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

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ABSTRACT

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 throughout

the duration of stimulus presentation (Bradley et al., 2001; Pace-Schott et al., 2011). Thus, if a stimulus is considered emotionally arousing, it will generate a greater initial HRD during the orientating phase than if the stimulus is considered neutral (Bradley et al., 2001). Importantly, Abercrombie et al. found that increased phasic HRD predicted subsequent memory at recognition 48 h later. While each of these studies clearly indicates that the degree of psychophysiological reactivity predicts subsequent memory for emotionally arousing stimuli, none of them examined whether sleep might be involved in the process.

Thus, in the present study we examined, for the first time, how a night of sleep influences changes in heart rate and skin conductance to negative and neutral images compared to a day of wakefulness, as well as how visceral reactivity in response to images at encoding predicts subsequent memory following a delay of sleep or wakefulness. We hypothesized that sleep would lead to a diminished HRD response and a reduction in skin conductance reactivity, mirroring the reduction previously seen in amygdala activation (van der Helm et al., 2011), while no change would be seen in the wake group. We also predicted that while the intensity of visceral reactivity in response to images at encoding would predict subsequent memory at recognition for both groups, due to sleep's active role in emotional memory consolidation, the effect will be strongest in the sleep group.

2. Materials and methods

2.1. Participants

Forty-six University of Notre Dame students participated for payment or class credit. The University of Notre Dame Institutional Review Board approved all testing procedures and written consent was obtained before the experiment. All participants were instructed to refrain from tobacco, caffeine, alcohol, and recreational drugs for 24 h before and throughout the study. They were native English speakers and had normal or corrected-to-normal vision. Prior to the study, participants were screened via an online Qualtrics form for current or prior sleep disorders, disabilities that lead to disturbed sleep, substance abuse, major mental illness, and the use of sleep aid medications or other medications affecting the central nervous system. If any of these conditions was indicated, participants were not admitted into the study. Seven participants were excluded post-hoc from analysis; four due to equipment failure, one for napping during the delay period in spite of instructions not to do so (see below), and two due to an undisclosed sleep or mental disorder that was discovered during debriefing. Thus, thirty-nine participants (female = 18) were included in the analyses (wake group = 21, sleep group = 18).

2.2. Materials

2.2.1. Encoding materials

During the encoding task, participants viewed a set of 68 scenes that portrayed negatively arousing or neutral objects (34 of each valence) placed on plausible neutral backgrounds (e.g. a snake or a chipmunk in a forest, a taxi cab accident or a taxi cab on a street). For each of the scenes, we created four different versions by placing two similar neutral objects (e.g. two images of a taxi cab) and two similar negative objects (e.g. two images of a taxi cab accident) on two neutral backgrounds (e.g. two images of a street) in order to create four different but related scenes (Payne et al., 2008, 2012). Similar images were used to avoid the possibility of image-specific outcomes. By varying the type of object (neutral or negative) and the background version (one of the two paired backgrounds), four different lists of 68 scenes were created. Each participant saw only one list at encoding, which was randomly determined using a mixed Latin Square design. The images within each list were also presented randomly to avoid order effects.

2.2.2. Recognition materials

At recognition, objects and backgrounds were presented separately and one at a time, in random order. Each of these items had either been studied previously ('old') or was entirely new and had never been seen before ('new'). Items on the recognition test were 34 'old' negative objects, 34 'old' neutral objects, 34 'old' backgrounds previously shown with a negative object (although the actual content of all backgrounds was neutral, for convenience we refer to these as "negative backgrounds" because of their original pairing with negative objects), 34 'old' backgrounds previously shown with a neutral object, 34 'new' negative and neutral objects, and 34 'new' backgrounds (all neutral and unpaired with previously viewed objects). We note here that our focus in the current study is on memory for, and physiological reactivity to, negative and neutral objects following delays of sleep versus wakefulness as they represent the emotional focus of the scenes and determine each scene's valence (see Payne & Kensinger, 2010, 2011; Payne et al., 2008, 2012 for additional consideration of background memory).

Participants in a previous study had rated all images (studied and foils) for valence and arousal, using 7 point scales (Kensinger, Garoff-Eaton, & Schacter, 2006); all negative images had received arousal ratings of 5–7 (with high scores representing an arousing image) and valence ratings lower than 3 (with low scores representing a negative image). All neutral items (objects and backgrounds) had been rated as un-arousing (arousal values lower than 4) and neutral (valence ratings between 3 and 5). Subjective ratings taken from our own participants at encoding verified that negative scenes were rated as low in valence (mean: 2.78 ± 0.41) and high in arousal (mean: 4.94 ± 0.48), while neutral scenes were rated as non-arousing (mean: 3.86 ± 0.32) and neutral (mean: 4.47 ± 0.30). This rating task was used both to assess subjective ratings of valence and arousal and to maximize attention and encoding.

2.3. Equipment

To perform the encoding and recognition tasks, participants were escorted to a soundproof viewing booth where they were fitted with noise-reducing headphones to minimize distraction. In the viewing booth, the images were presented using E-Prime (Psychology Software Tools) on a rear-projected 64″ screen located 59″ away from the participant using a NEC NP40 projector. Heart Rate and Skin Conductance Response were recorded using a Biopac MP 150 Data Acquisition System equipped with an SPO2 Pulse Oximeter and a GSR EDA Galvanic Skin Response Amplifier. The viewing booth was equipped with a microphone that projected the participant's responses into a separate control room. For the sleep group, polysomnography (PSG) was recorded with a Grass Comet polysomnography system.

2.4. Procedure

2.4.1. Wake condition

Participants completed the encoding session between 8:00 am and 10:00 am. Prior to beginning the encoding task, subjects were allowed to acclimate to the viewing booth while baseline psychophysiological measures were taken. They were then given a practice picture to become familiar with the rating scales and to ensure that they understood the procedure. After the practice trial, each participant viewed a set of 68 scenes, each of which was displayed for 6000 ms. After each scene was removed from the

display, the subject was prompted to make their ratings of valence and arousal. Because the focus of our study was on changes of objective measures of arousal, these subjective ratings were only collected during the initial session to confirm previous picture norms and ensure attention at encoding. To reduce movement artifact in the psychophysiological waveforms, participants verbally announced their valence and arousal ratings for each image aloud. Participants were alone in the viewing booth for the duration of picture viewing to minimize any social expectancy or emotional contagion effects. Participant audio was picked up via a microphone in the booth and projected into a separate control room where the experimenter logged their responses into the computer. Once the experiment began, the experimenter did not communicate with the participant until session completion. After each picture rating was given, a 10-second inter-stimulus interval (ISI) allowed physiological reactions to return to baseline. In between sessions, wake participants were encouraged to go about their typical weekday routine but were instructed not to nap.

Participants returned to the lab between 8:00 pm and 10:00 pm on the same day (always 12 h from their encoding session) and were informed that they would be participating in an unexpected memory test. They were escorted to the same viewing booth and again equipped with noise-reducing headphones to complete the task. Participants again indicated aloud whether each item was old or new. Images were displayed for 6000 ms regardless of how fast participants announced their answers and there was again a 10-second ISI between items. If they did not answer their response was logged as missing data and was excluded from further analysis.

2.4.2. Sleep condition

The sleep protocol was identical to the wake protocol, except participants arrived in the evening for the encoding session between 8:00 pm and 10:00 pm and completed the recognition task 12 h later between 8:00 am and 10:00 am following a night of sleep. Sleep participants spent the night in the Sleep, Stress, and Memory Laboratory in an adjacent building at the University of Notre Dame. Electrodes were attached to allow for digital PSG recording while participants watched a non-arousing video. The montage included 7 electroencephalogram (EEG) leads (O1, O2, C1, C2, Cz, F1, F2) as well as two electromyogram (EMG) and two electrooculogram (EOG) leads, with each electrode referenced to the contralateral mastoid. After a full night of sleep, the participants were awakened and allowed 30 min to recover from sleep inertia prior to recognition testing. All sleep stages were scored according to the criteria described by Rechtschaffen and Kales (1968) and discussion of stages use their nomenclature (i.e. REM sleep, SWS) in order to be consistent with most studies of sleep and memory consolidation (e.g. Payne et al., 2008, 2012; Diekelmann & Born, 2010). Although the sleep data are not the focus of this study, descriptive statistics are reported in Table 1, and we note that sleep quality in the laboratory was generally good with subjects sleeping for 7.3 ± 0.80 h on average.

Table 1
All measures are in minutes unless indicated.

Sleep parameter	Mean ± SD	% Total sleep time ± SD
Sleep parameters for overnight in lab		
Total sleep time	440.9 ± 50.0	
Wake after sleep onset	47.9 ± 52.5	
Sleep efficiency (%)	87.3 ± 11.2	
Sleep latency	7.5 ± 5.8	
Stage 1	25.2 ± 6.9	5.9 ± 2.2
Stage 2	236.9 ± 42.1	53.6 ± 5.5
SWS	91.8 ± 22.1	21.1 ± 5.3
REM	85.8 ± 19.4	19.4 ± 3.1

SWS = slow wave sleep, REM = rapid eye movement sleep, sleep latency = latency to sleep onset.

2.5. Psychophysiological measures

2.5.1. Heart rate

During both encoding and recognition sessions, a BIOPAC SPO2 Pulse Oximeter was attached to the pointer finger of each participant's dominant hand for inter-beat interval (IBI) collection. HR in beats-per minute (BPM) was derived from the pulseox series collected by AcqKnowledge (ACQ) 4.1. Inaudible tones were acquired synchronously in ACQ immediately prior to stimulus onset to allow for precise alignment of stimulus onset with psychophysiological data. Sampling rate was 312.5 Hz. In order to measure HR changes during orientation and picture presentation, HR was estimated for 16 one-second bins starting 1 s prior to stimulus presentation and continuing for 15,000 ms after stimulus onset (Abercrombie et al., 2008; Graham, 1978). The one-second bin prior to stimulus onset was used as a baseline for each presentation. Heart rate deceleration (HRD) is a phasic response that maps onto the affective arousal of a stimulus (i.e. the greater the arousal, the larger the deceleration; Abercrombie et al., 2008; Bradley et al., 2001; Lang, 1995; Pace-Schott et al., 2011), and this response persists throughout the duration of stimulus presentation (Bradley et al., 2001; Pace-Schott et al., 2011). If a stimulus is perceived as emotionally arousing, it will generate a greater initial HRD during the orientating phase than if the stimulus is considered neutral (Bradley et al., 2001). HRD was calculated by subtracting the baseline BPM during the 1 s prior to stimulus onset from the minimum BPM within the first four 1-s bins. Thus, reported HRD for our study refers to the maximum BPM deceleration during the initial 4 s of stimulus presentation for each trial.

2.5.2. Skin conductance response

Measures of SCR were collected during both encoding and recognition as a marker of sympathetic activation in response to the stimuli (Lang, 1995). Along with HR sensors, participants were prepped with BIOPAC EL507 disposable adhesive EDA sensors on the fingertips of the ring and pointer fingers of their non-dominant hand for SCR collection. Sampling rate was 312.5 Hz during which tonic electrodermal activity (EDA) was calculated. Tonic EDA represents the baseline skin conductance level for each participant. Using ACQ for post-experiment data analysis, phasic EDA waveforms were created by running the tonic EDA waveform through a 0.05 Hz high pass filter. Finally, SCR was calculated. SCR represents localized changes within the tonic EDA. Each SCR was identified by ACQ detection algorithms as a change in electrical conductance $\geqslant$0.02 microsiemens (μS; Dawson, Schell, & Filion, 2000) within the same 15,000 ms window after stimulus onset. Only the first SCR after stimulus presentation was included in analysis. The skin conductance level at the onset of each scene was used as the baseline SCR for each individual trial from which to compare change during later analysis. Due to the time-locked, event-related design of the study we focused on the individual responses of the participants to the stimuli (Mendes, 2009). We calculated SCR proportion by dividing the number of responses that passed threshold during each session by the total number of items seen during that session (Gavallas, 1968).

2.6. Data analysis

2.6.1. Psychophysiological measures

For all measures of HRD and SCR, mean scores were calculated as the average response to each scene aggregated separately at encoding by scene valence (i.e. negative and neutral scenes), and aggregated separately at recognition by valence and scene

component (i.e. negative object, neutral object, negative background, and neutral background). Following Payne and Kensinger (2011), changes in objective visceral reactivity were calculated by comparing responses to entire scenes at encoding to responses to the central object that determined the valence of the scene at recognition. Again, HRD for our study was calculated as the maximum BPM deceleration during the initial viewing of the stimulus for each trial (Abercrombie et al., 2008), and SCR proportion was calculated by dividing the number of responses that passed threshold during each session by the total number of items seen during that session (Gavallas, 1968).

2.6.2. Behavioral data

Subjective ratings of the scenes were assessed as the mean rating of valence and arousal during the encoding session, and these scores were calculated both across all participants and separately for each condition (sleep vs. wake). Memory retention of the objects was calculated separately for each valence (negative and neutral) as the number of items accurately remembered (i.e. hits) divided by the number of items originally viewed. To correct for response bias, we calculated corrected memory by subtracting the proportion of false alarms ('old' judgments to new pictures) of each object type from the proportion of hits (Snodgrass & Corwin, 1988).

3. Results

3.1. Self-report measures

To exclude possible confounds of sleepiness and mood between the sleep and wake groups, self-reported measures of sleepiness, anxiety, and mood were collected prior to encoding and recognition sessions. The groups did not differ in ratings of sleepiness at encoding [$t(37) = 0.29$, $p = 0.77$] or at recognition [$t(30) = -0.21$, $p = 0.98$], as measured by the Stanford Sleepiness Scale (SSS; Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973). There were also no group differences on the state version of the State-Trait Anxiety Inventory (STAI; Spielberger, 2010), [$t(37) = -.023$ $p = 0.82$], and or the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988). This was true both for the positive affect scale of the PANAS [$t(37) = 1.54$, $p = 0.13$], and the negative affect scale of the PANAS [$t(37) = 1.17$, $p = 0.25$]. Finally to check for more pervasive differences in mood, participants also completed the STAI trait measure, the Beck Depression Inventory-II (BDI-II; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961), the Beck Anxiety Inventory (BAI; Beck, Epstein, Brown, & Steer, 1988) and the Mood and Anxiety Symptoms Questionnaire (MASQ; Watson & Clark, 1991). Again, the sleep and wake groups did not differ in any of these measures [STAI trait: $t(37) = .108$, $p = 0.92$; BDI-II: $t(37) = -1.30$, $p = 0.20$; BAI: $t(37) = -1.57$, $p = 0.13$; MASQ: $t(37) = 0.01$, $p = 0.99$].

3.2. Subjective ratings and psychophysiological reactivity at baseline

Using measures generated during initial encoding of the images, we first confirmed that the negative scenes were perceived as being more emotionally salient than the neutral scenes. Across all participants, paired sample *t*-tests revealed that negative scenes were subjectively rated as being more negative [$t(38) = 20.86$, $p < 0.001$] and more arousing [$t(38) = 11.08$, $p < 0.001$] than neutral scenes (see Table 2a). These findings are supported by SCR results indicating that negative scenes provoked a significantly larger proportion of SCRs than neutral scenes [$t(38) = 2.39$, $p = 0.02$]. Although initial analysis of HRD did not show an overall distinction between negative and neutral scenes [$t(38) = .29$, $p = 0.77$], a continuum of negative images was employed in our study that varied from slightly negative to very negative. Given that heart rate shows a linear increase with the degree of arousal (Lang et al., 1993), the inclusion of minimally negative pictures may have reduced the power to sufficiently compare the initial HRD differences at encoding. For this reason we analyzed a subset of negative scenes that received an average valence rating of less than 2, which resulted in a subset of 18 scenes that were perceived as being highly negative. When we compared these images to a matched set of 18 randomly selected neutral scenes (with an avg. valence rating = 4 ± 0.01), the negative scenes produced a significantly larger HRD at encoding compared to their neutral counterparts [$t(17) = 3.51$, $p = 0.003$]. Together these results indicate that the negative scenes were indeed experienced as more emotionally salient than the neutral scenes upon initial exposure.

Independent sample *t*-tests confirmed that the wake and sleep groups did not differ in their subjective ratings of negative [valence: $t(37) = 0.77$, $p = 0.45$; arousal: $t(37) = 1.1$, $p = 0.28$] or neutral scenes [valence: $t(37) = 0.63$, $p = 0.53$; arousal: $t(37) = 0.60$, $p = 0.56$]. Prior to initiating the session, the participants engaged in a scripted conversation to allow for acclimation. This period was also used to obtain a baseline of heart rate at the beginning of the encoding session. Average heart rate was calculated across a 10 s portion of this interview, and we found that there was not a significant difference during this baseline period between the sleep and wake groups ($t(37) = 1.1$, $p = .28$). Due to the binary nature of our SCR analysis (# of responses/# viewed) we could not establish a baseline measure prior to the start of the session, but later analyses revealed that the sleep and wake groups did not differ in the proportion of pictures that elicited an SCR response during the encoding task (see Section 3.4). See Table 2b for average subjective rating and psychophysiological reactivity data at baseline and encoding.

3.3. Change in HRD over time

Our first objective was to determine how HRD reactivity to the central object of scene was affected by the passage of time, and more critically, to determine if it was depotentiated by sleep. First we verified that the sleep group and the wake group did not differ in average HRD to all negative [$t(37) = 1.43$, $p = 0.16$; see Table 2b] or neutral scenes [$t(37) = 0.97$, $p = 0.34$] at encoding (see Fig. 1a). The same was true for the subset of 18 highly negative pictures [valence < 2; $t(17) = 0.38$, $p = 0.74$] and the matched neutral set [$t(17) = 0.14$, $p = 0.89$]. Next we conducted a 2 (valence: negative, neutral) × 2 (HRD measurement for each session: encoding, recognition test) × 2 (condition: sleep, wake) mixed ANOVA, with valence and session as repeated measures. One wake subject was excluded from this analysis due to heart rate equipment failure during recognition. Interestingly and contrary to our prediction that negative images would be most affected, the 3-way interaction was not significant [$F(1,36) = 0.07$, $p = 0.79$]. There was, however, a significant condition × session interaction demonstrating that the sleep group had a significantly reduced HRD, but to *both* negative and neutral information, while there was no change in the wake group [$F(1,36) = 5.00$, $p = 0.032$, $h^2 = 0.12$; see Fig. 1a]. This result indicates a *general* depotentiation of emotional reactivity as measured by the degree of HRD from encoding to recognition when a delay includes sleep, but not when the delay is spent awake. Paired sample *t*-tests show that the sleep group had a significant reduction in HRD from encoding to the subsequent recognition test [$t(17) = 2.4$, $p = 0.03$], while the wake group did not change [$t(19) = 0.84$, $p = 0.41$]. The sleep and wake groups did not differ at encoding [$t(36) = 1.16$, $p = 0.25$], or at recognition [$t(36) = 1.04$, $p = 0.31$], thus minimizing concerns about time of day effects.

Table 2
(a) Average subjective and visceral reactivity to negative and neutral scenes at encoding show that the negative scenes are perceived as being significantly more negative and more arousing than the neutral scenes. (b) No differences in these measurements exist between the sleep and wake groups at baseline or encoding, allowing us to rule out time of day influences.

Measurement type	Stimuli type				Difference	
	Negative		Neutral			
	Mean	SEM	Mean	SEM	*t*	*p*
Subjective ratings and psychophysiological reactivity at encoding						
All participants						
Valence ratings	2.78	.04	4.47	.03	20.86	<.001*
Arousal ratings	4.94	.05	3.86	.03	11.08	<.001*
SCR	.61	.05	.58	.06	2.39	.022*
HRD all	−4.62	.39	−4.53	.47	.29	.77
HRD restrict[t]	−5.49	.37	−3.77	.39	3.51	.003*

Measurement type	Group					
	Sleep (n = 18)		Wake (n = 20)		Difference	
	Mean	SEM	Mean	SEM	*t*	*p*
Time of day effects						
Baseline						
Heart rate (BPM)	81.2	2.72	77.2	2.33	1.11	.28
Encoding						
Negative stimuli						
Valence ratings	2.85	.09	2.75	.10	.77	.49
Arousal ratings	5.01	.10	4.84	.12	1.10	.28
SCR	.65	.07	.58	.08	.67	.51
HRD (BPM)	−5.21	.60	−4.10	.51	1.43	.16
Neutral stimuli						
Valence ratings	4.50	.07	4.44	.07	.57	.53
Arousal ratings	3.88	.09	3.80	.09	.60	.56
SCR	.62	.07	.54	.09	.68	.50
HRD (BPM)	−5.01	.71	−4.11	.61	.97	.34

Note: Valence was measured on a Likert scale from 1 (negative) to 7 (positive). Arousal was measured on a Likert scale from 1 (calming/relaxing) to 7 (agitating/exciting). SCR was calculated as the proportion of scenes to which individuals had an SCR response over the total number of scenes viewed. HRD is average decrease in heart rate from baseline within the first 4 s while viewing the scene. [t]HRD restrict includes a restricted subset of negative scenes with an average valence < 2 and a matched set of neutral scenes (average valence ⩾ 4).
* $p < .05$.

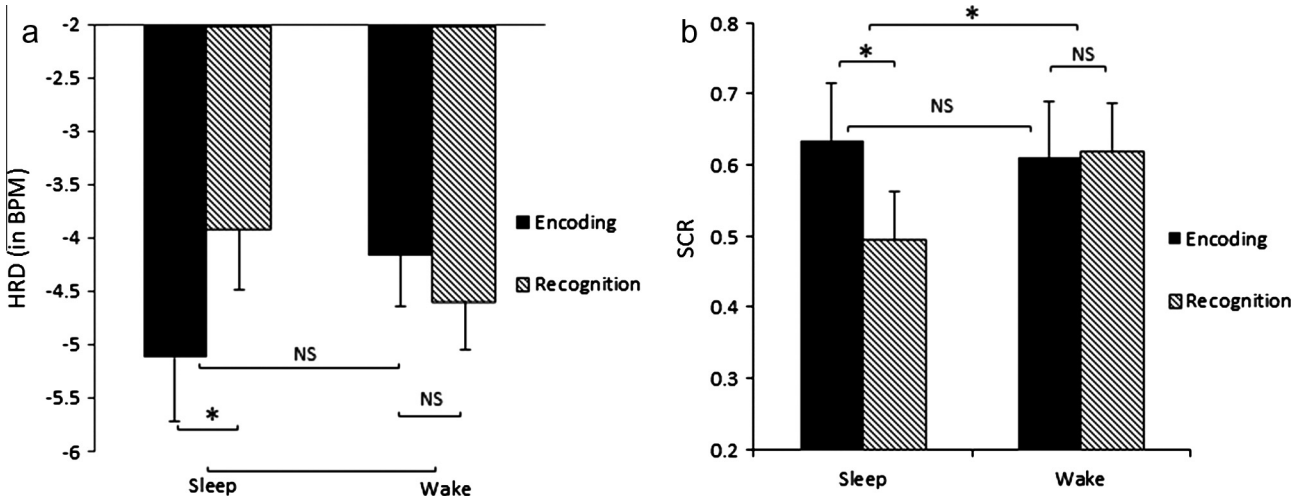

Fig. 1. (a) Mean overall HRD at encoding and recognition in the sleep and wake groups across valences. Note that the sleep group had a significant reduction in HRD from encoding to recognition, but the wake group experienced no change. The bottom-most bracket denotes the significant condition × time interaction. (b) Mean overall SCR for encoding and recognition in the sleep and wake groups across valences. In agreement with heart rate data, there was a significant reduction in the number of SCRs experienced when the delay was filled with sleep, but no change in the number of SCRs when the delay was spent awake. The top-most bracket denotes the condition by time interaction. *$p < .05$.

3.4. Change in SCR over time

Next, we determined how visceral reactivity to the central object of the scenes, as measured by SCR, changed over time. We also examined whether there was a difference in SCR change across a delay including sleep and a delay spent awake. First, we determined that the sleep and wake groups did not differ in the percentage of SCR responses elicited by negative [$t(37) = 0.67$, $p = 0.51$; see Table 2b] or neutral scenes [$t(37) = 0.68$, $p = 0.50$] at encoding (see Fig. 1b). We then conducted a 2 (valence: negative, neutral) × 2

(SCR measurement for each session: encoding, recognition test) × 2 (condition: sleep, wake) mixed analysis of variance (ANOVA). Again, while the 3-way interaction was not significant [$F(1,37) = 0.67$, $p = 0.41$], there was a significant condition × session interaction revealing that the sleep group had significantly reduced SCR to both negative and neutral information, while once again there was no change in the wake group [$F(1,37) = 5.91$, $p = 0.02$, $h^2 = 0.14$; see Fig. 1b]. These results are consistent with the HRD results, providing additional evidence for a *general* depotentiation of physiological reactivity to stimuli over time, regardless of their perceived valence, when the delay includes sleep, but no change in visceral reactivity when the delay is spent awake. Paired sample *t*-tests show that the sleep group had a significant reduction in SCR from encoding to recognition [$t(17) = 3.26$, $p = 0.005$], while the wake group did not show any change [$t(20) = 0.19$, $p = 0.85$]. Again, the sleep and wake groups did not differ at encoding [$t(37) = 0.59$, $p = 0.56$] or at recognition [$t(37) = 0.68$, $p = 0.50$].

3.5. Memory performance: group differences and the relationship between physiological reactivity at encoding and subsequent memory retrieval

A comparison of how object memory differed between the two groups indicated that the sleep group had significantly better memory for objects than the wake group [$t(37) = 2.13$, $p = 0.04$], providing additional support for the theory that sleep is important for memory consolidation (see Rasch & Born, 2013; Stickgold, 2005 for review). However, while memory for negative objects was marginally better in the sleep group than the wake group [$t(37) = 1.84$, $p = 0.07$], a 2 (valence: negative, neutral) × 2 (Scene component: object, background) × 2 (condition: sleep, wake) mixed ANOVA revealed that the group variable did not interact with object valence [$F(1,37) = 0.05$, $p = 0.83$]. In fact, neutral object memories were also marginally better remembered in the sleep group compared to the wake group [$t(37) = 1.88$, $p = 0.07$], which may help explain the general depotentiation results reported above (see Section 4). However, it is worth noting that the sleep group showed preferentially enhanced memory for negative objects relative to memory for the neutral backgrounds on which they were originally placed [$t(17) = 2.8$, $p = 0.01$], while there was no difference in memory of objects and backgrounds for the neutral scenes [$t(17) = 0.21$, $p = 0.83$, see Fig. 2]. The wake group did not show this preferential enhancement for negative objects over associated backgrounds [$t(20) = 1.2$, $p = 0.24$, see Fig. 2]. This finding suggests

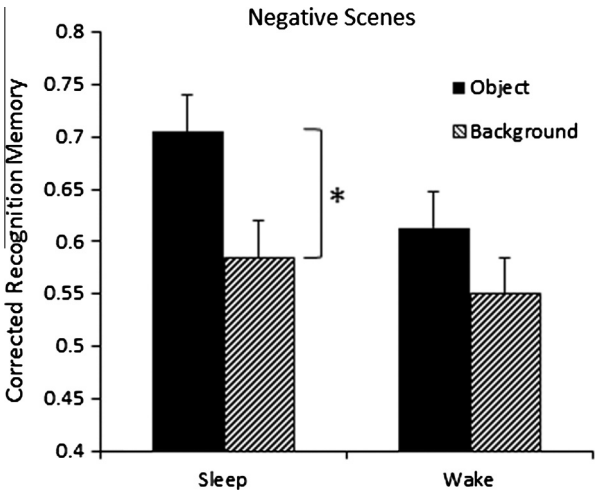

Fig. 2. Sleep benefits memory for negative objects relative to their associated (neutral) backgrounds, while wake results in equivalent memory for the two scene components. *$p < .05$.

that while sleep did not benefit negative over neutral objects overall in this study, it nevertheless did hone in on the negative arousing components of a scene, selectively benefiting the consolidation of negative objects over their paired neutral backgrounds. This result is partially consistent with our prior studies of sleep and the emotional memory trade off effect (Payne & Kensinger, 2010; Payne et al., 2008, 2012, 2011).

The purpose of this experiment was not so much to look at memory performance per se (as that has been done numerous times and reported elsewhere, see Payne & Kensinger, 2010; Payne et al., 2008, 2012, 2011), as it was to determine how visceral reactivity to the full scene at encoding predicted memory for the central scene component (i.e. the negative vs. neutral object) at recognition in the sleep and wake groups. Thus, we correlated physiological measurements at encoding with memory scores for negative and neutral objects at recognition. When including all participants, average HRD at encoding correlated with object memory score across valences at recognition ($r = -.42$, $p = 0.008$). However, when looking at this correlation separately in the sleep and wake groups, we found that average HRD at encoding and object memory at recognition are significantly correlated in the sleep group ($r = -0.53$, $p = 0.02$) but not the wake group ($r = -0.21$, $p = 0.37$). Further dividing these group specific correlations by valence, average HRD to negative scenes at encoding correlated with memory scores for just the negative objects at recognition, but only in the sleep group ($r = -0.67$, $p = 0.002$; see Fig. 3a) and not the wake group ($r = -0.21$, $p = 0.36$). No other significant correlations for HRD and subsequent memory emerged for either the sleep or wake groups (see Table 3). Based on the a priori hypothesis that physiological reactivity at encoding would better predict memory scores for the emotionally salient negative objects, we conducted a one-tailed Fisher *r*-to-*z* transformation (Preacher, 2002) and found that the correlation in the sleep group was significantly different than the correlation in the wake group ($z = -1.71$, $p = 0.04$). This finding strengthens our claim that increased physiological reactivity at encoding tags an item as important such that consolidation processing that occurs specifically during sleep enhances later recognition.

Similarly we correlated SCR at encoding with object memory at recognition. When all participants were included, there was not a significant correlation between SCR and object memory across both valences ($r = 0.20$, $p = 0.22$). Separating this analysis by group also did not lead to any significant correlations (sleep: $r = 0.27$, $p = 0.27$, wake $r = 0.13$, $p = 0.58$). However, dividing the scores by group and valence, we found that SCR to negative scenes at encoding predicted memory for negative objects at recognition, but again, this was true only in the sleep group ($r = 0.48$, $p = 0.04$; see Fig. 3b) but not the wake group ($r = -0.24$, $p = 0.29$), parallel to the HRD results. Again, there were no other significant correlations between SCR and subsequent memory for the sleep or wake groups (see Table 3). We again performed a one-tailed Fisher *r*-to-*z* transformation and again found that the correlation in the sleep group was significantly different than the correlation in the wake group ($z = 2.2$, $p = 0.01$). Together these results indicate that people who are more reactive to negative stimuli at encoding also have enhanced memory for negative information at recognition, but only if they sleep in the delay interval.

4. Discussion

Sleep's role in mediating affective reactivity is a new area of research that is currently a subject of debate, with competing theories arguing that sleep acts to protect (Baran et al., 2012; Groch et al., 2013), potentiate (Lara-Carrasco et al., 2009; Wagner et al., 2002) or depotentiate (van der Helm et al., 2011; Walker & van der Helm, 2009) emotional reactivity. We intended to contribute

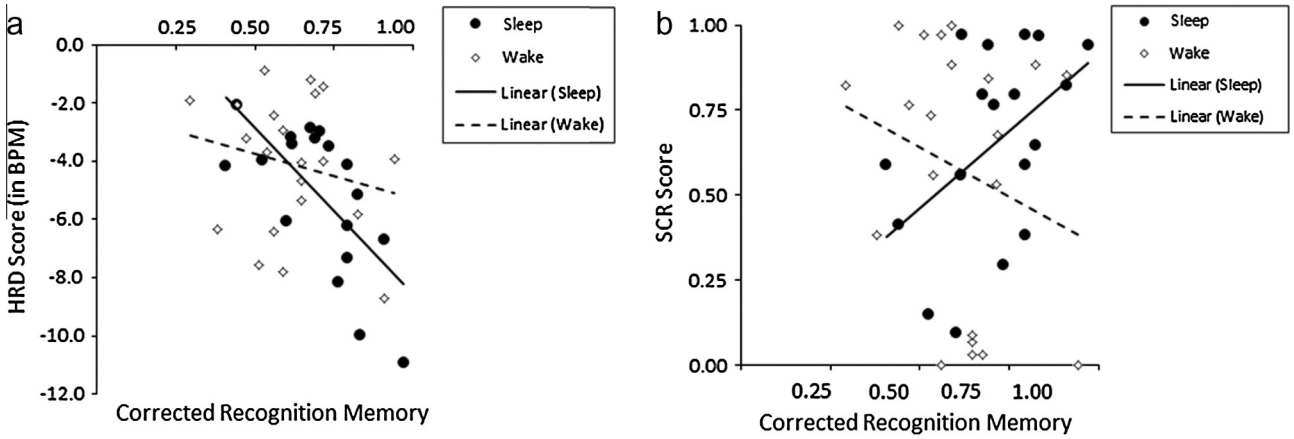

Fig. 3. (a) A larger average HRD to negative scenes during encoding correlates with increased memory for negative objects at recognition for participants in the sleep group. This correlation is not significant for participants in the wake group. (b) Similarly, greater average SCR scores to negative scenes during encoding correlates with increased memory for negative objects at recognition for participants in the sleep group. This correlation is not significant for participants in the wake group.

Table 3
Correlations (*r* values) of average HRD and SCR with memory scores show that greater reactivity to negative scenes at encoding predicts enhanced memory for negative objects at recognition in the sleep group. No other significant correlations exist. Fisher *r*-to-*z* analyses revealed that the correlations for negative object memory and HRD ($z = -1.71$, $p = 0.04$) and SCR ($z = 2.2$, $p = 0.01$) were significantly different between the sleep group and the wake group.

	Negative object	Negative background	Neutral object	Neutral background
Correlations of physiological measurements with memory for scene components				
Sleep group				
HRD	−0.67*	−0.21	−0.30	−0.29
SCR	0.48*	−0.23	0.09	−0.12
Wake group				
HRD	−0.21	0.21	−0.03	0.03
SCR	−0.24	0.16	0.20	−0.16

* $p < .05$.

to this emerging literature by examining how objective, physiological measures of reactivity to negative and neutral images changed over a full night of sleep compared to a day of wakefulness, and extend it by tracking changes in reactivity to the emotional focus of these images (i.e. the objects) over time. Even more critically, we examined how emotional memories might be identified or "tagged" for long-term consolidation processes through acute measures of physiological arousal at the time of learning. To do this, we investigated how reactivity to scenes at encoding predicted subsequent memory for the central objects of the scenes at recognition and, crucially, whether sleep had a moderating influence on this phenomenon. Such an extension is important and ecologically relevant given that the emotional focus of an event, such as the face of an assailant or a weapon, is often viewed within a context initially (during a crime), but is later viewed independently (e.g. a lineup, weapon identification scenario).

Our results revealed a general depotentiation in which visceral reactivity to both negative and neutral objects decreased following sleep, while no such change occurred across a period of wakefulness. Importantly, this result emerged in both HRD and SCR measures, indicating that this effect is robust across multiple modes of physiological reactivity. Additionally, we found that subjects with greater physiological reactivity to negative scenes at encoding also had better memory for the negative objects during a later recognition test, but only if they slept in the delay interval. This effect was highly selective to negative object memory, as neither memory for backgrounds (negative or neutral) nor memory for neutral objects showed this relationship. Again, correlations with both HRD and SCR measures agreed, increasing the strength of our findings.

The result that increased reactivity at encoding predicted subsequent memory in participants who slept extends findings of a study by Abercrombie et al. (2008), in which subjects viewed negative and neutral pictures and then performed a recognition test two days later, and raises the interesting possibility that sleep may be *necessary* for such a result to emerge. While the two-day delay in the Abercrombie studies necessarily involved a period of sleep, here we showed that the correlations between HRD and SCR reactions at encoding and negative object memory at retrieval only held true in participants who received a sleep-filled delay. No such correlations arose for those who remained awake. An interesting possibility is that the elevated physiological reactivity at the time of learning may have helped 'tag' (Morris, 2006; Richter-Levin & Akirav, 2003) emotionally arousing experiences for downstream selective sleep-based consolidation processes. Thus, the more reactive a person is at encoding, the stronger the tag, and the better sleep will facilitate the long-term memory formation process. Another possibility is that increased reactivity benefits encoding, but since both the sleep and wake groups experienced the same level of reactivity during encoding, it would appear as though sleep is necessary to create the tie between visceral response and memory. In a recent study, we demonstrated a similar relation between elevated cortisol levels at encoding and better memory for negative objects in scenes, but again, only in participants who slept. Because cortisol has a sluggish time course, we postulated that it could aid in the effective tagging of salient stimuli, yet it left open the question of how stimuli were deemed significant in the first place. Our current data suggest that other measures of physiological arousal, which can fluctuate on a trial-by-trial basis (SCR, HRD), may help tag memories as salient at the time of learning, which may in turn prioritize them for sleep-based consolidation processes. Critically, in order for this tagging to lead to memory enhancement, sleep must follow learning, likely enabling selective consolidation processes to act. Together, these results provide novel evidence for interactions

between sleep and arousal/stress in the preferential consolidation of emotional memories.

While a night of sleep not only proved vital in tying physiological reactivity during learning to subsequent memory for negative objects, it was also necessary for changes in reactivity to stimuli. Our results revealed a general depotentiation effect in which reactivity was reduced to both negative and neutral stimuli, again only after a night of sleep, which falls in line with the Sleep to Remember, Sleep to Forget (SRSF) hypothesis of emotional memory processing (see van der Helm & Walker, 2012; Walker, 2009 for review). According to this hypothesis, over time, while the memory connected with an emotional event remains intact, the affective "blanket" that originally enveloped the memory during encoding is removed through processing during sleep. In other words, we sleep to retain the memory of the episode but also to reduce the emotional tone associated with it. Although the greatest change in affective tone would be expected for negative images that create the largest arousal response during encoding, even the processing of neutral stimuli creates an orienting response associated with some degree of arousal, which separates it from passive viewing (Abercrombie et al., 2008; Öhman, Eriksson, Fredriksson, Hugdahl, & Olofsson, 1974). Given this observation, we might expect a depotentiation in physiological response to both negative and neutral information after a single night of sleep, especially given that memory for negative and neutral objects was equally benefited by sleep in this study.

Although a general depotentiation effect falls in line with theories of diminished reactivity following sleep, it does not support studies reporting a potentiation or protection of reactivity over sleep (e.g. Baran et al., 2012; Lara-Carrasco et al., 2009; Wagner et al., 2002). The focus of our study was on the change in objective physiology, while many of these prior studies relied heavily on subjective ratings, which are 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). Psychophysiological measures, on the other hand, have been shown to capture underlying and unconscious manifestations of emotional reactivity (Bradley & Lang, 2007). For these reasons we chose not to ask the participants for subjective ratings at recognition, as we wanted a measure of pure visceral activity with minimal contamination from memory of the initial ratings.

A major strength of our memory and depotentiation findings is that both SCR and HRD results agree. However, one salient concern when reporting psychophysiological results is that differences could be attributed to time of day effects (Deryagina & Kraevskii, 1984; Michael et al., 2012). Yet as seen previously for measures of heart rate (see Kudielka, Schommer, Hellhammer, & Kirschbaum, 2004), there were no baseline differences for heart rate or encoding differences for SCR between the sleep and the wake groups, despite the different times of day at which encoding occurred. The absence of initial differences strongly suggests that time of day factors were not a concern in this study. With time of day concerns minimized, it would appear that processing during sleep is the major factor driving our results.

Rather than relying on subjective, self-reported ratings, the goal of this study was to objectively measure changes in visceral reactivity over periods of wake and sleep, and also to examine the relationship between reactivity at the time of learning and subsequent memory. Given this goal, it was necessary to depart from the methods used in previous studies of sleep and emotional memory tradeoff effects. For example, we increased the ISI time in order to minimize the possibility that reactivity to one image would be contaminated by reactions to the previously viewed image. These changes in methodology may explain why we did not fully replicate the emotional memory tradeoff effect as in our prior studies (Payne & Kensinger, 2010; Payne et al., 2008, 2012, 2011). Additionally, while our study revealed both a general depotentiation of reactivity over a period of sleep, and a novel correlation between reactivity at encoding and increased negative object memory post-sleep, a few limitations of the design should be noted. First, as previously mentioned, we did not ask the participants to give subjective ratings at recognition. While this decision was made intentionally (see above), it nevertheless has drawbacks, as it makes it impossible to determine whether subjective and objective measures of reactivity would diverge at recognition, and it limits our ability to compare our results to other studies. A second limitation was the collection of verbal reports while the participants were in the viewing booths. Again, while this decision was intentional in order to reduce movement artifact and ensure the quality of the heart rate and SCR waveforms collected from the fingertips, social expectancy effects cannot be completely ruled out (most notably to the subjective ratings at encoding). Another limitation was the use of only negative and neutral stimuli and no positive stimuli. Positively arousing events may involve a different kind of emotional processing that may alter how the reactivity changes over time, and should be the focus of future research. Finally, the intention behind our design was to track changes in reactivity to the emotional focus of the stimuli from initial viewing (where it was encoded as part of a scene) to recognition (where it was retrieved as an individual object). In so doing, we hoped to better understand the objective physiological response associated with the well-documented emotional memory tradeoff effect (Kensinger et al., 2007), in which memory for the emotional center of a complex scene is selectively preserved over the surrounding neutral information. Given that this effect is often enhanced by sleep (Payne & Kensinger, 2010, 2011; Payne et al., 2008, 2012), we were interested in tracking how reactivity and memory for the central objects that drive the affective response change across periods of wake and sleep. However, it is possible that presentation of the entire scene at recognition, with the central object in the same context as it was originally viewed, could elicit a different response. One key element from our study is that the stimuli were decoupled for both the sleep and the wake group such that each of them saw entire scenes at encoding and scene components at recognition, yet we only found a reduction in reactivity in the sleep group, indicating that this change is driven by an active process during sleep. Nonetheless, both of these limitations should be addressed in future research.

To our knowledge, this is the first study to demonstrate, (1) that SCR and HRD responses to both negative and neutral content are depotentiated over a night of sleep, but remain unchanged over a day of wakefulness, and (2) that individuals who are more reactive to negative images at encoding also have better memory for those images at recognition, but only if they sleep between training and test. These results suggest that reactivity to stimuli at the time of learning sets the stage for consolidation processes during sleep, and perhaps helps to explain how sleep selectively consolidates information that is salient and adaptive to remember while allowing less salient information to be forgotten (e.g. Hu et al., 2006; Payne et al., 2008, 2009; Fischer, Diekelmann, & Born, 2011; Payne & Kensinger, 2010; Saletin, Goldstein, & Walker, 2011). However, given that one of the most prevalent complaints in those suffering from Post-Traumatic Stress Disorder (PTSD) and mood disorders is sleep disturbance (Gottesmann & Gottesman, 2007; Mellman, Nolan, Hebding, Kulick-Bell, & Dominguez, 1997; Morrison, 1989; Tsuno, Besset, & Ritchie, 2005), it is worth considering how selective remembering might malfunction in these conditions. For example, if the visceral "charge" associated with negative memories persists due to sleep dysfunction, one may end up not with adaptive memory, but with chronic anxiety along with the continued strengthening of memories for negative

events. Considering the emotional and economic toll associated with mood and anxiety disorders, further research is essential to understand how sleep mediates the relationship between psychophysiological arousal and subsequent memory.

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