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Tracking explicit and implicit long-lasting traces of fearful memories in humans

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ABSTRACT

Recent accounts of Posttraumatic Stress Disorder (PTSD) suggest that the encoding of an episode within a fearful context generates different implicit and explicit memory representations. Whilst implicit memory traces include the associated emotional states, explicit traces include a recoding into an abstract or gist-based structural context of the episode. Theoretically, the long-term preservation of implicit memory traces may facilitate the often untreatable memory intrusions in PTSD. Here, we tracked in two experiments how implicit and explicit memory traces for fearful episodes dissociate and evolve over time. Subjects ($N = 86$) were presented with semantically-related word-lists in a contextual fear paradigm and tested for explicit memories either immediately (i.e., 30 min) or after a delay (i.e., 1 or 2 weeks) with a verbal recognition task. Skin Conductance Response (SCR) was used to assess implicit memory responses.

Subjects showed high memory accuracy for words when tested immediately after encoding. At test, SCR was higher during the presentation of verbatim but not gist-based words encoded in a fearful context, and remained unchanged after 2 weeks, despite subjects being unaware of words' encoding context. We found no clear evidence of accurate explicit memory traces for the fearful or neutral contexts of words presented during encoding, either 30 min or 2 weeks afterwards. These findings indicate that the implicit, but not the explicit, memory trace of a fearful context of an episode can be detected at long-term through SCR and is dissociated from the gist-based memory. They may have implications towards the understanding of how the processing of fearful memories could lead to PTSD.

1. Introduction

Different memory systems within the human brain encode and store distinct aspects of our fearful experiences (Bechara et al., 1995; Ledoux, 2000; Milner, Squire, & Kandel, 1998; Morris, Ohman, & Dolan, 1998). One system supports conscious retrieval of facts and event details (explicit memory), another supports the production of learned fear responses without conscious thought (implicit memory; Bechara et al., 1995; Milner et al., 1998). Although both systems normally act cooperatively (Schacter, 1987), in some cases they take different routes. Such memory systems divorce may produce paradoxical scenarios in which, for instance, a fearful memory emerges without the direct link to its spatiotemporal contextual origin. This is precisely one of the main, often untreatable, characteristics of anxiety disorders, which is the recurrent and involuntary re-experiencing of traumatic events, most notoriously in Posttraumatic Stress Disorder (PTSD).

One possible, yet theoretical, explanation for the explicit–implicit memory dissociation seen in PTSD is provided by the Dual Representation Theory (DRT; Brewin, 2001; Brewin, Gregory, Lipton, & Burgess, 2010). DRT assumes two different types of memory representations are encoded during the traumatic event. One type of representation includes sensory details and affective/emotional states experienced during the traumatic event (sensory-bound representation or S-rep). The other includes a subset of sensory input, recoded into an abstract or gist-based structural context of the event (contextual representation or C-rep). According to the DRT, involuntary activation and re-experiencing of S-reps occurs when

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the S-rep is strongly encoded, due to the affective salience of the traumatic episode, and the C-rep is either encoded weakly or without a tight association to the S-rep. Thus, the fact that the S-rep is not contextualized (i.e., bound to C-rep) leads to the brain responding as if the trauma is in fact reoccurring, producing a powerful sense of reliving as well as intense emotions. However, despite the relevance of DRT in orienting therapeutic interventions in several anxiety disorders (Brewin, 2001), the evidence of a detectable, and therefore tractable, S-rep/C-rep dissociation is at most parsimonious.

Experimentally, contextual fear memory paradigms have been used in laboratories to explore and recreate many of the behavioral patterns assumed to underlie the process and the long-term consequences of exposure to fearful or traumatic events. Animal research has been particularly relevant in exploring the implicit nature of the long-lasting trace of fearful event episodes. Animal research has provided three major contributions in regard to the representational structure of fearful memories. First, animals can retrieve fearful contexts after very long intervals, even at the end of their lives (Gale et al., 2004). Second, the implicit nature of long-lasting memory traces of fearful events has been postulated as the most plausible account for fear recovery (Bouton & Bolles, 1979; Bouton, Westbrook, Corcoran, & Maren, 2006; LeDoux, 2012; Monfils, Cowansage, Klann, & Joseph, 2009; Phelps & LeDoux, 2005; Vervliet, Craske, & Hermans, 2013). And third, it helped establishing the importance of the prefrontal cortex, the amygdala and the hippocampus in acquiring and expressing fearful memories (Adolphs, 2013; Lang et al., 2009; Maren, 2005).

In contrast, most of the research on how fearful events impact the representational nature of human memories has focused on explicit memory traces. This research has showed that the ability to recollect accurate detailed memories of a fearful episode tends to be impaired (Brewin, Kleiner, Vasterling, & Field, 2007). However, the increased level of forgetting for detailed or verbatim information is accompanied by a tendency to rapidly extract gist-based information of the fearful episode (Adolphs, Denburg, & Tranel, 2001). Such an unequal balance between decreased detailed and augmented contextual or gist-based memory content has been seen as a plausible explanation for the increased tendency with the passage of time of memory generalization of fearful episodes (Beck, Emery, & Greenberg, 1985; Van Ast, Cornelisse, Meeter, Joëls, & Kindt, 2013). Thus, the apparent duality of how fearful memory traces (i.e., implicit versus explicit) are preserved at long-term remains unclear and this constitutes the focus of the current investigation.

We conducted two experiments designed to track how implicit and explicit memory traces for fearful episodes dissociate and evolve over time in humans. We achieved that by combining experimental approaches from the animal and human literature. Contextual fearful episodes were experimentally generated through a fear conditioning paradigm used in previous human research, especially suitable to recreate important characteristics of anxiety disorders (Grillon, 2002; Grillon & Davis, 1997). We used a translational behavioral paradigm designed to test on healthy participants the dissociation of fear memory traces that is at the core of PTSD (Brewin et al., 2010) to provide insights relevant to the development and maintenance of PTSD in patients (Bechara et al., 1995). Fearful contexts were emulated by presenting to the subjects colored clocks (conditioned stimulus, CS) informing about the possible upcoming occurrence of a mild electric shock (unconditioned stimulus, US) or not (neutral context). Given the relevance of contextual conditioning for PTSD and anxiety disorders in general, CS-US association remained unpredictable during the experiment, thereby promoting sustained anxiety (Barlow, 2000; Grillon, 2008). Indeed, predictability is a fundamental aspect of classical conditioning, a process of associative learning during which organisms learn to anticipate events, aversive or otherwise (Rescorla & Wagner, 1972). When the intervals between CS and US are unpredictable, animals tend to rely on background stimuli present during conditioning, including experimental context. Aversive stimuli that are made predictable following CS–US pairing lead to substantial fear of the CS and little contextual fear, whereas unpredictable aversive events (i.e., unpaired CS–US) result in fear generalizing to the experimental context (Grillon, 2002; Grillon & Davis, 1997). Thus, information embedded within such CS–US intervals is susceptible to being encoded as part of the contextual fearful event and consequently vulnerable to suffer from long-term implicit/explicit dissociation.

In the present investigation, semantically related word-lists from the Deese–Roediger–McDermott (DRM; Roediger & McDermott, 1995) paradigm were included within CS–US intervals. Subjects were told that memories for the words were to be tested afterwards. We used the DRM paradigm because it consistently produces gist-based false memories, thereby providing a measure of abstract memory traces relatively independent of verbatim memory representations (Gallo, 2010). In brief, individuals reliably produce, during a memory test, high confidence but gist-based false memories for unstudied 'critical' words (e.g. window) that are semantically associated to the studied word-list (e.g. door, glass, pane, shade, ledge, etc.). We examined how the passage of time influenced explicit measures of verbatim (i.e., studied words) and gist-based contextual memories (i.e., unstudied critical words) of fearful episodes by testing separate groups of subjects with different time intervals between encoding and testing (i.e., 30 min, 1 week and 2 weeks). Subjects' fear levels during encoding and retrieval were assessed by their Skin Conductance Response (SCR). Autonomic system arousal is considered a primary symptom of fear (Cheng, Knight, Smith, & Helmstetter, 2006) and SCR has been shown to be a suitable measure to assess reactivation of fear-related memories in humans (Schiller et al., 2010), even without conscious access (Raio, Carmel, Carrasco, & Phelps, 2012).

2. Experiment 1

In this first experiment, we sought to test the hypothesis that the encoding of events within fearful contexts especially impairs the ability to explicitly retrieve verbatim memory for the details of the event episode, whereas gist-based memory remains unaffected. In addition, we further tested the idea that this contex-

Table 1
Recognition memory data.

	Fearful context		Neutral context		
	Gist-based items	Verbatim items	Gist-based items	Verbatim items	Unrelated items
Experiment 1					
Old Judgments					
30 min	.61 (.24)	.55 (.15)	.63 (.24)	.69 (.20)	.18 (.14)
1 week	.71 (.19)	.57 (.14)	.80 (.14)	.63 (.14)	.33 (.20)
d'					
30 min	1.37 (.73)	1.20 (.78)	1.42 (.73)	1.62 (.93)	
1 week	1.09 (.61)	.70 (.56)	1.37 (.61)	.85 (.61)	
Experiment 2					
Old Judgments					
30 min	.65 (.31)	.57 (.18)	.70 (.22)	.64 (.22)	.23 (.13)
2 weeks	.79 (.14)	.59 (.19)	.82 (.19)	.61 (.14)	.40 (.14)
d'					
30 min	1.20 (.74)	.98 (.51)	1.34 (.76)	1.24 (.69)	
2 weeks	1.08 (.53)	.50 (.57)	1.24 (.63)	.58 (.50)	

Recognition is shown by the mean proportion of correct old responses and *d'* for critical lures (gist-based memory rate), studied words (verbatim hit rate) and old responses to unrelated distractors (false-alarm rate). The unrelated distractors are not associated to any list and therefore are not separated depending on context. Standard deviations are shown in parenthesis.