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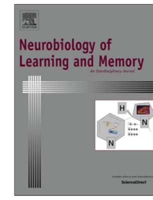

Psychophysiological arousal at encoding leads to reduced reactivity but enhanced emotional memory following sleep

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While sleep's role in emotional memory processing is gaining increasing support, its effect on emotion regulation remains equivocal. Moreover, little is known about the link between emotional reactivity at the time of encoding and subsequent sleep-based emotional memory consolidation. This study examined whether sleep would potentiate, protect, or depotentiate measures of heart rate and skin conductance in response to scenes containing emotional and neutral objects, and assessed how these measures of reactivity would predict subsequent memory for the objects across delays of sleep and wake. Heart rate deceleration (HRD) and skin conductance response (SCR) data were collected at encoding and recognition. Although HRD and SCR reactivity to objects were depotentiated after a sleep-filled delay, they remained unchanged after a delay containing wakefulness. Moreover, increased arousal responses to negative scenes at encoding as measured by HRD and SCR responses were positively correlated with subsequent memory for the negative objects of scenes, but only in the sleep group. This suggests that larger reactions to negative images at the time of encoding set the stage for the preferential consolidation of these images during a night of sleep. Although arousal responses are often thought to account for emotional enhancement in long-term memory, these findings suggest that both an arousal response at encoding and a subsequent period of sleep are needed to optimize selective emotional memory consolidation.

1. Introduction

Emotionally salient stimuli consistently elicit greater physiological responses than neutral stimuli (Abercrombie, Chambers, Greischar, & Monticelli, 2008; Lang, 1995; Lang, Greenwald, Bradley, & Hamm, 1993). The degree of change in physiological reactivity induced by a stimulus is governed by the intensity of arousal that the viewer associates with it (Lang et al., 1993). Research on the neurobiology of this phenomenon suggests that a stimulus perceived as negatively arousing can elicit changes in autonomic nervous system (ANS) output (Hauschildt, Peters, Moritz, & Jelinek, 2011; Lang et al., 1993) and increased activity in brain regions important for emotional processing (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Hoffman, & Kilts, 2002). For example, simple presentation of an emotionally arousing image can trigger changes in heart rate (HR), skin conductance response (SCR), facial movements (electromyogram; EMG; Lang et al., 1993; Pace-Schott et al., 2011), event-related potentials (ERPs; Diedrich, Naumann, Maier, & Becker, 1997; Schupp, Flaisch, Stockburger, & Junghöfer, 2006), and amygdala activation (Garavan et al., 2001), as well as increase subjective ratings of arousal (Lang, 1995; Lang et al., 1993).

Recently, attention has turned to how sleep modulates these initial affective responses (Baran, Pace-Schott, Ericson, & Spencer, 2012; Groch, Wilhelm, Diekelmann, & Born, 2013; Pace-Schott et al., 2011; van der Helm & Walker, 2012; van der Helm et al., 2011; Wagner, Fischer, & Born, 2002; Walker & van der Helm, 2009), although it is unclear at present whether sleep serves to protect (Baran et al., 2012; Groch et al., 2013), potentiate (Lara-Carrasco, Nielsen, Solomonova, Levrier, & Popova, 2009; Wagner et al., 2002), or depotentiate (Pace-Schott et al., 2011; van der Helm & Walker, 2012; van der Helm et al., 2011; Walker & van der Helm, 2009) reactivity to emotionally arousing stimuli. For example, Baran et al. (2012) investigated how nocturnal sleep modulates subjective ratings of valence and arousal to negative pictures compared to a delay of daytime wakefulness. While affective ratings of negative images were attenuated for subjects who remained awake, a night of sleep resulted in the maintenance of

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initial negative ratings. Given that the wake group experienced a change in subjective arousal while those who slept between ratings reported identical reactivity, the authors concluded that sleep helps protect the emotional salience of stimuli. Groch et al. (2013) reached a similar conclusion using ERPs to determine how responses to negative images changed over a night of sleep. In this study, the sleep period was divided into an early, slow wave sleep (SWS)-rich condition and a late, rapid eye movement sleep (REM)-rich condition in an attempt to assess the impact of each type of sleep. This study focused on changes in ERP responses in the frontal cortex during a late time window of 500–800 ms post-stimulus, which is a period linked to the largest ERP positivity effects of arousal evoked by emotional stimuli (Dolcos & Cabeza, 2002). Because stimuli perceived as negative elicit greater positivity during this late positive potential (LPP) window than neutral stimuli, the authors predicted that if sleep (particularly REM-rich sleep) had a depotentiating effect on visceral affectivity, a reduction in positivity would occur when comparing responses during encoding vs. recognition of the negative scenes. Groch et al. (2013) also assessed subjective ratings at encoding and recognition for each session. Similar to Baran et al. (2012), Groch and colleagues found no change in subjective ratings from encoding to recognition in either the SWS-rich or REM-rich condition. Likewise, no change was seen in the LPP from 500 to 800 ms after stimulus onset for either the REM-rich or SWS-rich condition, suggesting that processing negative stimuli during sleep does not alter the emotional reactivity associated with such images (Groch et al., 2013).

Unlike the previous two studies reporting no change in affective tone after a night of sleep, a study by Wagner et al. (2002) suggests that sleep has a potentiating effect on reactivity. When subjects received 3 h of early SWS-rich sleep, subjective ratings of negative pictures did not change from baseline. However, when subjects received 3 h of late REM-rich sleep, they reported an *increase* in experienced negativity. In a follow up study the authors allowed participants to receive an entire undisturbed night of sleep between sessions and found that the subjects again reported an increase in negative arousal ratings, similar to the participants who were allowed only a period of REM-rich sleep (Wagner et al., 2002). Similarly, Lara-Carrasco et al. (2009) asked subjects for valence and arousal ratings before and after either an undisturbed night of sleep, or a night of sleep with partial REM deprivation (REMD). They found that subjects who were REM deprived had reduced reactivity as measured by their subjective ratings compared to those that were allowed more REM sleep, and from this the authors suggest that REM sleep enhances 'aversive reactivity' to negative pictures. While these studies indicate that sleep may protect or even potentiate emotional affectivity over time, it is important to note that many of the results rely on subjective ratings, possibly more indicative of what participants think they should be feeling than what they actually experience. Moreover, because the images were seen and rated prior to sleep, memory of the initial rating may have affected the critical response after sleep (Groch et al., 2013).

Studies that have gone beyond subjective ratings to examine how objective, physiological reactions change over time suggest that sleep may have a depotentiating effect on emotional reactivity. For example, an fMRI study investigated how a night of sleep changed activation in limbic areas to a mixed set of emotionally salient and neutral pictures compared to a delay of daytime wakefulness (van der Helm et al., 2011). Participants were also asked to subjectively rate the scenes on their experienced level of 'intensity' during both viewings of the scenes. They found that after a night of sleep, amygdala activity was reduced in response to previously encountered negative stimuli. This reduced amygdala activity was accompanied by an increase in ventromedial prefrontal cortex (vmPFC) connectivity, an area involved in emotion regulation and indicated in top-down inhibitory effects on amygdala activity. These changes in activation for the sleep group were accompanied by a decrease in subjective emotional ratings between sessions. Participants who remained awake experienced an increase in amygdala activation, a decrease in vmPFC connectivity, and no change in subjective reactivity. The authors concluded that sleep may have a depotentiating effect on measures of behavior and psychophysiology (van der Helm et al., 2011). A similar effect was observed using SCR and EMG measures of physiological reactivity in a recent nap study (Pace-Schott et al., 2011). Although a difference in emotional reactivity failed to emerge in subjective ratings of valence and arousal between nap and control groups, repeated exposure to negative stimuli led to a reduction in SCR and EMG reactivity across sessions in the nap group, while the wake group showed no change in these measures of reactivity (although this pattern did not hold for heart rate deceleration; HRD).

As the previous studies indicate, sleep's role in altering or maintaining reactivity to emotional stimuli remains equivocal. Much more clear, however, is the beneficial role of sleep in emotional memory consolidation (see Payne & Kensinger, 2010; Walker, 2009 for review). For example, Hu, Stylos-Allan, and Walker (2006) showed participants negative and neutral images followed by a 12 h delay spanning daytime wakefulness or a night of sleep. When participants slept in-between sessions, they had enhanced memory accuracy for the emotionally arousing (but not neutral) images compared to when they remained awake. In addition to benefiting memory for entire emotional images, sleep can also selectively boost memory for emotional components of complex scenes (Payne, Stickgold, Swanberg, & Kensinger, 2008). Compared to a day of wakefulness, Payne and colleagues showed that a night of sleep selectively preserved memory for negative objects, but not memory for the (neutral) backgrounds on which they were placed (and also not for memory for neutral scenes). This finding suggests that, rather than preserving intact representations of scenes, the sleeping brain effectively "unbinds" scenes to consolidate only their most emotionally salient, and perhaps adaptive, emotional element (Payne, Chambers, & Kensinger, 2012; Payne & Kensinger, 2010). The emotional object of the scene may be "tagged" for long-term consolidation through arousal-related processes at encoding (Bennion, Mickley Steinmetz, Kensinger, & Payne, 2013). This effect becomes ecologically relevant in real life situations in which the emotional focus of an event, such as a weapon or the face of an assailant, is often viewed within a context initially (during a crime), but is later viewed independently (e.g. a weapon identification scenario or lineup).

What is not yet known is whether physiological reactivity to such emotional items at the time of encoding sets the stage for selective consolidation effects during sleep. This is an important question to ask given that several (non-sleep) studies have demonstrated that the intensity of visceral reactivity to stimuli at encoding predicts their accurate future retrieval. One such study found that within subsets of moderately arousing and neutral words, the words that elicited greater tonic heart rate activity and SCR responses at encoding were better recognized 1 h later than the words that did not elicit such autonomic activity (Buchanan, Etzel, Adolphs, & Tranel, 2006). Abercrombie et al. (2008) extended this research by investigating how the tonic increase in heart rate and the initial phasic heart orientating response (i.e. the heart rate deceleration response, or HRD) to stimuli at encoding would correlate with memory for emotional and neutral stimuli two days later. HRD is a phasic response that has been shown to map onto the affective arousal of a stimulus (i.e. the greater the arousal, the larger the deceleration; Abercrombie et al., 2008; Bradley, Codispoti, Cuthbert, & Lang, 2001; Lang et al., 1995; Pace-Schott et al., 2011), and this response has been shown to persist

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