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Sleep spindles provide indirect support to the consolidation of emotional encoding contexts

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ABSTRACT

Emotional memories tend to be strengthened ahead of neutral memories during sleep-dependent consolidation. In recent work, however, we found that this is not the case when emotion pertains to the contextual features of a memory instead of its central constructs, suggesting that emotional contexts are influenced by distinct properties of sleep. We therefore examined the sleep-specific mechanisms supporting representations of emotional context and asked whether these differ to those already implicated in central emotional memory processing, such as rapid eye movement sleep (REM). Participants encoded neutral foreground images that were each associated with an emotionally negative or neutral background (context) image. Immediate and delayed tests for the emotionality of the foreground/background image association were separated by a 4-h consolidation period, which consisted of either total wakefulness or included a 2-h polysomnographically monitored nap. Although memory for negative contexts was not associated with REM, or any other parameter of sleep, sleep spindles (12–15 Hz) predicted increased forgetting and slowed response times for neutral contexts. Together with prior work linking spindles to emotional memory processing, our data may suggest that spindles provide multi-layered support to emotionally salient memories in sleep, with the nature of such effects depending on whether the emotionality of these memories pertains to their central or contextual features. Therefore, whereas spindles may mediate a direct strengthening of central emotional information, as suggested in prior work, they may also provide concurrent indirect support to emotional contexts by working to suppress non-salient neutral contexts.

1. Introduction

Evidence obtained from both behavioural and physiological investigations indicates that memory consolidation is enhanced across overnight sleep relative to corresponding periods of daytime wakefulness (Born, Rasch, & Gais, 2006; Diekelmann, 2014; Diekelmann & Born, 2010; Ellenbogen, Payne, & Stickgold, 2006; Paller & Voss, 2004; Rasch & Born, 2013; Stickgold, 2005; Walker, 2008). Such sleep-dependent consolidation has been reported across a variety of declarative learning materials including word pairs (Gais, Lucas, & Born, 2006; Plihal & Born, 1997), category exemplars (Cairney, Durrant, Musgrove, & Lewis, 2011) and object-location associations (Rasch, Buchel, Gais, & Born, 2007; Wilhelm, Diekelmann, & Born, 2008), and has also been shown across daytime naps (Lau, Tucker, & Fishbein, 2010; Tucker et al., 2006; Wamsley, Tucker, Payne, & Stickgold, 2010).

Rather than impacting upon the consolidation of all newly-learned memories equally, recent work has suggested that sleep-dependent memory processes operate in a more discerning manner, such that information is selectively consolidated on the basis of its salience or relevance for future recall (Born & Wilhelm, 2012; Payne & Kensinger, 2010; Rasch & Born, 2013; Stickgold, 2013; Stickgold & Walker, 2013). Accordingly, emotionally negative memories are often strengthened over sleep to a greater extent than their neutral counterparts (Holland & Lewis, 2007; Hu, Stylos-Allan, & Walker, 2006), with several studies linking such effects to rapid eye movement sleep (REM) (Groch, Wilhelm, Diekelmann, & Born, 2013; Hockley, 2008; Nishida, Pearsall, Buckner, & Walker, 2009; Wagner, Gais, & Born, 2001), although see also Baran, Pace-Schott, Ericson, and Spencer (2012). In a seminal study by Payne, Stickgold, Swanberg, and Kensinger (2008), participants encoded various photographic scenes before a night of sleep or a day of wakefulness. Importantly, each scene

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contained a neutral background image and a superimposed object image, which was either emotionally negative (emotional scene) or neutral (neutral scene). Whereas time spent awake led to forgetting of the entire emotional scene, a night of sleep preserved representations of the negative objects, but not the neutral objects or the neutral backgrounds associated with either object type, suggesting that sleep-specific processes targeted only the centrally affective components of these newly-formed emotional memories.

In prior work, however, we showed that this effect does not hold true when the emotionality of a novel representation pertains to its contextual features, rather than the central memory information (Lewis, Cairney, Manning, & Critchley, 2011). In this study, participants encoded several neutral object images that were each superimposed on a negative or neutral background (context) image. After a period of sleep or equivalent wakefulness, participants were presented with each object image alone and asked to recall the emotionality of its associated background context. Contextual associations were generally better remembered after sleep than wake, but there was no selective sleep-related improvement in the recall of negative contexts. One potential reason for this finding is that centrally emotional memories are influenced by sleep in different manners to representations of emotional context. Accordingly, whereas Payne, Chambers, and Kensinger (2012) linked negative object retention to REM in recent work, distinct properties of sleep may support affective contextual information. Sleep spindles, for example, which are electroencephalographic (EEG) oscillations in the ~12–15 Hz frequency range, have been linked to the consolidation of both contextual (van der Helm, Gujar, Nishida, & Walker, 2011) and emotional representations (Kaestner, Wixted, & Mednick, 2013), and are thought to be integral to selective memory processing during sleep (Born & Wilhelm, 2012; Stickgold & Walker, 2013). In one study, spindles predicted better recall for newly-learned memories when they were made more salient prior to sleep (Wilhelm et al., 2011), whereas another study linked spindles to the retention of items that individuals were instructed to remember, as compared to items that they were instructed to forget (Saletin, Goldstein, & Walker, 2011). It is therefore possible, that spindles support emotionally salient information that is embedded within the context of newly-acquired memory representations.

In the current article, we provide the first report on an analysis of polysomnography (PSG) data recorded from individuals who napped between immediate and delayed testing for emotionally negative and neutral context memories. This allowed us to examine the sleep-specific mechanisms underpinning emotional memory consolidation in the contextual domain, and ask whether such mechanisms differ to those that support central emotional memory processing. Following the suggestion that sleep spindles may benefit emotionally salient contextual information, we predicted that these oscillations would support associations of negative context.

2. Material and methods

2.1. Participants

Thirty-eight (10 male) healthy participants (mean age 20.92, [S.D. ± 3.70]) free from any history of sleep, psychiatric or neurological disorders (as evaluated with pre-study screening questionnaires and telephone interviews) were recruited on a voluntary basis for two experimental sessions. Participants gave written informed consent in line with the School of Psychological Sciences Research Ethics Committee, University of Manchester, and refrained from consuming alcoholic or caffeinated products for 24 h prior to the study and throughout the study period. Participants were assigned to one of two experimental groups: 'nap' or 'wake', both contained 19 participants (5 male) with equivalent ages (wake group mean: 21.32 [S.D. ± 3.65], nap group mean: 20.53 [S.D. ± 3.78], $t(36)=0.66$; $p=0.52$). In order to check for group differences in alertness, participants completed the Stanford Sleepiness Scale (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973) in both experimental sessions. As an explicit test of alertness related to homoeostatic sleep pressure, we also calculated correlation coefficients between the amount of SWS (min) obtained by participants in the nap group and all post-sleep retrieval response times (RTs) (Cairney, Durrant, Power, & Lewis, in press; Durrant, Cairney, & Lewis, 2013; Durrant, Taylor, Cairney, & Lewis, 2011).

2.2. Experimental task

To investigate the relationship between sleep and emotional context memory, we employed an established source memory paradigm (Lewis et al., 2011; Smith, Henson, Rugg, & Dolan, 2005; Smith, Stephan, Rugg, & Dolan, 2006). At encoding, neutral foreground (object) images were superimposed on emotionally negative or neutral background (context) images. In the subsequent retrieval phases, participants were presented with object images alone and, for each, asked to indicate if it was old or new, and (if old) whether the context image it had been associated with at encoding was emotionally negative or neutral. Task procedures are illustrated in Fig. 1A.

2.3. Stimuli

One hundred and thirty-one images were taken from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2005) and supplemented with 29 images from the internet to create two sets of 80 negative and 80 neutral context images, which were counterbalanced for content (people/no people). IAPS pictures range from everyday scenes to images of injury, violence, decay and contaminated foods, and are rated on 9-point scales for both emotional valence (1=extremely negative, 5=neutral, and 9=extremely positive) and emotional arousal (1=very low arousal/boring and 9=very high arousal/exciting). The negative and neutral context image sets were significantly different in terms of mean valence rating (negative: 2.38 [S.D. ± 0.67], neutral: 5.14 [S.D. ± 0.46], $t(63)=23.28$; $p<0.0001$) and mean arousal rating (negative: 5.81 [S.D. ± 0.84], neutral: 3.36 [S.D. ± 0.76], $t(63)=17.25$; $p<0.0001$). Three hundred and twenty neutral object images were taken from the Hemera objects collection: < http://desktoppub.about.com/cs/stockphotovendors/gr/photoobjects1-2.htm > and each appeared on a square yellow background. Avoiding instances where a semantic relationship between an object and context image could be easily established, eight unique sets of 160 context/object image pairs were pseudorandomly generated for encoding. Lists 1–4 used one half of the 320 object images (160), whereas lists 5–8 used the rema ining half. The use of these lists was counterbalanced across participants.

2.4. Equipment

2.4.1. Task

The experimental tasks were created using Cogent 2000 (Functional Imaging Laboratory, University College London) and were both written and implemented using MatLab© (version 6.5) on a desktop PC with a dual-core Xeon processor and a 20″ computer screen. At encoding, participant responses were recorded using the PC keyboard, whereas retrieval session responses were recorded with a serial multi-button box attached to a Domino