability of FAs,³ and characterizes subjects' ability to discriminate *go* from *no go* stimuli. Hits, FAs, and d' values were averaged per trial block by condition (TSD or control), session (day 2 or day 3), and phase (1 to 3). Probe recall accuracy was analyzed separately as an overall accuracy score for phase one. Data were analyzed using mixed-effects analysis of variance with a random effect over subject on the intercept (Van Dongen et al., 2004), controlling for the order of the two task versions.

3. Results

Probe recall accuracy in phase 1 of the three-phase reversal learning decision task was analyzed with mixed-effects ANOVA with fixed effects for condition, session, and their interaction. Fig. 1 shows that average probe recall accuracy was consistently high (> 95%) in the control group and the TSD group on both days 2 and 3. There was no significant effect of condition ($F_{1,129} = 2.8$, $p = 0.10$), session ($F_{1,129} = 0.04$, $p = 0.84$), or condition by session interaction ($F_{1,129} = 0.01$, $p = 0.93$). Thus, there was no evidence that TSD impaired subjects' ability to process the stimuli presented.

The left panels of Fig. 2 show the discriminability index (d') in the two groups across each of the 3 task phases on day 2 and on day 3. The right panels of Fig. 2 show the proportion of hits and FAs across 4 trial blocks within each of the 3 task phases for both subject groups on each day. The three phases are visually separated for clarity, although all 3

³ https://en.wikipedia.org/wiki/sensitivity_index

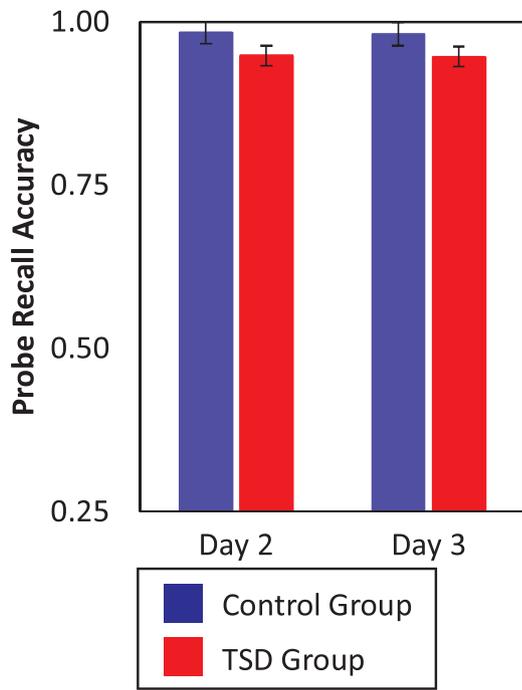


Fig. 1. Mean ± SE of probe recall accuracy in phase 1 of the three-phase reversal learning decision task, by session (day 2/day 3), for each condition. The accuracy axis ranges from 0.25 (chance performance) to 1.00 (perfect recall accuracy).

conditions in trial block 1 of phase 3 reflects the impact of the unannounced reversal (Fig. 2, top right). The improvement shown by trial block 2 of phase 3 indicates that, at baseline, subjects in both groups recognized the change in stimulus-response mappings and adjusted their response patterns accordingly. On the following day when the TSD group had been continuously awake for 30.5 h, subjects in that group had reduced discriminability (lower d') than the control group in all three phases, with the greatest impairment in phase 3 (Fig. 2, bottom left). In phase 3, after the reversal, the TSD group's hits and FAs did not show the rapid improvement after trial block 1 that would indicate adjustment to the reversal of the stimulus-response mappings, indicating a severe deficit in cognitive flexibility (Fig. 2, bottom right).

The d' data were analyzed across all three phases of the task using mixed-effects ANOVA with fixed effects for condition, session, phase, and their two-way and three-way interactions. There were significant main effects of condition ($F_{1,417} = 4.61, p = 0.032$), session ($F_{1,417} = 11.89, p < 0.001$), and phase ($F_{2,417} = 4.44, p = 0.012$); and a significant interaction of condition by session ($F_{1,417} = 15.10, p < 0.001$), and a trend for an interaction of session by phase ($F_{2,417} = 2.38, p = 0.093$). The condition by phase interaction was not significant ($F_{2,417} = 1.77, p = 0.17$), nor was the three-way interaction of condition by session by phase ($F_{2,417} = 0.20, p = 0.82$). Whereas task performance was consistently good across the three phases of the task on day 2 (baseline), performance was degraded in the sleep deprivation condition on day 3, and especially so in phase 3 after the reversal of the stimulus-response mappings.

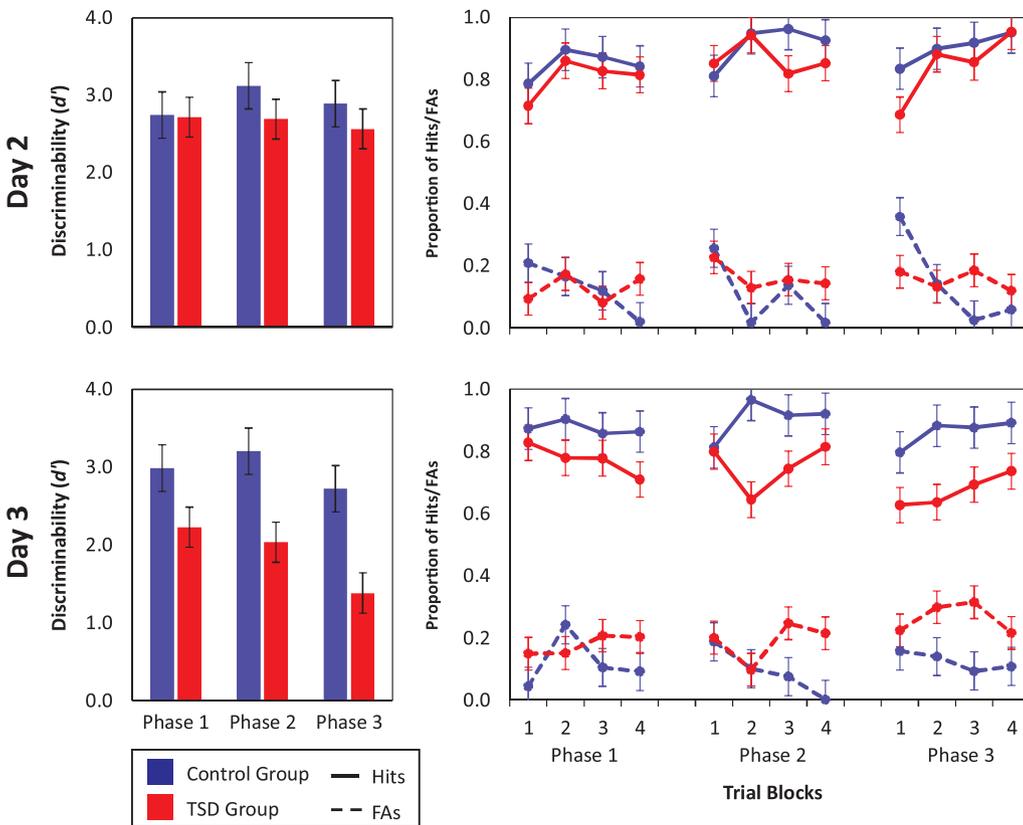


Fig. 2. Mean ± SE of performance on the three phases of the three-phase reversal learning decision task during day 2 (top) and day 3 (bottom). Discriminability index (d') scores, averaged across trial blocks, are shown on the left. The proportions of hits (solid lines) and false alarms (FAs; dashed lines), by trial block, are shown on the right. The gaps between task phases in the right panels serve to visually separate the phases for clarity, although the three phases were taken consecutively as a single task. There was only a brief pause for new instructions between phases 1 and 2, and no pause or instruction of any kind between phases 2 and 3 (the point of the unannounced reversal).

phases are taken collectively as a single task; there was a brief pause between phases 1 and 2 to present instructions for the next part of the task, and there was no pause between phases 2 and 3 as subjects only detected the reversal through the accuracy feedback. At baseline (day 2), the d' was high and stable for both conditions over the 3 phases (Fig. 2, top left). The decrease in hits and increase in FAs seen in both

4. Discussion

Feedback blunting during sleep deprivation may seriously limit cognitive flexibility in critical decision-making contexts (Whitney et al., 2015), and the present study provides new insights into the possible mechanisms underlying the effect. Our data allow us to address

whether sleep deprivation contributes to loss of cognitive flexibility through feedback blunting by: (1) producing a general diminution of performance because of an overwhelming sleep drive produced by extreme sleep deprivation; (2) reducing working memory or attentional maintenance resources available to perform the task; (3) contributing to incomplete or inadequate learning of stimulus-response mappings before reversal; and/or (4) interfering with detection of stimuli, as might be caused by lapses of attention. We discuss each of these possibilities here.

4.1. Does cognitive flexibility impairment depend on sleep deprivation dose?

The original report of cognitive flexibility impairment attributed to feedback blunting was in an experiment where subjects were continuously awake for 55 h (Whitney et al., 2015). This duration of sleep deprivation is not unheard of in operational settings (e.g., military operations), but is uncommon in most around-the-clock operations. The current study tested performance after a single night of sleep deprivation, after 30.5 h of continuous wakefulness. Nonetheless, the performance deficits associated with feedback blunting were still observed. To what extent feedback blunting would be observed at even less time awake remains to be investigated.

4.2. Does cognitive flexibility impairment only occur when attentional or working memory resources are greatly taxed?

The two-phase reversal learning task in the original study of feedback blunting employed 8 two-digit stimuli for which subjects needed to learn *go/no go* response mappings. This number of stimulus-response mappings could present a substantial working memory load (reflected by an average proportion of hits per trial block that remained under 0.8 and FAs that remained over 0.2 at baseline, with baseline pre-reversal d' values under 1.0). The current study employed a task with only 4 two-digit stimuli, which places a lower burden on subjects' working memory maintenance resources, supported by the larger proportion of hits, lower proportion of FAs, and higher d' values at baseline (Fig. 2, top panels). Therefore, the cognitive flexibility impairment associated with feedback blunting is not limited to conditions in which sleep-deprived individuals' ability to maintain information in the focus of attention is highly taxed.

4.3. Does cognitive flexibility impairment occur only with incomplete or inadequate learning of stimulus-response mappings before reversal?

In the previous report of cognitive flexibility impairment from feedback blunting, sleep-deprived subjects had difficulty attaining the level of performance accuracy prior to reversal of the stimulus-response mappings that they obtained when well rested. A lower level of performance prior to reversal would be expected to contribute to difficulty in adapting to reversal. Still, the results in the current study cast doubt on this factor being responsible for the cognitive flexibility impairment. In the previous report, with 55 h of sleep deprivation and 8 stimulus-response mappings to learn in the two-phase version of the task, pre-reversal discriminability (d') averaged 0.53 ± 0.19 (mean \pm SE) (Whitney et al., 2015). With only 30.5 h of sleep deprivation and 4 stimulus-response mappings to learn, the pre-reversal d' in phase 2 of the current task was about four times higher (2.07 ± 0.25 mean \pm SE; see Fig. 2). Nevertheless, the sleep-deprived subjects showed the post-reversal performance decline indicative of feedback blunting during phase 3. Thus, cognitive flexibility impairment in the reversal learning decision task occurs even in situations in which the pre-reversal stimulus-response mappings have been comparatively well-learned.

4.4. Does cognitive flexibility impairment occur because of failure to identify stimuli due to lapses of attention?

The possible role of attentional lapses as causal factors for feedback blunting has previously been addressed indirectly by means of a control experiment in a different group of subjects, who were well-rested (Whitney et al., 2015, supplemental material). In this experiment, lapses of attention were simulated by randomly omitting accuracy feedback from 0%, 20%, or 40% of trials (i.e., on a portion of trials, subjects would see a stimulus, make or withhold their response, and then *not* be shown whether their response was correct or incorrect). This served to mimic attentional lapses, when sleep-deprived subjects would presumably fail to detect some of the feedback, which would reduce their ability to learn the stimulus mappings. With this simulated attentional lapsing, subjects still exhibited higher post-reversal discriminability (d') than had been seen in the sleep-deprived subjects, thus suggesting that missing feedback due to lapses of attention could not, by itself, provide an adequate explanation for feedback blunting.

In the current study we examined the possible role of attentional lapses by directly assessing the accuracy of individuals' reports on stimuli observed on each trial. The phase 1 results during sleep deprivation (Fig. 1) show that subjects were correctly identifying the task stimuli with a near-perfect level of accuracy, comparable to the well-rested subjects. These results indicate that while occasional random lapses of attention can contribute to errors, it is not likely that they are a significant factor in producing feedback blunting.

4.5. Implications of feedback blunting for locus of sleep deprivation effects on performance

The results of our investigations of feedback blunting are not consistent with the idea that there is a single, unified cognitive mechanism by which sleep deprivation degrades performance. Although sleep deprivation produces lapses of attention on tasks that require vigilance, and such lapses are critical to performance on a variety of tasks (Lim & Dinges, 2008), there is now growing evidence that the patterns of preserved and impaired abilities during sleep deprivation cannot be explained solely by loss of stimulus information due to attentional lapsing (Jackson et al., 2013). Stimulus identification for familiar or well learned stimuli is not a fundamental difficulty arising from sleep deprivation (Tucker et al., 2010; Ratcliff and Van Dongen, 2017); see also Fig. 1. In addition, evidence presented in this study and work by others (Habeck et al., 2004; Chee & Chuah, 2007) indicates that stimulus information in the focus of attention is well maintained during sleep deprivation. Thus, those tasks for which the fundamental requirement is the robust maintenance of information are not necessarily impaired when people are sleep deprived (Tucker et al., 2010).

In contrast, tasks that require cognitive flexibility, including the reversal learning paradigm in which we have observed feedback blunting, require the acquisition of novel associations in the pre-reversal phase and the ability to use information from feedback to overcome interference from pre-potent response tendencies in the post-reversal phase. There is evidence that these specific abilities are impaired by sleep loss (Harrison & Horne, 1998; Drummond et al., 2000; Gevers et al., 2015). Together these two factors can account for the problems our sleep-deprived subjects experienced in the reversal learning decision task. Moreover, problems in acquiring novel information and the blunted efficacy of feedback to engender flexibility are especially likely to lead to problems when combined with intact ability to maintain information in working memory (Tucker et al., 2010). Under such conditions, we would expect to see people relying persistently on well-learned information and patterns of behavior. That is, we would expect to see perseverative behavior that is characteristic of people who are sleep deprived (Killgore, 2010).

Overall, the data suggest that people experiencing significant sleep loss have a fundamental problem with *dynamic attentional control*.

Dynamic attentional control is required in situations in which task-relevant information must be acquired through experience and must be updated depending on changing events. The central problem of dynamic attentional control is striking an optimal balance between the robust maintenance of task-relevant information in the face of interference from task-irrelevant information versus the timely updating of information as task-relevant information changes. If the balance between information maintenance and updating is compromised during sleep deprivation, performance that depends on adaptation to changing events should be specifically and severely compromised, leading to perseverative behavior. Here, we have demonstrated such impact on a reversal learning task.

Problems with dynamic attentional control represent a particularly significant challenge for fatigue risk management. Pharmacological interventions to improve alertness (e.g., caffeine or modafinil) mitigate deficits in sleep-deprived performance on vigilant attention tasks (Wesensten et al., 2005), but they are not equally effective at mitigating impairments in tasks requiring cognitive flexibility (Killgore et al., 2009). One of the standard techniques for promoting resilience to sleep loss and other stressors in the workplace is to provide extensive practice to promote readiness to respond. There is some evidence that some forms of cognitive flexibility can be improved by training (Edwards et al., 2010; Anguera et al., 2013). While training could be very helpful to performance under the right circumstances, when cognitive flexibility is required under conditions of sleep deprivation, training could lead to automaticity that may be deleterious to performance by increasing perseverative responses.

More research is needed to determine the generalizability of dynamic attentional control deficits as a primary mechanism underlying performance impairment due to sleep deprivation in real-world settings, and to investigate the usefulness of training interventions to mitigate the effects of sleep deprivation on dynamic attentional control. In addition, the impact of routine and experience in operators who have worked in safety-sensitive operations for many years needs to be examined, as this may further shape outcomes from dynamic attentional control deficits under conditions of sleep deprivation.

5. Conclusion

Our findings suggest that sleep deprivation involves an impairment in the dynamic reallocation of attentional resources to meet changing task demands. In the case of reversal learning tasks like the one used here, inflexibility of responding is sometimes attributed to failure to engage in top-down attentional control (Mitchell et al., 2008). Effects of sleep deprivation on task performance has also been attributed to deficits in top-down attentional control (Poh & Chee, 2017). Top-down attentional control is used to anticipate upcoming events based on expectations that have developed from prior predictable events. Expectations developed this way aid in detecting changes in circumstances through error signals that occur when expectations are violated, and loss of top-down attentional control due to sleep deprivation could potentially provide an explanation for the reversal learning task deficits seen in the present study. However, a recent sleep-deprivation study that used a task designed specifically to address this issue (Whitney et al., 2017) found strong evidence that sleep-deprived people do engage in top-down attentional control. Rather, they have difficulty reallocating attention away from information that is no longer task-relevant when circumstances change, resulting in reduced cognitive flexibility.

Evidence from a variety of tasks (Jennings et al., 2003; Killgore et al., 2009; Whitney et al., 2015; Satterfield et al., 2018; Whitney et al., 2017) indicates that dynamic attentional control problems produced by sleep loss are dissociable from problems with vigilant attention. Given the potential importance of both vigilant attention and attentional control impairments to real world errors produced by sleep deprivation, it is critical that future research address how sleep loss impairs these

distinct elements of performance and how to mitigate these effects.

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