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Review Article

The effects of sleep loss on capacity and effort

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ABSTRACT

Sleep loss appears to affect the capacity for performance and access to energetic resources. This paper reviews research examining the physical substrates referred to as resource capacity, the role of sleep in protecting that capacity and the reaction of the system as it attempts to respond with effort to overcome the limitations on capacity caused by sleep loss. Effort is the extent to which an organism will exert itself beyond basic levels of functioning or attempt alternative strategies to maintain performance. The purpose of this review is to bring together research across sleep disciplines to clarify the substrates that constitute and influence capacity for performance, consider how the loss of sleep influences access to those resources, examine cortical, physiological, perceptual, behavioral and subjective effort responses and consider how these responses reflect a system reacting to changes in the resource environment. When sleep deprived, the ability to perform tasks that require additional energy is impaired and the ability of the system to overcome the deficiencies caused by sleep loss is limited. Taking on tasks that require effort including school work, meal preparation, pulling off the road to nap when driving drowsy appear to be more challenging during sleep loss. Sleep loss impacts the effort-related choices we make and those choices may influence our health and safety.

1. Definition of effort

Recent research has begun to clarify how sleep loss affects capacity and access to energetic resources. Investigators across the sub-fields of sleep research have also identified cortical, physiological, perceptual, behavioral and subjective effort responses that reflect a system attempting to function normally in a resource environment changed by sleep loss. This research enhances our understanding of the physical substrates referred to as resource capacity, identifies how sleep protects that capacity and illuminates the impact of sleep loss on the normal utilization of those resources.

According to Kahneman [50] the extent to which a person can attend to or engage in activity is limited by a physiological maximal processing capacity. Information processing of differing types requires varying levels of attention and engagement and each makes unique demands on the limited processing capacity from moment to moment. Effort is an attempt by the system to meet the needs of the organism. When the system meets the organism's basic information processing needs it is operating under automatic control and though effort is needed, it is low and strain is not detected by the person. Increased time on task, time pressure and off-task distractions require resources in excess of that needed

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for basic information processing. When this happens, the person attempts to maintain performance by applying additional effort and further engaging the system. If resources are depleted or unavailable the person becomes fatigued or exhausted, reduces engagement and eventually gives up [1].

Speed of performance [75], work rates ([17,24,98] [87]), number of problems attempted [4,13,41]; Webb and Levy, 1984) and choice of tasks of various degrees of difficulty [7,79] have been used to determine performance effort. The subjective experience of effort is the sense of perceived exertion when performing beyond the fulfillment of basic task requirements [55] and the available energetic resources.

This review [6,96] will explore our current understanding of capacity, particularly with a focus on energy, how sleep loss affects energy resources and how effort is applied to maintain performance. In particular it will review research contributing to our understanding of capacity, how energy availability is affected by sleep loss, the cortical and physiological outcomes that influence capacity, the perceptual changes in task difficulty in response to sleep loss, how compensatory behavior has been applied in response to the limitations imposed by sleep loss, and the subjective experience of effort under sleep loss conditions.

2. Historical background—Capacity, sleep loss and effort

The impact of sleep loss on the availability of resources and the application of effort to accomplish goals has been of interest since the early days of sleep research. Researchers studying sleep deprivation approached the topic in three primary ways. They considered how performance was maintained through compensatory effort and evaluated the subjective reports of the expenditure of effort under conditions of sleep loss. The absence of performance deficits following sleep loss was considered to result from the application of compensatory effort [25,34,76] and assumed that without additional effort directed toward alert and focused engagement, poor performance would result. In one early study, the author and his wife, the only participants in the study, reported that they had to apply greater effort to perform efficiently on days following sleep loss. They proposed that voluntary 'effort' compensated for the subjective experience of impairment and surmised that expended effort increased in proportion to the amount of sleep lost. To prevent impairment on mental arithmetic, a person having slept 6 h instead of 8 would have to apply 25% greater "energy expenditure" [57].

3. Theoretical and applied value of examining capacity, sleep loss and effort

3.1. *Theoretical value*

Research in the area of sleep and effort has both theoretical and applied value. Such research enhances our understanding of the substrates that constitute and influence capacity for performance and clarifies the role of sleep in protecting those resources. Experimental work in this area helps also helps us consider the attempted compensatory responses and the interaction between genetic, cortical, physiological, perceptual and behavioral systems when sleep loss impacts the system.

3.2. *Applied value*

Adults and children delay sleep and curtail the sleep period deliberately by extending time at work, completing homework assignments and participating in computer and web-based activities [62,63]. Others lose sleep due to insomnia, apnea or medical conditions that interfere with sleep. Approximately 70% of US adults feel they get less sleep than they need and sleep an average of 6.5 h during the week but feel they need 7 h to function well (Sleep in America Poll, 2014). Adolescents (10–17 years) need 9 h of sleep [15] but over half of the 15–17 year olds, almost a third of the 12–14 year olds and 8% of the 6–11 year olds sleep 7 h or less (Sleep in America Poll, 2013). Overall, adults and children sleep less than they need and that loss of sleep influences the choices they make. When adolescent athletes, for example, had less sleep they had poorer mood and considered their drills in sports practice to be more difficult, and when they had more frequent awakenings they avoided the most challenging exercises [30]. Children and adolescents who have insufficient sleep may experience classroom work as more difficult than they would if they had sufficient sleep. Enhanced perceptions of difficulty may lead to decisions to work on easier tasks. Such perceptions and choices could influence students' educational growth.

Health-related choices made by adults in a preliminary study, were also affected by previous nights' sleep. Adults reporting problems with sleep latency, awakenings and total sleep time in comparison to those with no sleep problems were more likely to eat restaurant-prepared or fast-food rather than food made at home [27,29]. Meals prepared out of the home may require less effort but may be less healthful than meals prepared at home. Over time, persons with restricted sleep may have weight or health problems related to the reduced effort they expended by choosing to purchase rather than prepare their meals.

A dangerous outcome of sleep loss is the impact it has on a driver's ability to stay awake. The risk of car crashes with injuries has been associated with the loss of sleep [19]. In comparison to people who sleep eight or more hours, those who sleep 6 to 7 h are twice as likely, and those who sleep less than 5 h are four to five times as likely to be involved in a crash [91]. Many drivers drive when they are tired and 11% reported having nodded off or fallen asleep while driving within the past 12 months [93]. The drivers report having been aware of being tired before the crash. Their attempts to compensate for the fatigue was insufficient to overcome the limitations imposed by sleep loss and they did not expend the effort needed to locate a place to nap and delay arrival at their destinations.

Research exploring the effects of sleep loss on the capacity to perform, perception of task difficulty and willingness to engage may lead to a greater understanding of the limits caused by insufficient sleep on the performance of activities

at home, school and work. persist at difficult tasks at home, at school and Such investigations may lead to the development of strategies to promote educational success, healthy choices and public safety.

4. Hypotheses regarding capacity, sleep loss and effort

Robinson and Hermann [76] hypothesized that sleep loss negatively affected one's ability to perform and that additional effort through "muscular or ideational means" was necessary and responsible for the maintenance of performance when sleep was absent.

Two more recent hypotheses have attempted to explain the role of effort under sleep loss conditions. The first hypothesis posits that sleep loss causes sleepiness, impairs the arousal mechanism and reduces the supply of energy needed to power arousal, perceptual processes, motivation and effort. The outcome of this arousal deficit is a reduction in the desire to perform, a decrease in effort and performance impairments [101,102]. Sleepiness and the urge for sleep caused by sleep loss compete with interest in completing tasks [5], but motivational factors such as feedback can restore arousal, energy and motivation, and impact effort and performance at least for a short-time [81,54] as cited by Odle-Dusseau et al. [65]).

A second hypothesis suggests that energy resources and capacity are lost during sleep deprivation and these losses are responsible for the observed performance deficits. Under well-rested circumstances, the brain consumes the resources necessary to attend to, process and react to stimulation. However, under the influence of a stressor, such as the loss of sleep, the energy supply required for high quality performance is insufficient or unavailable. The effort mechanism can compensate for an insufficient energy supply if the person is aware of their current or potentially substandard performance. This awareness either leads to the mobilization of additional resources needed to sustain performance or the reduction of demands so that the discrepancy between the intention to perform well and actual performance will be aligned [89,50]). Hockey et al. [43] applying this model, proposed that when stress and fatigue caused by sleep loss threatens performance, participants will shift to less-demanding tasks to accommodate the decreased capacity.

The first hypothesis suggests that sleep loss affects the arousal system which affects attention. The predominant desire to sleep interferes with both the motivation to perform and performance. In the second, it is the organism's access to a robust energy system which is impaired. These two theories are not mutually exclusive. It is possible that sleep loss compromises access to or the availability of resources which fuel both attention and performance.

This review will consider energy availability at the source of capacity and it will explore how sleep loss impacts that energy. The cortical, physiological, perceptual, behavioral and subjective effort responses to the sleep loss induced limitations on capacity availability will be considered.

5. Capacity and sleep loss

5.1. *Capacity, energy, body temperature and sleep loss*

Sleep serves an important function in energy balance by reducing daily energy demands and conserving energy stores. Unlike wakefulness, during sleep energy expenditure caused by heat use and loss is limited by behavioral adaptations including the selection of sleep locations that minimize heat exchange with the environment and the assumption of species-specific heat-conserving postures. The conservation of energy within the sleep period also occurs through a reduction in muscle activity including an overall decline in muscle tension during non-Rapid Eye Movement (nREM) sleep and the inhibition of muscular activity during Rapid Eye Movement (REM) sleep [86].

Thermoregulation which requires significant energy to maintain high body temperatures during wakefulness is altered during sleep. In comparison to wakefulness the temperature set-point is reduced in nREM sleep and temperature is unregulated during REM sleep. Such body temperature alterations during sleep result in considerable energy savings [92].

The loss of sleep affects the ability to use energy to maintain normal body temperature. The loss of even a few hours of sleep has been shown to cause a drop in core body temperature in humans [84] and participants have reported feeling cold, added clothing and increased the ambient heat [46]. Sleep deprivation in rats resulted in an inability to retain body heat, an increase in energy expenditure, and an increase in food consumption [74]. The sleep deprivation alterations in energy use have been considered responsible for the observed decreases in body weight and the increases in food consumption [9,10]. Instead of conserving energy during sleep in the absence of sleep human subjects have been shown to use one third more energy [49].

Sleep loss affects the body's ability to store energy and control its availability. Sleep restricted for five days has been shown to result in a 40% slower insulin response and a reduction in the acute insulin response to glucose by 30% [85]. Gherlin, a hormone that stimulates appetite and Leptin, a hormone that inhibits appetite, are both involved in energy regulation and food intake [86]. After two nights of sleep limited to 4 h in bed Gherlin is increased by 28% and Leptin is decreased by 18% and appetites for high calorie foods is increased [87]. Sleep loss appears to create a physiological cascade in response to the detection of energy depletion. Instead of storing energy, energy becomes easily accessible and hormones signal that energy stores need immediate replacement.

5.2. *Capacity, energy metabolism, oxidative stress and sleep loss*

During wakefulness mitochondrial activity demands high levels of energy production. The metabolism of glycogen and other sources of stored energy results in the generation of oxidants or free radicals, and the non-radical products of oxygen and nitrogen. Sleep permits the removal of brain

oxidants including reactive oxygen species (ROS) and reactive nitrogen species (RNS) that accumulate during wakefulness [37]. Without the removal of these oxidants an imbalance between oxidant production and antioxidant defenses occurs leaving the brain in a state of hypermetabolism [33] and oxidative stress [40,95,51].

Sleep deprivation engenders an antioxidant response which is dependent on various factors including the duration of the sleep deprivation, brain area involved and the particular antioxidant. Increased antioxidant responses have been observed in the cortex, hippocampus, basal forebrain, brainstem and cerebellum of rats with short term (6 h) total sleep deprivation and decreased antioxidant responses in the hippocampus and brainstem with longer term (5–11 days) sleep deprivation [73]. With extended sleep deprivation the anti-oxidant imbalance can lead to cell death in rats [33]. Acute short term sleep loss may elicit an increase in antioxidant responses that serve to protect performance and prevent initial deterioration in working memory and behavior, however, the antioxidant response under long term sleep loss conditions appears to be inadequate to offset the presence and impact of these free radicals.

The imbalance between oxidant production and antioxidant defenses during sleep deprivation affects areas outside of the brain. Animals deprived of five days of sleep have shown oxidative stress in the liver with a decrease of 30% in antioxidants catalase and glutathione peroxidase resulting in increased cell membrane damage and permeability [33].

5.3. *Capacity, genetic transcription and sleep*

Gene expression in the brain is as extensive and specific during sleep as it is during wakefulness. The increase in particular gene expression during wakefulness appears to aid the brain in meeting waking energy demands, high synaptic excitatory transmission, high transcriptional activity, and the need for synaptic potentiation in the acquisition of new information. The increase in selected gene transcription during sleep appears to support brain protein synthesis and synaptic membrane maintenance [18]. Specific gene expression is dependent on the wake state or the sleep state and during that state proteins needed for that state are upregulated. Therefore, during sleep deprivation the upregulation of proteins needed for a variety of functions including protein synthesis and synaptic membrane maintenance may not occur.

5.4. *Capacity, energy homeostasis, locus coeruleus and sleep loss*

Locus coeruleus neurons (LC) which contain norepinephrine discharge at high rates during wakefulness, greatly reduced rates during non-rapid eye movement sleep (NREM) and near quiescence during REM sleep [3]. LC neurons maintain control of the awake state, attention, response to stress, novelty and inflammation, and response to behavioral needs [66] and as a result have significant metabolic demands during wakefulness [59].

Mitochondrial sirtuin (SirT3) a protein encoded by the *SIRT3* gene [103] is an important regulator of overall energy homeostasis [2]. SirT3 coordinates mitochondrial energy production and oxidation-reduction (redox) responses [8]. During short-term sleep loss, the metabolic needs of locus coeruleus neurons appear to be protected by the activation of the mitochondrial SirT3 [103]. Short-term sleep loss upregulates SirT3 and antioxidants in the locus coeruleus maintain energy homeostasis. However, sleep loss is a stressor to the locus coeruleus, and with extended sleep loss the adaptive mitochondrial metabolic responses fail. With longer term sleep loss SirT3 activity is reduced followed by an increased production of LC superoxides, LC mitochondrial protein acetylation and the loss of LC neurons through apoptosis [103].

5.5. *Capacity—Astrocytes meeting energy needs*

Glial cells include astrocytes and microglia. During periods of increased energy needs especially during wakefulness norepinephrine causes astrocytes, primarily through their adrenergic receptors, to anticipate and meet energy demands and maintain consistent ATP levels. The α1, α2 and β1 adrenergic receptors of astrocytes are involved in ion homeostasis, neurotransmitter clearance, and energy distribution with the β-adrenergic receptors responsible for eliciting the breakdown of glycogen during increased local neuronal activity [66]. Astrocytes release ATP which is quickly hydrolyzed to adenosine leading to the suppression of excitatory synaptic transmission and decreased arousal [67]. Extended wakefulness and the absence of sleep creates a mounting urge to sleep which appears to be controlled, at least in part, by adenosine affected by the astrocytes [39]. Greater sleep loss involves greater energy metabolism and increased adenosine in the system.

5.6. *Capacity—Removal of waste during sleep*

The waste products of neuronal activity accumulate during wakefulness. Included among these products is Aβ-amyloid (Aβ-) implicated in neurodegenerative diseases. During sleep cortical interstitial space increases by more than 60% and permits the convective exchange of cerebral spinal fluid and interstitial fluid surrounding brain cells, resulting in the removal of these interstitial waste products [102]. The absence of such waste removal from the brain's interstitial space appears to lead to an overload of intracellular calcium concentrations [56] and the interference with synaptic transmission [68]. The restriction of sleep appears to prevent the effective clearance of toxic waste from the system and impedes normal neuronal performance.

5.7. *Capacity—Summary*

Sleep permits the storage of energy and supports normal thermoregulation. The absence of sleep prevents energy savings and instead energy stores meant for normal waking activity are used during the sleep deprivation period. Thermoregulation which is dependent on the available energy supply is severely challenged and in rats studied attempts are made to compensate by increasing caloric intake however the animal does not store energy, loses weight and dies.

LC neurons are responsible for wakefulness and the *SIRT3* gene regulates overall energy homeostasis and the oxidation-reduction process. With extended loss of sleep the LC mitochondrial metabolic responses fail interfering with normal energy control and the anti-oxidant process. The generation of energy results in the production of waste materials including oxidants. During sleep cortical interstitial space increases and the convective exchange of cerebral spinal fluid and interstitial fluid surrounding brain cells results in the removal this waste. Sleep loss prevents the increase in interstitial space and the effective clearance of toxic waste impeding effective neuronal performance. Extended sleep loss results in an oxidant imbalance and cell death. Access to and normal use of energy stores is severely impaired by extended sleep loss.

6. Sleep loss, cortical changes and effort

The changes in cortical activation under the constraints of sleep deprivation and in response to external task demands have been the focus of scientific inquiry. This research identifies changes in cortical brain activity during sleep loss and strategies the brain uses to compensate for and maintain performance.

6.1. *Sleep loss, global brain activity and effort*

Global EEG activity has been thought to be marker of cortical activation in relation to effort. A decrease in high alpha power on the EEG was found to predict a decrease in global subjective vigor, which included a measure of subjective effort. These decreases in alpha power were not related to changes in reaction time [60] suggesting that decreases in high alpha power may be experienced as a reduction in vigor and effort in advance of its impact on behavior.

Functional magnetic resonance imaging (fMRI) maps dynamic changes in blood oxygen levels in the brain. Since changes in blood oxygen levels reflect neural activity in the structural region in which they occur fMRI maps provide an opportunity to observe localized brain activity. Using this technology, mental operations and functions can be associated with particular structural activity. Global cortical activation as assessed by functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) helps to identify how the brain responds when effort is applied and how individuals differ in their effort-related engagement when sleep deprived. Cortical activation as measured by the fMRI has been related to fatigue vulnerability. Using (fMRI) greater baseline cortical activation was associated greater tolerance for sleep deprivation in vigilance tasks [14].

The decline in left parietal activity has also been identified as one specific marker of the vulnerability to fatigue and sleep loss. Those with the greatest reductions in left parietal activation had the greatest variability in reaction time. This decline in activation of the left parietal area from wakefulness to sleep loss states and within the sleep loss assessments was consistent within participants suggesting individual differences in attention and vulnerability to sleep loss [61].

6.2. *Sleep loss, the prefrontal cortex and effort*

The identification of specific locations of cortical activation during sleep loss may clarify where in the brain compensatory actions occur to maintain performance. Increased activation of the prefrontal cortex (PFC) and bilateral parietal lobes, and decreased activation in the temporal lobes was found in participants deprived of 35 h of sleep while performing a memory recall task. PFC activation was associated with reported of sleepiness. Subjective reports of effort and perceived task difficulty were collected after the completion of the fMRI and memory task assessment and did not seem to be correlated with changes in brain activation [21]. Similarly, the fMRI changes in response to difficult words in a verbal learning task showed an increased activation in the bilateral inferior frontal gyrus, bilateral dorsolateral prefrontal cortex, and bilateral inferior parietal lobe following TSD compared with activation following a normal night of sleep. Better free recall of the difficult words was related to increased cerebral responses within the left inferior and superior parietal lobes and left inferior frontal gyrus.

When sleep deprived participants are asked to respond to tasks of high levels of difficulty without the opportunity to select tasks of lower levels of difficulty, some brain areas appear to increase neuronal activation possibly to compensate for the limitations imposed by sleep deprivation in verbal learning [22] and logical reasoning experiments [23].

Relative reductions in ventromedial prefrontal metabolic activity in risky decision making situations were found when participants were deprived of one night of sleep suggesting that the ventromedial prefrontal area may be particularly vulnerable to sleep deprivation [53]. Similarly, sleep deprivation appears to affect task switching, which requires effort to accommodate new informational and environmental demands. Since the prefrontal cortex controls task switching, it has been suggested that the resources normally available to the prefrontal cortex are limited and not well compensated when participants are sleep deprived [20].

6.3. *Sleep loss, the locus coeruleus, the nucleus accumbens and effort*

Increasing time spent awake has been linked to increased extracellular levels of adenosine in the basal forebrain. The presence of adenosine causes a reduction in EEG arousal and alertness [71] and the limitations it places on arousal may contribute to impairments in the application of effort. The presence of increasing quantities of adenosine in other brain locations interferes with dopamine transmission and with effortful performance as well. One such structure is the nucleus accumbens, where adenosine and dopamine appear to interact to regulate functions that require effort. The shell subregion of the nucleus accumbens receives moderately dense input from norepinephrine neurons [11] and lesions of locus coeruleus neurons influences the time course of recovery of baseline levels of extracellular dopamine [52]. In addition, norepinephrine derived from the LC produces an inhibition of the accumbens neurons which receive input from the hippocampus [94]. Salamone and his colleagues [80] reported that in rats, depletion or antagonism of dopamine in

the nucleus accumbens resulted in a greater sensitivity to increases in response costs and the reallocation of instrumental behavior away from more difficult tasks and toward the selection of easier ones. Since dopamine in the nucleus accumbens has a role in controlling effort applied to performance [80] it is possible that the apoptosis of locus coeruleus neurons caused by sleep loss induced oxidative stress may affect the release of dopamine in the nucleus accumbens. The amygdala, anterior cingulate cortex and ventral pallidum have also been identified in effort regulation though how sleep loss influences the functions of these structures with regard to effort has not been elucidated.

7. Sleep loss, physiology and effort

The changes to the energy supply and energy accessibility caused by sleep loss impact physiological functioning. These physiological changes reflect a system attempting to maintain normal functioning and performance under energy limitations.

The availability of energy resources likely affects the body's ability to expend effort. One means by which energy is released is through glucose metabolism. Glucose utilization as reflected by plasma glucose levels was reduced during the 24 h sleep deprivation period and was associated with decreases in a composite of self-reported alertness items including a measure of subjective effort. The greatest decreases in brain glucose utilization were found in those who felt least alert across the night. Changes in glucose levels were not correlated with vigilance performance, however [60]. In another study, sleep deprivation with 48 h with continuous work had no effect on resting blood glucose levels, however, participants perceived increases in imposed work load and reduced their walking pace [77].

Cardiovascular activity makes energy available throughout the system. Systolic blood pressure has been suggested to reflect increased effort. In a series of studies by Gendolla and colleagues, improved performance on tasks rated as difficult was positively correlated with changes in systolic blood pressure (SBP) and with the personal meaningfulness of the task [35]. In addition, insomniacs, those reporting chronically insufficient sleep, showed higher systolic blood pressure reactivity during a memory task than non-insomniacs, suggesting that those who get insufficient sleep apply greater cardiological effort when performing on tasks [82]. Other researchers who assessed heart rate reactivity in response to performance during sleep loss found phasic heart rate deceleration in persons who experienced 32 h of sleep deprivation and received feedback for their reaction time performance (Steyvers, 1987). However, neither fatigue nor anticipated effort has been found to be predictive of cardiovascular reactivity [36].

8. Perception

The increased reports of fatigue and changes in the perception of task difficulty with sleep deprivation may result from a finely-tuned mechanism by which the organism assesses its state, determines the resources needed to complete the task, and decides whether those resources are available or accessible or whether those resources need to be used or conserved for tasks of higher priority. When deprived of sleep for 48 h and required to perform continuous work, participants perceived that the work load had increased and reduced their walking pace in response [77]. Similarly, in a study of physically fit athletes, researchers found an increase in perception of task difficulty following fatigue [72]. Adolescent athletes who had insufficient sleep reported poorer mood and considered their drills in sports practice to be more difficult, and those with frequent awakenings avoided the most challenging exercises [30].

9. Objective effort with sleep loss

9.1. *Objective measures of effort with sleep loss*

The speed of task completion is considered representative of effort and motivation [75]. Under sleep loss conditions, reductions in work rates ([17]; Donnell, 1969; [99]) and the number of solutions participants attempt in response to experimenter-generated problems have been reported [4, 11, 38, Webb and Levy, 1984]. More direct indices of effort are choice preference [7,79] and opportunities to shift between varying effort-requiring work choices [45]. Using these strategies, the behavioral effects of sleep loss have been assessed by offering participants opportunities to select tasks of varying degrees of difficulty. When choices have been presented sleep deprived participants select less difficult math addition problems [31], less challenging non-academic tasks [28] and only the high priority tasks from a selection of both low and high priority offerings [43]. Time spent in daily routine activities which require additional energy decreases including time spent reading for school, dressing neatly and dressing fashionably following a night of sleep loss [31,28]. In addition, following sleep deprivation participants are more likely to break the rules of the task suggesting the adoption of expeditious task completion methods which include the use of heuristics or strategies that limit expended energy and effort [64]. Social loafing involves impaired performance when one works in a group in comparison to performance when one works individually [58]. It is suggested that effort is reduced when one believes others in the group will make equal or greater contributions to the outcome. In an assessment of the influence of sleep deprivation on social loafing, sleep deprived participants whose answers were combined to form a group score and knew that the group outcome rather than their own individual performance would be evaluated, completed fewer trials and had more incorrect responses than those who were sleep deprived and worked individually [44].

9.2. *Maintenance of objective effort*

Continued effort and engagement on a task following sleep loss can be maintained if the task qualities help sustain arousal, and motivational elements such as incentives and feedback are included ([99,47,88, 90]), task material is of interest to the participant [6,96], involve games that include high sensory stimulation, competition and motor output [26,38,97,100] or electric shock [83]. In one study, participants who actively controlled task events showed high levels of reported effort over the three work sessions. However, when the task was under experimenter control, reported effort was

not sustained past the first two sessions. Participants who experienced both experimenter control and sleep deprivation had slower reaction times and increases in premature responding [43]. In addition, when participants are aware they are entering the last assessment session or that the sleep deprivation experience is about to come to an end performance improvement is common [41]. Often, the final assessment session follows the study's longest period of sleep deprivation. The awareness of the upcoming completion of the sleep deprivation experience stimulates motivation, effort and performance.

The extent to which these task-related factors facilitate behavior and maintain performance under sleep deprivation conditions is limited. In one study, feedback decreased reaction time but did not increase accuracy (Steyvers, 1987). In another study, incentive maintained vigilance at baseline levels following one day of sleep deprivation though increasing incentives were unable to sustain baseline performance past 36 h of sleep deprivation [47]. In the absence of task qualities that stimulate engagement, subjective reports of motivation for both vigilance and cognitive tasks have been found to decrease over the course of the sleep deprivation period while reports of expended effort have been found to increase over this period [65].

10. Subjective effort with sleep loss

10.1. *Subjective effort measurement*

Effort under sleep loss conditions is most frequently assessed through self-report measurement. Participants are asked to report their experience with regard to the effort they expended. Often a Likert scale is used in which respondents indicate the effort applied to the previous task by choosing a number ranging from 1 to 10 on symmetric agree-disagree scales or on computerized visual analogue scales with effort represented on a 100 mm line. The wording of the questions regarding the subjective effort varies between laboratories. Participants have been requested to estimate the difficulty of the upcoming task and their anticipated success on the task (Gendolla et al., 2011), their effort during the task (Drummond, 2000, 2005; [64,70]; Odle-Dusseau et al. [65,31]; Hockey et al., 1996) [42], the effort required by the task [22], task difficulty [21,22], the demanding nature of the task [43], effort involved in maintaining primary work goals or performance [43] concentration on the task [70,22,43] motivation to perform the task well (Drummond, 2005 [22]; Odle-Dusseau et al. [65]) and estimated performance [70].

10.2. *Subjective report of effort applied to performance*

Reports of effort applied to performance on reaction time, vigilance, short-term memory, math addition and complex cognitive tasks under sleep loss conditions have been collected. The experience of increased effort has been reported by participants deprived of 24 h of sleep on cognitive vigilance tasks [70], complex cognitive tasks [43] and tasks involving physical work [77]. Participants in one study reported increasing effort and decreasing motivation over the course of the sleep deprivation period. The less participants wanted to participate the more effort they believed they were expending [65]. When increased subjective effort has been reported, objective task performance during sleep deprivation has not necessarily been maintained or improved over the baseline condition or in comparison to a rested control group on vigilance [65], cognitive reasoning [69] or on complex defensive maneuvers [16]. In addition, increased effort and motivation has not been related to improved performance on cognitive-vigilance tasks (Olde-Dusseau and Pilcher, 2010). Participant reports of having expended effort at levels reported when feeling rested and refreshed may reflect a personality style that results in consistent engagement in effort expended or of relative effort expended. For example, regardless of the resource limitations imposed by the sleep deprived state the person may think she is exerting her maximal effort given how she feels at that moment.

Sleep deprived participants do not always report increased effort when compared with those who are rested. No differences in reports of effort have been be found following addition tasks [31], memory tasks [21,64] and reaction time tasks [64] and simple arithmetic, object naming and storytelling [64]. No differences in reported effort with sleep loss may reflect participants' continued effort as they attempt to maintain task accuracy in a compromised state.

The absence of differences in effort reports when the rested and sleep deprived states are compared could also be a function of the means by which subjective effort is measured. The particular effort questions used can affect reported effort. The experience of effort is abstract and also depends on the participant's idiosyncratic physical and emotional sensations. Participants may conjure a sense of the minimum and maximum effort they could expend at that instant, and compare their sensations and current behavior with what they feel they want to do or can do at that moment. The determination of effort to be expended is not made in comparison to some fixed idea of minimum and maximum quantities. Likely, the subjective minimum and maximum effort one can expend at that moment shifts according to an algorithm which includes the interpretation of the effort question being asked, the demands of the task, past experience with that task, the considered importance of the task, the person's current state of resource availability and the emotional and physical sensations that reflect resource availability.

Researchers' interpretations effort responses also require consideration. Reports of increased effort by those deprived of sleep could have several interpretations. The person may perceive a change in resource availability and tasks thought to be simple when resources were available are now perceived to be more difficult since current resources are sensed to be insufficient. Reports of increased effort could also reflect the determination to use voluntary, focused and alternative strategies to engage cortical and physiological resource reserves.

The report of reduced effort could reflect the sense that the task demands require more work than the person can produce at that time and a decision to reduce or withdraw effort given the limited resources. Alternatively, a reduction in reported effort could indicate the task was perceived as insufficiently

challenging or captivating to maintain effort. The relationship between sleep loss and effort reports would be better understood if researchers agreed upon a set of uniform questions clarified with specific instructions to be used across laboratories, under various conditions and tested for reliability. Such consistency in measurement might result in a consistent metric by which participants can share their experience of effort and by which researchers can understand that experience.

10.3. *The timing of the subjective effort assessment*

The variability in the delay between the performance of a task when effort is expended and the time at which the effort questions are asked also may be responsible for the variation in self-reported effort found between studies. Mood and fatigue self-reports show more negative responses if the subjective assessment is conducted within the work period than if the assessment occurs after the work period has been completed or during a rest break [41]. This may be the case for reported effort as well. Drummond et al. [21], for example, found no changes in reports of effort in participants deprived of 35 h of sleep assessed for their perception of effort and task difficulty more than 10 min after performance on the learning task. In another study, when the subjective ratings of effort followed the completion of a battery of memory and reaction time tasks, it was unclear whether the participants deprived of over 30 h of hours of sleep could fully recall their effort and no difference between the rested and sleep deprived groups was found on reported effort [64]. The absence of sleep loss-induced effort report differences could be a function of interference with and the loss of memory for the effort expended.

10.4. *The relationship between subjective experience and objective effort*

The measurement of both subjective and objective effort in sleep deprivation studies is infrequent. Reports of sleepiness and fatigue were associated with the selection of lower difficulty tasks [31], reading less for school following a night of sleep loss [28] and greatest social loafing impairment [44]. In another sleep deprivation study engagement in the high priority tasks continued while performance on lower priority tasks decreased and subjective effort increased [43].

11. Individual differences

Hockey et al. [43] found that while some participants reported exerting less effort, most reported expending more effort when sleep deprived than when fully rested. In a study of two medical residents monitored for physiological and effort over a three month period, one resident's report showed no relationship between subjective effort and cortisol, and adrenaline and reported low workload, high levels of support and control, low levels of fatigue and anxiety and high levels of positive affective states. In comparison, data collected from the second resident showed relationships between subjective effort and cortisol, between subjective effort and noradrenaline, and perceived work demands, fatigue, subjective effort and adrenaline [42]. One marker of vulnerability to sleep deprivation, a decrease in left parietal activation, has been correlated with within subject variability of reaction times [61]. Genetic differences may account for the differences in vulnerability to sleep deprivation and the ability of the system to compensate for the limitations caused by sleep loss. A comparison of three mice strains found differences in the distribution of sleep and the time course of slow wave activity in response to sleep deprivation [48]. In addition, species differences in attention, learning ability, memory and cortical responsiveness to exogenous substances suggests unique genetic sensitivities to stress on the system's capacity. For example, in rats attention and memory behavior [12] and learning to press a lever for food when amphetamine injected into the nucleus accumbens [78] differs depending on the species. Mice show species-specific responses to scopolamine with regard to speed of response and spatial recognition memory [32]. Such strain differences support the genetic basis of sleep loss vulnerability and suggest the existence of genetically determined differences in effort expenditure in response to sleep loss.

12. Summary

Sleep loss appears to affect access to energetic resources and the capacity for performance. Cortical, physiological, perceptual, behavioral and subjective responses reflect a system reacting to changes in the resource environment caused by the absence of sleep. This paper reviews research examining the physical substrates referred to as resource capacity, the role of sleep in protecting that capacity and how the system attempts to respond with effort to overcome the limitations on capacity caused by sleep loss.

Effort is the extent to which an organism will exert itself beyond basic levels of functioning or attempt alternative strategies to maintain performance. The subjective report of effort is the participant's experience of that exertion. Sleep deprivation creates limitations on the ability to perform consistently and at non-sleep deprived and rested levels. The purpose of this review is to bring together research across sleep disciplines to clarify the substrates that constitute and influence the capacity for performance, consider the various roles sleep plays in protecting those resources, review how effort is objectively measured and experienced in response to the limitations on the resources caused by sleep loss.

Children and adults in the United States feel they get less sleep than they need and the loss of sleep influences the choices they make. Sleep loss appears to influence ability to apply sufficient effort needed to live healthy, safe and focused lives. Car crashes, for example, have been associated with loss of sleep. Though drivers report knowing they were sleepy before the crash, they report not taking the time or making the effort to nap and delay the arrival at their destination. Adolescent athletes, when sleep impaired consider their practice drills to be more difficult and avoid the most challenging maneuvers. Adults who report sleep problems appear to eat restaurant-prepared or fast food rather than food made at home. Through a growing appreciation of the role of sleep in effort expenditure and the limits of effort

when capacity is compromised, the public will be better positioned to develop strategies for better sleep and for the promotion of sleep-related educational, health and safety goals.

12.1. Capacity

An early hypothesis proposed that sleep loss negatively affected one's ability to perform and that additional effort was necessary for the maintenance of performance. A more recent theory based on attention suggests that sleep loss specifically impairs the arousal mechanism and reduces the supply of energy needed to power arousal, perceptual processes, motivation and effort. A second theory suggests that capacity in the form of energy resources is lost during sleep deprivation and this loss is responsible for the observed performance deficits. When the capacity is sufficiently reduced effort can no longer be applied and there is a shift to less-demanding tasks.

Capacity includes the body's stored and available energy. Sleep results in both a reduction in performance-based energy demands and thermoregulatory needs. In the absence of sleep, energy is not stored and instead one third more energy is used. Waking mitochrondrial activity requires considerable energy demand and high levels of energy metabolism in the mitochondria results in the production of brain oxidants that can damage cells. The sleep process initiates an antioxidant response removing brain oxidants that accumulate during wakefulness.

Locus coeruleus neurons (LC) maintain control of arousal and response to behavioral needs. Mitochondrial sirtuin (SirT3) is a protein encoded by the *SIRT3* gene which coordinates mitochondrial energy production, regulates energy homeostasis and controls oxidation-reduction (redox) responses. Extended sleep loss reduces SirT3 activity, and increases the production of LC superoxides and the loss of LC neurons..

Astrocytes, a type of glial cell anticipate and meet energy demands and maintain consistent ATP levels. The effects of sleep deprivation on the arousal system seem to be controlled, at least in part, by adenosine affected by the astrocytes. Greater time spent awake is linked to neuronal metabolic activity, increased extracellular levels of adenosine in the basal forebrain and a reduction in EEG arousal and alertness. The nucleus accumbens, adenosine and dopamine appear to interact to regulate functions that require effort. A depletion or antagonism of dopamine in the nucleus accumbens leads to a greater sensitivity to response costs and the reallocation of instrumental behavior away from more difficult tasks and toward the selection of easier ones. Apoptosis of locus coeruleus neurons caused by sleep loss induced oxidative stress may affect the release of dopamine in the nucleus accumbens thereby affecting effort behavior.

Waking neuronal activity also involves the production of waste. During sleep the cortical interstitial space increases by more than 60% and permits the convective exchange of cerebral spinal fluid and the removal of interstitial waste products. In the absence of sleep, such waste removal does not occur and an overload of toxic material can interfere with synaptic transmission.

12.2. Cortical changes with sleep loss

Cortical changes reflect energetic and resource limitations imposed by sleep loss and in some cases mirror experienced vigor and effort. Greater baseline cortical activation is associated greater tolerance for sleep loss and reductions in high alpha power on the EEG is associated with decreases in global subjective vigor including subjective effort.

Brain areas not typically associated with tasks appear to become activated under sleep deprivation conditions. Functional magnetic resonance imaging studies have identified decrements in left parietal activity and reductions in ventromedial prefrontal metabolic activity as indicators of vulnerability to sleep loss. Increased activation of the prefrontal cortex and bilateral parietal lobes appear to be associated with reports of sleepiness, with better recall of difficult words related to increased responsiveness within the left inferior and superior parietal lobes and left inferior frontal gyrus.

12.3. Physiological changes with sleep loss

Physiological changes reflect a system that seems to be working to maintain performance. Increased plasma glucose levels has been associated with decreases in a composite of self-reported alertness items including a measure of subjective effort and may reflect decreased cerebral glucose utilization found during the sleep deprivation period. In contrast, in a separate study resting blood glucose levels were unchanged during sleep loss, though participants perceived increases in imposed work load and reduced their walking pace.

Cardiovascular activity makes energy available throughout the system. Those who get insufficient sleep appear to apply greater cardiac effort when performing tasks. Insomniacs showed higher systolic blood pressure reactivity during a memory task than non-insomniacs and changes in systolic blood pressure was positively correlated with improved performance on tasks rated as difficult. Phasic heart rate deceleration has also been found in persons who experienced sleep deprivation and received feedback for their reaction time performance.

12.4. Perception and sleep loss

The organism assesses its state, determines the resources needed to complete the task, considers the accessibility of those resources or whether those resources need to be used for tasks of higher priority. Without changes in the task requirements sleep deprived participants, have perceived increases in work load, and physically fit but fatigued athletes have reported increases in the perception of the difficulty of a task.

12.5. Objective measures of effort and sleep loss

Sleep deprivation results in objective changes in effort including reductions in the speed of task completion, work rates and the number of solutions attempted. A preference for lower effort tasks, less challenging non-academic tasks, and the selection of only high priority tasks have been observed. With regard to daily functioning, reductions have been found in time spent in daily routine activities, reading for school, and dressing less neatly

and less fashionably following a night of sleep loss. Sleep deprived persons are also more likely to break the rules of the task suggesting the adoption of heuristics which limit expended energy and effort and in socially-based tasks, sleep deprived participants use social loafing in a group setting to conserve energy.

12.6. *Subjective effort with sleep loss*

Subjective effort is assessed by asking participants to report their experience of the effort they expended. The wording of the questions regarding subjective effort expended varies between laboratories with each question tapping into slightly different self-report information.

During or following sleep deprivation, participants have reported increased effort on cognitive vigilance tasks, complex cognitive tasks and tasks involving physical work. Feelings of decreasing motivation and increasing effort over the course of the sleep deprivation period have been described. Reports of increased subjective effort have not necessarily lead to the maintenance or improvement of objective performance and reports of decreased subjective effort have preceded impairments in performance on a vigilance task. Reports of sleepiness and fatigue have been associated with the selection of lower difficulty tasks. In applied settings, though effort reports of participants who had less sleep than they needed were equivalent to those of participants who were rested, those who had less sleep reported greater sleepiness and fatigue, read less for school, selected less demanding academic and non-academic tasks and had increased reaction times. Effort reports have been found to be unchanged or reduced during sleep deprivation on vigilance tasks, addition tasks and memory tasks and those tasks have shown impairments in recall memory, simple arithmetic, object naming and storytelling.

The differences in effort reports between studies may be a function of the methods by which subjective effort is measured, the particular language used to assess the experience of effort and the abstract nature of the experience of effort. In addition, how one answers the effort question is based on a person's idiosyncratic physical and emotional sensations.

In addition, the demands of the task, the considered importance of the task, the perceived connection between their effort and the outcome, and context in which the report effort is being given impacts the effort response.

The reports of effort appear to be ephemeral, may be difficult to remember and could depend on the timing of the subjective effort assessment. An understanding of participants' experience of effort would be better understood if researchers agreed upon a set of uniform questions, asked at particular time in the assessment and clarified with specific instructions and tested for reliability.

12.7. *Individual differences*

Sleep loss affects humans differently with some showing greater vulnerability in reaction times and decreased activation in the left parietal areas. Similarly, different participants respond to the sleep deprivation experience with varying exertion. Most participants report having expended more effort when sleep deprived than when fully rested, but some report having exerting less. Comparisons of the performance of rodent species suggest differences in response to sleep loss as well as differences in learning, attention and memory. These findings suggest genetically based differences in capacity and ability to compensate for changed internal and external environments.

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